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Fish diversity in European lakes: geographical factors dominate over anthropogenic pressures

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SUMMARY

1. We aimed to distinguish the relative contributions of natural and anthropogenic local factors on patterns of fish diversity in European lakes at different geographical scales.

2. We compiled data from standardised fish monitoring using multimesh benthic gill nets, information on lake morphometry and on geographical, climatic and anthropogenic pressure variables from 1632 lakes in 11 European countries. By means of regression trees, we determined those natural and anthropogenic factors and their thresholds that best predicted local fish diversity, density and mean size. Generalised linear models were used to assess the influence of anthropogenic factors at smaller geographical and morphometric scales.

3. Local fish species richness and diversity were related mainly to morphometric and (bio)geographical/climatic variables. Larger and deeper lakes in warm areas tended to be the most species rich and diverse. Fish density was related mainly to anthropogenically driven productivity but also was sensitive to geographical/climatic factors. Thus, warmer and shallower lower-altitude European lakes, which are usually more eutrophic, had higher fish densities than cold and deeper higher-altitude lakes. Fish size increased with altitude and declined with increasing seasonality and temperature.

4. After controlling for the natural factors, productivity had a positive effect on fish species richness and diversity, whereas it negatively influenced fish size.

5. Our results suggest that macroecological patterns of lake fish diversity across Europe are best predicted by natural factors. The contribution of anthropogenic factors to fish diversity was evident only via the effect of eutrophication at smaller geographical scales, whereas no effect could be found from hydromorphological pressures. From an applied perspective, these results suggest that bioassessment and biodiversity evaluation might be most effectively conducted and interpreted locally, where

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anthropogenic effects on biodiversity become more apparent. At a macroecological scale, the strong effect of environmental temperature on most components of fish diversity suggests future changes in fish diversity as a consequence of climate change.

Introduction

Freshwater ecosystems hold an estimated 12% of the world's animal species, and the biodiversity of these habitats is declining at an alarming and unprecedented rate due to anthropogenic activities (Abramovitz, 1996; Sala *et al.*, 2000; Johnson, Revenga & Echeverria, 2001). Determining the processes responsible for modifying of biodiversity patterns is a crucial issue for conservation strategies in the face of current and future global and regional anthropogenic impacts (Kerr, Kharouba & Currie, 2007). However, there has been surprisingly little effort to distinguish the effects of natural and anthropogenic factors on macroecological patterns of freshwater diversity, because most studies focus on understanding 'natural' processes alone, disregarding the potential problems caused by the addition of current anthropogenic effects (La Sorte, 2006). Particularly, in densely populated regions such as Europe, where aquatic systems are greatly affected by humans (Abramovitz, 1996; EEA, 2010), anthropogenic factors may well override the well-known effects of natural gradients on local and regional aquatic diversity.

Lakes, being natural relatively isolated ecosystems, can be considered as biogeographical islands and are thus ideal for studying the macroecological effects of local and regional processes on assemblage composition (Heino, 2011). For example, regional fish species richness generally declines from the tropics to the poles (Abell *et al.*, 2008), but is modulated by historical effects on biogeography in European lakes (Griffiths, 2006; Jeppesen *et al.*, 2010) that sometimes interact with climate. Similarly, richness and endemism of riverine fish faunas were higher in the Mediterranean regions than in Central, Eastern and Northern Europe (Reyjol *et al.*, 2007). These studies point to a strong effect of regional factors on the composition of European fish assemblages.

Lake morphometry (area and depth) is considered the most important natural factor influencing local fish assemblage composition (Jeppesen *et al.*, 2000; Olin *et al.*, 2002; Mehner *et al.*, 2005, 2007). Many studies have shown that local fish species richness in lakes is strongly linked to area, probably as a result of a higher complexity

and stability of habitats in large lakes (e.g. MacArthur & Wilson, 1967; Barbour & Brown, 1974). In a study covering a wide latitudinal gradient in north-eastern U.S.A., lake morphometry even overrode the effect of regional processes on fish richness (Allen *et al.*, 1999). In contrast, few studies have addressed the effect of anthropogenic factors on local fish diversity. Fish species richness was unimodally or positively related to anthropogenically increased productivity in Danish (Jeppesen *et al.*, 2000) and Finnish lakes (Olin *et al.*, 2002), respectively, and lake productivity was an important predictor of fish abundance and biomass in German lakes (Mehner *et al.*, 2005).

The mean size of fish is another component of diversity which interacts with species richness and density (Magurran, 2004). Natural predictors of the life-history traits of fish, such as body size, are primarily climatic factors, and there is increasing evidence that the mean body size of fish declines with increasing mean annual temperature (Griffiths, 2006; Teixeira-de Mello *et al.*, 2009; Jeppesen *et al.*, 2010). Simultaneously, anthropogenically enhanced productivity causes a decline in the mean size of fish, caused by density-dependent growth in highly productive lakes (Jeppesen *et al.*, 2000). In addition to cultural eutrophication, hydromorphological alterations, exploitation as fisheries and the use of lakes for recreation have been found significantly to affect fish species richness, density and body size (e.g. Jennings *et al.*, 1999; Allan *et al.*, 2005).

Studies on fish diversity in lakes suggest that there is presumably no single factor that simultaneously predicts diversity, size and density of fish across large spatial gradients. Natural factors and anthropogenic pressures may strongly interact in determining the local fish assemblage in lakes. In the face of the freshwater biodiversity crisis (Dudgeon *et al.*, 2006; Vörösmarty *et al.*, 2010), it is therefore important to estimate the relative contribution of natural and anthropogenic factors on the macroecological patterns of fish diversity in lakes. However, to do this, large data sets are needed which have to be obtained by systematic sampling including fish species, density and size. Furthermore, the lakes included should cover broad geographical, climatic and morphometric gradients, and

data on local anthropogenic pressures should be of sufficient precision.

Here, we compiled a fish database consisting of standardised, multimesh-sized gillnet catches from 1632 lakes from 11 European countries covering a wide latitudinal and longitudinal gradient. The lakes also represent a wide range of morphometric and environmental variables/stressors. Our overall aim was to assess whether current anthropogenic pressures have already changed large-scale macroecological patterns of fish diversity in European lakes. Specifically, we addressed the following questions: (i) Are local fish species richness and diversity in European lakes primarily determined by the latitudinal and morphometric gradients, or has the effect of locally enhanced productivity by human-induced eutrophication disrupted these macroecological patterns? (ii) Alternatively, is the effect of anthropogenic pressures on biodiversity visible only at smaller geographical scales? (iii) Is the average size of fish primarily determined by environmental temperature, or has anthropogenic disturbance replaced the dominant effect of temperature? (iv) Is the density of fish in lakes related primarily to productivity, or can other predictors explain a part of the variability observed over large spatial gradients?

Methods

Data set

We used a fish database including 1632 European lakes sampled from 1993 to 2009. The database was created as part of a Water Framework Directive 2000/60/EC Intercalibration exercise, supplemented by additional data from the authors. The database included 11 countries and covered a latitudinal gradient between 41.96 and 69.69°N (maximum distance between lakes of 3083 km) and a longitudinal gradient between −10.17 and 31.30°E (maximum distance between lakes of 3395 km; Fig. 1). All lakes were sampled from June to September with Nordic benthic multimesh gill nets, largely in accordance with the European standard (Appelberg *et al.*, 1995; CEN 14757, 2005). Benthic gill nets (12 mesh sizes between 5.0 and 55 mm in a geometric series, each panel being 2.5 m long and 1.5 m high) were set in a random stratified sampling design in the benthic habitat. Nets were generally set for a 12- to 16-h period from before dusk and lifted after dawn. The total fishing effort per lake (number of benthic nets) was standardised by lake area and maximum depth according to CEN 14757 (2005). The sampling procedure employed in the Ger-
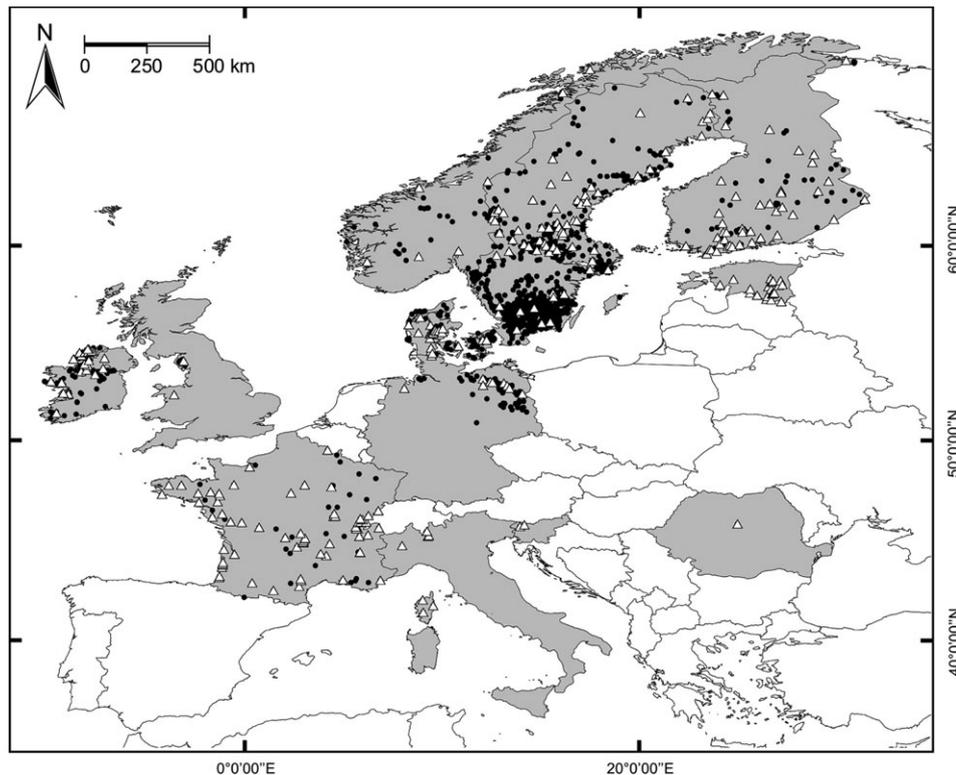

Fig. 1 Geographical distribution of the 1632 lakes across 11 European countries (black circles) and balanced data set with 272 lakes (white triangles).

man lakes differed slightly from the standard protocol, as the sampling was split, with the first half of the effort (number of nets) set during late summer and early autumn and the second half set during the subsequent spring (Mehner *et al.*, 2005). In that case, a sampling campaign is the sum of two sampling periods. The data set (n = 1632 lakes) contained only lakes with pH > 6, to exclude the structuring effect of acidification on fish assemblages, which otherwise might obscure the effects of the main anthropogenic pressures assessed in this study, that is, eutrophication and hydromorphological degradation. This was needed as a large part of the Nordic data were from lakes recovering from acidification.

Descriptors of fish assemblages

Species richness was calculated as the total number of fish species collected in a lake. Shannon–Wiener diversity (H) was calculated according to Shannon and Wiener (Pielou 1969). Fish density was expressed as catch per unit effort, determined as the number per unit effort (NPUE, number of fish) and the biomass per unit effort (BPUE, wet mass of fish), standardised with respect to gillnet area (m^2) and fishing duration (h). Shannon–Wiener diversity was calculated from both fish numbers (H_{NPUE}) and biomass (H_{BPUE}). The biomass/number ratio (BPUE/NPUE) was estimated as a proxy of the average fish body size and hereafter called body size.

Table 1 Fish descriptors and explanatory variables analysed, their minima, means and maxima. The percentage of lakes for each level of the categorical variables is also shown [from 1 (less pressure) to 5 (more pressure)]

	Mean	Minimum	Maximum	Std. deviation	n
Fish descriptors					
Fish number (number fish net m^{-2} per h)	0.09	<0.01	1.69	0.13	1632
Fish biomass (g fish net m^{-2} per h)	3.20	0.01	29.09	3.04	1632
Richness	5.23	1	17	2.80	1632
H_{NPUE}	1.20	0	2.78	0.59	1632
H_{BPUE}	1.49	0	2.99	0.65	1632
Body size (BPUE/NPUE; g WW)	55.79	0.76	981.56	68.47	1632
Lake morphometry					
Lake area (km^2)	2.55	0.02	116.51	8.36	1629
Maximum depth (m)	13.71	0.20	137	13.36	1591
Mean depth (m)	4.69	0.07	97.00	5.29	1259
Climate					
Sum of precipitation (mm)	738.3	423.6	3173.6	254.5	1632
Mean temperature (°C)	5.65	−3.83	14.33	2.83	1632
Minimum temperature (°C)	−3.60	−16.80	8.00	4.54	1632
Maximum temperature (°C)	15.34	6.80	23.10	1.77	1632
Amplitude temperature (°C)	18.90	8.40	30.10	3.88	1632
Location					
Latitude (°)	57.4109	41.9697	69.6972	4.28	1632
Longitude (°)	1.3000	−10.1763	31.3019	7.43	1632
Altitude (m)	186.6	−1.00	1739	206.6	1593
Pressures (continuous)					
pH	7.09	6.00	9.95	0.78	1214
Total phosphorus ($\mu g\ L^{-1}$)	40.1	1.0	3334.0	128.6	918
Percentage agriculture land cover (%)	22.7	0	100	27.5	727
Percentage natural land cover (%)	72.0	0	100	30.2	732
Percentage of shoreline bank modified	17.2	0	100	25.4	111

	Percentage of lakes					
	1	2	3	4	5	n
Pressures (categorical)						
Population density class	2.8	73.1	11.2	1.0	–	718
Morphometric pressures (shoreline bank modification)	36.9	2.0	0.6	0.3	1.3	668

n, number of lakes; H_{NPUE}, diversity based on fish number; H_{BPUE}, diversity based on fish biomass; BPUE, biomass per unit effort; NPUE, number per unit effort.

Environmental and anthropogenic pressure variables

Lake area (km^2), altitude (m) and maximum depth (Z_{max}) were extracted from the national databases (Table 1). Climatic data were obtained from the climate CRU model (New *et al.*, 2002). The amplitude of temperature (T_{amp}; a proxy for seasonality) was calculated as the difference between mean temperature (T_{mean}) in July and that in January.

The anthropogenic pressures considered are listed in Table 1. Enhanced in-lake productivity (eutrophication) was estimated by annual mean total phosphorus (TP; $\mu g\ L^{-1}$) and land use and population density in the catchment. TP was measured as the mean of a minimum of four samples taken in a single year (one for each season) for all lakes (except a small number of Swedish lakes for which we selected TP data for another year matching the last fish sampling campaign as closely as possible). Land use was estimated as the percentage of natural and agricultural land cover in the lake catchment using Corine Land Cover. For a subset of the lakes, population density in the catchment was assessed according to expert judgment on a four-step scale (low, medium, high and very high; Table 1). Morphometric modification was estimated as the percentage of shoreline bank modified according to expert judgment and in application of the Lake Habitat Survey (Rowan *et al.*, 2006) on a ranked scale [five classes, from 1 (no modification) to 5 (highly modified)].

Statistical analysis

We applied a two-step approach. First, we conducted regression tree analyses to explore which factors dominate in the prediction of fish diversity (richness, diversity, size, density) in the lakes. Second, for those fish descriptors that were influenced mainly by natural factors according to the regression tree analysis, we controlled for the dominant effects of these factors and then tested explicitly for the effects of anthropogenic factors by applying generalised linear models (GLM). We log_{10}-transformed all variables except pH, richness and diversity.

Regression tree analyses were performed to trace the relationship between the natural and anthropogenic variables (predictors) and fish diversity descriptors (responses) and to identify thresholds of the predictor variables best discriminating the resulting fish assemblage structure. Regression trees are a binary partitioning approach whereby a data set is progressively split into subsets that most significantly reduce the variability of the response variable. This type of regression gives a clear picture of the structure of the data and provides a highly intuitive insight into the kinds of interactions between variables (Crawley, 2002). It simultaneously handles categorical and continuous data, is insensitive to outliers and multicollinearity (Breiman *et al.*, 1984) and is therefore highly suitable for the complex data set we have accumulated here. Regression trees can also accommodate missing data in predictor variables by using other independent variables, known as surrogates, that best agree (i.e. classify the same subjects in the same way) with the original splitting variable (Breiman *et al.*, 1984). Surrogates are selected by the algorithm according to their performance in the percentage of agreement in the allocation of cases to the two groups. To avoid over-fitting, we 'pruned' the tree using a 10-fold cross-validation and the one standard error (1-SE) rule (Breiman *et al.*, 1984). A 10-fold cross-validation test consists in splitting the data, constructing a new model from a subset of samples and then testing the predictive accuracy of those sample(s) not included in its construction (Breiman *et al.*, 1984; Bahn & McGill, 2007). In more detail, the data were divided into 10 parts and one part was omitted. The tree was then estimated using 90% of the data and the omitted 10% were used to obtain a prediction error. This process was then repeated by omitting each of the 10 data sets in turn. We chose the 1-SE rule to estimate the best tree because this method usually results in smaller trees than suggested by the minimum cross-validated error, but with minimal increase in the estimated error rate (Breiman *et al.*, 1984; De'ath & Fabricius, 2000).

We ran a separate regression tree for each of the six descriptors of fish diversity. Categorical predictors (Table 1) were included as nominal variables. We excluded highly redundant predictors from regression tree analyses (Table 2). Hence, since minimum temperature (T_{min}), T_{mean} and T_{amp} covaried strongly (Table 2; average Spearman's $r_s = 0.9$), we subsequently included only T_{max} and T_{amp}. The percentages of natural and agricultural land cover were also strongly negatively correlated ($r_s = -0.9$), so we included only the latter in the analyses. Longitude was strongly correlated with T_{amp} ($r_s = 0.7$) and with precipitation ($r_s = 0.7$) and was therefore also excluded. Alternative splits (i.e. splits that had as many correct classifications as the original splitting variable) and surrogate variables were examined to obtain a more complete understanding of the dependencies and relationships within the data (De'ath & Fabricius, 2000). Thus, we inspected strongly competing alternative splits to test whether the resulting tree could

Table 2 Correlation matrix of the environmental and anthropogenic pressure variables

	Lat	Long	T_{max}	T_{min}	T_{mean}	T_{amp}	Precip	Altit	Area	TP	Z_{max}	%agric	%nat	pH
Lat	–	0.646	−0.486	−0.950	−0.935	0.691	−0.310	0.367	−0.013	−0.382	−0.107	−0.619	0.619	−0.452
Long	<0.001	–	0.011	−0.664	−0.607	0.723	−0.718	0.055	−0.021	−0.245	−0.073	−0.397	0.359	−0.341
T_{max}	<0.001	0.657	–	0.487	0.603	−0.269	−0.298	−0.580	0.063	0.369	−0.104	0.428	−0.422	0.337
T_{min}	<0.001	<0.001	<0.001	–	0.981	−0.929	0.325	−0.499	−0.012	0.422	−0.114	0.603	−0.554	0.438
T_{mean}	<0.001	<0.001	<0.001	<0.001	–	−0.858	0.236	−0.566	0.016	0.444	−0.105	0.655	−0.602	0.494
T_{amp}	<0.001	<0.001	<0.001	<0.001	<0.001	–	−0.457	0.344	0.057	−0.349	0.123	−0.477	0.432	−0.303
Precip	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	–	0.228	−0.004	−0.005	0.132	0.134	−0.108	−0.021
Altit	<0.001	0.028	<0.001	<0.001	<0.001	<0.001	<0.001	–	−0.046	−0.473	0.215	−0.474	0.493	−0.444
Area	0.594	0.390	0.011	0.614	0.519	0.021	0.877	0.066	–	−0.071	0.411	0.107	−0.047	0.182
TP	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.881	<0.001	0.032	–	−0.440	0.568	−0.603	0.423
Z_{max}	<0.001	0.004	<0.001	0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	–	−0.223	0.259	0.041
%agric	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.004	<0.001	<0.001	–	−0.912	0.663
%nat	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.003	<0.001	0.206	<0.001	<0.001	<0.001	–	−0.656
pH	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.472	<0.001	<0.001	<0.001	0.157	<0.001	<0.001	–

Spearman's r_s values above the diagonal and the corresponding *P*-values below the diagonal. Values over 0.7 and variables not included in the regression tree analysis are given in grey background. Lat, latitude; Long, longitude; T_{max}, maximum temperature; T_{min}, minimum temperature; T_{mean}, mean temperature; T_{amp}, amplitude of temperature; Precip, precipitation; Altit, altitude; TP, total phosphorus; Z_{max}, maximum depth; %agric, percentage of agricultural land cover; %nat, percentage of agricultural land cover.

better explain the data. Finally, when a variable with missing data was selected, we checked to ensure that data were evenly distributed across response and predictor variables.

Since the initial database was dominated by Swedish lakes (Fig. 1), and this geographical bias could have influenced the results, we split the lakes into three categories (regions) based on latitude and four based on longitude and subsampled an equal number of lakes from each of the 12 subregions. Next, we re-ran regression tree analyses using this unbiased data set (in total 272 lakes). Therefore, we significantly reduced the proportion of missing values for productivity variables (100% and 84% of data available for TP and percentage of agricultural land cover, respectively). Subsequently, we compared the results of these two approaches.

For those fish descriptors that were influenced mainly by natural factors according to regression tree analysis, we ran GLM (McCullagh & Nelder, 1989) for each of the two subsets defined by the primary splits of regression trees and by using anthropogenic pressures as predictors. Thus, if for example a fish descriptor was mainly influenced by T_{max}, we took the two T_{max} categories defined by the primary tree split and calculated GLMs within each tree category. We compared the models with main effects of two anthropogenic predictors (TP and % agriculture) and their interaction by using the Akaike Information Criterion corrected (AICc). We used a Poisson error distribution and a logarithmic link function for richness variable and normal error distribution and identity link function for diversity and body size variables.

Regression tree analyses were performed in 'R' version 2.9.1 (Development Core Team, 2009) using the BRODGAR v. 2.7.2 statistical package (Highland Statistics Ltd., Newburgh, U.K.). GLMs were performed using SPSS 17.0 (SPSS Inc., Chicago, IL, USA, 1989–2006).

Results

In the regression tree analysis of species richness, the primary split was defined by lake area, which was positively related to richness. Surrogate variables of lake area were maximum depth (Z_{max}) and latitude (positively and negatively related to fish richness, respectively). Lakes were further divided according to T_{max}, which in total contributed almost as much explanatory power as lake area (Table 3; Fig. 2). Surrogate variables for the three nodes related to T_{max} were precipitation, latitude and altitude, indicating a relationship between T_{max} and the geographical gradients.

Shannon–Wiener diversity based on both fish numbers (H_{NPUE}) and biomass (H_{BPUE}) was primarily affected by T_{max}, with both altitude and latitude as surrogate variables (Table 3). For H_{NPUE}, a second split divided the lakes above and below the temperature threshold according to their area with surrogate Z_{max}. For H_{BPUE}, T_{max} and area again defined the second and third nodes, respectively (Table 3; Fig. 2).

The density of fish was primarily predicted by productivity (in-lake TP concentration; Table 3; Fig. 2), with thresholds of 23.7 µg L^{-1} (number) and 20 µg L^{-1} (biomass). Surrogate variables for TP were altitude and

Table 3 Results of regression tree analysis (n = 1632 lakes) for each fish assemblage descriptor

| | Regression tree | | | | | |
	Richness	H_{NPUE}	H_{BPUE}	Body size	NPUE	BPUE
Total variance explained	45%	30%	31%	20%	33%	25%
Node 1	Area (Z_{max}, latitude)	T_{max} (altitude, latitude)	T_{max} (altitude, latitude)	Altitude (T_{max})	TP (altitude, pH)	TP (altitude, pH)
Threshold	0.68 km^2	15.7 °C	15.7 °C	484.2 m	23.7 μg L^{-1}	20.0 μg L^{-1}
Variance explained	22%	14%	16%	11%	20%	20%
Node 2	T_{max} (precipitation)	Area (Z_{max})	T_{max} (altitude)	(−)T_{amp} (precipitation)	T_{max} (latitude)	(−)Z_{max} (area)
Threshold	16.0 °C	0.67 km^2	13.6 °C	16.4 °C	15.3 °C	6.9 m
Variance explained	5%	7%	7%	9%	6%	3%
Node 3	T_{max} (latitude)	Area (Z_{max})	Area (precipitation)		(−)altitude (latitude)	Altitude (T_{amp})
Threshold	16.0 °C	0.50 km^2	0.31 km^2		108.4	53 m
Variance explained	14%	6%	5%		3%	2%
Node 4	T_{max} (altitude)	(−)altitude (T_{max})	Area (Z_{max})		T_{max} (altitude)	
Threshold	13.6 °C	248.3 m	0.67 km^2		12.4 °C	
Variance explained	4%	3%	3%		2%	
Node 5					(−)Z_{max} (area)	
Threshold					14.8 m	
Variance explained					2%	

Main variables, thresholds defining each node and percentage of variance explained are listed. For each node, main surrogate variables (i.e. those with maximum agreement) are shown in brackets (first two main surrogates for the node explaining the highest variance and the first one for the rest of the nodes). Fish number (NPUE), fish biomass (BPUE), diversity based on fish number (H_{NPUE}), diversity based on fish biomass (H_{BPUE}) and body size. TP, total phosphorus; T_{max}, maximum temperature; T_{amp}, amplitude of temperature; Z_{max}, maximum depth; BPUE, biomass per unit effort; NPUE, number per unit effort.

pH, which were negatively and positively related to fish density, respectively. A second node was defined by T_{max} for fish number and by Z_{max} for fish biomass. The interaction between TP and temperature in predicting fish numbers is shown in Fig. 3: for the same TP concentration, more fish were found in warmer lakes (T_{max} > 15 °C). Fish body size was predicted by altitude, with T_{max} as a surrogate. A second split divided lower-altitude lakes according to their T_{amp} (Table 3; Fig. 2).

Additional regression trees were trained using a geographically unbiased data set (i.e. subsampling a similar proportion of lakes in three latitude and four longitude categories leaving 272 lakes in total). The results were similar to those obtained from the whole database, suggesting that the strong dominance of Scandinavian lakes in the large data set did not influence the main conclusions. However, the variance explained increased for

each regression tree, except for fish richness and H_{CPUE} (that remained similar; Table 4). The only differences occurred for fish species richness, which was mainly related to T_{max} and explained 30% of the variance for the model, and for body size, which was mainly positively related to precipitation. Nevertheless, lake area appeared at the second split for fish richness explaining 10% of the variance. The main surrogate variable for the first split was the percentage of agricultural land cover for all fish descriptors, except for fish size and number for which T_{amp} and latitude were the main surrogates, respectively.

Generalised linear models showed that fish descriptors (richness, diversity and body size) were in all cases significantly affected by anthropogenic factors (TP and percentage of agricultural land cover) when accounting for the dominant effects of natural predictors, as found in the regression tree (Table 5; Fig. 4). The AICc indicated that TP was the main anthropogenic factor
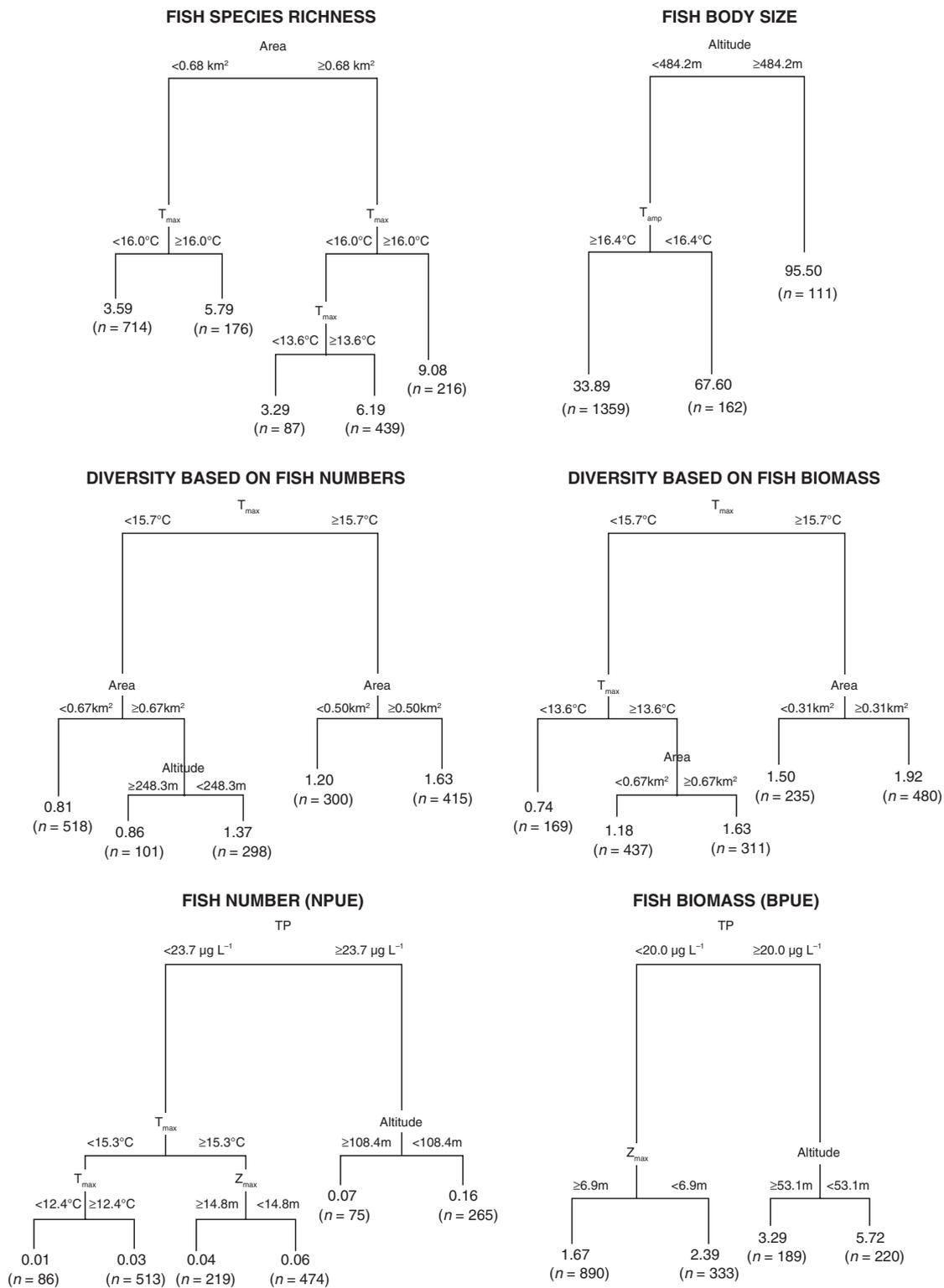
Fig. 2 Regression trees of fish assemblage descriptors for 1632 European lakes. The higher a variable in the tree, the more important it is for differentiating fish assemblage descriptors. Each node of the tree is described by the splitting variable. The longer the line, the higher the variance explained by the splitting variable. Each leaf is labelled with the mean rating and the number of observations in the group (in parentheses). For surrogate variables and explained variance, see Table 3. Fish number (NPUE; number fish net m^{-2} per h), fish biomass (BPUE; g fish net m^{-2} per h), diversity based on fish number (H_{NPUE}), diversity based on fish biomass (H_{BPUE}) and body size (BPUE/NPUE ratio; g wet weight). TP, total phosphorus; T_{max}, maximum temperature; T_{amp}, amplitude of temperature; Z_{max}, maximum depth; BPUE, biomass per unit effort; NPUE, number per unit effort.
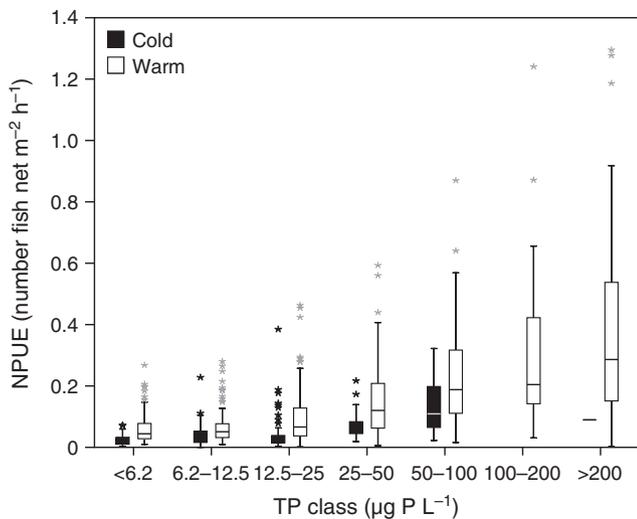
Fig. 3 Box plot showing the abundance of fish (NPUE) in different total phosphorus (TP) classes ($\mu g\ L^{-1}$) for two lake categories defined by the regression tree in Table 3: cold lakes ($T_{max} < 15\ °C$) and warm lakes ($T_{max} > 15\ °C$). Minimum and maximum number of lakes within box plots are one and 91, respectively, for cold lakes and 26 and 166, respectively, for warm lakes. T_{max}, maximum temperature; NPUE, number per unit effort.

explaining changes in richness, H_{NPUE}, H_{BPUE} and body size, except for richness in small lakes and fish body size in higher-altitude lakes for which the percentage of agriculture land cover was more significant than TP (Table 5). Both factors were positively related to fish species richness and diversity, but negatively related to body size (Fig. 4).

Discussion

Our study of patterns of fish diversity in European lakes, based on probably the most comprehensive and large-scaled data set ever produced in lakes, suggests that several of the well-documented statistical correlations between local fish diversity and natural gradients are still intact. Local species richness was strongly related to lake morphometry and environmental temperature, whereas average fish size and Shannon–Wiener diversity were determined primarily by environmental temperature related to altitudinal and latitudinal gradients. Furthermore, the geographical gradients found in our analyses agree with a previous study of fish species richness in lakes at European scale that reported a decline in regional species richness in the northern and western regions due to influence of biogeographical aspects, such as barriers and glaciation events (Griffiths, 2006).

Primary productivity, as a measure of the amount of energy available at a base of food webs, is presumably one of the major determinants of species richness and diversity (e.g. Currie, 1991), and primary productivity is strongly related to the TP concentration in lakes. The increased energy available, and the greater food-web complexity in more productive lakes, allows more species to coexist (Gaston, 2000). Here, we showed that agriculture in the catchment was the primary surrogate of natural predictors when using a geographically unbiased data set (i.e. where Mediterranean and Scandinavian lake samples were more balanced), suggesting that anthropogenic stressors may have modified natural macroecological gradients of fish diversity in lakes. Similarly, when taking into account the most important geographical, climatic and morphometric differences between the lakes, both enhanced TP concentration and agriculture in the catchment contributed significantly to an increase in fish species richness and diversity. Thus, the anthropogenic effects on biodiversity become more visible at smaller geographical and morphometric scales,

Table 4 Results of regression tree analysis for each fish assemblage descriptor using a reduced data set where lakes were evenly distributed among three latitude and four longitude categories ($n = 272$ lakes)

	Regression tree					
	Richness	H_{NPUE}	H_{BPUE}	Body size	NPUE	BPUE
Total variance explained	40%	28%	39%	37%	46%	32%
Node 1	T_{max} (agriculture)	T_{max} (agriculture)	T_{max} (agriculture)	Precipitation (T_{amp})	TP (latitude)	TP (agriculture)
Variance explained	30%	22%	22%	20%	27%	23%
Threshold	15.0 °C	15.0 °C	15.0 °C	668.34 mm	20.1 $\mu g\ L^{-1}$	17.6 $\mu g\ L^{-1}$

The variables defining the first node and their thresholds are listed. Main surrogate variable is given in brackets. Fish number (NPUE), fish biomass (BPUE), diversity based on fish number (H_{NPUE}), diversity based on fish biomass (H_{BPUE}) and body size. TP, total phosphorus; T_{max}, maximum temperature; T_{amp}, amplitude of temperature; Z_{max}, maximum depth; BPUE, biomass per unit effort; NPUE, number per unit effort.

Table 5 Results of generalised linear models on the effect of anthropogenic factors on fish diversity

Variable	Data set	Factor	AICc	*P* value
Richness	Small lakes < 0.68 km²	lg TP	2484.14	0.539
		lg% agriculture	**1783.59**	**0.001**
		lg TP	6846.64	0.972
		lg% agriculture		0.233
		lg TP*lg% agriculture		0.230
	Large lakes > 0.68 km²	**lg TP**	**2983.26**	**0.036**
		lg% agriculture	6620.03	0.011
		lg TP	45166.61	0.561
		lg% agriculture		0.159
		lg TP*lg% agriculture		0.428
H_{NPUE}	Cold lakes < 15.7 °C	**lg TP**	**1374.94**	**<0.001**
		lg% agriculture	1949.45	<0.001
		lg TP	8437.30	<0.001
		lg% agriculture		<0.001
		lg TP*lg% agriculture		<0.001
	Warm lakes > 15.7 °C	**lg TP**	**989.13**	**<0.001**
		lg% agriculture	2467.83	<0.001
		lg TP		<0.001
		lg% agriculture		<0.001
		lg TP*lg% agriculture		<0.001
H_{BPUE}	Cold lakes < 15.7 °C	**lg TP**	**1475.74**	**<0.001**
		lg% agriculture	1997.03	<0.001
		lg TP	8439.77	<0.001
		lg% agriculture		<0.001
		lg TP*lg% agriculture		<0.001
	Warm lakes > 15.7 °C	**lg TP**	**1011.18**	**<0.001**
		lg% agriculture	2490.04	<0.001
		lg TP		<0.001
		lg% agriculture		<0.001
		lg TP*lg% agriculture		<0.001
Body size	Lower altitude < 484.2 m a.s.l.	**lg TP**	**8542.74**	**<0.001**
		lg% agriculture	8568.76	<0.001
		lg TP	28169.67	<0.001
		lg% agriculture		<0.001
		lg TP*lg% agriculture		<0.001
	Higher altitude > 484.2 m a.s.l.	lg TP	902.08	<0.001
		lg% agriculture	**566.88**	**<0.001**
		lg TP		<0.001
		lg% agriculture		<0.001
		lg TP*lg% agriculture		<0.001

Each fish descriptor variable was split into two data sets following the first node of the regression tree analysis (see Table 3). Each data set was tested for one (TP or percentage of agricultural land cover) or both anthropogenic factors together. The top-ranked models (lowest AICc) are highlighted in boldface. Richness (species number), diversity based on fish number (H_{NPUE}), diversity based on fish biomass (H_{BPUE}), TP, total phosphorus; % agriculture, percentage of agricultural land cover; AICc, Akaike Information Criterion corrected; BPUE, biomass per unit effort; NPUE, number per unit effort.

whereas they are less obvious across larger spatial extents. This suggests that even though global or continental bioassessment and evaluation of biodiversity is needed, they might be most effectively analysed and interpreted at smaller geographical scales (Heino, 2013).

Our results corroborate those of earlier studies covering smaller geographical gradients, which revealed that the response of fish assemblages to changing productivity varies considerably depending on lake morphometry and fish species composition (Olin *et al.*, 2002; Mehner

et al., 2005, 2007). A dominant effect of lake morphometry over those induced by anthropogenic descriptors was also found for broad-scale richness of benthic macroinvertebrates, birds and zooplankton (Allen *et al.*, 1999). In turn, productivity was the main positive determinant of fish density in our study (Fig. 5), corroborating earlier studies on lake fish assemblages covering smaller geographical and trophic gradients (Jeppesen *et al.*, 2000; Olin *et al.*, 2002) and studies on zooplankton biomass at European scale (Gyllström *et al.*, 2005).
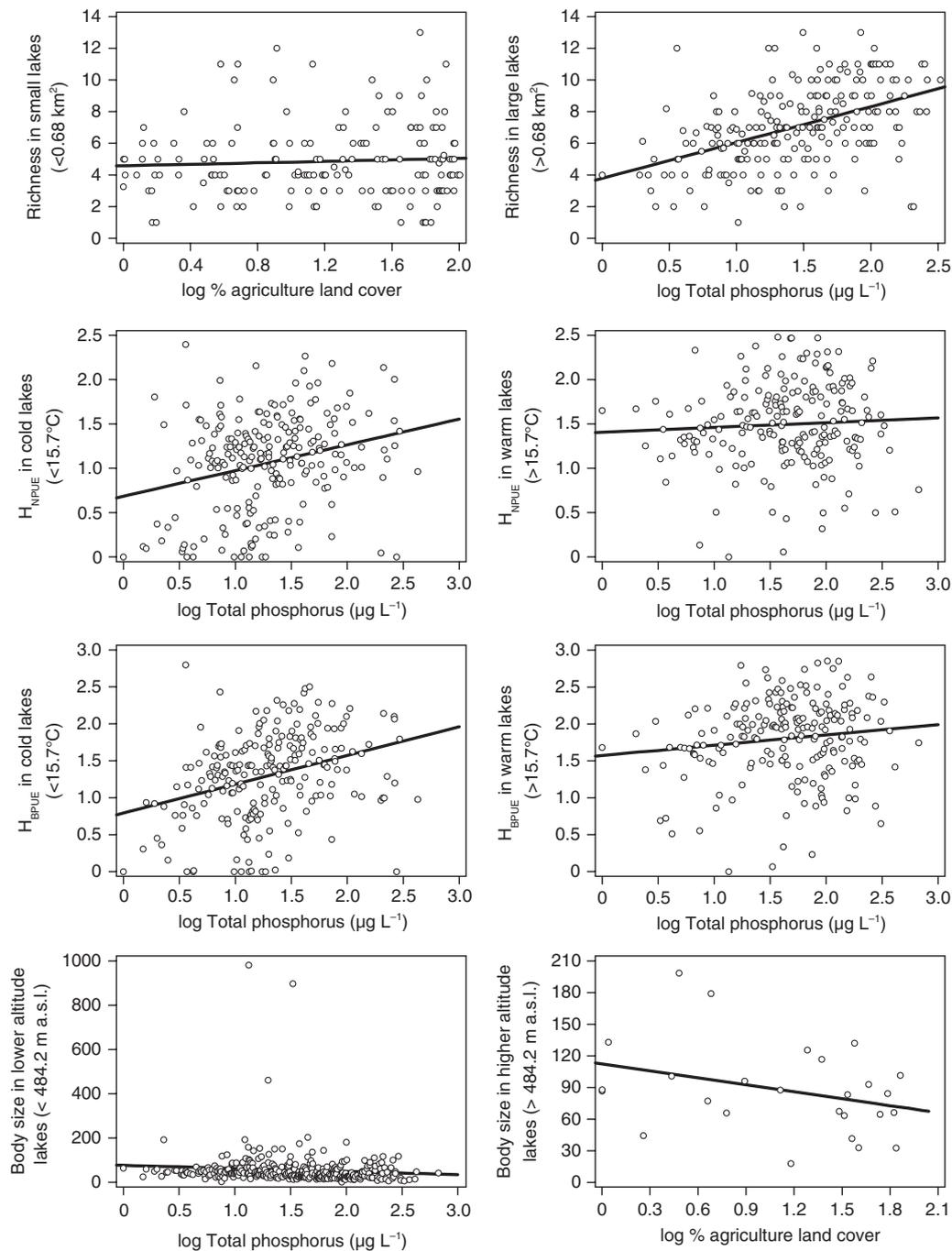
Fig. 4 Effects of total phosphorus and agricultural land cover on fish descriptors (see Table 5 for statistical results). Fish diversity based on fish number (H_{NPUE}), diversity based on fish biomass (H_{BPUE}). NPUE, number per unit effort.

According to our results, a TP concentration of around 20–25 µg L^{-1} represents a threshold for a significant increase in lake fish numbers and biomass.

Our regression tree approach also detected some effects, hitherto poorly described, of temperature and lake morphometry on fish density. Thus, warmer and lower-altitude European lakes, which are usually more eutrophic, had higher fish density than cold and higher-altitude European lakes (Fig. 5). The temperature-related effects on fish density (due to both latitudinal or altitudinal differences) may act independently of lake trophic status since, for a similar TP concentration, we found generally a greater number of fish in warm than in cold lakes. So far, this had been found only for fish biomass in a comparative study of shallow subtropical and temperate lakes, showing a twofold higher fish biomass per
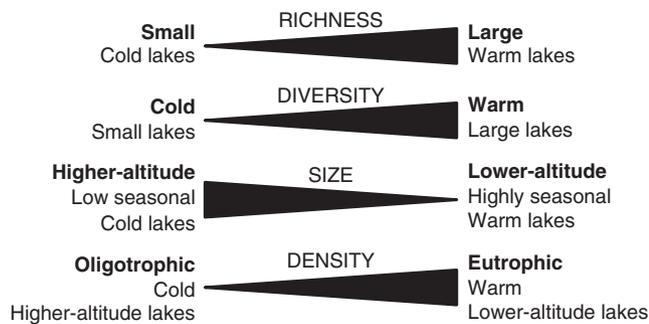
Fig. 5 Scheme showing changes (increase and decrease) for each fish assemblage descriptor in European lakes. Main variables driving changes in each descriptor are given in boldface.

unit of TP in the warmer subtropical lakes (Teixeira-de Mello *et al.*, 2009).

With regard to fish body size, geographical and climatic factors remained the dominant predictors, but the effect of anthropogenic factors emerged when geographical differences between the lakes were taken into account. Most importantly, fish body size was larger in high-altitude than in low-altitude lakes and declined with increasing temperature (Fig. 5). These findings agree with previous studies on fish (Blanck & Lamouroux, 2007; Jeppesen *et al.*, 2010) and invertebrates [e.g. beetles, Vamosi & Vamosi (2007); zooplankton, Gillooly & Dodson (2000)] and support the predictions of the metabolic theory of ecology (Brown *et al.*, 2004). Our results suggested a decrease in fish body size with enhanced eutrophication, which is in accordance with previous local studies of fish and zooplankton (Jeppesen *et al.*, 2000). This decrease in fish body size with eutrophication was more obvious in higher-altitude lakes, which are naturally more oligotrophic than those at lower altitudes, and suggests that, in the former, fish assemblages may be more sensitive to changes in lake productivity.

In our study, body size was also associated with the amplitude of temperature and precipitation, variables that are both highly correlated with longitude. The results suggest that lakes in Eastern Europe, normally exhibiting greater variations in temperature, and higher summer temperatures, tend to have smaller fish. Supporting this argument, Carlson, Olsen & Vøllestad (2008) found that small body size could be an advantage for fish inhabiting strongly seasonal environments. The positive relationship between fish density and air temperature, and smaller fish in warmer lakes, agrees with the results of cross-comparisons of fish populations in Europe. These showed that fish species from lower latitudes are typically smaller, grow faster, mature earlier and have shorter lifespans and allocate less energy (as go-

nadosomatic index) to reproduction than populations and species at higher latitudes (Griffiths, 2006; Blanck & Lamouroux, 2007; Jeppesen *et al.*, 2010). Such changes are evident even in the same species along a latitudinal gradient (Blanck & Lamouroux, 2007; Jeppesen *et al.*, 2010).

Overall, our results indicated that larger and deeper lakes in warmer areas were the richest and most diverse in fish species (Fig. 5). The positive relationship between richness and lake area, depth or volume might reflect a greater environmental stability in large and deep lakes than in small and shallow lakes (Jeppesen *et al.*, 2000; Irz, Argillier & Oberdorff, 2004; Volta *et al.*, 2011) and increased habitat heterogeneity favouring the coexistence of more species (MacArthur & Wilson, 1967).

Differences in maximum temperature made a similar contribution to fish species richness as did lake area. Similarly, diversity indices were mainly influenced by maximum temperature, which agrees with a recent model, supported by terrestrial, freshwater and marine taxa data, that quantifies the role of biochemical kinetics in generating biodiversity (Allen, Brown & Gillooly, 2002). According to this model, environmental temperature, through its effects on individual metabolic rates, influences the rates of genetic divergence among populations and rates of speciation in communities. In our analysis, lake altitude appeared as the main surrogate for the maximum temperature in the fish diversity regression trees. The effects of altitude on fish diversity can probably be attributed to its direct barrier effects on colonisation and its indirect effects due to collinearity with temperature, which is in accordance with the findings in a previous study of lakes in China (Zhao *et al.*, 2006).

Apart from eutrophication, we did not find any effect of anthropogenic alterations, such as hydrological and morphometric degradation, on fish diversity in lakes. This result agrees with a previous study in German lakes (Mehner *et al.*, 2005). In contrast to our findings, previous studies restricted to North American lakes, in which lake shores were sampled by electrofishing (e.g. Jennings *et al.*, 1999; Schindler, Geib & Williams, 2000), have shown that fish richness declines in response to shoreline modifications and that the strength of the changes depends on the complexity of the artificially created habitats (Jennings *et al.*, 1999). The weak effect of hydromorphological pressures on fish diversity in European may be attributable to the fact that, in some cases, our measures were based on expert judgment, which might be too coarse to detect subtle impacts. It could also be attributed to the fact that the respective information was available only for a small subset of lakes. Nevertheless, when the same analyses were car-

ried out using only these lakes where the information was available, the main variables determining the fish diversity descriptors did not change. Therefore, the opposite outcomes between European and North American studies suggest that: (i) fish in European lakes are less sensitive or are more resilient to these anthropogenic pressures, or (ii) the impact of these pressures is obscured by the effect of strong biological interactions, such as predation and competition, in European lakes, or (iii) a strong effect is only seen if a certain degree of pressure intensity is exceeded, which was not the case for the lakes included here. In addition, (iv) we cannot exclude the possibility of an effect of hydromorphological pressures on some other traits that were measured in North American fish but were not measured in our study (e.g. small cyprinids). Furthermore, gillnet sampling may not be the most effective method to document the effects of hydromorphological pressures, since these pressures mostly influence shoreline fish assemblages, which are more reliably monitored by electrofishing (Diekmann *et al.*, 2005; Erős, Specziár & Bíró, 2009). It is highly likely that all these explanations strongly interact in causing the differing response of temperate fish diversity to anthropogenic stressors between Europe and North America. The regional fish diversity in Europe is highly depauperate compared to North America, mainly as a consequence of the relative importance of historical processes such as glaciations (Tonn *et al.*, 1990; Griffiths, 2006). Therefore, the dominant fish species in Europe are less specialised, have broader niches and a more flexible life history than their American counterparts (Tonn *et al.*, 1990), making them less vulnerable to the effects of anthropogenic stressors. In turn, the fish diversity in European lakes is less variable, and hence less sensitive to local predictors, than is found in similar studies of North American fish assemblages. Nevertheless, we cannot exclude that using only benthic gillnet data could have led to an underestimation of fish species richness (Erős *et al.* 2009), though a study of Danish lakes indicated that benthic nets catch most species (Menezes *et al.*, in press).

Some of our models, particularly those obtained using the whole data set, explained a low percentage of the variance (e.g. 20% for body size), indicating that their predictive ability may be limited, and thus, conclusions should be carefully drawn. However, when cross-validating by using smaller, more balanced training sets, better models were overall obtained, which allows for more robust ecological insights.

In conclusion, our results indicate that most components of lake fish diversity at a European scale are mainly determined by natural factors. Some effects of anthropogenic stressors on fish diversity became particularly obvious when subsets of lakes with similar natural environmental factors were evaluated. In contrast, fish numbers and biomass responded to anthropogenically enhanced productivity even at a macroecological (here European) scale. From an applied perspective, these findings have important implications for unravelling the causes of freshwater biodiversity loss and for the development of fish-based systems for assessing the ecological status of lakes (i.e. in the implementation of the European Water Framework Directive, WFD). Our results confirm that (i) fish density is sensitive to some anthropogenic pressures, which must be considered when developing biotic indicators, and (ii) geographical and morphometric factors should be accounted for when attempting to quantify the effects of anthropogenic factors on fish diversity at large geographical scales (Irz *et al.*, 2007; Argillier *et al.*, 2013). This agrees with the WFD requirement for setting reference conditions for subsets of lakes defined by geography and morphometry (e.g. European Commission, 2010; Brucet *et al.*, 2013). Our results also suggest that (iii) temperature differences, mainly related to geographical gradients and lake morphometry, strongly predict most components of fish diversity, emphasising the importance of temperature in determining broad-scale patterns of fish diversity in European lakes. Therefore, subtle changes in fish diversity in lakes may be early indicators of the effects of global warming, a process that is already evident in European lakes (Jeppesen *et al.*, 2012)

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