

Spatial patterns and determinants of trait dispersion in freshwater fish assemblages across Europe

Jessica Côte^{1*}  | Lucie Kuczynski^{1,2*}  | Gaël Grenouillet^{1,3}

¹UMR Laboratoire Evolution et Diversité Biologique, UPS, Toulouse, France

²Department of Biology, University of Oklahoma, Norman, Oklahoma

³Institut Universitaire de France, Paris, France

Correspondence

Jessica Côte, Laboratoire Evolution et Diversité Biologique, IRD 253, CNRS 5174, UPS, 118 Route de Narbonne, Toulouse 31062 CEDEX 9, France.
Email: cote.jessica33@gmail.com

Editor: Fabien Leprieur

Abstract

Aim: Understanding how species assemble into assemblages and identifying the determinants of assembly processes remains a key challenge in ecology. Within assemblages, functional trait dispersion can be used to infer assembly processes, but this inference could depend on the trait considered. Here, using both single and multiple trait-based approaches, we analysed dispersion patterns for alpha (i.e., related to niche partitioning) and beta (i.e., related to environmental tolerance) traits in freshwater fish assemblages and characterized how trait dispersion patterns vary along environmental gradients at large spatial scale.

Location: Western Palaearctic, 290 river catchments.

Time period: Contemporary.

Major taxa studied: Freshwater fish.

Methods: Based on freshwater fish occurrence records in 290 European river catchments, we computed dispersion indices (mean pairwise distance) using standardized effect sizes for each single trait and multiple traits. We then used linear models including climatic, geo-morphological, biotic and human-related factors to determine the key drivers shaping freshwater fish dispersion patterns across Europe.

Results: We highlighted spatial variation in trait dispersion, with both underdispersion and overdispersion simultaneously observed for a given trait, but also distinct patterns of trait dispersion, even within beta and alpha traits. We provided evidence that elevation range and current and past climatic conditions mainly structured trait dispersion patterns. Finally, our results revealed that spatial patterns in trait dispersion based on multiple traits were less pronounced than those based on individual traits.

Main conclusions: Our results highlighted that traits showed different spatial and environmental patterns, reflecting different ecological patterns. This could lead to potential problems when using functional indices computed on multiple traits and challenges their relevance to describe diversity patterns and to infer the assembly processes shaping community structure.

KEYWORDS

diversity, environmental filtering, environmental gradients, European catchments, functional traits, mean pairwise distance, stream fish assemblages, trait dispersion

*These authors contributed equally to this work.

1 | INTRODUCTION

The functional facet of diversity aims to answer to the need for an integrative view (Díaz & Cabido, 2001; Petchey & Gaston, 2002; Tilman et al., 1997) by taking into account species characteristics (Violle et al., 2007) in the measurements. Several components of functional diversity can be used to describe assemblage structure (Mason, Moullot, Lee, & Wilson, 2005; Mouchet, Villéger, Mason, & Moullot, 2010), including functional trait dispersion (e.g., Ingram & Shurin, 2009). Functional dispersion refers to the variability of traits within a community. Underdispersion for one trait suggests similar values across species within a given sample (i.e., low variability), whereas overdispersion indicates the opposite pattern (i.e., high variability around mean trait values). Trait dispersion is regularly studied using indices based on several traits (e.g., de Bello et al., 2013; de Souza Queiroz, Da Silva, & de Cerqueira Rossa-Feres, 2015; Schleuter et al., 2012). However, traits might show different responses to environmental or spatial gradients, and one might blur the detected patterns by combining all traits in a single measure of diversity (Tsianou & Kallimanis, 2016).

According to Lopez et al. (2016), a dichotomy based on the function they support has been proposed to classify functional traits as alpha or beta traits according to the expected main determinant of their diversity within community. Traits related to behaviour, small-scale habitat preferences or resource use and thus to the coexistence of species within the assemblage are defined as alpha traits, whereas traits linked to environmental requirements and tolerance along environmental gradients are defined as beta traits (Kraft et al., 2015; Lopez et al., 2016; Mayfield & Levine, 2010). Consequently, overdispersion is expected on alpha traits, because processes such as competition and niche differentiation might occur, whereas underdispersion is expected on beta traits, on which environmental filtering can act (Ackerly & Cornwell, 2007; Lopez et al., 2016). In this context, in order to infer assembly processes more precisely, previous studies have recommended that functional diversity for alpha and beta traits should be analysed separately, because they can be defined as different axes of species niche (Kraft et al., 2015; Lopez et al., 2016; Mayfield & Levine, 2010) and because this provides a framework to disentangle the influence of competition and environmental filtering on multivariate diversity patterns.

Patterns of dispersion of traits vary along environmental gradients partly because alpha and beta traits respond to different environmental filters (Lopez et al., 2016). For instance, Katabuchi, Kurokawa, Davies, Tan, and Nakashizuka (2012) showed that soil characteristics influenced dispersion patterns of forest tree communities. Likewise, Vogt, Peres-Neto, and Beisner (2013) found that environmental characteristics of lakes had an influence on the trait diversity of zooplankton communities. Climate (past and present) is known to be a key factor determining spatial patterns of trait dispersion (e.g., Ordóñez & Svenning, 2015, 2016; Shiono et al., 2015), and the direction of this influence is likely to vary according to the trait considered. For instance, Swenson et al. (2012) found strong mean temperature effects on trait dispersion, either positive or negative,

and low trait dispersion was mainly observed in environments characterized by a strong climate seasonality. Dispersion patterns of beta traits (i.e., related to environmental requirements) are more likely to vary according to climatic conditions than patterns of alpha traits (i.e., related to resource use).

Human-related factors are also known to play a major role in patterns of trait dispersion, although the directionality of this influence is still not clear. For instance, Forrest, Thorp, Kremen, and Williams (2015) have shown that land use, especially conventional intensive agriculture, decreased trait dispersion of bee communities. On the contrary, degraded systems present higher trait dispersion than unimpacted bird communities (Bregman et al., 2015). Thus, one might expect that human-related land use is likely to affect trait dispersion, especially the dispersion patterns of beta traits, although the intensity of the influence might depend on the type of disturbance and on the trait considered (Schellenberger Costa et al., 2017).

Another component of human-related factors is non-native species (NNS), which are now recognized as an important determinant in community reorganization (Vitousek, D'Antonio, Loope, Rejmanek, & Westbrooks, 1997). The impact of NNS on trait dispersion may depend on the trait considered, but also on competitive ability and niche similarity. In particular, NNS might have similar environmental requirements to native species (Diez, Sullivan, Hulme, Edwards, & Duncan, 2008; Thuiller et al., 2010), and in that case, their establishment would not increase beta trait dispersion. On the contrary, NNS should have different alpha traits to avoid niche overlapping with native species (Schaefer, Hardy, Silva, Barraclough, & Savolainen, 2011; Strauß et al., 2016), leading to an increase in alpha trait dispersion. Overall, the impacts of human-related factors such as land use and NNS appear complex and hard to predict, because the direction and the intensity might depend of the type of factor and on the type of trait considered.

In this study, we decomposed the known patterns of multivariate functional diversity for European fish assemblages and determined the environmental drivers that are important for each trait individually. While few studies were interested in dispersion in freshwater fish assemblages, they mainly used multivariate approaches (e.g., Dolbeth, Vendel, Pessanha, & Patricio, 2016; Schleuter et al., 2012). For instance, Schleuter et al. (2012) used a multivariate approach to characterize spatial patterns in functional diversity across Europe. They suggested that geographical isolation but also harsh environmental conditions (especially extreme temperatures) could lead to low functional divergence. However, the approach used by the authors (i.e., using multivariate indices) did not allow them to determine whether the global observed pattern was attributable to either the same traits that were underdispersed simultaneously at low and high temperatures or to different traits that were underdispersed at one side of the thermal gradient. Moreover, as far as we know, none of these studies aimed to understand the determinants of several individual trait dispersion patterns at a large scale.

The aim of the present study was fourfold. First, we described dispersion patterns of five functional traits, including both alpha (e.g., trophic position) and beta (e.g., locomotion-related and

reproductive) traits (Astor et al., 2014; Troia & Gido, 2015). Second, we compared single and multiple trait approaches in the inference of spatial patterns of trait dispersion. Third, we assessed to what extent NNS influenced the observed patterns. Fourth, we identified the main determinants (i.e., climatic, land use and NNS) of these large-scale patterns of trait dispersion.

2 | MATERIALS AND METHODS

2.1 | Fish data and species traits

Freshwater fish occurrence records in 290 European river catchments were compiled from published data on species lists at the river catchment scale (Tedesco et al., 2017). Only river catchments with at least five fish species were retained for analyses. We used five quantitative functional traits linked to feeding [trophic position (TP)], life-history strategies [fecundity (number of eggs spawned at each spawning) and egg diameter] and dispersal ability (body length and swimming factor, determined by the ratio of minimal depth of the caudal peduncle to the maximal caudal fin depth; Lamouroux, Poff, & Angermeier, 2002).

Alpha and beta traits have been defined according to the framework proposed by Lopez et al. (2016) and other studies (Kraft et al., 2015; Mayfield & Levine, 2010) (Table 1). We classified trophic position and fecundity as alpha traits, because trophic position is related to resource partitioning at the local scale (Lopez et al., 2016; Pease, González-Díaz, Rodiles-Hernández, & Winemiller, 2012; Saito, Cianciaruso, Siqueira, Fonseca-Gessner, & Pavoine, 2016) and fecundity could be related to competitive ability and, consequently, resource partitioning (Sibbing & Nagelkerke, 2001). On the contrary, we classified egg size and swimming factor as beta traits. Indeed, in freshwater fish, some studies showed a strong relationship between these traits and environmental conditions, especially hydrological and thermal conditions (Pease et al., 2012; Tedesco et al., 2008). Moreover, hydrodynamic morphological ratios are related to locomotion and habitat use and are strongly driven by environmental conditions (Lamouroux et al., 2002; Sagnes & Statzner, 2009). Body length was defined as both an alpha and a beta trait, because some studies showed that it could be implicated in resource partitioning (feeding) but could also be driven by environmental factors (habitat use, locomotion) (Pease et

al., 2012; Sibbing & Nagelkerke, 2001). Trait values were taken from the literature (Kottelat & Freyhof, 2007), FishBase (Froese & Pauly, 2018) and derived from one picture per species from these two references for swimming factor. The completeness of trait information collected from the literature varied from 40% to 97% among traits. Consequently, we used from 285 to 290 river catchments and a pool from 143 to 355 and from 176 to 402 species, depending on the trait considered, for native and complete assemblages, respectively. We assessed correlations among species traits using pairwise Spearman's correlation tests. Apart from a marked positive correlation between body length and fecundity ($\rho = .80$, $p < .001$), all other correlations were $< .35$ (Supporting Information Appendix S1).

2.2 | River catchment descriptors

We described each river catchment in terms of climatic, geo-morphological and anthropogenic features. Four climatic variables were extracted from the WorldClim database (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005): mean annual temperature (TEMP), total annual precipitation (PREC), seasonality of temperature (TSEAS) and seasonality of precipitation (PSEAS). We extracted the percentage of surface covered by ice during the Last Glacial Maximum (LGM) from Ehlers, Gibbard, and Hughes (2011). Regarding to geo-morphological factors, the area of river catchment (AREA) was extracted from the CCM2 database (Vogt, Soille, Colombo, Paracchini, & de Jager, 2007) and the elevation range (ELE) from the HYDRO1k database available from the U.S. Geological Survey. Anthropogenic features were described using variables extracted from the Global Land Cover Network (GLCN) database (artificial areas, cultural areas, forest and shrub-herb areas), and the density of population was extracted from the HYDE 3.0 database for each catchment (Klein Goldewijk, Beusen, Dreht, & Vos, 2011). To reduce the multidimensionality of anthropogenic variables, we performed a principal component analysis on land use and population density variables and kept the first axis (accounting for 38.4% of the total variability and showing a strong positive correlation with the density of population, artificial and cultural areas) to obtain a synthetic variable (HUM) describing the intensity of human activities. Then, we also quantified the species richness (SR) and the proportion of NNS for each European river catchment using Kottelat & Freyhof (2007).

TABLE 1 Description of the five studied traits

Trait	Functional category	Filter	Type of trait	Expected pattern	References
Trophic position	Feeding	Niche partitioning	α	Overdispersion	Saito et al. (2016) and Lopez et al. (2016)
Fecundity	Life history strategy	Niche partitioning	α	Overdispersion	Sibbing and Nagelkerke (2001)
Body length	Feeding	Niche partitioning	α	Overdispersion	Pease et al. (2012)
	Life-history strategy, habitat use, locomotion	Environment	β	Underdispersion	Pease et al. (2012), Lopez et al. (2016)
Egg size	Life-history strategy	Environment	β	Underdispersion	Pease et al. (2012)
Swimming factor	Locomotion	Environment	β	Underdispersion	Pease et al. (2012)

2.3 | Trait dispersion and null models

To quantify trait dispersion, we computed mean pairwise distance (MPD; Webb, Ackerly, McPeck, & Donoghue, 2002) based on Gower distance matrices (Gower, 1971) for each trait separately and then based on all traits (i.e., multivariate MPD). Given that NNS can influence the patterns of trait dispersion, we carried out the analysis once while considering all co-occurring species in assemblages (including NNS; i.e., complete assemblages) and once while based only on native co-occurring species (without NNS; i.e., native assemblages). We performed null models to obtain unbiased indices that are comparable across studies and allow the testing of under- and overdispersion. Null models have been used following Leprieur, Beauchard, Hugueny, Grenouillet, and Brosse (2008) in order to be comparable with similar studies (Schleuter et al., 2012; Villéger, Blanchet, Beauchard, Oberdorff, & Brosse, 2011). In particular, we randomized 999 times the trait matrix corresponding to native or complete conditions (without and including NNS, respectively) and computed MPD for each randomization. Next, we computed standardized effect sizes (SES) of MPD for each trait and each catchment as follows: $SES = (obs - \text{mean}(rand))/SD(rand)$, where *obs* is the observed MPD and *rand* is the vector of 999 random MPD. SES of MPD are the opposite of the Nearest Relative Index (NRI), proposed by Webb et al. (2002). Positive values of SES indicate that species present more different trait values than those expected under a random hypothesis, which suggests overdispersion for the considered trait, whereas negative SES values indicate that species present more similar trait values than those expected under a random hypothesis, which suggests underdispersion for this trait. To determine whether an SES differed significantly from the random expectation, we used the distribution of the 999 random MPD for each catchment. An observed MPD higher than the 97.5th percentile or lower than the 2.5th percentile of this distribution was significant (i.e., $\alpha = .05$). A positive coefficient indicates that higher values of SES (i.e., stronger overdispersion or weaker underdispersion) are associated with higher values of the environmental variable. On the contrary, a negative relationship indicates that higher values of SES are associated with lower values of the environmental variable. Regarding second-order terms, a positive estimate indicates a convex response curve (i.e., higher SES values are observed at both upper and lower limits of the environmental gradient), whereas a negative estimate indicates a concave curve (i.e., lower SES values are observed at both extremes of the environmental gradient).

2.4 | Robustness of MPD indices to missing trait data

Given that functional diversity indices are sensitive to missing trait data (Májeková et al., 2016; Pakeman, 2014), we assessed the completeness of the species trait data and its impact on the spatial patterns of trait dispersion. To address potential geographical and phylogenetic bias in the trait data, we mapped, for each trait, the proportion of missing trait data per catchment and plotted the available versus missing data along the phylogeny (Supporting Information Appendix S2, Figures S2.1 and S2.2). The phylogenetic signal was estimated for each trait by the *D* value, which quantifies the sum of

changes in estimated nodal values of the presence-absence of missing data along the edge of the time-calibrated molecular phylogeny from Rabosky et al. (2013), and was tested using the null distribution of *D* values obtained by randomly shuffling the tips of the phylogeny 1,000 times (Fritz & Purvis, 2010).

To address the robustness of MPD indices to missing trait data, we used the framework proposed by Pakeman (2014) and simulated different degrees of trait data completeness by progressively removing trait information. Given that the proportion of missing trait data per species was highly correlated with species occurrence (Supporting Information Appendix S2, Figure S2.3), we analysed the impact of progressive removal of the traits of the rarer species on the computation of the MPD indices (Májeková et al., 2016; Pakeman, 2014). This scenario was applied to the most complete trait (i.e., swimming factor, completeness = 97%), and MPD values were expressed for each catchment as a proportion of the metric value at the full species complement.

Finally, we assessed the impact of missing data on spatial patterns of trait dispersion by computing the rank correlation between original MPD values and values obtained at each step of the removal procedure.

2.5 | Statistical analyses

To determine to what extent trait dispersion was influenced by the consideration of NNS, we used Spearman correlation tests between native and complete SES. Next, to identify the potential drivers of the observed spatial patterns, we performed a multi-model inference procedure with each measure of trait dispersion separately as the response variable. We considered all possible multi-predictor models ($n = 1,585$ for complete assemblages and $n = 637$ for native assemblages) that included five terms or fewer, including second-order terms (i.e., quadratic) (Supporting Information Appendix S3). Only mean annual temperature and annual precipitation were included as second-order terms, because humped-shaped relationships have been shown between these variables and diversity (Schleuter et al., 2012). We used generalized least squares (GLS) models in order to take into account spatial autocorrelation. The area and elevation were ln-transformed, and the predictors were transformed to z-scores (i.e., normalized) to standardize their slope coefficients, and pseudo- R^2 values were calculated for each model (Nagelkerke, 1991). We kept the models for which the difference between their Akaike information criterion (AIC) from the lowest AIC was less than or equal to two.

From the selected models (Supporting Information Appendix S3), we calculated model-averaged slopes based on the AIC weights of each model (Burnham & Anderson, 2002) and the associated 95% confidence intervals (Johnson & Omland, 2004). We checked for spatial autocorrelation using Moran's *I* (Fan & Myint, 2014), which ranged between .09 and .21 (Table 3). We chose the structure of spatial autocorrelation by fitting semi-variograms and took into account the spatial autocorrelation in all the models (Table 3). Moreover, we checked for multicollinearity between

explanatory variables (variance inflation factors all lower than six; Zuur, Ieno, & Smith, 2007).

All statistical analyses were performed with R software version 3.2.1 (R Core Team, 2017). Models were performed with the *nlme* package, and the autocorrelation structure was assessed with the *gstat* package. The package *MuMIn* was used for the multi-model inference procedure.

3 | RESULTS

Overall, the completeness of the species trait data varied among river catchments from 47.7 to 96.7% [median = 90.5, interquartile range (IQR) = (81.4, 94.3)] and showed a strongly right-skewed distribution for each trait, with the lowest values mainly observed in south-eastern Europe (Supporting Information Appendix S2, Figure S2.1). Completeness varied among fish families, with lower values for Cobitidae and Nemacheilidae, resulting in significant phylogenetic non-randomness of missing data observed for four of the traits (D values ranging from .53 to .85, $p < .001$), except swimming factor, for which missing values were randomly distributed along the phylogeny ($D = .92$, $p = .293$). However, fish species with at least one missing trait value occurred in very few river basins [median = 2, IQR = (1, 4)], whereas species with complete trait data represented 78% of the occurrence records (Supporting Information Appendix S2, Figure S2.3). Consequently, when analysing the impact of progressive removal of

the traits of the rarer species, most of the MPD indices showed little change across all the river basins (mean absolute deviation of 4.8% for 80% of the species removed). Consequently, the correlation between original MPD values and values obtained during the removal procedure revealed very resilient spatial patterns in trait dispersion ($\rho = .96$ for 80% of species removed; Supporting Information Appendix S2, Figure S2.4).

3.1 | Spatial patterns of trait dispersion

Regarding trophic position, underdispersion was mainly observed in Europe, except in small catchments around Mediterranean Sea (especially in Italy, Greece and Turkey) where overdispersion was noticed (Figure 1; Table 2). Overdispersion was the main observed pattern regarding body length, although few catchments presented significant negative SES values (Table 2). Likewise, we observed strong overdispersion for fecundity, with an increase of overdispersion from the north to the south of Europe (Figure 1; Table 2). For egg diameter, underdispersion was mainly observed in large catchments (Table 2), but a north–south gradient was observed, with overdispersion reported in catchments from northern Europe (Figure 1). For swimming factor, except for some catchments, we observed a south–north gradient of dispersion, with overdispersion near the Mediterranean Sea and underdispersion in the northern continental areas (Figure 1). When considering all the traits together, overdispersion seemed to

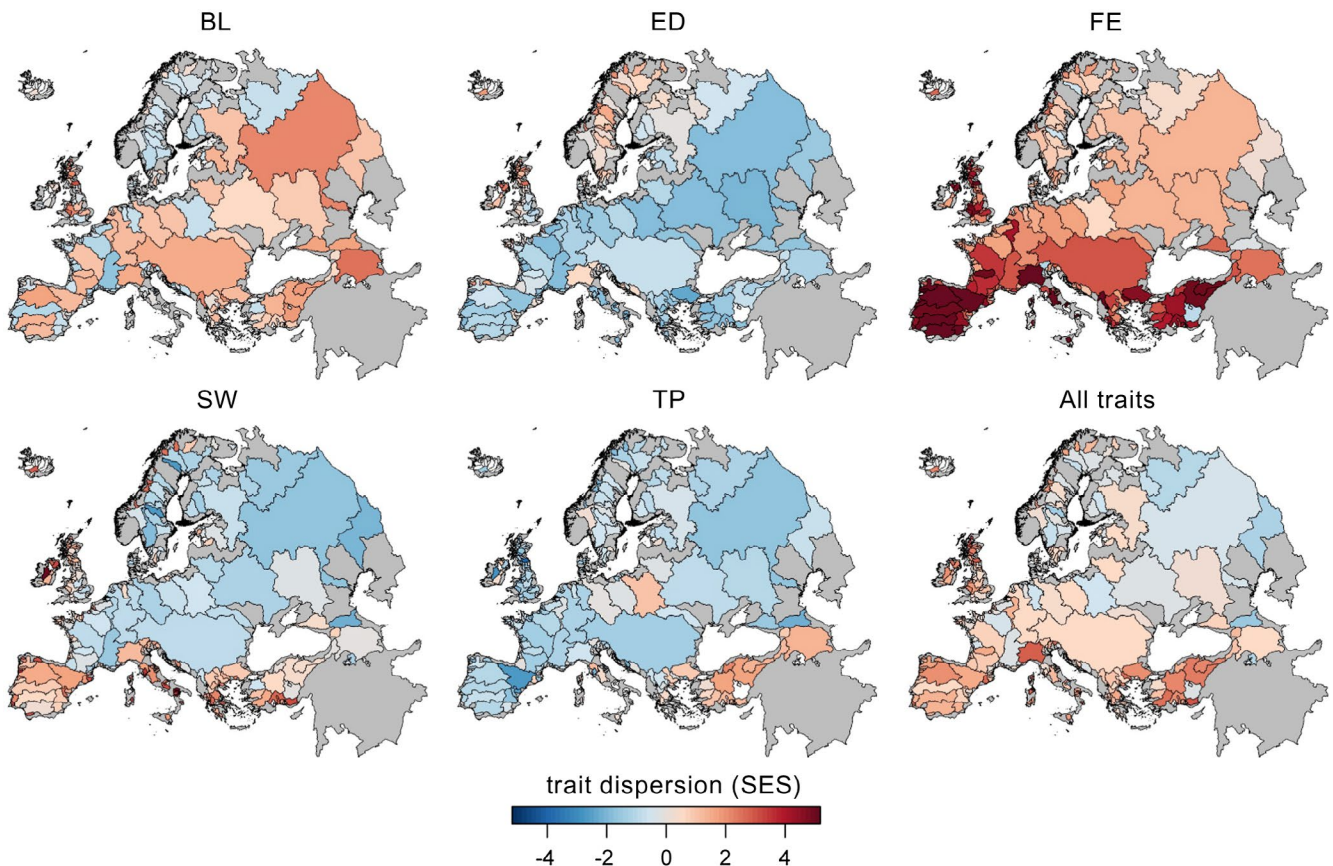


FIGURE 1 Spatial patterns of standardized effect sizes (SES) of mean pairwise distances calculated on native assemblages (i.e., native species only) for body length (BL), egg diameter (ED), fecundity (FE), swimming factor (SW), trophic position (TP) and all traits

TABLE 2 Number of river catchments for which positive (i.e., overdispersed) and negative (i.e., underdispersed) values of standardized effect sizes (SES) of the trait dispersion index was observed in body length, egg diameter, fecundity, swimming factor, trophic position and all traits

		α		Both	β		
		Trophic position	Fecundity	Body length	Egg diameter	Swimming factor	All traits
Native	Overdispersed	54 (1)	248 (50)	110 (7)	106 (7)	194 (26)	239 (22)
	Underdispersed	205 (11)	8 (0)	147 (0)	157 (16)	83 (3)	51 (0)
Complete	Overdispersed	80 (1)	278 (46)	121 (4)	154 (9)	164 (12)	240 (12)
	Underdispersed	207 (8)	9 (0)	167 (0)	131 (7)	126 (4)	50 (0)

Note.. Standardized effect sizes were computed on both native and complete assemblages, and the percentages of significant ($p < .05$) values are given in parentheses.

be observed more often than underdispersion (Table 2), although no clear spatial pattern was apparent (Figure 1).

Standardized effect sizes calculated on native and complete assemblages were significantly correlated for all traits (R^2 ranging from .78 to .88, all $p < .001$; Figure 2). Nevertheless, NNS led to a global decrease of SES values for fecundity and swimming factor, whereas we observed an increase of SES values for egg diameter (Figure 2). No such change in SES values when considering NNS was observed for body length and trophic position, or for dispersion computed on all traits (Figure 2). Overall, changes in dispersion patterns observed when comparing native and complete assemblages were not homogeneously distributed across Europe (Supporting Information Appendix S4). For instance, concerning fecundity, we observed a clear east–west gradient, with a strong decrease of SES values with NNS in the western part of Europe and a weak increase of SES values in the eastern part of Europe. Regarding swimming factor, we observed a global decrease in western Europe of SES after integrating NNS, whereas no variation in SES for the eastern part of Europe was observed. Finally, for the index calculated on all traits, the results showed an increase of SES values in southern Europe and a decrease of SES values in north-eastern Europe with the introduction of NNS.

3.2 | Effects of environmental drivers on the patterns of trait dispersion

Regarding native assemblages, GLS models showed significant positive effects of the area, the mean annual temperature and its quadratic term, the precipitation seasonality and the elevation on fecundity values, whereas a negative effect of the temperature seasonality was observed (Table 3). Concerning egg diameter, the results showed a negative effect of the annual mean temperature, the temperature seasonality and the species richness, and we observed a switch from overdispersion to underdispersion along the annual mean temperature and the temperature seasonality gradients for both complete and native assemblages (Table 3; Figure 3). A positive effect of the LGM and of annual precipitation on dispersion of egg diameter values was observed (Table 3). For body length, a negative effect of the temperature seasonality and a positive effect of the species richness, the LGM and elevation were noticed, whereas swimming factor was positively influenced by the annual mean temperature and its quadratic term and by elevation

and negatively by the area. Finally, we observed a positive effect of the precipitation seasonality for trophic position and a negative effect of the quadratic term of temperature. For index of all traits, we observed a negative effect of the species richness and positive effects of the annual mean temperature, the LGM and elevation.

Concerning the complete assemblages including NNS, we observed similar results to those found on assemblages with native species only, although the signal of some drivers was blurred. No effect of human impact was observed for dispersion computed on all traits. Finally, the rate of NNS had no influence on dispersion of traits (Table 3; Figure 3).

4 | DISCUSSION

Our study showed evidence of strong spatial variation in trait dispersion. We especially highlighted clear differences in patterns of trait dispersion within each type of trait (alpha and beta), suggesting that expectations linked to alpha and beta niches are not observed for all the traits. The contrasting patterns observed in trait dispersion were partly explained by different geo-morphological and climatic gradients. Our study suggests that univariate dispersion indices should be considered as a complementary tool to multivariate dispersion indices computed over several traits in studies assessing trait-based assembly rules. Moreover, we also showed that NNS strongly modify the dispersion patterns for almost all traits in a different direction, depending on the trait considered.

4.1 | Spatial patterns in trait dispersion

We found strong spatial patterns of dispersion for studied traits, especially regarding life-history traits (egg diameter and fecundity) and dispersal-related morphology (swimming factor), in contrast to previous studies (Šímová et al., 2015). At a more local scale, Ingram and Shurin (2009) found a decrease in dispersion, regarding several morphological and diet traits with the latitude.

We expected alpha traits (i.e., those linked to resource use) to be overdispersed, because they are linked to the coexistence of species within the assemblage, whereas beta traits (i.e., those linked to environmental requirements) were expected to be underdispersed, because these traits are likely to be filtered by the environment (Ackerly & Cornwell, 2007; Lopez et al., 2016). Our results did not corroborate this hypothesis for all the traits, contrary to what was found in snails at a local scale (Astor et al., 2014), highlighting a

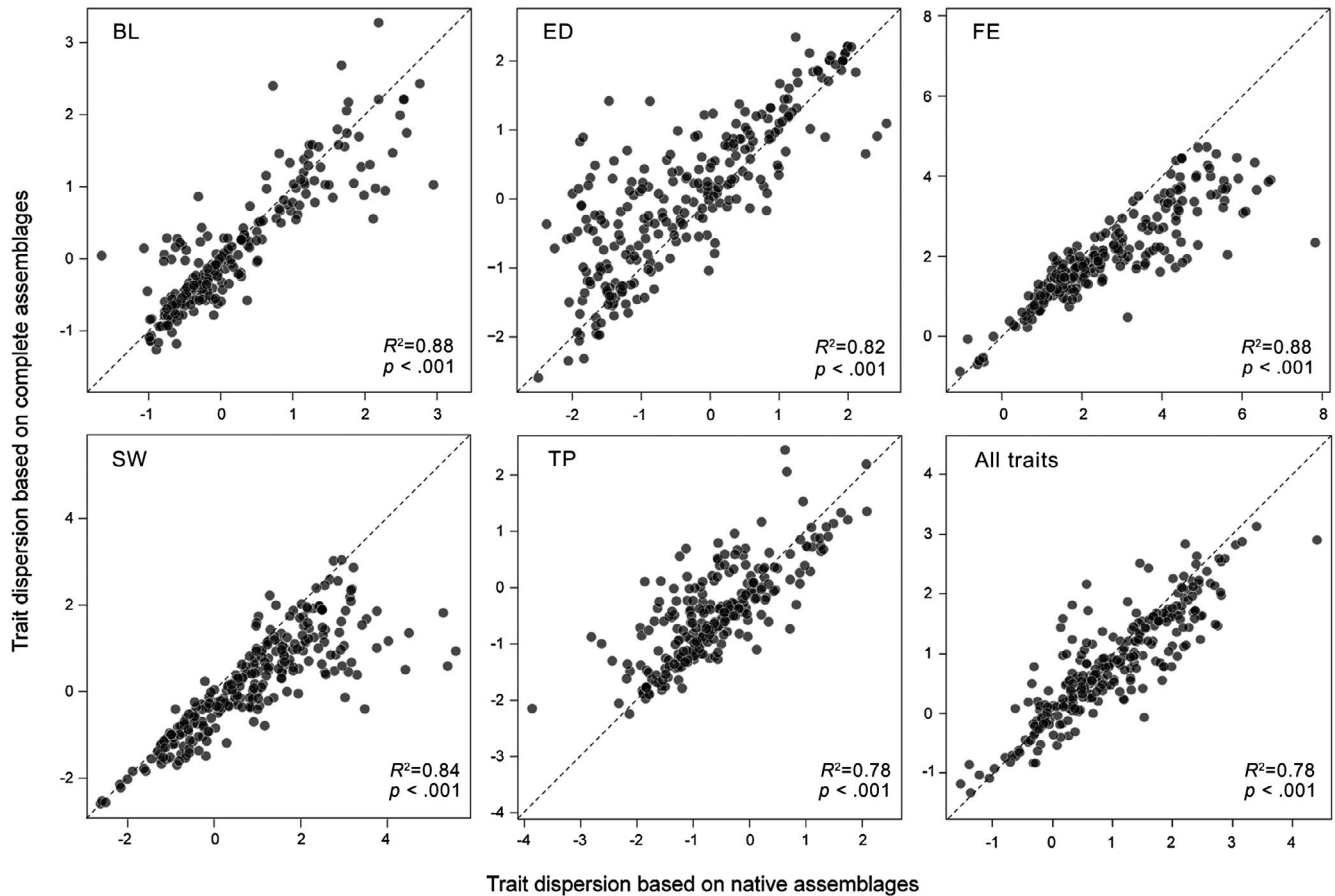


FIGURE 2 Correlations between trait dispersion [standardized effect sizes (SES)] calculated on native and complete assemblages for body length (BL), egg diameter (ED), fecundity (FE), swimming factor (SW), trophic position (TP) and all traits

potential effect of the spatial scale at which studies are conducted. Astor et al. (2014) found strong underdispersion in traits driven by environmental filtering, whereas they did not show evidence of overdispersion for traits linked to diet or body size, which is in agreement with what is currently expected (Lopez et al., 2016). In our study, overdispersion was mainly observed for the fecundity trait in almost every river catchment across Europe, whereas underdispersion was mainly noticed for egg diameter, trophic position and swimming factor, traits from both alpha and beta niches.

Our results are not in agreement with those found by Schleuter et al. (2012). They found evidence of a north–south gradient of functional dispersion, with the highest values in central Europe and the lowest values in the Balkans and Mediterranean areas. On the contrary, in our study, we found high values of dispersion for the multi-trait index for basins located in the Balkans and Mediterranean areas. This discrepancy between the two studies might be attributable to the choice of functional traits, mainly morphological for Schleuter et al. (2012), and/or of the index of divergence used.

Our results suggest that patterns of dispersion are not easily generalizable at the trait level, even among alpha and beta types of traits. This result highlights the fact that separating alpha and beta traits, as recommended in previous studies (Lopez et al., 2016), is important but not sufficient in the inference of patterns of dispersion and that the spatial variation of traits within each

category should be taken into account in future studies. Moreover, such distinction between different axes of species niche does not take into account the fact that traits can be implied simultaneously in both categories. For instance, pleiotropic effects (i.e., multiple functions for a trait) of a trait that may be related to both species coexistence and tolerance along large environmental gradients could explain why we observed both underdispersion and overdispersion in different areas for a given category.

4.2 | Abiotic and biotic determinants of trait dispersion

Although the determinants of trait dispersion were trait dependent, our results highlighted the importance of elevation range and both present and past climatic conditions in structuring trait dispersion patterns. Among geo-morphological factors, elevation range seemed greatly to influence the patterns of dispersion for all beta and alpha traits. We observed an increase of trait dispersion with elevation range, a surrogate of habitat diversity in river catchments. Previous studies have already highlighted the importance of the elevation gradient on diversity patterns (e.g., Bahram, Polme, Koljalg, Zarre, & Tedersoo, 2012; Frenzel, Everaars, & Schweiger, 2016; García-López, Micó, & Galante, 2012; Matono, Bernardo, Costa, & Ilheu, 2014; Melo, Rangel, & Diniz-Filho, 2009) and mean values of

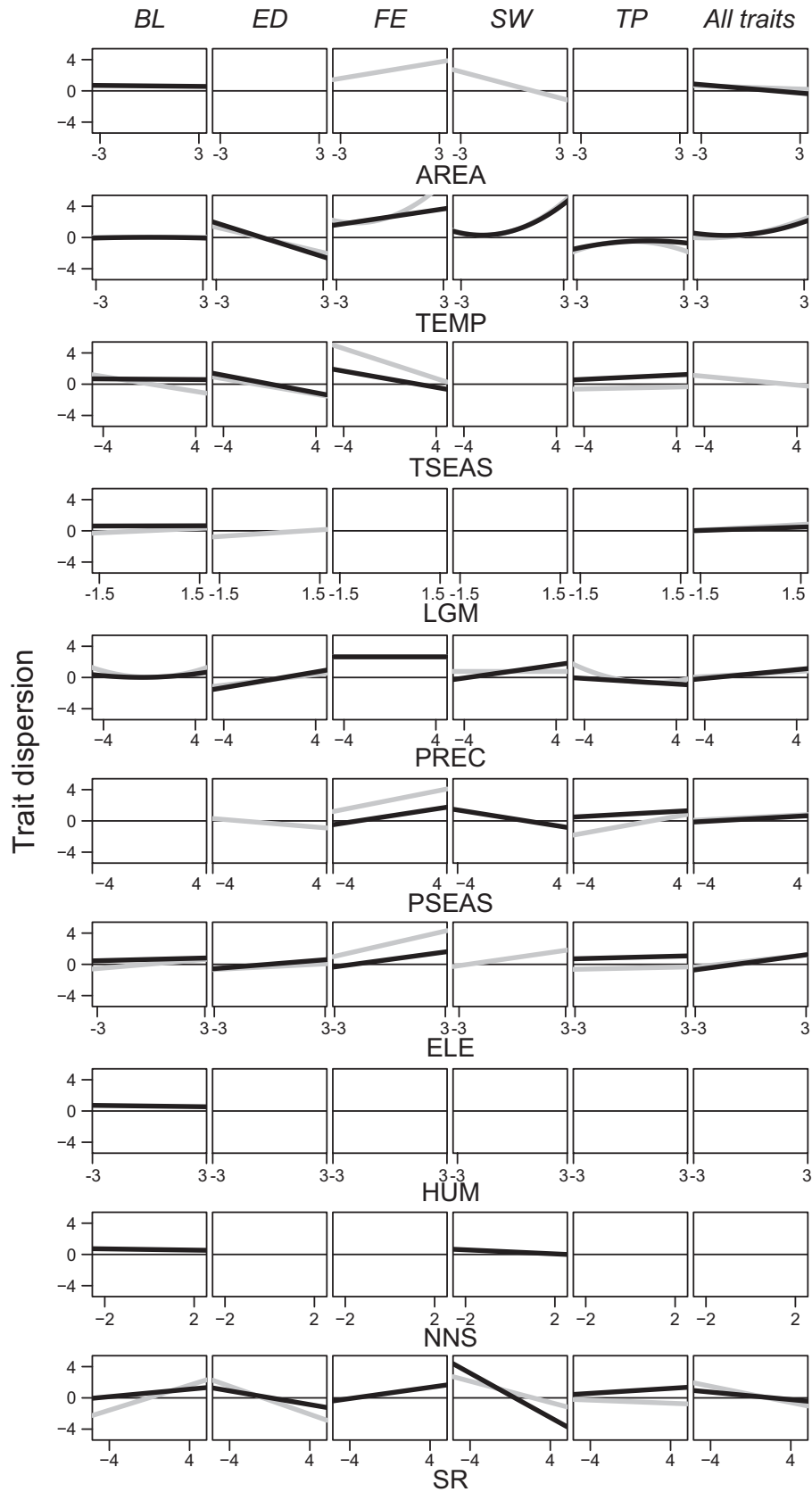


FIGURE 3 Relationship between trait dispersion and each environmental driver (normalized). Black and grey lines refer to native and complete assemblages, respectively, drawn from model coefficients computed in Table 3. The horizontal line corresponds to $y = 0$. Abbreviations are as in Table 3

TABLE 3 Results of generalized least squares models relating standardized effect sizes (SES) of the trait dispersion indices to catchment descriptors (\log_{10} -transformed when the distribution was not Gaussian)

	Moran's I Spatial autocorrelation	Spatial autocorrelation structure	Climate										Geomorphology			Human-related use			Biotic	
			TEMP	TEMP ²	TSEAS	LGM	PREC	PREC ²	PSEAS	AREA	ELE	HUM	NNS	SR						
Trophic position	0.20	Exponential	-	-0.13	0.03	-	-0.19	0.05	0.33	-	0.05	-	-	-	-	-	-	-	-	-0.05
Fecundity	0.21	Exponential	0.81	0.21	-0.48	-	-	-	0.36	0.35	0.54	-	-	-	-	-	-	-	-	-
Body length	0.09	Exponential	-	-	-0.24	0.19	-	-	0.05	-	0.20	-	-	-	-	-	-	-	-	0.40
Egg diameter	0.18	Exponential	-0.54	-	-0.25	0.28	0.17	-	-	-0.15	-	0.12	-	-	-	-	-	-	-	-0.45
Swimming factor	0.16	Gaussian	0.64	0.21	-	-	-	-	-	-0.56	0.34	-	-	-	-	-	-	-	-	-0.34
All traits	0.18	Exponential	0.40	-	-0.14	0.24	0.08	-	0.09	-0.07	0.26	-	-	-	-	-	-	-	-	-0.26
Trophic position	0.20	Exponential	0.12	-0.06	0.07	-	-0.09	-	0.10	-	0.06	-	-	-	-	-	-	-	-	0.08
Fecundity	0.21	Exponential	0.34	-	-0.26	-	-	-	0.28	-	0.32	-	-	-	-	-	-	-	-	0.18
Body Length	0.09	Exponential	-	-0.01	-0.01	0.01	0.03	0.02	-	-0.02	0.06	-0.03	-0.04	0.12	-	-	-	-	-	-0.22
Egg diameter	0.18	Exponential	-0.72	-	-0.28	-	0.25	-	-	0.19	-	-	-	-	-	-	-	-	-	-0.71
Swimming factor	0.16	Exponential	0.60	0.19	-	-	0.21	-	-0.29	-	-	-	-0.13	-0.71	-	-	-	-	-	-0.71
All traits	0.18	Exponential	0.25	0.09	-	0.14	0.14	-	0.10	-0.18	0.32	-	-	-	-	-	-	-	-	-0.12

Note.. AREA = area of river catchment; ELE = elevation range; HUM = human use; LGM = percentage of surface covered by ice during the Last Glacial Maximum; NNS = percentage of non-native species; PREC = total annual precipitation; PSEAS = seasonality of precipitation; SR = fish species richness; TEMP = mean annual temperature; TSEAS = seasonality of temperature. The values are slope regression coefficients (in bold when significant at $p < .05$). HUM and NNS, considered to be recent effects, have not been tested on native assemblages. Models have been run using as response variables SES values computed from trophic position, body length, fecundity, egg diameter, swimming factor and all traits for both native and complete fish assemblages. Moran's I values and the structure of autocorrelation are given for each multi-model inference procedure (i.e., response variable and each selection procedure). Bold coefficients are significant (i.e., Confidence interval (IC_{95}) does not comprise zero). If no estimate is given, it indicates that the explanatory variable was not selected by the multi-model inference procedure.

traits (Bässler et al., 2016; de Bello et al., 2013), but there are few studies on the dispersion of these traits (de Bello et al., 2013).

Regarding climatic conditions, our results highlighted the importance of temperature mean and seasonality but also precipitation seasonality in structuring trait dispersion patterns. An increase of dispersion with mean temperature was observed for the alpha and beta traits fecundity and trophic position, respectively, whereas a decrease was observed for egg size. Overall, a negative relationship between seasonality of temperature and dispersion of traits was noticed, whereas a positive relationship was observed between seasonality of precipitation and dispersion of traits, except for egg size, for which the relationship was negative. These results suggest underdispersion in thermally unstable environments and overdispersion in hydrologically unstable environments, except for egg size, where underdispersion is predominant. Environmental stability appears to be a key feature influencing patterns of trait dispersion for fish species (Tedesco et al., 2008) but also for other groups (e.g., Brendonck, Jocqué, Tuytens, Timms, & Vanschoenwinkel, 2014). These results are in agreement with one previous study on plants, which provided evidence for either a positive or a negative influence of temperature seasonality on dispersion of traits, depending on the trait considered (Shiono et al., 2015).

Contrary to our expectations, both over- and underdispersion could occur in climatically unstable environments. In such environments, overdispersion might occur because several strategies enable organisms to cope with important climatic variations. However, underdispersion might also be observed because several species can select a unique optimal strategy in order to respond to one type of pressure. Regarding the climatic history, past climatic events such as glaciation events might lead to mass extinctions and consequently have a negative impact on diversity (Oberdorff, Hugué, & Guegan, 1997; Tedesco, Oberdorff, Lasso, Zapata, & Hugué, 2005) by decreasing functional richness and functional evenness but increasing functional dispersion (Schleuter et al., 2012). Our results are in agreement with this hypothesis, because an increase in dispersion with the percentage of ice cover during the last glaciation event was observed for reproductive traits, suggesting overdispersion in areas exposed to strong glaciation episodes and underdispersion in refuge areas.

Concerning quadratic effects, we observed significant effects only for temperature. For trophic position, our results support the harshness hypothesis, which expects lower diversity in harsh environments (Currie et al., 2004; Mason, Irz, Lanoiselée, Mouillot, & Argillier, 2008). For this trait, we observed a concave relationship with underdispersion for extreme values, suggesting habitat filtering for this trait. Previous study on beach food webs showed similar results, with underdispersion of trophic position values on beaches with extreme morphodynamic environments (Bergamino, Lercari, & Defeo, 2011). On the contrary, our results did not support the harshness hypothesis for fecundity and swimming factor, for which a convex relationship was observed (i.e., overdispersion for extreme values). This result suggests that niche partitioning is the main filter of community assemblages for these two traits and is peculiarly high at extreme temperatures.

Nevertheless, overdispersion for these two traits was mainly observed in small Mediterranean river basins, which have been identified as diversity hotspots with strong endemism (Reyjol et al., 2007).

Although several studies showed the impact of human activities on functional diversity (e.g., Flynn et al., 2009; D'agata et al., 2014), we found no effect of human-related land use on spatial patterns of trait dispersion, although this might be attributable to the coarse resolution of characterization of human use in the present study. However, regardless of the environmental conditions, the presence of NNS blurred the relationship between the patterns of trait dispersion and the environmental drivers, suggesting that NNS might respond differently to these drivers. Moreover, our results suggest that NNS impact trait dispersion patterns. Surprisingly, the effect of NNS did not depend on the type of trait. For instance, NNS have a negative influence on dispersion patterns of body length and fecundity, leading to an increased redundancy between species (i.e., similar values of trait for both native and NNS). In contrast, egg diameter (also a beta trait) showed overdispersion when several NNS were present in the basin, indicating that NNS are complementary to native species in terms of their egg diameter (i.e., different values of traits between native and NNS).

4.3 | Single versus multiple trait-based approaches

Our results showed different patterns between indices calculated on single and multiple traits, suggesting that multi-trait indices can present a different view of dispersion patterns. Indeed, besides the fact that we found less clear patterns of dispersion using multiple trait-based approaches, our results also showed that combining multiple traits could blur the effects of environmental variables on trait dispersion patterns and mask some of them. Liu, Swenson, Zhang, and Ma (2013) found similar results in tropical tree communities, with different patterns observed between univariate and multivariate measures. Different processes can select different traits and, consequently, give opposing signals in null model analyses (Saito et al., 2016). Indeed, functional diversity is a combination of the diversities of each individual trait, and although some of the traits considered can be restricted to a very narrow range of values (i.e., low diversity regarding those traits, or underdispersion), others could take a wide range of values (i.e., high diversity concerning those traits, or overdispersion). By associating all these traits in a single diversity measure, for which the range of values taken by co-occurring species can be highly trait specific, one could (and probably would) blur spatial patterns of functional diversity. It now appears necessary to decompose the currently known spatial patterns and mechanisms structuring functional diversity trait by trait to deepen our understanding of these overall patterns and their determinants (Astor et al., 2014; Ingram & Shurin, 2009). In this context, our results highlight the usefulness of approaches addressing several functional traits separately to understand trait-based assembly rules that could not be apprehended by a global measure of trait dispersion.

4.4 | Conclusion

Our study highlighted strong among-trait variations in spatial patterns of trait dispersion. It thus appears necessary to take this insight into account, because different traits within the alpha and beta dichotomy can present opposite patterns of dispersion, especially at a large scale, and can mask an important trait dispersion signal for an individual trait when using all traits together (Lopez et al., 2016; Saito et al., 2016). Thus, it seems essential for community ecologists to select traits correctly in the study of assembly processes (Saito et al., 2016). Even if the separation of traits into alpha and beta traits is important to disentangle interacting processes, it appears not to be sufficient. Indeed, although hypotheses concerning patterns of dispersion in beta and alpha traits have been formulated clearly in previous studies, they can vary drastically within each type of trait, across space and along environmental gradients. Among them, climatic conditions appeared to be the most important drivers of spatial patterns in trait dispersion. Finally, the presence of NNS can drastically modify the patterns of trait dispersion and blur the effects of environmental drivers on assemblage composition. Although the influence of NNS on functional diversity has been assessed recently (Toussaint et al., 2018), the present study suggests that change in functional dispersion related to NNS should be decomposed trait by trait to gain a better understanding of which component of functional diversity is impacted.

ACKNOWLEDGMENTS

The Evolution et Diversité Biologique laboratory was supported by 'Investissement d'Avenir' grants (CEBA, ref. ANR-10-LABX-0025; TULIP, ref. ANR-10-LABX-41). J.C. was supported by Agence française pour la biodiversité (AFB). We thank the reviewers for their comments that helped to improve this manuscript. We also thank Pablo Tedesco and Céline Jezequel for their help in Geographic Information System (GIS) analysis.

DATA ACCESSIBILITY

All climatic GIS layers are available as raster grids from the WorldClim database: <http://www.worldclim.org/>. Environmental and topographic GIS layers are available on CCM2 and Hydro1k databases: <http://ccm.jrc.ec.europa.eu/php/index.php?action=view&id=24> and <https://lta.cr.usgs.gov/HYDRO1K>. The percentage of surface covered by ice is available in Ehlers et al. (2011): https://booksite.elsevier.com/9780444534477/digital_maps.php. Anthropogenic features (land use and population density) have been extracted from GLCN and HYDE 3.0: <https://www.eea.europa.eu/data-and-maps/data/global-land-cover-250m> and <ftp://ftp.pbl.nl/~hyde/>. The occurrences database is available in Tedesco et al. (2017).

ORCID

Jessica Côte  <https://orcid.org/0000-0003-4965-1915>

Lucie Kuczynski  <https://orcid.org/0000-0002-4448-2836>

REFERENCES

- Ackerly, D. D., & Cornwell, W. K. (2007). A trait-based approach to community assembly: Partitioning of species trait values into within- and among-community components. *Ecology Letters*, 10, 135–145. <https://doi.org/10.1111/j.1461-0248.2006.01006.x>
- Astor, T., Strengbom, J., Berg, M. P., Lenoir, L., Marteinsdóttir, B., & Bengtsson, J. (2014). Underdispersion and overdispersion of traits in terrestrial snail communities on islands. *Ecology and Evolution*, 4, 2090–2102. <https://doi.org/10.1002/ece3.1084>
- Bahram, M., Polme, S., Koljalg, U., Zarre, S., & Tedersoo, L. (2012). Regional and local patterns of ectomycorrhizal fungal diversity and community structure along an altitudinal gradient in the Hyrcanian forests of northern Iran. *New Phytologist*, 193, 465–473. <https://doi.org/10.1111/j.1469-8137.2011.03927.x>
- Bässler, C., Halbwegs, H., Karasch, P., Holzer, H., Gminder, A., Kriegelsteiner, L., ... Brandl, R. (2016). Mean reproductive traits of fungal assemblages are correlated with resource availability. *Ecology and Evolution*, 6, 582–592. <https://doi.org/10.1002/ece3.1911>
- Bregman, T. P., Lees, A. C., Seddon, N., MacGregor, H. E. A., Darski, B., Aleixo, A., ... Tobias, J. A. (2015). Species interactions regulate the collapse of biodiversity and ecosystem function in tropical forest fragments. *Ecology*, 96, 2692–2704. <https://doi.org/10.1890/14-1731.1>
- Bergamino, L., Lercari, D., & Defeo, O. (2011). Food web structure of sandy beaches: Temporal and spatial variation using stable isotope analysis. *Estuarine Coastal and Shelf Science*, 91, 536–543.
- Brendonck, L., Jocqué, M., Tuytens, K., Timms, B. V., & Vanschoenwinkel, B. (2014). Hydrological stability drives both local and regional diversity patterns in rock pool metacommunities. *Oikos*, 124, 741–749. <https://doi.org/10.1111/oik.01710>
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach* (2nd ed.). New York, NY: Springer.
- Currie, D. J., Mittelbach, G. G., Cornell, H. V., Field, R., Guégan, J. F., Hawkins, B. A., ... Turner, J. R. G. (2004). Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters*, 7, 1121–1134. <https://doi.org/10.1111/j.1461-0248.2004.00671.x>
- D'agata, S., Mouillot, D., Kulbicki, M., Andréfouët, S., Bellwood, D. R., Cinner, J. E., ... Vigliola, L. (2014). Human-mediated loss of phylogenetic and functional diversity in coral reef fishes. *Current Biology*, 24, 555–560. <https://doi.org/10.1016/j.cub.2014.01.049>
- de Bello, F., Vandewalle, M., Reitalu, T., Lepš, J., Prentice, H. C., Lavorel, S., & Sykes, M. T. (2013). Evidence for scale- and disturbance-dependent trait assembly patterns in dry semi-natural grasslands. *Journal of Ecology*, 101, 1237–1244. <https://doi.org/10.1111/1365-2745.12139>
- de Sousa Queiroz, C. S., Da Silva, F. R., & de Cerqueira Rossa-Feres, D. C. (2015). The relationship between pond habitat depth and functional tadpole diversity in an agricultural landscape. *Royal Society Open Science*, 2, 150165. <https://doi.org/10.1098/rsos.150165>
- Díaz, S., & Cabido, M. (2001). Vive la différence: Plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution*, 16, 646–655.
- Diez, J. M., Sullivan, J. J., Hulme, P. E., Edwards, G., & Duncan, R. P. (2008). Darwin's naturalization conundrum: Dissecting taxonomic patterns of species invasions. *Ecology Letters*, 11, 674–681. <https://doi.org/10.1111/j.1461-0248.2008.01178.x>
- Dolbeth, M., Vendel, A. L., Pessanha, A., & Patricio, J. (2016). Functional diversity of fish communities in two tropical estuaries subjected to anthropogenic disturbance. *Marine Pollution Bulletin*, 112, 244–254. <https://doi.org/10.1016/j.marpolbul.2016.08.011>
- Ehlers, J., Gibbard, P. L., & Hughes, P. D. (2011). *Quaternary glaciations – Extent and chronology, volume 15*. Amsterdam: Elsevier Science.
- Fan, C., & Myint, S. (2014). A comparison of spatial autocorrelation indices and landscape metrics in measuring urban landscape

- fragmentation. *Landscape and Urban Planning*, 121, 117–128. <https://doi.org/10.1016/j.landurbplan.2013.10.002>
- Flynn, D. F. B., Gogol-Prokurat, M., Nogeire, T., Molinari, N., Richers, B. T., Lin, B. B., ... DeClerck, F. (2009). Loss of functional diversity under land use intensification across multiple taxa. *Ecology Letters*, 12, 22–33. <https://doi.org/10.1111/j.1461-0248.2008.01255.x>
- Forrest, J. R. K., Thorp, R. W., Kremen, C., & Williams, N. M. (2015). Contrasting patterns in species and functional-trait diversity of bees in an agricultural landscape. *Journal of Applied Ecology*, 52, 706–715. <https://doi.org/10.1111/1365-2664.12433>
- Frenzel, M., Everaars, J., & Schweiger, O. (2016). Bird communities in agricultural landscapes: What are the current drivers of temporal trends? *Ecological Indicators*, 65, 113–121. <https://doi.org/10.1016/j.ecolind.2015.11.020>
- Fritz, S. A., & Purvis, A. (2010). Selectivity in mammalian extinction risk and threat types: A new measure of phylogenetic signal strength in binary traits. *Conservation Biology*, 24, 1042–1051. <https://doi.org/10.1111/j.1523-1739.2010.01455.x>
- Froese, R., & Pauly, D. (2018). *FishBase*. Retrieved from www.fishbase.org
- García-López, A., Micó, E., & Galante, E. (2012). From lowlands to highlands: Searching for elevational patterns of species richness and distribution of scarab beetles in Costa Rica. *Diversity and Distributions*, 18, 543–553. <https://doi.org/10.1111/j.1472-4642.2011.00846.x>
- Gower, J. C. (1971). A general coefficient of similarity and some of its properties. *Biometrics*, 857–871. <https://doi.org/10.2307/2528823>
- Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25, 1965–1978. <https://doi.org/10.1002/joc.1276>
- Ingram, T., & Shurin, J. B. (2009). Trait-based assembly and phylogenetic structure in northeast Pacific rockfish assemblages. *Ecology*, 90, 2444–2453. <https://doi.org/10.1890/08-1841.1>
- Johnson, J. B., & Omland, K. S. (2004). Model selection in ecology and evolution. *Trends in Ecology and Evolution*, 19, 101–108. <https://doi.org/10.1016/j.tree.2003.10.013>
- Katabuchi, M., Kurokawa, H., Davies, S. J., Tan, S., & Nakashizuka, T. (2012). Soil resource availability shapes community trait structure in a species-rich dipterocarp forest. *Journal of Ecology*, 100, 643–651. <https://doi.org/10.1111/j.1365-2745.2011.01937.x>
- Klein Goldewijk, K., Beusen, A., van Drecht, G., & de Vos, M. (2011). The HYDE 3.1 spatially explicit database of human-induced global land-use change over the past 12,000 years. *Global Ecology and Biogeography*, 20, 73–86. <https://doi.org/10.1111/j.1466-8238.2010.00587.x>
- Kottelat, M., & Freyhof, J. (2007). *Handbook of European freshwater fishes*. Cornol, Switzerland: Publications Kottelat.
- Kraft, N. J. B., Adler, P. B., Godoy, O., James, E. C., Fuller, S., & Levine, J. M. (2015). Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology*, 29, 592–599. <https://doi.org/10.1111/1365-2435.12345>
- Lamouroux, N., Poff, N. L., & Angermeier, P. L. (2002). Intercontinental convergence of stream fish community traits along geomorphic and hydraulic gradients. *Ecology*, 83, 1792–1807. [https://doi.org/10.1890/0012-9658\(2002\)083\[1792:ICOSFC\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[1792:ICOSFC]2.0.CO;2)
- Leprieux, F., Beauchard, O., Hugué, B., Grenouillet, G., & Brosse, S. (2008). Null model of biotic homogenization: A test with the European freshwater fish fauna. *Diversity and Distributions*, 14, 291–300. <https://doi.org/10.1111/j.1472-4642.2007.00409.x>
- Liu, X., Swenson, N. G., Zhang, J., & Ma, K. (2013). The environment and space, not phylogeny, determine trait dispersion in a subtropical forest. *Functional Ecology*, 27, 264–272. <https://doi.org/10.1111/1365-2435.12018>
- Lopez, B., Burgio, K., Carlucci, M., Palmquist, K., Parada, A., Weinberger, V., & Hurlbert, A. (2016). A new framework for inferring community assembly processes using phylogenetic information, relevant traits and environmental gradients. *One Ecosystem*, 1, e9501. <https://doi.org/10.3897/oneeco.1.e9501>
- Májeková, M., Paal, T., Plowman, N. S., Bryndová, M., Kasari, L., Norberg, A., ... de Bello, F. (2016). Evaluating functional diversity: Missing trait data and the importance of species abundance structure and data transformation. *PLoS ONE*, 11, e0149270. <https://doi.org/10.1371/journal.pone.0149270>
- 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. <https://doi.org/10.1111/j.1365-2656.2007.01350.x>
- 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. <https://doi.org/10.1111/j.0030-1299.2005.13886.x>
- Matono, P., Bernardo, J. M., Costa, A. M., & Ilheu, M. (2014). Fish response to anthropogenic pressures in temporary streams: The importance of environmental drivers. *River Research and Applications*, 30, 1281–1295.
- Mayfield, M. M., & Levine, J. M. (2010). Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters*, 13, 1085–1093. <https://doi.org/10.1111/j.1461-0248.2010.01509.x>
- Melo, A. S., Rangel, T. F. L. V. B., & Diniz-Filho, J. A. F. (2009). Environmental drivers of beta-diversity patterns in New-World birds and mammals. *Ecography*, 32, 226–236. <https://doi.org/10.1111/j.1600-0587.2008.05502.x>
- Mouchet, M. A., Villéger, S., Mason, N. W. H., & Mouillot, D. (2010). Functional diversity measures: An overview of their redundancy and their ability to discriminate community assembly rules: Functional diversity measures. *Functional Ecology*, 24, 867–876. <https://doi.org/10.1111/j.1365-2435.2010.01695.x>
- Nagelkerke, N. J. D. (1991). A note on a general definition of the coefficient of determination. *Biometrika*, 78, 691–692. <https://doi.org/10.1093/biomet/78.3.691>
- Oberdorff, T., Hugué, B., & Guegan, 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. <https://doi.org/10.1111/j.1365-2699.1997.00113.x>
- Ordóñez, A., & Svenning, J. C. (2015). Geographic patterns in functional diversity deficits are linked to glacial-interglacial climate stability and accessibility. *Global Ecology and Biogeography*, 24, 826–837. <https://doi.org/10.1111/geb.12324>
- Ordóñez, A., & Svenning, J. C. (2016). Strong paleoclimatic legacies in current plant functional diversity patterns across Europe. *Ecology and Evolution*, 6, 3405–3416. <https://doi.org/10.1002/ece3.2131>
- Pakeman, R. J. (2014). Functional trait metrics are sensitive to the completeness of the species' trait data? *Methods in Ecology and Evolution*, 5, 9–15.
- Pease, A. A., González-Díaz, A. A., Rodiles-Hernández, R., & Winemiller, K. O. (2012). Functional diversity and trait–environment relationships of stream fish assemblages in a large tropical catchment. *Freshwater Biology*, 57, 1060–1075. <https://doi.org/10.1111/j.1365-2427.2012.02768.x>
- Petchey, O. L., & Gaston, K. J. (2002). Functional diversity (FD), species richness and community composition. *Ecology Letters*, 5, 402–411. <https://doi.org/10.1046/j.1461-0248.2002.00339.x>
- R Core Team. (2017). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Rabosky, D. L., Santini, F., Eastman, J., Smith, S. A., Sidlauskas, B., Chang, J., & Alfaro, M. E. (2013). Rates of speciation and morphological evolution are correlated across the largest vertebrate radiation. *Nature Communications*, 4, 1958. <https://doi.org/10.1038/ncomms2958>
- Reyjol, Y., Hugué, B., Pont, D., Bianco, P. G., Beier, U., Caiola, N., ... Virbickas, T. (2007). Patterns in species richness and endemism of

- European freshwater fish. *Global Ecology and Biogeography*, 16, 65–75. <https://doi.org/10.1111/j.1466-8238.2006.00264.x>
- Sagnes, P., & Statzner, B. (2009). Hydrodynamic abilities of riverine fish: A functional link between morphology and velocity use. *Aquatic Living Resources*, 22, 79–91. <https://doi.org/10.1051/alr/2009008>
- Saito, V. S., Cianciaruso, M. V., Siqueira, T., Fonseca-Gessner, A. A., & Pavoine, S. (2016). Phylogenies and traits provide distinct insights about the historical and contemporary assembly of aquatic insect communities. *Ecology and Evolution*, 6, 2925–2937. <https://doi.org/10.1002/ece3.2081>
- Schaefer, H., Hardy, O. J., Silva, L., Barraclough, T. G., & Savolainen, V. (2011). Testing Darwin's naturalization hypothesis in the Azores: Predicting invasiveness in the Azores. *Ecology Letters*, 14, 389–396. <https://doi.org/10.1111/j.1461-0248.2011.01600.x>
- Schellenberger Costa, D., Gerschlaue, F., Pabst, H., Kühnel, A., Huwe, B., Kiese, R., ... Kleyer, M. (2017). Community-weighted means and functional dispersion of plant functional traits along environmental gradients on Mount Kilimanjaro. *Journal of Vegetation Science*, 28, 684–695. <https://doi.org/10.1111/jvs.12542>
- Schleuter, D., Daufresne, M., Veslot, J., Mason, N. W. H., Lanoiselee, C., Brosse, S., ... Argillier, C. (2012). Geographic isolation and climate govern the functional diversity of native fish communities in European drainage basins. *Global Ecology and Biogeography*, 21, 1083–1095. <https://doi.org/10.1111/j.1466-8238.2012.00763.x>
- Shiono, T., Kusumoto, B., Maeshiro, R., Fujii, S.-J., Goetzenberger, L., de Bello, F., & Kubota, Y. (2015). Climatic drivers of trait assembly in woody plants in Japan. *Journal of Biogeography*, 42, 1176–1186. <https://doi.org/10.1111/jbi.12503>
- 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.
- Šimová, I., Violle, C., Kraft, N. J. B., Storch, D., Svenning, J.-C., Boyle, B., ... Enquist, B. J. (2015). Shifts in trait means and variances in North American tree assemblages: Species richness patterns are loosely related to the functional space. *Ecography*, 38, 649–658. <https://doi.org/10.1111/ecog.00867>
- Strauß, A., Guilhaumon, F., Randrianiaina, R. D., Wollenberg Valero, K. C., Vences, M., & Glos, J. (2016). Opposing patterns of seasonal change in functional and phylogenetic diversity of tadpole assemblages. *PLoS ONE*, 11, e0151744. <https://doi.org/10.1371/journal.pone.0151744>
- Swenson, N. G., Enquist, B. J., Pither, J., Kerkhoff, A. J., Boyle, B., Weiser, M. D., ... Noltling, K. M. (2012). The biogeography and filtering of woody plant functional diversity in North and South America: Functional trait biogeography. *Global Ecology and Biogeography*, 21, 798–808. <https://doi.org/10.1111/j.1466-8238.2011.00727.x>
- Tedesco, P. A., Huguency, B., Oberdorff, T., Dürr, H. H., Mérigoux, S., & de Mérona, B. (2008). River hydrological seasonality influences life history strategies of tropical riverine fishes. *Oecologia*, 156, 691–702. <https://doi.org/10.1007/s00442-008-1021-2>
- Tedesco, P. A., Oberdorff, T., Lasso, C. A., Zapata, M., & Huguency, B. (2005). Evidence of history in explaining diversity patterns in tropical riverine fish. *Journal of Biogeography*, 32, 1899–1907. <https://doi.org/10.1111/j.1365-2699.2005.01345.x>
- Tedesco, P. A., Beauchard, O., Bigorne, R., Blanchet, S., Buisson, L., Conti, L., ... Oberdorff, T. (2017). A global database on freshwater fish species occurrence in drainage basins. *Scientific Data*, 4, 170141. <https://doi.org/10.1038/sdata.2017.141>
- Thuiller, W., Gallien, L., Boulangeat, I., De Bello, F., Münkemüller, T., Roquet, C., & Lavergne, S. (2010). Resolving Darwin's naturalization conundrum: A test for evidence. *Diversity and Distributions*, 16, 461–475. <https://doi.org/10.1111/j.1472-4642.2010.00645.x>
- 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. <https://doi.org/10.1126/science.277.5330.1300>
- Toussaint, A., Charpin, N., Beauchard, O., Grenouillet, G., Oberdorff, T., Tedesco, P. A., ... Villéger, S. (2018). Non-native species led to marked shifts in functional diversity of the world freshwater fish faunas. *Ecology Letters*, 21, 1649–1659. <https://doi.org/10.1111/ele.13141>
- Troia, M. J., & Gido, K. B. (2015). Functional strategies drive community assembly of stream fishes along environmental gradients and across spatial scales. *Oecologia*, 177, 545–559. <https://doi.org/10.1007/s00442-014-3178-1>
- Tsianou, M. A., & Kallimanis, A. S. (2016). Different species traits produce diverse spatial functional diversity patterns of amphibians. *Biodiversity and Conservation*, 25, 117–132. <https://doi.org/10.1007/s10531-015-1038-x>
- Villéger, S., Blanchet, S., Beauchard, O., Oberdorff, T., & Brosse, S. (2011). Homogenization patterns of the world's freshwater fish faunas. *Proceedings of the National Academy of Sciences USA*, 108, 18003–18008. <https://doi.org/10.1073/pnas.1107614108>
- Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional! *Oikos*, 116, 882–892.
- Vitousek, P. M., D'Antonio, C. M., Loope, L. L., Rejmanek, M., & Westbrooks, R. (1997). Introduced species: A significant component of human-caused global change. *New Zealand Journal of Ecology*, 21, 1–16.
- Vogt, J., Soille, P., Colombo, R., Paracchini, M. L., & de Jager, A. (2007). Development of a pan-European river and catchment database. *Digital Terrain Modelling*, 121–144.
- Vogt, R. J., Peres-Neto, P. R., & Beisner, B. E. (2013). Using functional traits to investigate the determinants of crustacean zooplankton community structure. *Oikos*, 122, 1700–1709. <https://doi.org/10.1111/j.1600-0706.2013.00039.x>
- Webb, C. O., Ackerly, D. D., McPeck, M. A., & Donoghue, M. J. (2002). Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, 33, 475–505. <https://doi.org/10.1146/annurev.ecolsys.33.010802.150448>
- Zuur, A. F., Ieno, E. N., & Smith, G. M. (2007). *Analyzing ecological data* (p. 672). New York, NY: Springer.

BIOSKETCHES

JESSICA CÔTE is a postdoctoral researcher in the laboratory 'Évolution et Diversité Biologique' (University of Toulouse, France). She is interested in the impact of global change and anthropogenic disturbances on organisms at population and community levels. She particularly studies the effect of environmental disturbances on functional and phylogenetic diversity and assemblage rules.

Lucie Kuczynski is a postdoctoral researcher in the Biology Department of Oklahoma University. She is interested in understanding the evolutionary and ecological processes that structure diversity at multiple temporal and spatial scales and at different levels of biological organization. She is currently working on linking the phylogeographical structure and community diversity patterns of North American amphibians.

SUPPORTING INFORMATION

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

How to cite this article: Côte J, Kuczynski L, Grenouillet G.

Spatial patterns and determinants of trait dispersion in freshwater fish assemblages across Europe. *Global Ecol Biogeogr.* 2019;28:826–838. <https://doi.org/10.1111/geb.12896>