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**Size diversity and species diversity relationships in fish assemblages of Western Palearctic lakes**

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**Abstract**

Body size, coupled with abundance and taxonomy, may help to understand the mechanisms shaping community structure. Since the body size of fish is closely related to their trophic niche, size diversity (based on individual body size) of fish communities may capture intraspecific variations in fish trophic niches that are not detected by species diversity. Thus, the relationship between size diversity and species diversity may help to integrate variation at both intraspecific and interspecific levels. We studied the relationship between species diversity and size diversity as a measure of the degree of overlap in size among species and thereby the potential overlap in niches in a community. We hypothesized that the relationship between size diversity and species would be different across the European continent due to different levels of size overlap in fish communities. The data were derived from samplings of fish communities using standardised benthic gill nets in 363 lakes. At the continental scale, size diversity increased with species diversity; at the ecoregion scale, the slope of the relation changed across the continent, with the greatest mismatch occurring in northern Europe where communities comprised only one or a few species, but each of which exhibited a great range in size. There was an increase in slope towards the south with significant relations for four out of six ecoregions. The steeper size diversity-species diversity slope at lower latitudes is attributable to a lower overlap in fish size and thus likely to finer niche separation. Our results also suggest that size diversity is not a strong surrogate for species diversity in European lake fish communities. Thus, particularly in fish communities composed of few species, measuring size diversity may help to detect potential functional variation which may be neglected by measuring species diversity alone.

## Introduction

Biodiversity has a multifaceted nature since it embraces biological variation of taxonomic, functional (i.e. traits), and genetic components (Díaz and Cabido 2001, Cadotte et al. 2011, Hooper et al. 2005). While some studies at large-scale gradients have shown strong relationships between these three different diversity components (e.g. Stuart Smith et al. 2013), others have revealed mismatches (e.g. Safi et al. 2011). These contradictory outcomes of comparisons may challenge the interchangeable use of different diversity measures (de Victor et al. 2010, Safi et al. 2011, Violle et al. 2014).

Body size is one of the most important animal traits because it affects physiology and determines competitive and predator–prey interactions (Peters 1983, Cohen et al. 1993, De Roos, et al. 2003, Woodward et al. 2005); furthermore, it is easy to measure. Additionally, body size is a key trait for defining ecological niches, especially so in aquatic ecosystems where organisms that are comparable in size often occupy similar niches (Woodward and Hildrew 2002, Jennings et al. 2001). Body size has been used as a trait in several functional diversity indices, but usually it refers to just one estimate of the size of the adult per species. A simple and intuitive way to assess variation in the individual body size structure of a community is to use its size diversity (Bruce et al. 2006, 2010, Quintana et al. 2008, Ye et al. 2013, García-Comas et al. 2016). Size diversity, based on the Shannon diversity index (Pielou 1969), integrates the amplitude of the size range and evenness in the same way as the Shannon species diversity index integrates the number of species and their relative abundance. Since body size aggregates multiple traits influencing community functioning (e.g. Woodward et al. 2005), the use of size diversity index based on individual body size facilitates studying part of the functional variation of a community expressed as the size variation among individuals. Size diversity based on individual body size may capture interspecific variability, as well as intraspecific variability, the importance of which is being increasingly recognized for many ecological and evolutionary processes (Violle et al. 2012).

The relationship between species diversity and size diversity will depend on the extent to which different species in a community exhibit similar body sizes. If the species differ strongly in adult and/or maximum

size (e.g. they have different sizes at sexual maturity), the addition of new species to a community will likely increase body size diversity, resulting in a linear positive relationship between species and size diversity (Micheli and Halpern 2005, Guillemot et al. 2011; Fig. 1, A and B). The slope of this function indicates the rate of increasing new body sizes: a steep slope means that the diversity of body sizes increases rapidly with species diversity (Fig. 1, A), whereas a shallower slope implies an increasing overlap in size while species accumulate (Fig. 1, B). A weak correspondence between species and size diversity will occur in communities composed of a single or of few species which have a wide size range and thus high size diversity (Fig. 1, C). Hence the strength and the shape of the relationship reflect the overlap in size, and likely an overlap of niches, among species in a community. A low overlap in size may imply that size-related traits are lost from a system as species diversity declines, as has been found in some studies relating species diversity and functional diversity (Micheli and Halpern 2005, Guillemot et al. 2011). A relationship between species and size diversity has not yet been demonstrated at large geographical scales, while varying patterns have been observed in local-scale studies (Bruce et al. 2006, Gascón et al. 2009).

Fish are well-suited for studying the relationship between species diversity and size diversity because they are of key importance for the functions and services of aquatic ecosystems in numerous ways. Thus, they are, for instance, important for the transfer of energy and cycling of nutrients and they also supply food and recreational activities (Holmlund and Hammer, 1999). Furthermore, intraspecific size variation within fish species strongly affects the dynamics and structure of lake communities even at low species diversity (Jansson et al. 2007, Lemmens et al 2017). Since the body size of fish is closely related to their trophic niche (Jennings et al. 2001, Romanuk et al. 2011), size diversity of fish communities may capture intraspecific variations in fish trophic niches that are not detected by taxonomic approaches.

Although the patterns of variation of the size-species diversity relationship at large scale have not yet been studied, we may expect shifts along the latitudinal gradient, as has been observed for the relationship between fish functional and species diversity in marine systems at a global scale (Stuart-Smith et al. 2013). The different patterns for the size-species relationship along latitude will be potentially driven by biogeographical and ecological processes (Micheli and Halpern 2005, Guillemot et al. 2011, Stuart-Smith et al. 2013, Arran et al. 2017). Glaciations in central and northern Europe have caused an impoverished fish fauna (Dynesius and Jansson 2000, Griffiths 2006, Lévêque et al. 2008), with dominance of large-

bodied ecological generalist species capable of exploiting a variety of ecological niches and with increased levels of intraspecific variability (Robinson and Schluter 2000, Griffiths 2006, Blanchet et al. 2010). Since body size is a good proxy of niche separation, we may expect a higher size overlap in fish species of these regions and, as a consequence, a weaker coupling between size diversity and species diversity. In contrast, fish communities in southern lakes (e.g. Mediterranean region) have had longer time for speciation due to the lack of widespread major glaciations (Griffiths 2006). These different biogeographical histories may have resulted in different relationships between size and species diversity.

Other potential factors influencing fish size diversity should be taken into account when studying the size-species relationship. Previous studies on the lake fish communities across large-scale gradients in Europe (Emmrich et al. 2014) showed that environmental temperature is a main driver negatively affecting fish body size. This is because for fish, as for many ectotherms, an increase in developmental temperature leads to a decrease in adult body size [i.e. temperature–size rule (Atkinson, 1994)]. The effects of lake morphometry and productivity on mean size of fish community at macroecological scale only emerged when geographical differences between the lakes were taken into account (Brucet et al. 2013, Emmrich et al. 2014). In contrast, a negative relationship between productivity and fish size diversity was found at local scale and was explained by competitive interactions for resources in less productive systems, promoting diversification of communities by size (Emmrich et al. 2011, Quintana et al. 2015). Finally, fish body size can also be influenced by human activities, such as fish species introductions or stockings and intensive removal fisheries, with different implication on fish community size diversity (Klemetsen et al. 2002). Species introductions may shift the fish community towards larger sizes because non-native species are larger than their native counterparts (Blanchet et al. 2010), whereas intensive fisheries often leads to removal of large-bodied individuals and indirectly causes an increase of their smaller prey due to released predation (Blanchard et al. 2005).

In this study, we used data from Western Palearctic lakes to assess the relationship between size diversity and species diversity in freshwater fish communities at European scale and in different ecoregions. We hypothesized a stronger correspondence between size diversity and species diversity in low latitude compared to high latitude regions (i.e. the diversity of body sizes will increase more rapidly with species diversity in warmer lakes) due to the biogeographical and ecological processes mentioned above. This would mean that there is lower overlap in fish body size in southern regions compared with northern

regions. We also hypothesized a decrease to occur in size diversity in warmer lakes due to the overriding influence of temperature (compared to local predictors) on fish mean size which leads to a higher dominance of small-sized fish in these lakes (Brucet et al. 2013, Emmrich et al. 2014). Finally, we tested for a potential bias caused by human impacts (i.e. fish introductions, fisheries, reservoirs) in our analyses.

## Methods

### Data set

We used a fish database including 363 Western Palearctic lakes located in eleven countries (mostly in Europe) and covering latitudes between 69°69'N to 36°69'N (Fig. 2). The lakes were sampled once between 1993 and 2012 using stratified random sampling with benthic multi-mesh gillnets (type NORDIC: length 30 m; height 1.5 m; 12 panels of 2.5 m each with bar mesh sizes between 5 and 55 mm knot to knot). The database was created to facilitate implementation of the European Union Water Framework Directive 2000/60/EC (for details see Brucet et al. 2013) and was supplemented with additional data from the authors. Samplings were undertaken during late summer and early autumn with a pre-defined number of nets per lake set randomly in each depth stratum depending on lake area and depth in accordance with a European standard protocol (Appelberg et al. 1995; CEN 14757 2005). Captured fish were identified to species level and measured (total length rounded to the nearest cm). For more details on the samplings and lake environmental characteristics, see Brucet et al. (2013), Emmrich et al. (2014), Boll et al. (2016) and Mehner et al. (2017).

Four abiotic variables known to influence fish species diversity and size structure (Brucet et al. 2013, Emmrich et al. 2014) were used (Table 1): maximum lake depth (m), total phosphorus concentration (TP,  $\text{mg m}^{-3}$ ), longitude and maximum air temperature at the geographic location of the lake [obtained from the Climate Research Unit (CRU) climate model and based on the maximum monthly mean temperature]. Maximum air temperature was used as an approximation to maximum lake temperature because previous studies have shown that it is a reliable surrogate for epilimnetic lake temperature (Livingstone and Lotter, 1998) and because fish diversity and size structure are more sensitive to maximum than to average local temperatures (Brucet et al. 2013, Emmrich et al. 2014). In the models, we did not include lake area because it was correlated with lake depth, nor latitude as it was strongly correlated with maximum

temperature (Pearson correlation 0.44 and -0.87, respectively,  $P < 0.001$ ). We  $\log_{10}$ -transformed all variables in order to achieve normally distributed variables.

The 363 lakes were situated in 11 freshwater ecoregions (Abell et al. 2008; Fig. 2). However, freshwater ecoregions that had less than five lakes were removed from the analysis (Barents Sea Drainages, Norwegian Sea Drainages, Dniester–Lower Danube, Thrace, Central Anatolia). Thus, a total of 346 lakes was used for the analysis and the number of lakes per freshwater ecoregion is presented in Table 2. In Eastern Iberia, the dataset was composed only of reservoirs, and in Cantabric Coast-Languedoc and Central & Western Europe there were 7 and 22 reservoirs, respectively. The remaining water bodies sampled were natural lakes.

In order to test for a potential bias in our analyses caused by fish species introductions or supplementation of existing populations (i.e. introduction of small or big fish that may change that natural patterns of size diversity), we calculated the percentage of non-native individuals out of the total number of individuals in each water body. We considered non-native species to be those that had been introduced or translocated. The native/translocated/introduced status of each fish species was defined to at least a lake basin-specific level according to the literature (Filipsson 1994, Tammi et al. 2003, Kottelat & Freyhof 2007, Brosse et al. 2013, Dias et al. 2014, Tarkan et al. 2015, Boll et al. 2016, Trochine et al. 2017). For some ecoregions (Northern and Western Anatolia and Northern Baltic Drainages) information was available for each individual study lake.

### **Species diversity and size diversity calculations**

Species richness was calculated as the total number of fish species sampled in a lake. Shannon diversity (H) was calculated according to Shannon and Wiener (Pielou 1969) using catch per unit effort (CPUE, number of fish  $\text{net}^{-1} \text{night}^{-1}$ ). We calculated size diversity for each fish community in each lake by using individual length measurements (total length) (Bruce et al. 2006, Quintana et al. 2008) and the methodology proposed in Quintana et al. (2008), applying the open source software “diversity08” available at [www.limnolam.org](http://www.limnolam.org). The size diversity index ( $\mu$ ) is computed based on the Shannon diversity expression adapted for a continuous variable, such as body size. This measure takes the form of an integral involving the probability density function (pdf; i.e. a function that describes the relative

likelihood for a random variable to take on a given value) of the size of the individuals described by the following equation:

$$H = - \int_0^{\infty} p_X(x) \log_2 p_X(x) dx$$

where  $p_X(x)$  is the pdf of size  $x$ . The non-parametric kernel estimation was used as a pdf, which is applicable to any type of size distribution. A kernel function is essentially a pdf, usually symmetric, whose dispersion is controlled by a bandwidth parameter. The estimator is a sum of kernel functions centered at the sample points (Quintana et al. 2008). Before computing size diversity, data are automatically standardised by division of each size value by the geometric mean of the size distribution (Quintana et al. 2008). This standardisation allows comparison with data from other studies whose samples are measured with different units, such as length, weight or volume, while it does not alter the results. The size diversity index ( $\mu$ ) is the continuous analogue of the Shannon diversity index and it produces values in a similar range to those of the Shannon species diversity index (Quintana et al. 2008). The use of size diversity for analysis of the shape of size distribution has the advantages that (1) it is a single-value metric that simplifies comparisons between samples (Bruçet et al. 2010); (2) its meaning is easy to interpret since the concept of diversity is well established: high size diversity means a wide size range and similar proportions of the different sizes along the size distribution (i.e. Emmrich et al. 2011). All lakes had more than 50 measured individuals, which corresponds to a size diversity error estimation lower than 10%.

#### **Estimation of body size overlap among fish species**

In order to have an estimation of the degree of size overlap among species, we built frequency distribution plots of 1 cm size classes and then we calculated the average number of species overlapping in each size class for each single lake. Thereafter, we calculated log(mean overlap) per lake and tested for statistical differences between ecoregions by means of an ANOVA and Tukey post hoc tests. We first excluded all lakes with only one species.

### Statistical analysis

To evaluate species diversity and size diversity relationships across the environmental gradient and ecoregions, we ran a Linear Mixed-Effects Model (LMM) with size diversity as dependent variable. As independent variables we included species diversity, ecoregion, interaction between species diversity and ecoregion, lake depth, TP, longitude, maximum temperature and percentage of non-natives. Lakes were used as a random factor. We searched for the most parsimonious model by an automatic stepwise backward selection of one predictor variable at a time by minimising the Akaike information criterion (AIC) (Akaike 1974). The most parsimonious model was the combination of variables having the strongest impact on outcomes. Spatial autocorrelation of the residuals of the best model was examined using Moran's  $I$  (Legendre and Legendre 1998).

A significant interaction between species diversity and ecoregion indicated that the slope between fish size diversity and species diversity differed among the ecoregions. Thus, subsequently, we calculated ecoregion-specific linear regressions between species and size diversity (Table 2). Additionally, we plotted the slope of the size-species diversity relationship calculated from simple linear regression for each ecoregion separately (Table 2) against the temperature [both average maximum and average annual temperature (averaged across monthly mean temperatures)] of each ecoregion in order to see the general trend in the ecoregion-specific slope along the climatic gradient. We calculated the correlation strength between the ecoregion-specific slopes and the average maximum and average annual temperature (we did not run regressions because the number of points was too small).

The same LMM analysis was repeated using species richness instead of species diversity as an independent variable. Similar results were obtained, but with less variation of fish size diversity explained than when using species diversity. For this reason, and because both size diversity and species diversity use Shannon diversity formulae and have similar range of values, we do not present the results for species richness here.

We tested for the effects of reservoirs, where human intervention is expected to be highest, by re-doing LMM and Moran  $I$  spatial autocorrelation on a subset of water bodies only including lakes (Supplementary material Appendix 1, Table A1). We also used an ANOVA on a subset of lakes for which fisheries intensity data was available ( $n=175$ ) to compare the size diversity in lakes having reported high

fisheries intensity with lakes with no or low fisheries intensity. The size diversity of fish communities did not differ between the two sets of lakes (ANOVA,  $p > 0.05$ ); thus, we did not consider this aspect any further.

For all analyses, we checked that assumptions of normal distribution of residuals and homoscedasticity were not violated. We inspected the variance inflation factor (VIF) to assure that there was no multicollinearity among predictors in the final set used for the analyses. Analyses were performed in ‘R’ version 2.9.1 (Development Core Team 2009) using “nlme” (Pinheiro et al. 2011), “ape”, (Paradis et al. 2004) and “MuMIn” (Bartoń 2009).

## Results

Size diversity ( $\mu$ ) and species diversity ranged between minima of 0.65 and 0 and maxima of 3.34 and 2.55, respectively. Three different combinations of species and size diversity of fish communities were observed: high species and high size diversity (Fig. 3, A and B), low species and low size diversity (Fig. 3, C) and low species diversity and high size diversity (Fig. 3, D). The average body size of fish tended to decrease with increasing temperature ( $r^2=0.37$ ,  $p<0.001$ ). No significant relationship ( $r^2=0.01$ ,  $p=0.07$ ) was found between size diversity and the total number of measured fish suggesting that the increase in size diversity was not a consequence of measuring more fish.

LMM results (Table 3) showed that fish species diversity, lake maximum depth, maximum temperature, ecoregion and the interaction between species diversity and ecoregion were significant predictors of the variation of fish size diversity. Size diversity was influenced positively by both species diversity and lake depth and negatively by temperature. Altogether, the model explained 38.5% of the variation of fish size diversity at the continental scale. No significant relationships were found between size diversity and TP, longitude and percentage of non-natives. The slope of the relationship between size and species diversity was 0.13 ( $\pm 0.04$  SE) and size diversity was higher at low species diversity but quantitatively more similar at higher species diversity (Fig. 4).

The LMM analysis was performed on a subset of water bodies ( $n= 301$  lakes) excluding reservoirs and the significant predictors of the variation of fish size diversity were the same as for the whole dataset

(Supplementary material Appendix 1, Table A1). The model explained 35.6% of the variation of fish size diversity. No significant spatial dependence was shown (Moran's  $I$ ,  $p > 0.05$ ) in the whole dataset or in the subset excluding reservoirs, which is in agreement with previous studies using the same database (Trochine et al. 2017).

The significant interaction between species diversity and ecoregion indicated that the slope between fish size diversity and species diversity differed among the ecoregions (Table 2 and 3; Fig. 4). Accordingly, we calculated ecoregion-specific linear regressions between species and size diversity. Notably, these regressions had the steepest slope in Northern Anatolia and Western Anatolia, an intermediate slope in Iberia and Cantabric Coast-Languedoc, and the shallowest slopes in Central & Western Europe and the Northern Baltic Drainages (Table 2; Fig. 4). Thus, overall there was a tendency to increase the slope of the within-ecoregion size-species diversity relationship when increasing the maximum and average air temperature in each ecoregion (Pearson correlations of 0.967 and 0.852, respectively) (Fig. 5).

The strongest relationships (highest  $R^2$  of linear regression) between size and species diversity were found in Northern and Western Anatolia, followed by Cantabric Coast-Languedoc (Table 2; Fig. 4). In Central & Western Europe and Eastern Iberia, size diversity and species diversity followed a similar trend, but the slope was not significant. This may to some extent reflect that the number of water bodies available was low for Eastern Iberia.

Particularly in the Northern Baltic Drainages, several lakes held fish communities with low species diversity and high size diversity (29 lakes from this region had communities composed of  $\leq 3$  species and a size diversity  $\geq 2$ ). This was the case, for example, for lake fish communities composed of a single species, such as Arctic charr (*Salvelinus alpinus*) (Fig. 3, D) or brown trout (*Salmo trutta*), covering a wide size range and thus having high size diversity (average size diversity 2.2 and 1.8 for fish communities composed of only *Salvelinus alpinus* or *Salmo trutta*, respectively).

The average of fish size overlap per lake differed among ecoregions (ANOVA,  $F = 31.26$ ,  $p < 0.001$ ). Overall there was a decrease in size overlap at lower latitudes, except for fish communities in the Northern Baltic Drainages which on average had a low size overlap, probably due to low species diversity in several of these lakes (Supplementary material Appendix 1, Fig. A1). The highest size overlap was found in Central & Western Europe (an average of almost 4 species overlapping in size, particularly in

size classes of less than 30 cm) and the lowest in the ecoregions of Northern and Western Anatolia (with an average of only 2 species overlapping in size, particularly in size classes of less than 20 cm).

## Discussion

The size diversity of lake fish communities at the continental scale was overall positively related to the species diversity. This means that addition of species results in some increase in size diversity in fish communities at the continental scale, which is in accordance with previous studies using multiple functional traits (e.g. trophic breadth, trophic group, body depth, eye position, etc.; Micheli and Halpern 2005, Safi et al. 2011, Stuart Smith et al. 2013). The shallow slope ( $\ll 1$ ) of the size diversity to species diversity relationship at a continental scale suggests that size diversity increases much slower than species diversity, and hence an increase in species diversity leads to a greater overlap in size among species and hence likely in a greater overlap of their niches. This may reflect the fact that many fish species grow over large body size ranges (Fig. 3, B and D) and change niche during ontogeny (Persson 1986, 1990, Romanuk et al. 2011). In fact, several lake fish communities in our study showed low species diversity but high size diversity suggesting that fish communities with low species diversity may potentially be functionally diverse.

However, results at the ecoregion level showed that the slope of the size diversity and species diversity relationship increased towards warmer low-latitude ecoregions (Table 2, Fig. 4 & 5), though the regression was significant only for four out of six tested ecoregions. At the extreme of this gradient, lakes from Northern and Western Anatolia showed the steepest slopes and the strongest relationship between the two diversity measures. Therefore, towards low latitudes, size diversity increased almost at the same rate as species diversity. These fish communities in warmer lakes also have species that in general overlap less in their body sizes (Supplementary material Appendix 1, Fig. A1), maybe reflecting that biogeographical differences and ecological processes (e.g. higher interspecific competition) at local or evolutionary scales lead to increased niche specialisation towards low latitudes, as has been found in several previous studies (Griffiths 2006, Reyjol et al. 2007, Mason et al. 2008, Tedesco et al. 2012, Schleuter et al. 2012, Cirtwill et al. 2015).

Lake depth also positively contributed to the variation of size diversity, probably because deep lakes provide larger space and habitat heterogeneity to a wider range of fish sizes, in accordance with the Habitat Diversity Hypothesis which states that diversity is controlled by the availability of different habitat types (Williams 1943). This contribution was also significant when reservoirs were excluded from the analysis. Total phosphorus concentration and longitude did not influence size diversity at the continental scale.

In accordance with the temperature–size rule (Atkinson 1994) and empirical observations (Emmrich et al. 2014, Arranz et al. 2016), the average body size of fish tended to decrease with increasing temperature, which may explain in part the decrease in size diversity with temperature. This is also shown by the fact that for some widely distributed species, the smallest body sizes occurred in the warmest ecoregion (Supplementary material Appendix 1 Table A2). Our results agree with observed variations in life-history traits with latitude and temperature, showing small body size in low-latitude warm lakes (Blanck and Lamouroux 2007).

The higher slope of the size diversity to species diversity relationship towards lower latitude regions suggests that fish communities in southern ecoregions are composed of species which are less similar in size (Fig. 1, A; Fig. 3, A; Supplementary material Appendix 1, Fig. A1) and probably in their niches and functional roles. A similarly strong coupling between species and functional diversity (measured from several traits) was observed in the highly diverse marine fish communities of coral reefs (Micheli and Halpern 2005, Guillemot et al. 2011) and the Galapagos Archipelago (Stuart-Smith et al. 2013) and was explained by the high partitioning of resources among species and the relatively low overlap in their niches.

The patterns found at the latitudinal extremes of our study may also reflect biogeographic differences. Due to the lack of widespread major glaciations (except for the mountain areas during the Quaternary period), fish communities in Northern and Western Anatolian lakes may have had longer time for speciation, which may have resulted in a less body size overlap (Supplementary material Appendix 1, Fig. A1). Furthermore, Anatolian lakes belong to basins that have historically been isolated for longer periods than most of the remaining lakes and thus display higher levels of endemism and beta diversity (Dias et al. 2014). Dispersal limitation, caused by the rise of the Anatolian Plateau whose average height is 1100

m with mountains forming barriers between the river basins, may also have promoted speciation in Anatolian lakes along with a lack of major glaciation (Kosswig 1955, Boll et al. 2016). In contrast, in central and northern European ecoregions, the fish fauna is impoverished as a result of climatic changes caused by periods of glaciations (Dynesius and Jansson 2000, Griffiths 2006, Lévêque et al. 2008). These climatic changes and the resulting cycles of range expansion and contractions have favoured the dominance of ecological generalist species, capable of exploiting several ecological niches (Robinson and Schluter 2000, Griffiths 2006). This agrees with the higher number of species which overlap within small to intermediate size classes, and might indicate an average of more than three abundant species with regular recruitment and similar growth (i.e. overlapping size) co-occurring in these lakes. Alternatively, high species overlap per size class may also be caused by co-occurrence of considerably more than three abundant (i.e. regularly recruiting) species with more dissimilar growth (i.e. less overlap in size in each of the youngest age classes).

The greatest mismatch between species and size diversity was found in lakes in the northern ecoregions, particularly in some lakes in the Northern Baltic Drainages where fish communities were composed of a single or a few species, but had high size diversity (Fig. 1, C; Fig. 3, D). In these northern and previously glaciated lakes, the diminished fish fauna shows high levels of intraspecific variability related to resource polymorphism (Griffiths 2006, Robinson and Schluter 2000), and these eco-morphs mimic the co-occurrence of several species. Fish species in these lakes have a relatively large size range and change their trophic niche as they grow (e.g. *Salvelinus alpinus*; Fig. 3, D; Griffiths 2006). As a result, overall these lakes have higher fish size diversity relative to species diversity than lakes further south in Europe. Consequently, the concept of species diversity is misleading in this context because it prevents detecting the potentially much higher size or functional diversity in these communities. In this ecoregion, we found an average of two species within most size classes up to 20 cm, which fits the fact that perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) are the two most abundant species in most of these lakes.

Human actions like introductions and fishing are not size-independent phenomena (e.g. Benoît & Rochet 2004). Some fish species are introduced as juveniles or adults, particularly in reservoirs. This may disrupt the natural patterns of size diversity by causing changes in the relative abundance of size classes and because the introduced species may predate on the native ones. However, we did not find a significant influence of human intervention on the overall patterns of size diversity. For some ecoregions such as the

Northern Baltic Drainages, the reason may be that reported introductions did not result in established populations as revealed by the low numbers of non-native individuals even many years later (Trochine et al. 2017). Although some of the data were compiled for monitoring rather than for research purposes and were based on a single sampling over some years only, we believe that the magnitude of the data set (one of the most comprehensive and large scale data set for lakes; Bruce et al. 2013) and the fact that sampling was highly standardised give strength to the results.

We are also aware that we only studied one fish trait. However, indices of functional diversity integrating multiple traits (e.g. morphological traits related to diet and habitat niche) very often do not include intraspecific variability but rather use average trait values for species (Cianciaruso et al. 2009). The size-based approach as applied here overcomes this issue because body size is easily measured for all individuals in a population and hence helps to detect the potential intraspecific functional trait variation, which may have large effects on the dynamics and structure of aquatic communities (Jansson et al. 2007, Persson and De Roos 2013, Norkko et al. 2013).

Given the fact that body size is a key trait for defining ecological niches and the strong relationship between organism body size and several ecological traits (e.g. Woodward et al. 2005), it might be possible to draw links between the variations in size diversity and changes in the structure and functioning of communities (Ye et al. 2013, García-Comas et al. 2016). For example, according to the Niche Diversification Hypothesis (Connell 1978), which suggests that systems of higher diversity could take greater advantage of the niche opportunities in an environment, a highly size-diverse community may be able to capture a greater proportion of resources relative to a less size-diverse one. Thus, size diversity may indicate diet niche partitioning, as has already been reported for zooplankton and invertebrate communities (Bruce et al. 2006, Rudolf 2012, Ye et al. 2013). In this sense, the high fish size diversity in species-poor communities of northern lakes would indicate trophic niche partitioning among different sizes of the same species (Fig. 1). We assumed, with many precedents from the literature, that for European fish, trophic function changes with body size (Romanuk et al. 2011). Therefore, since large fish are more predatory than small ones, increased size diversity may also reflect higher chances for between- and within-guild predation (Jennings et al. 2001).

In warmer low-latitude lakes, the potentially lower overlap of fish sizes (Fig. 1, A; Fig. 3, A; Supplementary material Appendix 1, Fig. A1) may render these communities more vulnerable to extinctions compared with the communities in colder lakes (Fig. 1, B; Fig. 3, B; Supplementary material Appendix 1, Fig. A1) (except for lakes with only one species) in that the removal of one species could result in loss of a size-related trait. An exception would be when the existing species is able to expand its niche and occupy the new available niche. It is also important to take into account that, in some ecosystems, size niche may be decoupled from functional niche, and niche specialisation may become manifest along morphological traits in similar-sized species (e.g. cichlids in ancient and highly productive African lakes, Steele and López-Fernández 2014). In this case, loss of a species may mean loss of a function even if species have the same body size.

In conclusion, at a continental scale, the size diversity of lake fish communities is similarly high for different levels of species diversity. This result suggests that most fish species show relatively similar size distributions and thus may potentially cover similar trophic niches, instead of forming distinct size groups. However, the slope of the size-species diversity regression changed across the continent, suggesting different levels of size overlap, with increasing overlap toward higher latitude. Our results also suggest that size diversity is not a strong surrogate for species diversity in European lake fish communities. The main reason for this discrepancy is that there are fish communities composed of one or a few species but with high size diversity. In this case, species diversity is less informative of the functional role than the size diversity and, thus, the use of species diversity alone as a measure of biodiversity may compromise our ability to understand the fish community functioning. This study represents a step towards understanding the link between species diversity and size diversity and community functioning over large-scale gradients. More research is needed to measure individual size overlap in fish communities and to understand how the different levels of size overlap at the continental scale affect their vulnerability to environmental change and its implications for conservation ecology.

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**Table Legends****Table 1.** Environmental variables analysed (minima, maxima, and means) and number of lakes.

	N	Minimum	Maximum	Mean
Lake area (km <sup>2</sup> )	363	0.001	113.0	3.08
Maximum depth (m)	363	0.550	115.7	17.63
Total phosphorus (mg m <sup>-3</sup> )	363	1.000	401.9	35.74
Maximum temperature (°C)	363	7.400	33.2	17.30

**Table 2.** Slope (size diversity divided by species diversity),  $R^2$ , significance ( $p$ ) and number of lakes (N) for the linear relationship between size diversity and species diversity within each ecoregion.

Ecoregion	Slope	$R^2$	$p$	N
Northern Baltic Drainages	0.097	0.028	0.03	179
Central & Western Europe	0.089	0.016	0.20	103
Cantabric Coast-Languedoc	0.363	0.241	<0.001	20
Eastern Iberia	0.342	0.146	0.15	16
Northern Anatolia	0.730	0.624	<0.001	19
Western Anatolia	0.846	0.417	0.06	9

**Table 3.** Results for the Linear Mixed Model for fish size diversity. Species diversity x ecoregion

	<b>AIC</b>	<b>Estimate</b>	<b>Std. Error</b>	<b><i>df.</i></b>	<b><i>t/F</i></b>	<b><i>p-value</i></b>
<b>Full model</b>	<b>161.98</b>					
(Intercept)		2.44	0.44	329	5.55	<0.001***

(interaction between species diversity and the factor ecoregion).

Species diversity	0.13	0.04	329	2.96	<0.01**
Maximum depth (m)	0.11	0.05	329	2.08	<0.05*
Maximum temperature (°C)	-0.65	0.38	329	-1.70	0.09
Total phosphorus (mg . m <sup>-3</sup> )	-0.04	0.05	329	-0.81	0.42
Longitude (°)	-0.004	0.005	329	-0.74	0.46
Non-natives species (%)	-0.08	0.09	329	-0.91	0.36
Ecoregion			329	8.25	<0.001***
Species diversity x ecoregion			329	6.60	<0.001***

**Full model:**

Size diversity ~ species diversity + maximum depth + maximum temperature + total phosphorus + longitude + non-native species + ecoregion + species diversity x ecoregion

**Stepwise selection**


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**Model 1 = Full model except longitude**      **160.56**

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**Model 2 = Model 1 except total phosphorus**      **158.97**

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**Best model = Model 2 except non-natives species**      **157.81**

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(Intercept)	2.47	0.43	332	5.76	<0.001***
Species diversity	0.12	0.04	332	2.88	<0.01**
Maximum depth (m)	0.13	0.05	332	2.81	<0.01**
Maximum temperature (°C)	-0.77	0.37	332	-2.09	<0.05*
Ecoregion			332	9.73	<0.001***
Species diversity x ecoregion			332	6.59	<0.001***

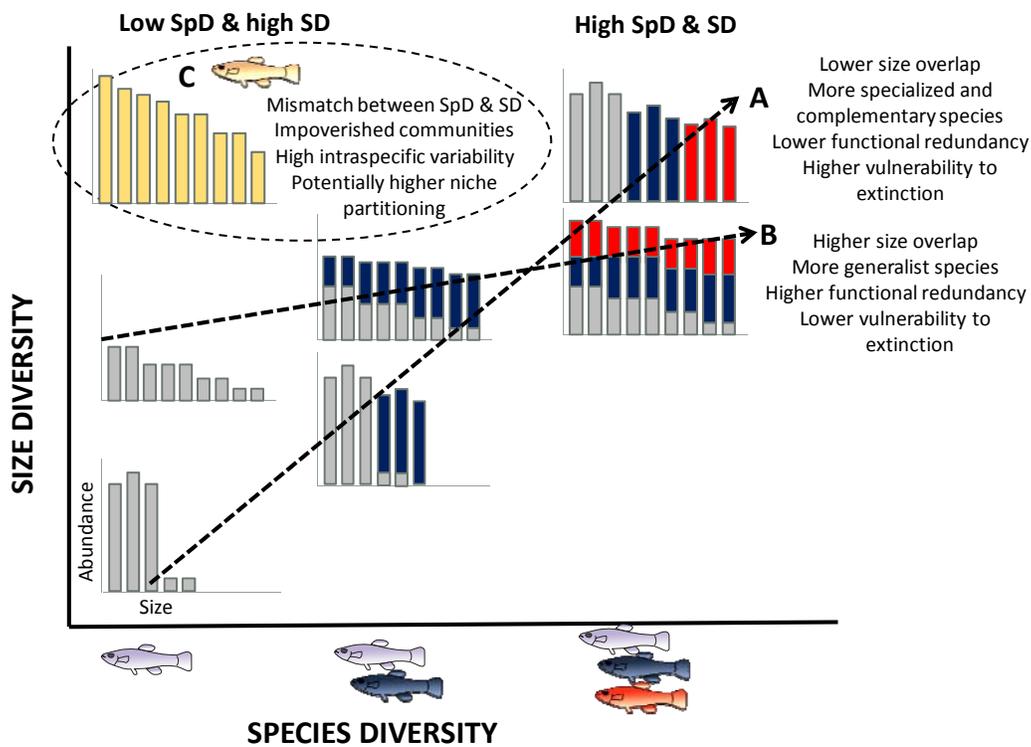
**Best model:**

Size diversity ~ species diversity + maximum depth + maximum temperature + ecoregion + species diversity x ecoregion

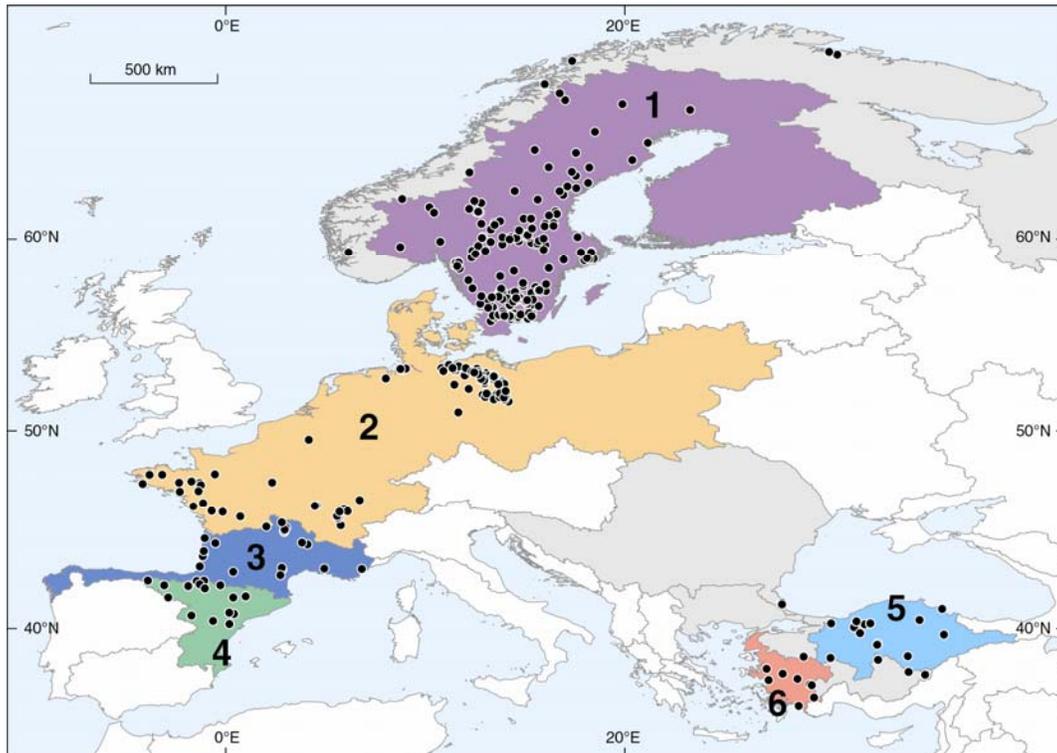
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## Figure Legends

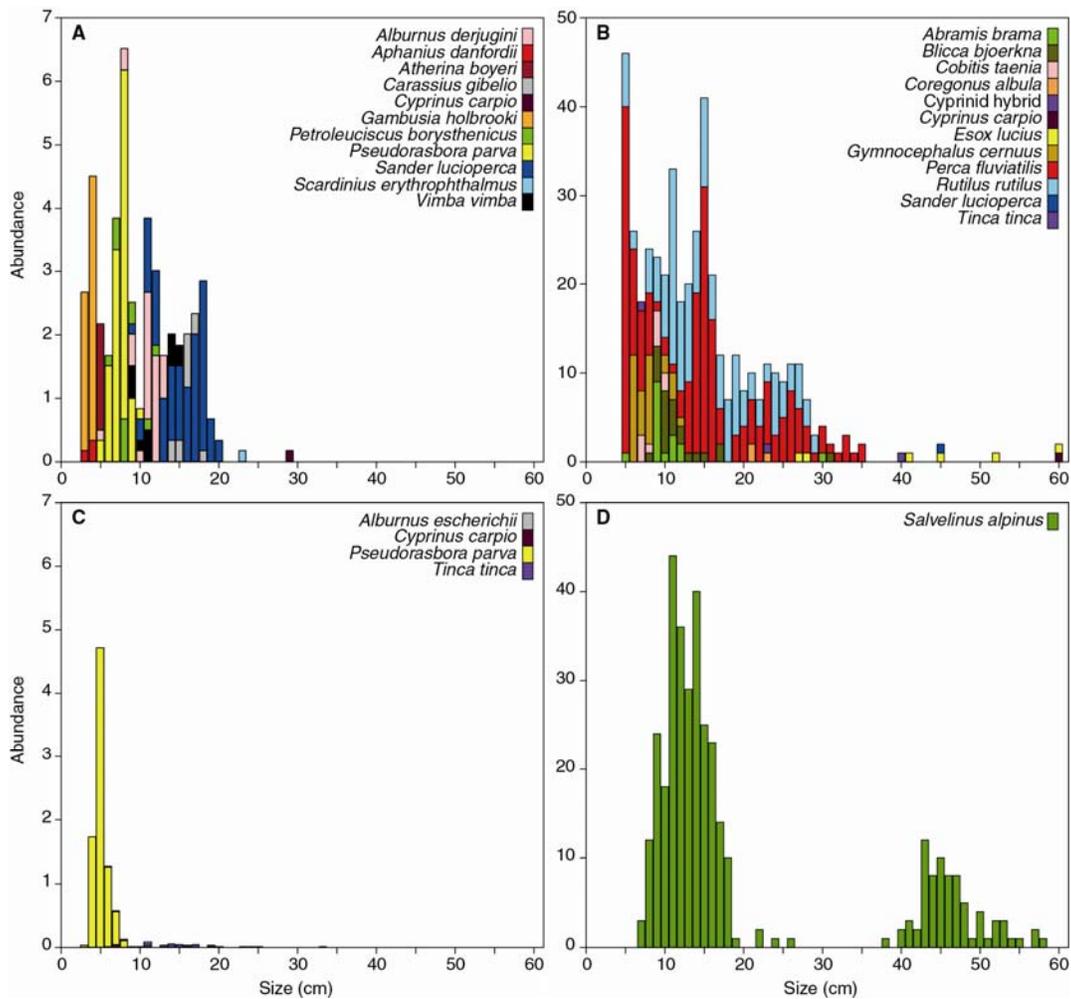
**Figure 1.** Hypothetical relationships between species diversity (SpD) and size diversity (SD). (A) The two types of diversity increase at a similar rate and the relationship is strongest; (B) linear relationship with slope  $\ll 1$ ; (C) no relationship between size diversity and species diversity: example of communities composed of a single or a few species with high size diversity. For each situation, the potential ecological and functional implications are explained. Each colored fish represents a new species which is added into the community as species diversity increases. The frequency distribution plots represent the abundance of each species in each size class.



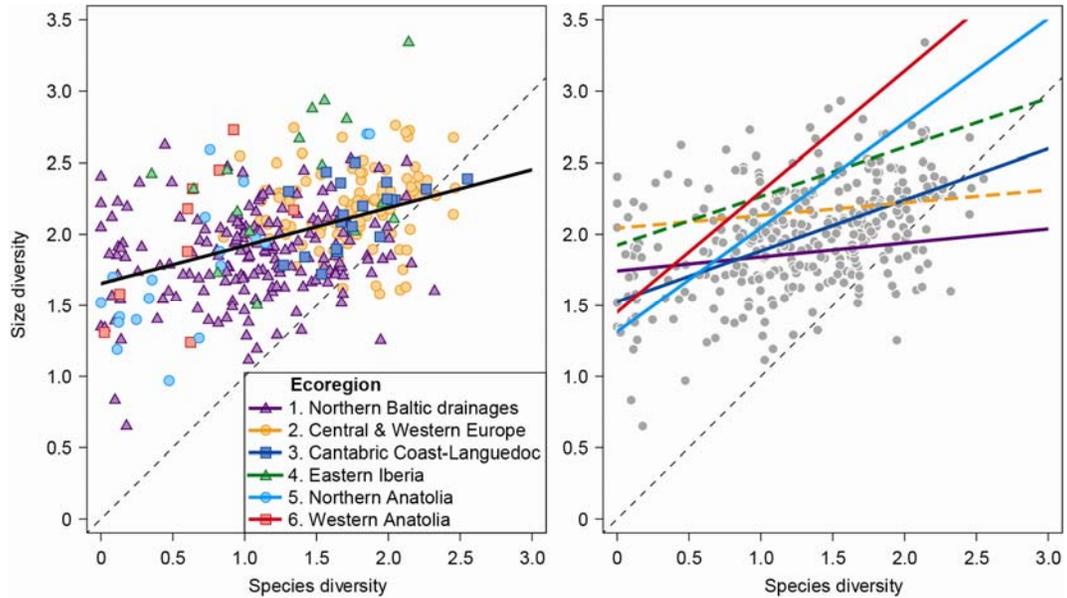
**Figure 2.** Geographical distribution of 363 lakes. Freshwater ecoregions (colored) are defined according to Abell et al (2008): (1) Northern Baltic Drainages, (2) Central & Western Europe, (3) Cantabric Coast-Languedoc, (4) Eastern Iberia, (5) Northern Anatolia and (6) Western Anatolia. Lakes in grey ecoregions were not considered because there were too few to allow statistical analysis.



**Figure 3.** Examples of size distributions [abundance in CPUE (fish net<sup>-1</sup> night<sup>-1</sup>) as a function of size classes in cm] and species composition of a fish community in different lakes: (A) high species diversity ( $H = 1.9$ ) and size diversity ( $\mu = 2.7$ ) in a community composed of fish species of relatively different sizes in a lake from Northern Anatolia; (B) high species diversity ( $H = 2.1$ ) and size diversity ( $\mu = 2.8$ ) in a community composed of species growing over large size ranges in a lake in Central and Western Europe; (C) low species diversity ( $H = 0.3$ ) and size diversity ( $\mu = 1.4$ ) in a lake in Turkey and (D) low species diversity ( $H = 0$ ) and high size diversity ( $\mu = 2.4$ ) in a lake in the Northern Baltic Drainages.



**Figure 4.** Relationship between species diversity and size diversity for all lakes (left) and for different ecoregions (right). In both panels stippled black lines indicate the 1:1 relationship for comparison purposes. In the right panel, the non-significant relationships are represented by discontinuous lines.



**Figure 5.** Relationship between the temperature (A; maximum and B; mean) in each ecoregion and the slope of the within-region size-species diversity regression (C). Closed circles are ecoregions with significant ( $p < 0.1$ ) slope for species diversity and size diversity relationship. Open circles are ecoregions with non-significant ( $p > 0.1$ ) slope for species diversity and size diversity relationships.

