ORIGINAL ARTICLE

Contrasting patterns and mechanisms of spatial turnover for native and exotic freshwater fish in Europe

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ABSTRACT

Aim We compare the distribution patterns of native and exotic freshwater fish in Europe, and test whether the same mechanisms (environmental filtering and/or dispersal limitation) govern patterns of decrease in similarity of native and exotic species composition over geographical distance (spatial species turnover).

Locations Major river basins of Europe.

Methods Data related to geography, habitat diversity, regional climate and species composition of native and exotic freshwater fish were collated for 26 major European river basins. We explored the degree of nestedness in native and exotic species composition, and quantified compositional similarity between river basins according to the beta-sim (independent of richness gradient) and Jaccard (dependent of richness gradient) indices of similarity. Multiple regression on distance matrices and variation-partitioning approaches were used to quantify the relative roles of environmental filtering and dispersal limitation in shaping patterns of decreasing compositional similarity over geographical distance.

Results Native and exotic species exhibited significant nested patterns of species composition, indicating that differences in fish species composition between river basins are primarily the result of species loss, rather than species replacement. Both native and exotic compositional similarity decreased significantly with increasing geographical distance between river basins. However, gradual changes in species composition with geographical distance were found only for exotic species. In addition, exotic species displayed a higher rate of similarity decay (higher species turnover rate) with geographical distance, compared with native species. Lastly, the majority of explained variation in exotic compositional similarity was uniquely related to geography, whereas native compositional similarity was either uniquely explained by geography or jointly explained by environment and geography.

Main conclusions Our study suggests that large-scale patterns of spatial turnover for exotic freshwater fish in Europe are generated by human-mediated dispersal limitation, whereas patterns of spatial turnover for native fish result from both dispersal limitation relative to historical events (isolation by mountain ranges, glacial history) and environmental filtering.

Keywords

Biogeography, dispersal limitation, distance decay, Europe, environmental filtering, exotic species, freshwater fish, nestedness.

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INTRODUCTION

Enhancing our knowledge of the processes that shape spatial variability in community structure (species turnover or beta diversity) remains one of the fundamental challenges in contemporary community ecology and conservation biogeography (Tuomisto *et al.*, 2003; Olden, 2006; Gaston *et al.*, 2007). Spatial patterns of species turnover provide valuable insight into how biological communities respond to climate and environmental change, and help inform the design of protected area networks for conservation (Wiersma & Urban, 2005). Ecological interest in these phenomena is perhaps best exemplified by the increasing scientific exploration of the distance decay of similarity in plant and animal communities, whereby the compositional similarity of any two localities decreases with increasing geographical distance separating them (Nekola & White, 1999; Soininen *et al.*, 2007; Morlon *et al.*, 2008).

The distance decay of similarity in ecological communities has now been studied across a wide spectrum of organisms, environments and geographies (reviewed by Soininen *et al.*, 2007). This body of literature suggests that the decay process is caused by at least two, not necessary mutually exclusive, mechanisms. First, the environmental filtering hypothesis (Keddy, 1992) predicts that changes in community composition are a result of species-specific niche differences in adaptive responses that have evolved along environmental gradients (niche-based processes). Niche-based processes produce a decay of compositional similarity with geographical distance when environmental conditions are spatially autocorrelated, so that nearby sites tend to be more similar in their environmental conditions than distant sites (Nekola & White, 1999; Steinitz *et al.*, 2006). Second, the dispersal limitation hypothesis (Hubbell, 2001) posits that: (1) differences in species dispersal capabilities produce patterns of distance decay in community similarity even in homogeneous environments (neutral processes), and (2) spatial configuration of the landscape (e.g. the size and isolation of habitats, characteristics of dispersion corridors) influences species turnover by controlling habitat patch connectivity and hence the permeability of the landscape to organism movement. A landscape with major geographical barriers to movement is expected to produce greater rates of community similarity decay compared with a more homogeneous and well connected landscape.

Recent studies have reported a decline in similarity of exotic plant species (species established from outside the biogeographical zone considered) with increasing distance between localities (La Sorte & McKinney, 2006; Qian & Ricklefs, 2006; La Sorte *et al.*, 2008), a pattern also observed for a number of native communities (Nekola & White, 1999; Soininen *et al.*, 2007). What remains unclear, however, is whether the same or different mechanisms govern patterns of distance decay in native and exotic compositional similarity. Biogeographical patterns of exotic species offer a unique opportunity to test the hypotheses of environmental filtering and dispersal limitation for shaping patterns of distance decay in community similarity.

Indeed, the distributions of exotic species are not constrained by historical factors (e.g. glacial and geological events) that partly explain the current distribution of native species (Ricklefs & Schluter, 1993; Oberdorff *et al.*, 1997; Svenning & Skov, 2007). For this reason, exotic species are likely to be less dispersally limited than native species due to human-assisted introductions that breach natural geographical barriers to movement (e.g. Olden, 2006; Rahel, 2007). We may therefore expect that dispersal limitation for native species will play a more predominant role in driving rates and patterns of distance decay compared with exotic communities, and that exotic species would exhibit a lower rate of similarity decay with geographical distance (i.e. a lower species turnover with distance).

To explore the distance decay of similarity and subsequent processes (environmental filtering and dispersal limitation), previous studies have primarily used traditional similarity indices, including Jaccard's and Sørensen's coefficients (e.g. Nekola & White, 1999; Qian & Ricklefs, 2006; Steinitz *et al.*, 2006; Soininen *et al.*, 2007). Although these indices provide a 'broad-sense' measure of spatial turnover, they do not adjust for differences in composition attributable to richness gradients (see Koleff *et al.*, 2003). Consequently, the compositional differences arising from differences in species richness (species loss associated with nestedness) cannot be distinguished from differences in species composition that are independent of species richness (true species turnover that involves species replacements) (Baselga *et al.*, 2007). The decay in community similarity with geographical distance and subsequent processes refer to true species-turnover patterns (Nekola & White, 1999; Baselga, 2007) and hence should not be confounded with nested patterns of species composition (Harrison *et al.*, 1992; Baselga *et al.*, 2007). Nestedness occurs when assemblages in species-poor sites are composed of species that constitute subsets of species that occur in successively richer sites (Wright *et al.*, 1998; McAbendroth *et al.*, 2005). This distribution pattern can result from different mechanisms: selective colonization, differential extinction, nestedness of habitats, interspecific variation in tolerance of environmental conditions and passive sampling (reviewed in Whittaker & Fernández-Palacios, 2007). According to Baselga (2007), similarity indices that account for differences in species richness (nestedness) may lead to misleading interpretations of the processes (environmental filtering and dispersal limitation) shaping true species-turnover patterns. To overcome this problem, the application of 'narrow-sense' beta diversity indices, such as the beta-sim index that reflects the relative magnitude of species gains and losses rather than local richness gradients, is highly recommended (Koleff *et al.*, 2003; Baselga, 2007).

Currently, few studies have explored large-scale distribution patterns of fish in freshwater ecosystems (Soininen *et al.*, 2007). Yet freshwater environments represent an ideal study system because river basins are separated from one another by barriers that are insurmountable for freshwater fish (land or ocean), thus forming what can be considered biogeographical islands with distinct species pools (Sepkoski & Rex, 1974;

Hugueny, 1989; Tedesco *et al.*, 2005). Therefore, in contrast to vagile terrestrial species, freshwater fish are uniquely constrained because their ability to respond to environmental change is limited to movement defined by the connectivity of water. In recent times, however, human activities have assisted the ability of fish species to overcome these natural biogeographical barriers through the intentional and accidental introduction of individuals, in addition to creating new routes and pathways for colonization (García-Berthou *et al.*, 2005; Rahel, 2007). As a result, ecologists are now required to reconcile the contrasting biogeographical histories of native and exotic species, which poses both a significant challenge and a unique opportunity to test long-standing theory in biogeography (Sax *et al.*, 2007).

In the present study, we analyse patterns of spatial turnover for native and exotic freshwater fish across major river basins of Europe, a region with steep environmental gradients and a rich biogeographical history (Oberdorff *et al.*, 1997; Griffiths, 2006; Reyjol *et al.*, 2007). Specifically, we explore patterns of nestedness in native and exotic fish community composition, and test whether the same mechanisms (environmental filtering and/or dispersal limitation) govern patterns of distance decay in native and exotic compositional similarity. By using variation-partitioning approaches to statistical analysis, we are able to quantify the relative (and covarying) roles of environmental filtering and dispersal limitation in shaping patterns of distance decay in compositional similarity.

MATERIALS AND METHODS

Data sources

This study explores patterns of European fish biogeography from the Iberian Peninsula and France in the west to the Ural Mountains in the east (Fig. 1). We compiled freshwater fish occurrences for native species and exotic species (i.e. originating from outside Europe) for the major European river basins from published data (see Leprieur *et al.*, 2008a). In this study, fish occurrences for the Dälalven river basin (Sweden) were also collected to ensure an equal sample size between northern and southern river basins. This led to a total of 26 major river basins with 138 native and 38 exotic species. Only strictly freshwater fish were considered because migratory and brackish species would introduce potential bias in the analysis as we considered each river basin as a biogeographical island (Hugueny, 1989).

We collected environmental data related to habitat diversity and climatic conditions for each river basin. The mean values of 10 climatic variables were first calculated over the surface area of each river basin from $0.5° \times 0.5°$ grid climate data (Leemans & Cramer, 1991; New *et al.*, 1999). These climatic variables have previously been found to be correlated with large-scale patterns of freshwater animal diversity (e.g. Mandrak, 1995; Oberdorff *et al.*, 1997; Beauchard *et al.*, 2003). Variables included: annual precipitation (P_{ann}), precipitation of driest month (P_{min}), precipitation of wettest month (P_{max}),
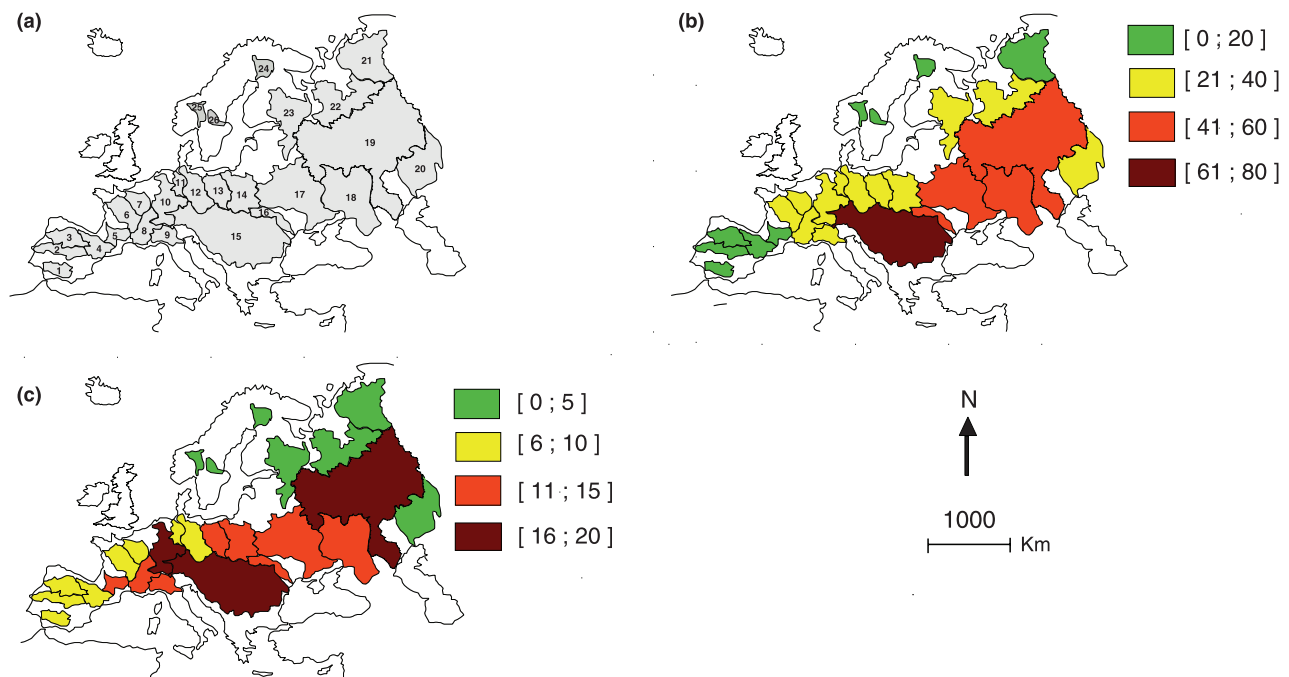
Figure 1 (a) Map of the 26 major European river basins examined in this study (1, Guadalquivir; 2, Tagus; 3, Douro; 4, Ebro; 5, Garonne; 6, Loire; 7, Seine; 8, Rhône; 9, Pô; 10, Rhine; 11, Weser; 12, Elbe; 13, Oder; 14, Wisla; 15, Danube; 16, Dniestr; 17, Dniepr; 18, Don; 19, Volga; 20, Ural; 21, Petchora; 22, Dniva; 23, Neva; 24, Kemijoki; 25, Glomma; 26, Dälalven; (b) species richness of native fishes; (c) species richness of exotic fishes.

coefficient of variation of monthly precipitation (P_{cv}), annual number of days with precipitation (N_{rd}), annual mean temperature (T_{ann}), mean temperature of warmest month (T_{max}), mean temperature of coldest month (T_{min}), coefficient of variation of monthly mean temperature (T_{cv}), mean monthly temperature range (T_{amp}). Lastly, the surface area (km^2) and altitudinal range (m) was compiled for each river basin from a global compilation of river basin characteristics (World Resources Institute, 2003) to describe basin-level habitat diversity (Hugueny, 1989).

Principal components analysis (PCA) was performed to account for observed collinearity among the 10 climatic variables and to reduce the number of variables in our analyses to a set of composite principal components (i.e. climate PCA1, PCA2 and PCA3) describing dominant gradients of variation in the original climate variables. The three first PCA axes accounted for 90.6% of the total variance in the climatic data (see Appendices S1 & S2 in Supporting Information). The first axis PCA1 was (1) strongly and positively correlated with N_{rd} and T_{cv}, and (2) strongly and negatively correlated with T_{ann} and T_{min}. Positive PCA1 scores characterized northern and eastern European river basins that displayed a higher number of rainy days and lower temperature and precipitation than western and southern river basins. The second axis, PCA2, was strongly and negatively correlated with T_{amp} and positively correlated with P_{min}. Negative PCA2 scores characterized river basins of the Iberian Peninsula that displayed highest values of mean monthly temperature range and lowest values of precipitation in the driest month. The third axis, PCA3, was strongly and negatively correlated with P_{cv}.

Data analysis

Nestedness in species distributions

We used the binary matrix nestedness temperature calculator (BINMATNEST; Rodríguez-Gironés & Santamaría, 2006) to quantify the level of nestedness in native and exotic species distributions. The calculator's algorithm permutes rows (fish species) and columns (river basins) in such a way that matrix nestedness is maximized and a temperature T ranging from 0 (complete order) to 100° (complete disorder) is calculated. In an ordered dataset, every site contains a proper subset of the species at all of the sites above it. To determine the statistical significance of the observed T value, BINMATNEST provides three probability values, associated with different null models. As recommended by Rodríguez-Gironés & Santamaría (2006), the most conservative null model 3 was examined. In this null model, the probability of each cell being occupied during simulations (i.e. 5000 null matrices) is the average of the probabilities of occupancy of its row and column in the observed matrix. This null model accounts for the incidences of species (column totals) and richness of river basins (row totals) while sampling the null space uniformly (Rodríguez-Gironés & Santamaría, 2006). Because passive sampling could generate nestedness (Wright *et al.*, 1998), the observed tem-

perature matrix was also compared with those obtained by the null model 2. In this null model, the probability of occupancy of each species is proportional to its observed frequency of occurrence and the total number of species per basin is equiprobable (Fischer & Lindenmayer, 2002). One of the conditions necessary for the development of nestedness is that localities and their biotas are comparable (i.e. same species pool, see Wright *et al.*, 1998). Because the Iberian native fish fauna is derived from a distinct species pool compared with western, central and northern Europe (Reyjol *et al.*, 2007), we excluded four river basins of the Iberian Peninsula when analysing nestedness in native species distributions.

To identify the determinants of nestedness, the order in which river basins are sorted from the maximally packed matrix (the nestedness rank order) can be compared with the rank order of possible independent correlates (Patterson & Atmar, 2000). For both native and exotic species, simple and partial Spearman rank correlation tests (Gibbons, 1993) were used to relate the nestedness rank order to habitat diversity (basin area and altitudinal range) and basin-wide climate (climate PCA axes). Because the current distribution of native species may also be explained by historical factors (e.g. glaciation events), the relationship between the nestedness rank order and the isolation of each river basin from Ponto-Caspian Europe was quantified. The Ponto-Caspian region is recognized as a refuge zone during the Last Glacial Maximum (from 24,000 to 18,000 years ago; see Reyjol *et al.*, 2007). Following Reyjol *et al.* (2007), basin isolation was quantified as the geographical distance (Euclidean distance based on mean latitude and longitude of each basin) separating each basin from the centre of the Black Sea.

Patterns of compositional similarity

To identify patterns in compositional similarity between river basins, we applied hierarchical cluster analysis using Ward's method (Legendre & Legendre, 1998) on the similarity matrix between river basins for the native (136 species in 26 basins) and exotic species pools (38 exotic species in 24 basins). Compositional similarity was estimated using the beta-sim index (β_{sim}), which is a 'narrow-sense' beta diversity metric that focuses on compositional differences that are independent of species-richness gradients (Koleff *et al.*, 2003). Jaccard's index of similarity (β_{jac}) was also calculated because of its wide application in ecology and more particularly in studies exploring the distance decay of similarity (Soininen *et al.*, 2007). β_{jac} is considered a 'broad-sense' measure of beta diversity that incorporates differences in composition attributable to species-richness gradients (Koleff *et al.*, 2003).

Spatial and environmental correlates of native and exotic compositional similarity

The geographical distance between basins was quantified according to the straight-line Euclidean distance (based on mean latitude and longitude of each basin). The straight-line

distance can present several limitations when considering heterogeneous environments such as riverine landscapes (Olden *et al.*, 2001). For example, this distance measure does not take into account the presence of major geographical barriers that may be important for limiting the dispersal of freshwater fish. For this reason, we included an additional geographical distance measure (hereafter called geographical barrier). This pairwise distance measure consisted of assigning (1) a value of one for two river basins separated by the Pyrenees or the Alps Mountains (the major geographical barriers in Europe), and (2) a value of zero for two river basins that are not separated by these geographical barriers.

The distance decay of similarity was investigated by regressing the pairwise similarity in species composition between basins against the geographical distance separating them. We performed a randomization procedure described in Nekola & White (1999) and Steinitz *et al.* (2006) to test for differences in the rate of decay in species similarity with geographical distance (the slope of the linear regression that is a measure of species turnover) between native and exotic species pools. Next, we applied a simple Mantel test (9999 permutations) to assess the significance of the distance decay of similarity. This randomization test quantifies the magnitude of the linear relationship between two distance matrices (Legendre & Legendre, 1998). Simple Mantel tests were also used to assess the relationship between exotic and native compositional similarity and other distance matrices of explanatory variables related to geography (geographical barrier) and environment (surface area, altitudinal range and climate PCA axes). The Euclidean distance was employed to quantify the difference in surface area, altitudinal range and climatic variables (the climate PCA axes) between pairs of river basins.

Standard Mantel tests measure the average correlation between all objects of the matrices involved, which may obscure changes in the direction or magnitude of autocorrelation at different geographical distance lags. The pattern and significance of spatial autocorrelation across different geographical distance lags were therefore examined using simple Mantel correlograms. The geographical distance matrix was divided into nine distance classes using Sturge's rule to set the range of pairwise distances in each class (Legendre & Legendre, 1998). Mantel correlation coefficients were calculated at each distance class and tested for significance with a permutation test (using 9999 permutations) based on a sequential Bonferroni correction ($\alpha = 0.05$; Legendre & Legendre, 1998). The shape of the Mantel correlogram was also interpreted to describe the spatial structure in species composition (e.g. gradients, patchy structures or random distributions; Legendre & Fortin, 1989). All Mantel analyses were performed using the ECODIST package implemented in the open-source R software (R Development Core Team, 2006).

Because environmental similarity is expected to decline with increasing geographical distance (Appendix S3), disentangling the relative roles of environmental filtering and dispersal limitation in shaping patterns of distance decay in composi-

tional similarity is not straightforward (Gilbert & Lechowicz, 2004). Multiple regression on distance matrices (using PERMUTE! 3.4.9; Casgrain, 2001) and variation partitioning (Legendre & Legendre, 1998) were therefore applied to distinguish between the effect of variables describing dispersal limitation (geographical distance and geographical barriers) vs. environmental conditions (surface area, altitudinal range and climate PCA axes).

Multiple regression on distance matrices is conceptually similar to traditional linear regression, except that the dependent and independent variables are square distance matrices instead of single vectors (Legendre & Legendre, 1998). For a given explanatory variable, calculation of the standardized partial regression coefficients (β) enabled us to compare their per-unit effect on compositional similarity, while controlling for the effect of the other variables. To overcome the problem of lack of independence between site pairs, the significance of the standardized partial regression coefficients and the coefficients of multiple determination (R^2) were assessed using a permutation test ($n = 999$; Casgrain, 2001). We performed a forward selection procedure to ensure that each of the variables in the final model made a statistically significant ($P < 0.05$ after Bonferroni correction) contribution to the amount of variance explained (Legendre & Legendre, 1998; Casgrain, 2001).

Variation partitioning was applied to the final model to decompose the total variation in species similarity into four fractions: (1) uniquely explained by geography (support for the dispersal limitation hypothesis), (2) uniquely explained by environment (support for the environmental filtering hypothesis), (3) jointly explained by geography and environment (the spatially structured environmental component that also provides support for the environmental filtering hypothesis), and (4) unexplained (Steinitz *et al.*, 2005; Qian & Ricklefs, 2006; Bjorholm *et al.*, 2008).

RESULTS

Nestedness in species distributions

Both native and exotic species composition showed significant nested subset patterns ($T_{native} = 18.40$, $P < 0.0001$; $T_{exotic} = 10.20$, $P < 0.0001$ for the two null models considered). For native species, the order in which river basins are sorted from the maximally packed matrix was negatively correlated with the rank order of basin area (Spearman correlation: $r_S = -0.626$, $P < 0.001$; Table 1). This relationship remained statistically significant after accounting for the variation explained by basin isolation from the Black Sea (partial Spearman correlation: $r_S = -0.443$, $P = 0.035$). Native species nestedness was also positively correlated with basin isolation (Spearman correlation test: $r_S = 0.770$, $P < 0.001$; Table 1); an association that remained significant after controlling for the effect of basin area (partial Spearman correlation test: $r_S = 0.679$, $P < 0.001$). For exotic species, the nestedness rank order was negatively correlated with the rank order of basin area ($r_S = -0.590$, $P = 0.002$; Table 1).

Table 1 Spearman rank correlation (r_S) between the degree of nestedness in species distributions of native and exotic fishes in European river basins and each explanatory variable (see Materials and Methods for more details).

Variable	Native species		Exotic species	
	r_S	P	r_S	P
Isolation†	0.770**	< 0.001	–	–
Habitat diversity				
Surface area	−0.626**	0.001	−0.590**	0.002
Altitudinal range	−0.012	0.965	−0.144	0.500
Climate				
PCA1	0.057	0.803	0.058	0.785
PCA2	−0.220	0.334	0.293	0.163
PCA3	0.166	0.468	0.394	0.057

*$P < 0.05$; **$P < 0.005$ (Bonferroni correction, $\alpha = 0.05/11$).
†Basin isolation was quantified as the geographical distance (Euclidean distance based on mean latitude and longitude of each basin) separating each river basin from the centre of the Black Sea.

Patterns of compositional similarity

Patterns of native and exotic compositional similarity showed marked spatial trends across the major European river basins. It was seen from β_{jac} that geographically close river basins showed higher levels of community similarity according to the hierarchical cluster analysis, whereas more distant basins showed little commonality in species membership (Fig. 2a,b). Not surprisingly, river basins grouped together by the cluster analysis (Fig. 2a,b) also tended to exhibit similar levels of species richness (Fig. 1b,c). Results from a Mantel test verified this finding by showing a negative relationship between similarities based on basin community composition and species richness for both native ($r_M = −0.273$, $P = 0.01$) and exotic species ($r_M = −0.469$, $P < 0.001$). Four groups of river basins were identified as exhibiting high similarities in native community composition (Ward linkage = 1.5; Fig. 2a): (1) river basins of the Iberian Peninsula in south-western Europe (1–4), (2) river basins of the Ponto-Caspian region in eastern Europe (15–20), (3) river basins of western–central Europe (21, 22, 24–26), and (4) river basins of northern Europe (5–14, 23). Overall, similar groupings of basins were observed when analysing exotic compositional similarity (Fig. 2b). This pattern was confirmed by a Mantel test showing that the native and exotic similarity matrices were significantly correlated ($r_M = 0.361$, $P = 0.003$), that is, basins that were similar in their native species composition tended to be similar in their exotic species composition.

Statistical analyses according to β_{sim} provided a novel insight into patterns of spatial turnover due to the independence of β_{sim} from differences in species richness for both native (Mantel test: $r_M = 0.055$, $P = 0.104$) and exotic species ($r_M = 0.137$, $P = 0.07$). For example, river basins of northern Europe (23–26) exhibiting low native species richness (Fig.1b) were grouped with species-rich river basins of the Ponto-Caspian region (Fig. 2c). On the other hand, the species-rich

Danube river basin (15) was classified with less species-rich river basins of western Europe (Figs 1b & 2c). Similar examples existed for exotic species (Fig. 2d) where several river basins characterized by low species richness (5–6; 11–12; 24–26) were grouped with species-rich river basins of central Europe [the Danube (10) and Rhine (15) river basins]. Overall, patterns of spatial turnover revealed by β_{sim} were consistent with the observed nestedness in native and exotic species composition. In contrast to the situation observed with the Jaccard's index, river basins that were significantly similar in their native species composition were not significantly similar in their exotic species composition (Mantel test: $r_M = 0.197$, $P = 0.07$).

Spatial and environmental correlates of native and exotic compositional similarity

Pairwise species similarity based on β_{jac} or β_{sim} decreased significantly with increasing distance between river basins for native (Mantel test: $r_M = −0.417$ and $−0.368$ for β_{jac} and β_{sim}, respectively; $P < 0.001$) and exotic species ($r_M = −0.689$ and $−0.652$ for β_{jac} and β_{sim}, respectively; $P < 0.001$) (Table 2). Inspection of the Mantel correlogram, however, showed contrasting patterns of species spatial turnover for native and exotic species (Fig. 3). For native species, the Mantel correlogram (using both β_{jac} and β_{sim}) indicated significant and positive spatial autocorrelation among the smallest distance classes. In other words, geographically close river basins showed a greater level of community similarity than would be expected by chance alone. However, few negative spatial autocorrelations were significant for the largest distance classes, implying that geographically distant river basins did not tend to have lower levels of community similarity than those expected by chance alone (Fig. 3a,c). Overall, this pattern of spatial autocorrelation indicates abrupt changes in native species composition with geographical distance (a patchy spatial structure). In contrast, the Mantel correlogram computed for exotic species indicated positive spatial autocorrelation among the smallest distance classes and negative spatial autocorrelation among the largest distance classes (using both β_{jac} and β_{sim}; Fig. 3b,d). Contrary to native species, this pattern of spatial autocorrelation indicates gradual changes in exotic species composition with geographical distance (a spatial gradient).

The randomization procedure indicated that native species were characterized by a lower rate of decay in similarity with increasing distance between basins compared with exotic species (regression slopes = −0.006 and −0.010 for native and exotic species, respectively; two-tailed test: $P = 0.0001$). Using β_{sim} provided similar results (regression slopes = −0.007 and −0.014 for native and exotic species, respectively; two-tailed test: $P = 0.0001$).

When considering β_{jac}, simple Mantel tests (Table 2) showed that pairwise similarity in native species decreased significantly with increasing differences in climatic conditions between river basins (PCA1: $r_M = −0.427$, $P < 0.001$; PCA2:
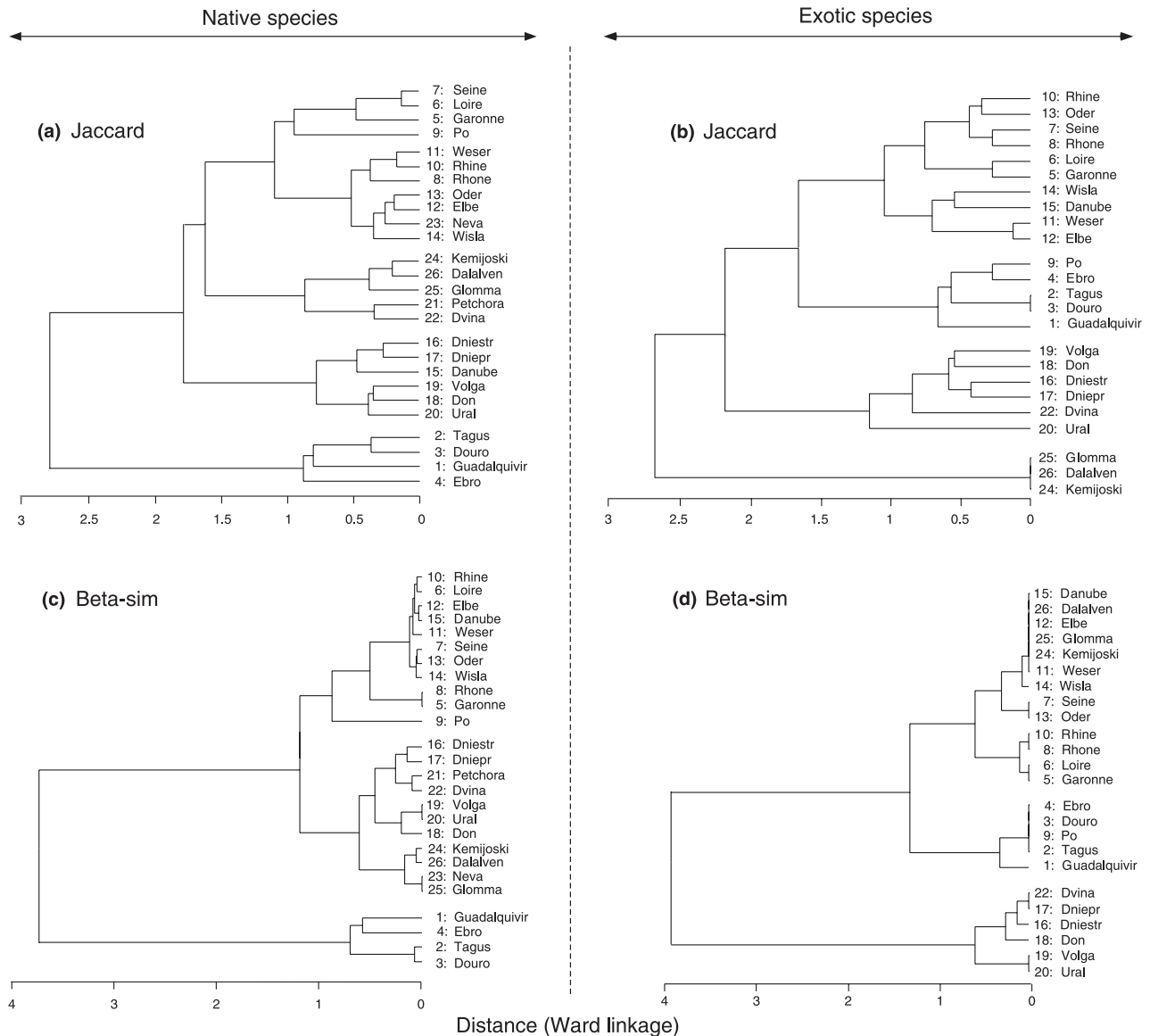
Figure 2 Clustering of European river basins according to native and exotic freshwater fish compositional similarity. The hierarchical cluster analysis was performed according to two similarity indices (β_{sim} and β_{jac}) and the Ward linkage method. (a) Native species compositional similarity using β_{jac}; (b) exotic species compositional using β_{jac}; (c) native species compositional similarity using β_{sim}; (d) exotic species compositional similarity using β_{sim}.

$r_M = -0.453$, $P < 0.002$). River basins that were not separated by the major European geographical barriers (the Pyrenees and Alps mountains) displayed the greatest level of pairwise similarity in native species (Mantel test: $r_M = -0.789$, $P < 0.002$). Similar results were obtained using β_{sim} (Table 2). For exotic species, using β_{jac} revealed that pairwise similarity decreased significantly with increasing differences in river basin area (Mantel test: $r_M = -0.406$, $P < 0.002$) and climatic conditions (Mantel test: $r_M = -0.550$, $P < 0.002$ for climate PCA1; see Table 2). These correlations were marginally significant according to β_{sim} (Table 2).

Regression models testing the combined effects of geographical and environmental distance-based variables on native compositional similarity accounted for 72.4% and

84.5% of the variation in β_{jac} and β_{sim}, respectively (Table 3). Except for geographical distance, the same distance-based explanatory variables were selected by forward selection as making a significant contribution to the amount of explained variation in β_{jac} and β_{sim} (Table 3). Standardized partial regression coefficients indicated that the geographical barrier variable was the strongest predictor of native compositional similarity ($\beta = -0.686$ and -0.778 for β_{jac} and β_{sim}, respectively). In contrast, distance-based variables related to habitat diversity and climate displayed the lowest standardized partial regression coefficients. These results were confirmed by the variation-partitioning analysis, which showed that the proportion of variance explained uniquely by environment was relatively low ($< 10\%$) in both the models according to

Table 2 Results from simple Mantel correlation tests between native and exotic fish compositional similarity and several explanatory variables related to geography, habitat diversity and climate (see Materials and Methods for more details).

| Variables	Native species		Exotic species	
	β_{jac}	β_{sim}	β_{jac}	β_{sim}
Geography				
Geographical distance	−0.417**	−0.368**	−0.689**	−0.652**
Geographical barrier	−0.789**	−0.886**	−0.065	−0.099
Habitat diversity				
Surface area	−0.074	0.119	−0.406**	−0.308*
Altitudinal range	−0.134*	−0.126	−0.179*	−0.159*
Climate				
PCA1	−0.427**	−0.389**	−0.550**	−0.215*
PCA2	−0.453**	−0.528**	−0.130*	−0.140
PCA3	−0.132	−0.111	−0.188*	−0.186

Analyses were performed using β_{jac} and β_{sim} indices of similarity.
*$P < 0.05$; **$P < 0.002$ (Bonferroni correction, $\alpha = 0.05/28$).

β_{jac} and β_{sim} (Fig. 4). In contrast, most of the variation in β_{jac} and β_{sim} was either uniquely explained by geography (34% and 43.1% for the Jaccard and beta-sim indices, respectively; Fig. 4) or jointly explained by environment and geography (28.3% and 39.1% for β_{jac} and β_{sim}, respectively; Fig. 4).

For exotic species, regression models accounted for 53.1% and 49.5% of the variation in β_{jac} and β_{sim}, respectively (Table 3). In contrast to native species, few distance-based variables related to the environment made a significant contribution to the amount of explained variation in exotic compositional similarity (Table 3). According to the standardized partial regression coefficients (β), geographical distance among basins contributed most to the variation in exotic compositional similarity ($\beta = -0.454$ and -0.872 for β_{jac} and β_{sim}, respectively). Furthermore, most of the explained variation in exotic compositional similarity according to β_{jac} was related to environment and geography in combination (37.4%), whereas almost all of the explained variation in exotic compositional similarity according to β_{sim} was uniquely related to geography (44.8%) (Fig. 4).

DISCUSSION

Whether the regional distribution of species is limited by constraints related to dispersal or environmental suitability has been a topic of continued debate among biogeographers and ecologists (Ricklefs & Schluter, 1993; Nekola & White, 1999; Gilbert & Lechowicz, 2004; Leathwick *et al.*, 2008). Recently a number of authors have suggested that distribution patterns of exotic species may provide new insight for advancing our understanding of the processes that govern the distribution
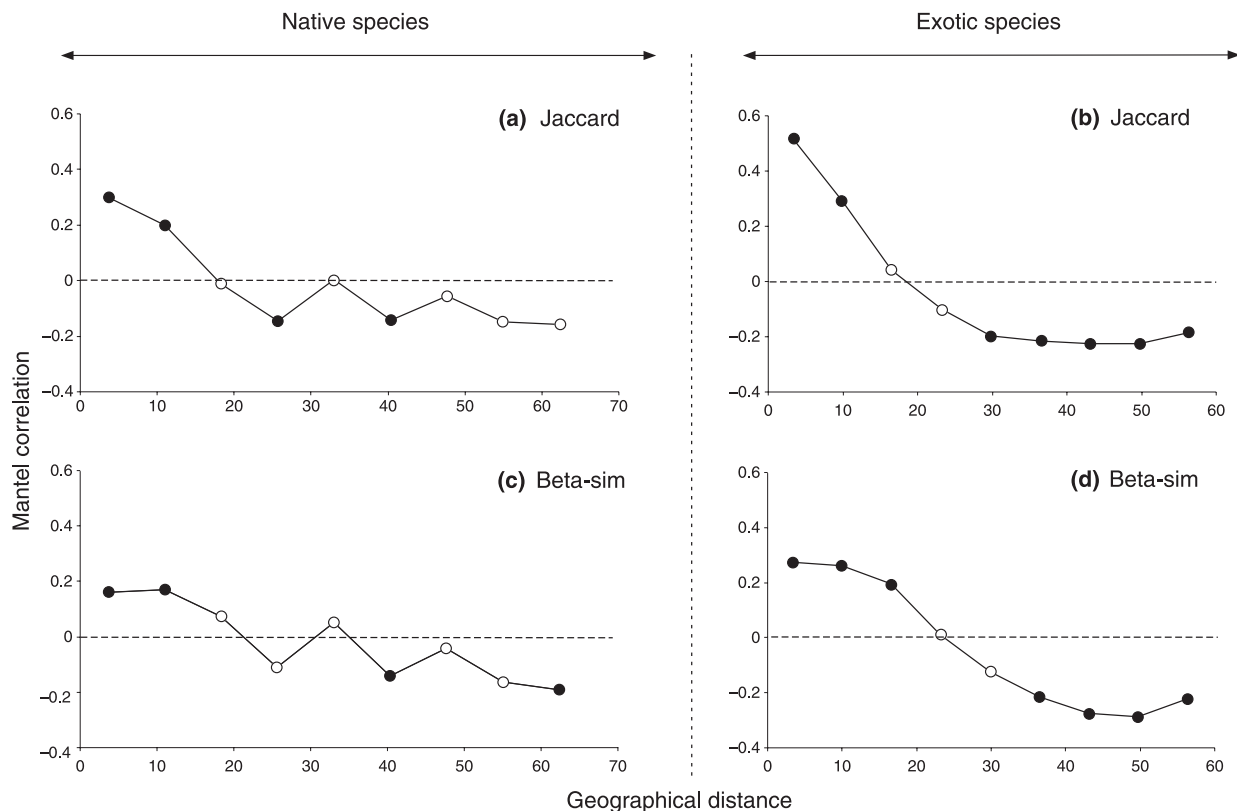

Figure 3 Mantel correlogram for spatial autocorrelation in native and exotic fish compositional dissimilarity between river basins using β_{jac} and β_{sim}. Dark circles, significant positive or negative correlations (assessed using sequential Bonferroni corrections with $\alpha = 0.05$) between compositional dissimilarity and geographical distance (based on mean longitude and latitude of each river basin).

Table 3 Regression of native and exotic fish compositional similarity against distance-based explanatory variables related to geography and environment (see Materials and Methods for more details), after a forward selection procedure (at $P < 0.05$ after Bonferonni correction).

Model	Partial standardized regression coefficients (β_{jac})	Partial standardized regression coefficients (β_{sim})
Native species		
Geographical distance	–	−0.094
Geographical barrier	−0.686	−0.778
Surface area	−0.146	0.073
Climate PCA1	−0.232	−0.123
Climate PCA2	−0.123	−0.127
Climate PCA3	−0.121	−0.090
R^2	0.724	0.845
Exotic species		
Geographical distance	−0.454	−0.872
Surface area	−0.240	–
PCA1	−0.213	0.343
R^2	0.531	0.495

–, Variables not selected in the final regression model.
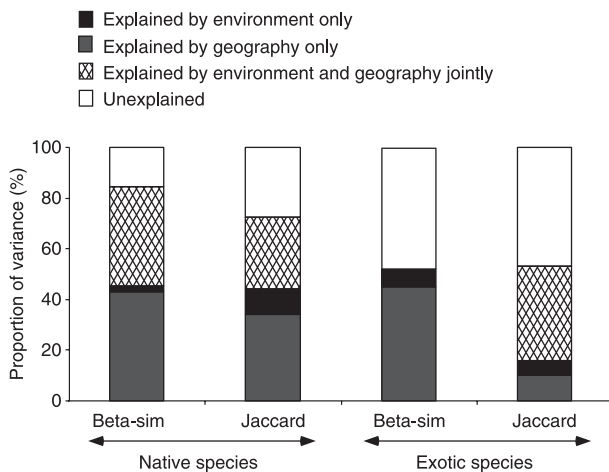
Figure 4 Relative importance of geography and environment in explaining variation in native and exotic fish compositional similarity between river basins. The diagrams are based on multiple regression on distance matrices to partition the variation into four independent fractions. Only explanatory variables that had statistically significant contributions to the final model after forward model selection were included in the variation partitioning (see Materials and Methods; Table 3). Results obtained using β_{jac} and β_{sim} are presented.

and diversity of organisms (e.g. Sax *et al.*, 2007). Many of the same authors have proposed that biogeographical patterns of native and exotic species are driven by similar ecological rules (Stadler *et al.*, 2000; Sax, 2001; Sax & Gaines, 2005), whereas others have suggested that the biogeography of exotic species is primarily a consequence of human, rather than natural processes (Blackburn *et al.*, 2008; Leprieur *et al.*, 2008b; Olden

et al., 2008). It is against this backdrop of recent scientific inquiry that the present study aimed to enhance our understanding of the patterns and mechanisms of nestedness and spatial turnover for native vs. exotic freshwater fish in Europe.

Our study revealed a significant nested subset pattern of native species composition in which fish faunas of species-poor, smaller river basins tended to be subsets of fish faunas of species-rich, larger river basins (except for the Iberian Peninsula, for which the freshwater fish fauna is derived from a distinct regional pool of species, Griffiths, 2006; Reyjol *et al.*, 2007). In addition, small and species-poor river basins of western and northern Europe were geographically distant from the more species-rich and large river basins of central and eastern Europe (see Fig. 1b). These results are not entirely surprising given the findings of Reyjol *et al.* (2007), who provided strong evidence that the European river basins can be considered as non-equilibrated islands in which species extinctions were not fully balanced by colonization from neighbouring river basins. In fact, small river basins located in western and northern Europe experienced higher rates of extinction than the large Ponto-Caspian river basins during the Pleistocene glaciations (the Danube, Dniestr, Dniepr, Don and Volga river basins; Griffiths, 2006; Reyjol *et al.*, 2007). Post-glacial colonization rates were probably highest for the river basins close to the Black Sea, which is recognized as a refuge zone during the Pleistocene glaciations.

An intriguing finding from our study is that exotic species also exhibited a significant nested subsets structure in species composition (including the Iberian Peninsula). As for native species, this distribution pattern was clearly related to the size of each river basin (the surface area), so that exotic fish faunas of smaller river basins tended to be subsets of exotic fish faunas of larger river basins (e.g. the Danube and Volga Rivers). Passive sampling may explain such a pattern because propagule pressure (the size, number and frequency of introduction events) is very likely to increase with area. However, no evidence was found for nestedness being an artefact of passive sampling. Therefore, assuming that freshwater fish introductions are a contemporary phenomenon (Rahel, 2007), selective extinctions associated with historical processes cannot explain patterns of nestedness in exotic species (whereas these processes are important drivers of native nestedness). An alternative hypothesis may be that larger river basins support higher-order stream channels (Matthews, 1998) that provide a greater range of available habitats (e.g. from cold-water upland streams to warm-water lowland rivers) for non-native freshwater fish. Indeed, habitat nestedness can lead to nestedness if species-rich sites are those that contain the greatest habitat heterogeneity or have environmental conditions tolerable by the largest number of species (Whittaker & Fernández-Palacios, 2007).

As discussed above, differences in exotic and native species composition between river basins may be more related to species loss than to species replacement. To disentangle the distance decay of similarity (true species turnover) from richness gradients (nestedness), the interpretation of species

similarity according to the beta-sim index is recommended (Baselga *et al.*, 2007). A significant decay of species similarity with increasing geographical distance between river basins was observed for both native and exotic species. However, the per-unit effect of geographical distance on native compositional similarity was weak when accounting for the influence of other variables related to environmental heterogeneity and geography. The simple fact that two river basins are isolated or not by a major European geographical barrier (the Pyrenees or the Alps mountains) explained much of the variation in native compositional similarity across Europe. This was evident from looking at the shape of the Mantel correlogram, which indicated abrupt changes in native species composition with geographical distance. Spatial discontinuity in fish faunal composition is mainly related to the Pyrenees Mountains, which prevented exchanges of freshwater fish between the Iberian Peninsula and the rest of Europe in response to past climatic fluctuations (Griffiths, 2006; Reyjol *et al.*, 2007). In support of this interpretation, the average similarity between the Iberian river basins ($n = 4$) and the other European river basins ($n = 22$) was very low (average $\beta_{sim} = 0.186$; Fig. 2c), indicating that the Iberian Peninsula displays a high level of fish fauna distinctiveness. This is consistent with a number of studies highlighting that the Iberian Peninsula differs from the rest of Europe in its high level of fish endemism (Griffiths, 2006; Reyjol *et al.*, 2007). In contrast, a high level of similarity was found between the river basins outside the Iberian Peninsula (average $\beta_{sim} = 0.758$, $n = 22$), which is consistent with the fact that beta diversity is low when the degree of nestedness is high (Wright & Reeves, 1992).

Unlike native species, gradual changes in species composition with geographical distance were observed for exotic species, and the major European geographical barriers did not account for a significant amount of variation in exotic compositional similarity across Europe. Such a result is not surprising, as human-assisted freshwater fish introductions breach natural geographical barriers to movement in Europe (García-Berthou *et al.*, 2005), leading to greater fish fauna homogenization in southern Europe (Clavero & García-Berthou, 2006; Leprieur *et al.*, 2008a). However, this does not imply that dispersal limitation played a minor role in shaping large-scale distribution patterns of exotic fish in Europe. In fact, geographical distance in isolation accounted for most of the explained variation in exotic compositional similarity between river basins (Fig. 4). Dispersal limitation for exotic fish species is likely to be related to the spatial structure in introduction pathways. For instance, García-Berthou *et al.* (2005) identified pathways of freshwater fish species introductions in Europe and showed that these pathways were spatially structured. Mid-latitude western European countries (e.g. France and Germany) received many exotic species from North America and donated many of them to both southern (Spain) and northern (Sweden) countries. In contrast, mid-latitude eastern European countries (e.g. Romania and Poland) received some exotic species from the former Soviet Union, but provided no species to other countries.

Non-random geographical structure in introduction pathways results from the intentional human-selected nature of freshwater fish introductions (García-Berthou *et al.*, 2005). In fact, many freshwater fish introductions are intentional (and therefore geographically localized) because they are strongly associated with human uses (e.g. sport fishing; Clavero & García-Berthou, 2006). This may explain why exotic freshwater fish in Europe displayed a higher rate of similarity decay (a higher species turnover rate) with distance than natives, a result that contrasts with our initial prediction and contradicts previous large-scale studies on exotic plant species in North America (La Sorte & McKinney, 2006; Qian & Ricklefs, 2006; Qian *et al.*, 2008, which used Jaccard's index of similarity). These previous studies found a lower rate of similarity decay for exotic plant species, and hence suggested that exotic plants were less dispersally limited than natives due to intentional or/ and accidental introductions over long distance. Such a difference between our results and these previous studies is also likely to be related to other factors. First, plant distribution patterns were analysed using political units (county, province and state), as opposed to what might be considered a more relevant biogeographical scale, such as the river basin examined in our study. Indeed, by defining regional species pools according to political units, one does not take into account biogeographical barriers (e.g. mountain ranges, large rivers) that define the historical floral distinctiveness of a region. Second, exotic plants are probably less dispersally limited than exotic freshwater fish due to intrinsic differences in mobility between freshwater fish and plants. These factors may explain why exotic plants in North America are more widely distributed over large spatial scales compared with exotic fish species in Europe.

Although our results support the hypothesis of dispersal limitation for both native and exotic species, they do not completely refute the environmental filtering hypothesis for native species. We found that spatially structured climatic gradients (e.g. temperature and the number of rainy days associated with PCA1) accounted for a large portion of the variation in native compositional similarity. This is not surprising, as broad-scale physiological and ecological requirements of freshwater fish species are largely driven by temperature and hydrology (Matthews, 1998). In the present study, the number of rainy days decreases from northern to southern Europe, which may account for temporal persistence of suitable habitats for freshwater fish (Beauchard *et al.*, 2003). Compared with northern European river systems, Mediterranean-type streams in southern Europe experience strong seasonal patterns in flow (low flow in summer that restricts aquatic habitats to small isolated pools, and high flow in autumn and spring), and long periods of high temperature. Species sorting according to hydrological stability has been reported for both temperate and tropical freshwater fish communities at different spatial scales (Hoeinghaus *et al.*, 2007; Tedesco *et al.*, 2008). For example, Tedesco *et al.* (2008) showed that the distributions of tropical freshwater fish at the river-basin scale

can be partly explained by the match between life-history strategies and the degree of hydrological variability.

To summarize, our results suggest that the present-day distribution of the native European freshwater fish fauna results from both dispersal limitation (associated with past historical events) and environmental filtering, which removed species that were unable to persist under a given set of climatic conditions. The combined effect of post-glacial dispersal limitation and climatic gradients in structuring fish communities has been also reported at the regional scale in North America (Jackson & Harvey, 1989; Tonn et al., 1990; Mandrak, 1995). More generally, our results support recent research highlighting that environmental filtering and dispersal limitation are not mutually exclusive in explaining spatial variability in assemblage structure (Gilbert & Lechowicz, 2004; Cottenie, 2005; Beck & Vun Khen, 2007; Baselga, 2008).

Before concluding, it is important to discuss a number of analytical considerations for biogeographical studies of spatial turnover. The choice of the appropriate index of compositional similarity has been long debated among ecologists and biogeographers (see discussions in Koleff et al., 2003). Contrasting results due to the incorporation of richness gradients in similarity measure have been recently discussed by Baselga (2007) and Baselga et al. (2007). As pointed out by these authors, the appropriateness of the similarity measure to test the hypothesis addressed should guide the choice of similarity measure. For exotic species, the results obtained using Jaccard's index provided support for the environmental filtering hypothesis, but not for the dispersal limitation hypothesis; a finding that markedly contrasts with the conclusions drawn from the use of the beta-sim index. This discrepancy is related to the intrinsic nature of Jaccard's index, which accounts for differences in species richness between localities (Koleff et al., 2003). We found that river basins were primarily classified according to their similarity in exotic species richness when using Jaccard's index (Fig. 2b), hence contrasting with the observed nested subset structure in exotic species composition. Furthermore, differences in exotic species richness between river basins were found to be significantly associated with their differences in climatic conditions (Mantel test: $r_M = 0.255$, $P = 0.007$) and surface area (Mantel test: $r_M = 0.386$; $P < 0.001$) (Appendix S3). Consequently, the spatially structured environmental factors (climate PCA1 and surface area) are more likely to account for differences in exotic species richness between river basins than differences in exotic species identities (true species turnover). Interestingly, the lack of difference between the two indices for native species is probably related to the strong native species turnover (independent of richness gradient) that was present between the Iberian river basins and those of the rest of Europe. Overall, in the context of a strong richness gradient (nestedness), our results provide evidence that the beta-sim index should be employed when quantifying the relative roles of environmental filtering vs. dispersal limitation for shaping patterns of distance decay in community similarity.

CONCLUSIONS

Previous studies on plants and birds concluded that exotic and native species can exhibit similar biogeographical patterns (Stadler et al., 2000; Sax, 2001; Kühn et al., 2003; Labra et al., 2005; Sax & Gaines, 2005). Although our results indicate that both native and exotic fish species exhibit a significant nested subset pattern of species composition, they do not entirely agree with these previous terrestrial studies. Indeed, our results do not support the prediction that environmental conditions act as filters generating similar distribution patterns for native and exotic species (Stadler et al., 2000; Kühn et al., 2003). In contrast, our findings suggest that large-scale patterns of spatial turnover for exotic freshwater fish result from human-mediated dispersal limitation, whereas patterns of spatial turnover for native fish result from both dispersal limitation relative to historical events (isolation by mountain ranges, glacial history) and environmental filtering. However, complementary analyses incorporating species traits would be particularly valuable to further support our findings. For instance, species-level analysis would permit the environmental filtering hypothesis to be tested, while controlling for the influence of biogeographical and historical factors (Hoeinghaus et al., 2007) and a traits-based approach would provide complementary insight into the mechanisms leading to community nestedness (McAbendroth et al., 2005).

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SUPPORTING INFORMATION

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

Appendix S1 The first three principal components based on the correlation matrix between the 10 climate variables used to characterize climatic conditions of the European river basins ($n = 26$).

Appendix S2 Results from a PCA analysis summarizing climatic conditions in the 26 major European river basins: PCA scores on (a) the first axis; (b) the second axis.

Appendix S3 Mantel correlation (r_M) between each distance-based explanatory variable.

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BIOSKETCH

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