

Article (refereed) - postprint

Brucet, Sandra; Pedron, Stephanie; Mehner, Thomas; Lauridsen, Torben L.; Argillier, Christine; Winfield, Ian J.; Volta, Pietro; Emmrich, Matthias; Hesthagen, Trygve; Holmgren, Kerstin; Benejam, Lluís; Kelly, Fiona; Krause, Teet; Palm, Anu; Rask, Martti; Jeppesen, Erik. 2013. **Fish diversity in European lakes: geographical factors dominate over anthropogenic pressures.** *Freshwater Biology*, 58 (9). 1779-1793.
<https://doi.org/10.1111/fwb.12167>

© 2013 John Wiley & Sons Ltd

This version available <http://nora.nerc.ac.uk/id/eprint/15241/>

NERC has developed NORA to enable users to access research outputs wholly or partially funded by NERC. Copyright and other rights for material on this site are retained by the rights owners. Users should read the terms and conditions of use of this material at <http://nora.nerc.ac.uk/policies.html#access>

This document is the author's final manuscript version of the journal article, incorporating any revisions agreed during the peer review process. Some differences between this and the publisher's version remain. You are advised to consult the publisher's version if you wish to cite from this article.

The definitive version is available at <https://onlinelibrary.wiley.com/toc/13652427/2013/58/9>

Contact CEH NORA team at
noraceh@ceh.ac.uk

1 **Fish diversity in European lakes: geographical predictors dominate over**
2 **anthropogenic pressures**
3
4
5
6
7
8
9

10 Brucet, S.^{1,2}, S. Pédrón³, T. Mehner⁴, T. L. Lauridsen^{5,6}, C. Argillier³, I. J. Winfield⁷, P.
11 Volta⁸, M. Emmrich⁴, T. Hesthagen⁹, K. Holmgren¹⁰, L. Benejam², F. Kelly¹¹, T. Krause¹², A.
12 Palm¹², M. Rask¹³, & E. Jeppesen^{5,6,14}
13
14
15
16
17
18

19 ¹European Commission, Joint Research Centre, Institute for Environment and Sustainability,
20 21027 Ispra, Italy
21
22
23

24 ² Department of Environmental Sciences, University of Vic, Vic, 08500, Catalonia, Spain
25

26 ³Irstea, UR HYAX, pôle Hydroécologie plans d'eau Onema/Irstea, 3275 Route de Cézanne,
27 CS 40061,13182, Aix-en-Provence Cedex 5, France
28
29
30

31 ⁴Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, 12561
32 Berlin, Germany
33
34

35 ⁵Department of Bioscience, Aarhus University, DK-8600 Silkeborg, Denmark
36
37

38 ⁶Sino-Danish Centre for Education and Research, Beijing, China
39

40 ⁷Centre for Ecology & Hydrology, Lancaster Environment Centre, Library Avenue, Bailrigg,
41 Lancaster LA1 4AP, U.K.
42
43
44

45 ⁸Consiglio Nazionale delle Ricerche, Institute of Ecosystem Study, 28922 Verbania Pallanza,
46 Italy
47
48

49 ⁹Norwegian Institute for Nature Research, P.O. Box 5685 NO-7485 Trondheim, Norway
50
51

52 ¹⁰ Swedish University of Agricultural Sciences, Department of Aquatic Resources, Institute of
53 Freshwater Research, Stångholmsvägen 2, SE-17893 Drottningholm, Sweden
54
55

56 ¹¹Inland Fisheries Ireland, Swords Business Campus, Swords, Co. Dublin, Ireland
57
58
59
60

1 25 ¹²Centre for Limnology at IAES, Estonian University of Life Sciences, 181 Riia St, 51014

2 26 Tartu, Estonia

3 27 ¹³Finnish Game and Fisheries Research Institute, Evo Fisheries Research Station, FIN-16970

4 28 Evo, Finland

5 29 ¹⁴Greenland Climate Research Centre (GCRC), Greenland Institute of Natural Resources,

6 30 Kivioq 2, P.O. Box 570 3900, Nuuk, Greenland

7 31

8 32

9 33 Corresponding authors: Sandra Brucet (sandra.brucet@uvic.cat) and Erik Jeppesen

10 34 (ej@dmu.dk)

11 35

12 36 Sandra Brucet

13 37 University of Vic

14 38 Sagrada Família, 7

15 39 08500 Vic, Catalonia, Spain

16 40

17 41

18 42 **Running head:** Fish assemblages along climatic and human pressure gradients

19 43

20 44 **Keywords:** Fish assemblage, species richness, eutrophication, hydromorphology,

21 45 biogeography

22 46

23 47

24 48

1 49 **Summary**

2
3
4 50

5
6
7 51 1. We aimed to distinguish the relative contributions of natural and anthropogenic local

8
9
10 52 factors on patterns of fish diversity in European lakes at different geographical scales.

11
12 53 2. We compiled data from standardized fish monitoring using multi-mesh benthic gill nets and

13
14 54 on lake morphometry, and geographical, climatic and anthropogenic pressure variables from

15
16 55 1632 lakes in 11 European countries. By means of regression trees we determined those

17
18 56 natural and anthropogenic factors and their thresholds that best predicted local fish diversity,

19
20 57 density and mean size. Generalized linear models were used to assess the influence of

21
22 58 anthropogenic factors at smaller geographical and morphometric scales.

23
24 59 3. Local fish species richness and diversity were related mainly to morphometric and

25
26 60 (bio)geographical/climatic variables. Larger and deeper lakes in warm areas tended to be the

27
28 61 most species rich and diverse. Fish density was related mainly to anthropogenically driven

29
30 62 productivity but also was sensitive to geographical/climatic factors. Thus, warmer and

31
32 63 shallower lower-altitude European lakes, which are usually more eutrophic, had higher fish

33
34 64 densities than cold and deeper higher-altitude lakes. Fish size increased with altitude and

35
36 65 declined with increasing seasonality and temperature.

37
38 66 4. After controlling for the natural factors, productivity had a positive effect on fish species

39
40 67 richness and diversity, whereas it negatively influenced fish size.

41
42 68 5. Our results suggest that macroecological patterns of lake fish diversity across Europe are

43
44 69 best predicted by natural factors. The contribution of anthropogenic factors to fish diversity

45
46 70 was evident only via by the effect of eutrophication at smaller geographical scales, whereas

47
48 71 no effect could be found from hydromorphological pressures. From an applied perspective,

1 72 these results suggest that bioassessment and biodiversity evaluation might be most effectively
2
3
4 73 conducted and interpreted locally, where anthropogenic effects on biodiversity become more
5
6 74 visible. At a macroecological scale, the strong effect of environmental temperature on most
7
8
9 75 components of fish diversity suggests future changes in fish diversity as a consequence of
10
11 76 climate change.

12
13
14 77

15
16
17 78

18
19
20 79

21
22
23 80

24
25
26 81

27
28
29 82

30
31
32 83

33
34
35 84

36
37
38 85

39
40
41 86

42
43
44 87

45
46
47 88

48
49
50 89

51
52
53 90

54
55
56 91

57 92 **Introduction**
58
59
60

1 93

2
3
4 94 Freshwater ecosystems hold an estimated 12% of the world's animal species and the
5
6 95 biodiversity of these habitats is declining at an alarming and unprecedented rate due to
7
8
9 96 anthropogenic activities (Abramovitz, 1996; Johnson, Revenga & Echeverria, 2001; Sala *et*
10
11 97 *al.*, 2000). Determining the processes responsible for modifying of biodiversity patterns is a
12
13 98 crucial issue for conservation strategies in the face of current and future global and regional
14
15
16 99 anthropogenic impacts (Kerr, Kharouba & Currie, 2007). However, there has been
17
18 100 surprisingly little effort to distinguish the effects of natural and anthropogenic factors on
19
20
21 101 macroecological patterns of freshwater diversity, because most studies focus on understanding
22
23 102 'natural' processes alone, disregarding the potential problems caused by the addition of
24
25 103 current anthropogenic effects (La Sorte, 2006). Particularly, in densely-populated regions
26
27 104 such as Europe, where aquatic systems are greatly affected by humans (Abramovitz, 1996;
28
29 105 EEA, 2010), anthropogenic factors may well override the well-known effects of natural
30
31
32 106 gradients on local and regional aquatic diversity.

33
34
35 107 Lakes, being natural relatively isolated ecosystems, can be considered as biogeographical
36
37 108 islands and are thus ideal for studying the macroecological effects of local and regional
38
39 109 processes on assemblage composition (Heino, 2011). For example, regional fish species
40
41
42 110 richness generally declines from the tropics to the poles (Abell *et al.*, 2008), but is modulated
43
44 111 by historical effects on biogeography in European lakes (Griffiths, 2006; Jeppesen *et al.* 2010)
45
46
47 112 that sometimes interact with climate. Similarly, richness and endemism of riverine fish faunas
48
49 113 were higher in the Mediterranean regions than in Central, Eastern and Northern Europe
50
51
52 114 (Reyjol *et al.*, 2007). These studies point to a strong effect of regional factors on the
53
54 115 composition of European fish assemblages.

1
2 116 Lake morphometry (area and depth) is considered the most important natural factor
3
4 117 influencing local fish assemblage composition (Jeppesen *et al.*, 2000; Olin *et al.*, 2002;
5
6 118 Mehner *et al.*, 2005, 2007). Many studies have shown that local fish species richness in lakes
7
8 119 is strongly linked to area, probably as a result of a higher complexity and stability of habitats
9
10 120 in large lakes (e.g. MacArthur & Wilson, 1967; Barbour & Brown, 1974). In a study covering
11
12 121 a wide latitudinal gradient in northeastern USA, lake morphometry even overrode the effect
13
14 122 of regional processes on fish richness (Allen *et al.*, 1999). In contrast, few studies have
15
16 123 addressed the effect of anthropogenic factors on local fish diversity. Fish species richness was
17
18 124 unimodally or positively related to anthropogenically increased productivity in Danish
19
20 125 (Jeppesen *et al.*, 2000) and Finnish lakes (Olin *et al.*, 2002), respectively, and lake
21
22 126 productivity was an important predictor of fish abundance and biomass in German lakes
23
24 127 (Mehner *et al.* 2005).

25
26
27
28
29
30 128 The mean size of fish is another component of diversity which interacts with species
31
32 129 richness and density (Magurran, 2004). Natural predictors of the life history traits of fish, such
33
34 130 as body size, are primarily climatic factors and there is increasing evidence that the mean
35
36 131 body size of fish declines with increasing mean annual temperature (Griffiths, 2006; Teixeira-
37
38 132 de Mello *et al.*, 2009; Jeppesen *et al.*, 2010). Simultaneously, anthropogenically enhanced
39
40 133 productivity causes a decline in the mean size of fish, caused by density-dependent growth in
41
42 134 highly productive lakes (Jeppesen *et al.*, 2000). In addition to cultural eutrophication,
43
44 135 hydromorphological alterations, exploitation as fisheries and the use of lakes for recreation
45
46 136 have been found to impact significantly fish species richness, density and body size (e.g.
47
48 137 Jennings *et al.*, 1999; Allan *et al.*, 2005).

49
50
51
52
53
54 138 Studies on fish diversity in lakes suggest that there is presumably no single factor that
55
56 139 simultaneously predicts diversity, size and density of fish across large spatial gradients.
57
58
59
60

1 140 Natural factors and anthropogenic pressures may strongly interact in determining the local
2
3
4 141 fish assemblage in lakes. In the face of the freshwater biodiversity crisis (Dudgeon *et al.*,
5
6 142 2006; Vörösmarty *et al.* 2010), it is therefore important to estimate the relative contribution of
7
8
9 143 natural and anthropogenic factors on the macroecological patterns of fish diversity in lakes.
10
11 144 However, to do this, large datasets are needed which have to be obtained by systematic
12
13 145 sampling including fish species, density and size. Furthermore, the lakes included should
14
15
16 146 cover broad geographical, climatic and morphometric gradients, and data on local
17
18 147 anthropogenic pressures should be of sufficient precision.

20
21 148 Here we compiled a fish database consisting of standardized, multi-mesh sized gill-net
22
23 149 catches from 1632 lakes from 11 European countries covering a wide latitudinal and
24
25 150 longitudinal gradient. The lakes also represent a wide range of morphometric and
26
27
28 151 environmental variables/stressors. Our overall aim was to assess whether current
29
30 152 anthropogenic pressures have already changed large-scale macroecological patterns of fish
31
32
33 153 diversity in European lakes. Specifically, we addressed the following questions: (1) Are local
34
35 154 fish species richness and diversity in European lakes primarily determined by the latitudinal
36
37 155 and morphometric gradients, or has the effect of locally enhanced productivity by human-
38
39 156 induced eutrophication disrupted these macroecological patterns? (2) Alternatively, is the
40
41
42 157 effect of anthropogenic pressures on biodiversity visible only at smaller geographical scales?
43
44 158 (3) Is the average size of fish primarily determined by environmental temperature, or has
45
46
47 159 anthropogenic disturbance replaced the dominant effect of temperature? (4) Is the density of
48
49 160 fish in lakes related primarily to productivity, or can other predictors explain a part of the
50
51
52 161 variability observed over large spatial gradients?

53
54
55 162

56
57
58 163
59
60

1 164 **Methods**

2
3
4 165 *Data set*

5
6
7 166 We used a fish database including 1632 European lakes sampled from 1993 to 2009. The
8
9
10 167 database was created as part of a Water Framework Directive 2000/60/EC Intercalibration
11
12 168 exercise, supplemented by additional data from the authors. The database included 11
13
14 169 countries and covered a latitudinal gradient between 41.96 and 69.69° N (maximum distance
15
16 170 between lakes of 3083 km) and a longitudinal gradient between -10.17 and 31.30° E
17
18 171 (maximum distance between lakes of 3395 km) (Fig. 1). All lakes were sampled from June to
19
20 172 September with Nordic benthic multi-mesh gill nets largely in accordance with the European
21
22 173 standard (CEN 14757, 2005; Appelberg *et al.*, 1995). Benthic gill nets (12 mesh sizes
23
24 174 between 5.0 and 55 mm in a geometric series, each panel being 2.5 m long and 1.5 m high)
25
26 175 were set in a random stratified sampling design in the benthic habitat. Nets were generally set
27
28 176 for a 12-16 h period from before dusk and lifted after dawn. The total fishing effort per lake
29
30 177 (number of benthic nets) was standardized by lake area and maximum depth according to
31
32 178 CEN 14757 (2005). The sampling procedure employed in the German lakes differed slightly
33
34 179 from the standard protocol, as the sampling was were split, with the first half of the effort
35
36 180 (number of nets) set during late summer and early autumn and the second half set during the
37
38 181 subsequent spring (Mehner *et al.*, 2005). In that case, a sampling campaign is the sum of two
39
40 182 sampling periods. The dataset (n = 1632 lakes) contained only lakes with pH>6, to exclude
41
42 183 the structuring effect of acidification on fish assemblages, which otherwise might obscure the
43
44 184 effects of the main anthropogenic pressures assessed in this study, i.e. eutrophication and
45
46 185 hydromorphological degradation. This was needed as a large part of the Nordic data were
47
48 186 from lakes recovering from acidification.
49
50
51
52
53
54
55
56
57
58
59
60

1 188 *Descriptors of fish assemblages*

2
3
4 189 Species richness was calculated as the total number of fish species collected in a lake.
5
6 190 Shannon-Wiener diversity (H) was calculated according to Shannon & Wiener (1949) in
7
8
9 191 Pielou (1969). Fish density was expressed as catch per unit effort, determined as the number
10
11 192 per unit effort (NPUE, number of fish) and the biomass per unit effort (BPUE, wet mass of
12
13 193 fish), standardized with respect to gill-net area (m²) and fishing duration (h). Shannon-Wiener
14
15 194 diversity was calculated from both fish numbers (H_{NPUE}) and biomass (H_{BPUE}). The
16
17 195 biomass: number ratio (BPUE:NPUE) was estimated as a proxy of the average fish body size
18
19
20
21 196 and hereafter called body size.
22
23

24 197

25
26
27 198 *Environmental and anthropogenic pressure variables*

28
29 199 Lake area (km²), altitude (m) and maximum depth (Z_{max}) were extracted from the national
30
31 200 databases (Table 1). Climatic data were obtained from the climate CRU model (New *et al.*,
32
33 201 2002). The amplitude of temperature (T_{amp}) (proxy for seasonality) was calculated as the
34
35 202 difference between mean temperature (T_{mean}) in July and January.
36
37
38

39 203 The anthropogenic pressures considered are listed in Table 1. Enhanced in-lake
40
41 204 productivity (eutrophication) was estimated by annual mean TP (µg L⁻¹), and land use and
42
43 205 population density in the catchment. Total phosphorus (TP) was measured as the mean of a
44
45 206 minimum of four samples taken in a single year (one for each season) for all lakes (except a
46
47 207 small number of Swedish lakes for which we selected TP data for another year matching the
48
49 208 last fish sampling campaign as closely as possible). Land use was estimated as the percentage
50
51 209 of natural and agricultural land cover in the lake catchment using Corine Land Cover. For a
52
53 210 subset of the lakes, population density in the catchment was assessed according to expert
54
55 211 judgment on a four-step scale (low, medium, high and very high) (Table 1). Morphometric
56
57
58
59
60

1 212 modification was estimated as the percentage of shoreline bank modified according to expert
2
3
4 213 judgment and in application of the Lake Habitat Survey (Rowan *et al.*, 2006) on a ranked
5
6 214 scale (five classes, from 1 no modification, to 5, highly modified).
7
8

9 215

10
11 216 *Statistical analysis*

12
13
14
15 217 We applied a two-step approach. First, we conducted regression tree analyses to explore
16
17 218 which factors dominate in the prediction of fish diversity (richness, diversity, size, density) in
18
19 219 the lakes. Second, for those fish descriptors that were influenced mainly by natural factors
20
21 220 according to the regression tree analysis, we controlled for the dominant effects of these
22
23 221 factors and then tested explicitly for the effects of anthropogenic factors by applying
24
25 222 Generalized Linear Models (GLM). We log₁₀-transformed all variables except pH, richness
26
27 223 and diversity.
28

29
30
31 224 Regression tree analyses were performed to trace the relationship between the natural and
32
33 225 anthropogenic variables (predictors) and fish diversity descriptors (responses) and to identify
34
35 226 thresholds of the predictor variables best discriminating the resulting fish assemblage
36
37 227 structure. Regression trees are a binary partitioning approach whereby a dataset is
38
39 228 progressively split into subsets that most significantly reduce the variability of the response
40
41 229 variable. This type of regression gives a clear picture of the structure of the data and provides
42
43 230 a highly intuitive insight into the kinds of interactions between variables (Crawley, 2002). It
44
45 231 simultaneously handles categorical and continuous data, is insensitive to outliers and
46
47 232 multicollinearity (Breiman *et al.*, 1984; De'ath, 2007), and is therefore highly suitable for the
48
49 233 complex dataset we have accumulated here. Regression trees can also accommodate missing
50
51 234 data in predictor variables by using other independent variables, known as surrogates, that
52
53 235 best agree (i.e. classify the same subjects in the same way) with the original splitting variable
54
55
56
57
58
59
60

1 236 (Breiman *et al.*, 1984). Surrogates are selected by the algorithm according to their
2
3
4 237 performance in the percentage of agreement in the allocation of cases to the two groups. To
5
6 238 avoid over-fitting, we ‘pruned’ the tree using a 10-fold cross-validation and the one standard
7
8
9 239 error (1-SE) rule (Breiman *et al.*, 1984). A 10-fold cross-validation test consists in splitting
10
11 240 the data, constructing a new model from a subset of samples and then testing the predictive
12
13 241 accuracy of those sample(s) not included in its construction (Breiman *et al.*, 1984; Bahn &
14
15
16 242 McGill, 2007). In more detail, the data were divided in 10 parts and one part was omitted. The
17
18 243 tree was then estimated using 90% of the data and the omitted 10% were used to obtain a
19
20
21 244 prediction error. This process was then repeated by omitting each of the 10 datasets in turn.
22
23 245 We chose the 1-SE rule to estimate the best tree because this method usually results in smaller
24
25 246 trees than suggested by the minimum cross-validated error, but with minimal increase in the
26
27 247 estimated error rate (at most <1SE) (Breiman *et al.*, 1984; Déath & Fabricius, 2000).
28
29
30 248 We ran a separate regression tree for each of the six descriptors of fish diversity. Categorical
31
32
33 249 predictors (Table 1) were included as nominal variables. We excluded highly redundant
34
35 250 predictors from regression tree analyses (Table 2). Hence, since minimum temperature (T_{\min}),
36
37 251 T_{mean} and T_{amp} co-varied strongly (Table 2; average Spearman’s $r_s=0.9$), we subsequently
38
39 252 included only T_{max} and T_{amp} . The percentages of natural and agricultural land cover were also
40
41
42 253 strongly negatively correlated ($r_s=-0.9$), so we included only the latter in the analyses.
43
44
45 254 Longitude was strongly correlated with T_{amp} ($r_s=0.7$) and with precipitation ($r_s=0.7$) and was
46
47 255 therefore also excluded. Alternative splits (i.e. splits that had as many correct classifications
48
49 256 as the original splitting variable) and surrogate variables were examined to obtain a more
50
51
52 257 complete understanding of the dependencies and relationships within the data (Déath &
53
54 258 Fabricius, 2000). Thus, we inspected strongly competing alternative splits to test whether the
55
56 259 resulting tree could better explain the data. Finally, when a variable with missing data was
57
58
59
60

1 260 selected, we checked to ensure that data were evenly distributed across response and predictor
2
3
4 261 variables.

5
6
7 262 Since the initial database was dominated by Swedish lakes (Fig. 1), and this geographical bias
8
9 263 could have influenced the results, we split the lakes into three categories (regions) based on
10
11 264 latitude and four based on longitude and sub-sampled an equal number of lakes from each of
12
13 265 the 12 sub-regions. Next, we re-ran regression tree analyses using this unbiased dataset (in
14
15 266 total 272 lakes). Thereby, we significantly reduced the proportion of missing values for
16
17 267 productivity variables (100% and 84% of data available for TP and percentage of agricultural
18
19 268 land cover, respectively). Subsequently, we compared the results of these two approaches.

20
21 269 For those fish descriptors that were influenced mainly by natural factors according to
22
23
24 270 regression tree analysis, we ran Generalized Linear Models (GLM; McCullagh & Nelder
25
26 271 1989) for each of the two subsets defined by the primary splits of regression trees and by
27
28 272 using anthropogenic pressures as predictors. Thus, if for example a fish descriptor was mainly
29
30 273 influenced by T_{\max} , we took the two T_{\max} categories defined by the primary tree split and
31
32 274 calculated GLMs within each tree category. We compared the models with main effects of
33
34 275 two anthropogenic predictors (TP and % agriculture) and their interaction by using the Akaike
35
36 276 Information Criterion corrected (AICc). We used a Poisson error distribution and a
37
38 277 logarithmic link function for richness variable and Normal error distribution and identity link
39
40 278 function for diversity and body size variables.

41
42
43 279 Regression tree analyses were performed in “R” version 2.9.1 (Development Core Team,
44
45 280 2009) using the Brodgar v. 2.7.2 statistical package (Highland Statistics Ltd., Newburgh,
46
47 281 UK). GLMs were performed using SPSS 17.0 (SPSS Inc., 1989-2006).

48
49
50 282

51
52
53 283 **Results**

1 284 In the regression tree analysis of species richness, the primary split was defined by lake
2
3
4 285 area, which was positively related to richness. Surrogate variables of lake area were maximum
5
6 286 depth (Z_{\max}) and latitude (positively and negatively related to fish richness, respectively).
7
8
9 287 Lakes were further divided according to T_{\max} , which in total contributed almost as much
10
11 288 explanatory power as lake area (Table 3; Fig. 2). Surrogate variables for the three nodes
12
13 289 related to T_{\max} were precipitation, latitude and altitude, indicating a relationship between T_{\max}
14
15
16 290 and the geographical gradients.

17
18
19 291 Shannon-Wiener diversity based both on fish numbers (H_{NPUE}) and biomass (H_{BPUE}) was
20
21 292 primarily affected by T_{\max} , with both altitude and latitude as surrogate variables (Table 3). For
22
23 293 H_{NPUE} , a second split divided the lakes above and below the temperature threshold according
24
25 294 to their area with surrogate Z_{\max} . For H_{BPUE} , T_{\max} and area again defined the second and third
26
27
28 295 nodes, respectively (Table 3; Fig. 2).

29
30
31 296 The density of fish was primarily predicted by productivity (in-lake TP concentration)
32
33 297 (Table 3, Fig. 2), with thresholds of $23.7 \mu\text{g L}^{-1}$ (number) and $20 \mu\text{g L}^{-1}$ (biomass). Surrogate
34
35 298 variables for TP were altitude and pH, which were negatively and positively related to fish
36
37
38 299 density, respectively. A second node was defined by T_{\max} for fish number and by Z_{\max} for fish
39
40 300 biomass. The interaction between TP and temperature in predicting fish numbers is shown in
41
42 301 Fig. 3: for the same TP concentration, more fish numbers were found in warmer lakes (T_{\max}
43
44 302 $>15^{\circ}\text{C}$). Fish body size was predicted by altitude, with T_{\max} as a surrogate. A second split
45
46
47 303 divided lower-altitude lakes according to their T_{amp} (Table 3; Fig. 2).

48
49
50 304 Additional regression trees were trained using a geographically unbiased dataset (i.e. sub-
51
52 305 sampling a similar proportion of lakes in three latitude and four longitude categories leaving
53
54
55 306 272 lakes in total). The results were similar to those obtained from the whole database
56
57
58 307 suggesting that the strong dominance of Scandinavian lakes in the large dataset did not
59
60

1 308 influence the main conclusions. However, the variance explained increased for each
2
3
4 309 regression tree, except for fish richness and H_{CPUE} (that remained similar; Table 4). The only
5
6 310 differences occurred for fish species richness, which was mainly related to T_{max} and explained
7
8 311 30% of the variance for the model, and for body size, which was mainly positively related to
9
10 312 precipitation. Nevertheless, lake area appeared at the second split for fish richness explaining
11
12 313 10% of the variance. The main surrogate variable for the first split was the percentage of
13
14 314 agricultural land cover for all fish descriptors, except for fish size and number for which T_{amp}
15
16 315 and latitude were the main surrogates, respectively.
17
18
19

20 316 Generalized linear models showed that fish descriptors (richness, diversity and body size)
21
22 317 were in all cases significantly affected by anthropogenic factors (TP and percentage of
23
24 318 agricultural land cover) when accounting for the dominant effects of natural predictors, as
25
26 319 found in the regression tree (Table 5; Fig. 4). The AICc indicated that TP was the main
27
28 320 anthropogenic factor explaining changes in richness, H_{NPUE} , H_{BPUE} and body size, except for
29
30 321 richness in small lakes and fish body size in higher altitude lakes for which the percentage of
31
32 322 agriculture land cover was more significant than TP (Table 5). Both factors were positively
33
34 323 related to fish species richness and diversity, but negatively related to body size (Fig. 4).
35
36
37
38
39

40 324

41 325

42 326 **Discussion**

43
44
45
46 327 Our study of patterns of fish diversity in European lakes, based on probably the most
47
48 328 comprehensive and large-scaled dataset ever produced in lakes, suggests that several of the
49
50 329 well-documented statistical correlations between local fish diversity and natural gradients are
51
52 330 still intact. Local species richness was strongly related to lake morphometry and
53
54 331 environmental temperature, whereas average fish size and Shannon-Wiener diversity were
55
56
57
58
59
60

1 332 determined primarily by environmental temperature related to altitudinal and latitudinal
2
3
4 333 gradients. Furthermore, the geographical gradients found in our analyses agree with a
5
6 334 previous study of fish species richness in lakes at European scale that reported a decline in
7
8 335 regional species richness in the northern and western regions due to influence of
9
10 336 biogeographical aspects, such as barriers and glaciation events (Griffiths, 2006).
11
12 337 Primary productivity, as a measure of the amount of energy available at a base of the food
13
14 338 webs, is presumably one of the major determinants of species richness and diversity (e.g.
15
16 339 Currie, 1991), and primary productivity is strongly related to the TP-concentration in lakes.
17
18 340 The increased energy available, and the greater food web complexity in more productive
19
20 341 lakes, allow more species to coexist (Gaston, 2000). Here, we showed that agriculture in the
21
22 342 catchment was the primary surrogate of natural predictors when using a geographically
23
24 343 unbiased dataset (i.e. where Mediterranean and Scandinavian lake samples were more
25
26 344 balanced), suggesting that anthropogenic stressors may have modified natural
27
28 345 macroecological gradients of fish diversity in lakes. Similarly, when taking into account the
29
30 346 most important geographical, climatic and morphometric differences between the lakes, both
31
32 347 enhanced TP concentration and agriculture in the catchment contributed significantly to an
33
34 348 increase in fish species richness and diversity. Thus, the anthropogenic effects on biodiversity
35
36 349 become more visible at smaller geographical and morphometric scales whereas they are less
37
38 350 obvious across larger spatial extents. This suggests that, even though global or continental
39
40 351 bioassessment and evaluation of biodiversity is needed, they might be most effectively
41
42 352 analysed and interpreted at smaller geographical scales (Heino, 2013).
43
44 353 Our results corroborate those of earlier studies covering smaller geographical gradients which
45
46 354 revealed that the response of fish assemblages to changing productivity varies considerably
47
48 355 depending on lake morphometry and fish species composition (Olin *et al.*, 2002; Mehner *et*
49
50 356 *al.*, 2005, 2007). A dominant effect of lake morphometry over those induced by
51
52
53
54
55
56
57
58
59
60

1 357 anthropogenic descriptors was also found for broad-scale richness of benthic
2
3 358 macroinvertebrates, birds, and zooplankton (Allen *et al.*, 1999). In turn, productivity was the
4
5
6 359 main positive determinant of fish density in our study (Fig. 5), corroborating earlier studies on
7
8
9 360 lake fish assemblages covering smaller geographical and trophic gradients (Jeppesen *et al.*,
10
11 361 2000; Olin *et al.*, 2002) and studies on zooplankton biomass at European scale (Gyllström *et*
12
13 362 *al.*, 2005). According to our results, a TP concentration of around 20-25 $\mu\text{g L}^{-1}$ represents a
14
15
16 363 threshold for a significant increase in lake fish numbers and biomass.

17
18 364 Our regression tree approach also detected some effects, hitherto poorly described, of
19
20
21 365 temperature and lake morphometry on fish density. Thus, warmer and lower-altitude
22
23 366 European lakes, which are usually more eutrophic, had higher fish density than cold and
24
25
26 367 higher-altitude European lakes (Fig. 5). The temperature-related effects on fish density(both
27
28 368 due to latitudinal or altitudinal differences) may act independently of lake trophic status since,
29
30 369 for a similar TP concentration, we found generally a greater number of fish numbers in warm
31
32
33 370 than in cold lakes. So far, similar findings had been found only for fish biomass in a
34
35 371 comparative study of shallow subtropical and temperate lakes, showing a twofold higher fish
36
37 372 biomass per unit of TP in the warmer subtropical lakes (Teixeira-de Mello *et al.*, 2010).

38
39
40 373 With regard to fish body size, geographical and climatic factors remained the dominant
41
42 374 predictors, but the effect of anthropogenic factors emerged when geographical differences
43
44
45 375 between the lakes were taken into account. Most importantly, fish body size was larger in
46
47 376 high-altitude than low-altitude lakes, and declined with increasing temperature (Fig. 5). These
48
49
50 377 findings agree with previous studies on fish (Blanck & Lamouroux, 2007; Jeppesen *et al.*,
51
52 378 2010) and invertebrates [e.g. beetles, Vamosi & Vamosi (2007);zooplankton, Gillooly &
53
54 379 Dodson (2000)] and support the predictions of the metabolic theory of ecology (Brown *et al.*,
55
56
57 380 2004). Our results suggested a decrease in fish body size with enhanced eutrophication, which
58
59
60

1 381 is in accordance with previous local studies of fish and zooplankton (Jeppesen *et al.* 2000).

2
3
4 382 This decrease in fish body size with eutrophication was more obvious in higher altitude lakes,
5
6 383 which are naturally more oligotrophic than those at lower altitudes, and suggests that, in the
7
8
9 384 former, fish assemblages may be more sensitive to changes in lake productivity.

10
11 385 In our study, body size was also associated with the amplitude of temperature and
12
13
14 386 precipitation, variables that are both highly correlated with longitude. The results suggest that
15
16 387 lakes in Eastern Europe, normally exhibiting greater variations in temperature, and higher
17
18 388 summer temperatures, tend to have smaller fish. Supporting this argument, Carlson, Olsen &
19
20 389 Vøllestad (2008) found that small body size could be an advantage for fish inhabiting strongly
21
22 390 seasonal environments. The positive relationship between fish density and air temperature,
23
24 391 and smaller fish in warmer lakes, agrees with the results of cross-comparisons of fish
25
26 392 populations in Europe. They showed that fish species from lower latitudes are typically
27
28 393 smaller, grow faster, mature earlier, and have shorter life spans and allocate less energy (as
29
30 394 gonadosomatic index) to reproduction than populations and species at higher latitudes
31
32 395 (Griffiths, 2006; Blanck & Lamouroux, 2007; Jeppesen *et al.*, 2010). Such changes are
33
34 396 evident even in the same species along a latitudinal gradient (Blanck & Lamouroux, 2007;
35
36 397 Jeppesen *et al.*, 2010).

37
38
39
40
41
42 398 Overall, our results indicated that larger and deeper lakes in warmer areas were the richest
43
44 399 and most diverse in fish species (Fig. 5). The positive relationship between richness and lake
45
46 400 area, depth or volume might reflect a greater environmental stability in large and deep lakes
47
48 401 than in small and shallow lakes (Jeppesen *et al.*, 2000; Irz, Argillier & Oberdorff, 2004; Volta
49
50 402 *et al.*, 2011) and increased habitat heterogeneity favouring the coexistence of more species
51
52 403 (MacArthur & Wilson, 1967).

1 404 Differences in maximum temperature made a similar contribution to fish species richness
2
3
4 405 as did lake area. Similarly, diversity indices were mainly influenced by maximum temperature
5
6 406 which agrees with a recent model, supported by terrestrial, freshwater, and marine taxa data,
7
8 407 that quantifies the role of biochemical kinetics in generating biodiversity (Allen, Brown &
9
10 408 Gillooly, 2002). According to this model, environmental temperature, through its effects on
11
12 409 individual metabolic rates, influences the rates of genetic divergence among populations and
13
14 410 rates of speciation in communities. In our analysis, lake altitude appeared as the main
15
16 411 surrogate for the maximum temperature in the fish diversity regression trees. The effects of
17
18 412 altitude on fish diversity can probably be attributed to its direct barrier effects on colonization
19
20 413 and its indirect effects due to collinearity with temperature, which is in accordance with the
21
22 414 findings in a previous study of lakes in China (Zhao *et al.*, 2006).
23
24
25
26
27

28 415 Apart from eutrophication, we did not find any effect of anthropogenic alterations, such as
29
30 416 hydrological and morphometric degradation, on fish diversity in lakes. This result agrees with
31
32 417 a previous study in German lakes (Mehner *et al.*, 2005). In contrast to our findings, previous
33
34 418 studies restricted to North American lakes, in which lake shores were sampled by
35
36 419 electrofishing (e.g. Jennings *et al.*, 1999; Schindler, Geib & Williams, 2000), have shown that
37
38 420 fish richness declines in response to shoreline modifications and that the strength of the
39
40 421 changes depends on the complexity of the artificially created habitats (Jennings *et al.*, 1999).
41
42 422 The weak effect of hydromorphological pressures on fish diversity in European may be
43
44 423 attributable to the fact that, in some cases, our measures were based on expert judgment,
45
46 424 which might be too coarse to detect subtle impacts. It could also be attributed to the fact that
47
48 425 the respective information was available only for a small subset of lakes. Nevertheless, when
49
50 426 the same analyses were carried out using only these lakes where the information was
51
52 427 available, the main variables determining the fish diversity descriptors did not change.
53
54 428 Therefore, the opposite outcomes between European and North-American studies suggest
55
56
57
58
59
60

1 429 that: (1) fish in European lakes are less sensitive or are more resilient to these anthropogenic
2
3
4 430 pressures, or (2) the impact of these pressures is obscured by the effect of strong biological
5
6 431 interactions, such as predation and competition, in European lakes, or that (3) a strong effect
7
8
9 432 is only seen if a certain degree of pressure intensity is exceeded which was not the case for the
10
11 433 lakes included here. Additionally, (4) we cannot exclude the possibility of an effect of
12
13 434 hydromorphological pressures on some others traits that were measured in North American
14
15
16 435 fish but were not measured in our study (e.g. small cyprinids). Furthermore, gillnet sampling
17
18 436 may not be the most effective method to document the effects of hydromorphological
19
20
21 437 pressures, since these pressures may mostly influence shoreline fish assemblages, which are
22
23 438 more reliably monitored by electrofishing (Diekmann *et al.*, 2005; Erős *et al.*, 2009). It is
24
25 439 highly likely that all these explanations strongly interact in causing the differing response of
26
27
28 440 temperate fish diversity to anthropogenic stressors between Europe and North America. The
29
30 441 regional fish diversity in Europe is highly depauperate compared to North America, mainly as
31
32 442 a consequence of the relative importance of historical processes such as glaciations (Tonn *et*
33
34 443 *al.*, 1990, Griffiths, 2006). Therefore, the dominant fish species in Europe are less specialized,
35
36 444 have broader niches, and a more flexible life history than their American counterparts (Tonn
37
38
39 445 *et al.*, 1990), making them less vulnerable to the effects of anthropogenic stressors. In turn,
40
41 446 the fish diversity in European lakes is less variable, and hence less sensitive to local
42
43
44 447 predictors, than is found in similar studies of North-American fish assemblages. Nevertheless,
45
46 448 we cannot exclude that pelagic gillnet data used in this study could have led to an
47
48
49 449 underestimation of fish richness and thus may not adequately represent total lake diversity
50
51 450 (Erős *et al.*, 2009).

52
53
54 451 Some models, particularly those obtained using the whole dataset, explained a low
55
56 452 percentage of the variance (e.g. 20% for body size) indicating that their predictive ability may
57
58
59 453 be limited and thus conclusions should be carefully drawn. However, when cross-validating
60

1 454 by using smaller, more balanced training sets, better models were overall obtained, which
2
3
4 455 allows for more robust ecological insights.
5

6
7 456 In conclusion, our results indicate that most components of lake fish diversity at a European
8
9 457 scale are still mainly determined by natural factors. Some effects of anthropogenic stressors
10
11 458 on fish diversity became particularly obvious when subsets of lakes with similar natural
12
13 459 environmental factors were evaluated. In contrast, fish numbers and biomass responded to
14
15 460 anthropogenically enhanced productivity even at a macroecological (here European) scale.
16
17
18 461 From an applied perspective, these findings have important implications for unravelling the
19
20 462 causes of freshwater biodiversity loss and for the development of fish-based systems for
21
22 463 assessing the ecological status of lakes (i.e. in the implementation of the European Water
23
24
25 464 Framework Directive, WFD). Our results confirm that (1) fish densities are sensitive to some
26
27 465 anthropogenic pressures, which must be considered when developing biotic indicators, and (2)
28
29 466 geographical and morphometric factors should be accounted for when attempting to quantify
30
31 467 the effects of anthropogenic factors on fish diversity at large geographical scales (Argillier et
32
33 468 al., 2013, Irz et al., 2007). This agrees with the WFD requirement of setting reference
34
35 469 conditions for subsets of lakes defined by geography and morphometry (e.g. European
36
37 470 Commission, 2010; Brucet et al., 2013). Our results also suggest that (3) temperature
38
39 471 differences, mainly related to geographical gradients and lake morphometry, strongly predict
40
41 472 most components of fish diversity, emphasizing the importance of temperature in determining
42
43 473 broad-scale patterns of fish diversity in European lakes. Therefore, subtle changes of fish
44
45 474 diversity in lakes may be early indicators of the effects of global warming, a process that
46
47 475 presumably has only started to become visible.
48
49
50
51
52
53
54
55

56 477 **Acknowledgments**

57
58
59
60

1 478 This paper is a result of the project WISER (Water bodies in Europe: Integrative Systems to
2
3
4 479 assess Ecological status and Recovery) funded by the European Union under the 7th
5
6 480 Framework Programme, Theme 6 (Environment including Climate Change, contract No.
7
8
9 481 226273). The authors wish to thank all Lake Intercalibration experts who contributed to the
10
11 482 realization of the database and, particularly, David Ritterbusch and Uwe Brämick (Germany),
12
13 483 Otilia Mihail (Romania) and Robert Rosell (Northern Ireland). SB, EJ and TLL were also
14
15 484 supported by EU REFRESH, and EJ and TLL by CLEAR and CRES. PV was also supported
16
17 485 by INHABIT LIFE+ Project. KH was supported by the Swedish WATERS project. Some of
18
19 486 the UK fish data provided by IJW were collected under funding from Countryside Council for
20
21 487 Wales, the Environment Agency (England and Wales), Natural Environment Research
22
23 488 Council and Scottish Natural Heritage. We thank Anne Mette Poulsen and Tinna Christensen
24
25 489 for valuable editorial assistance; Simon Causse and Ayse Idil Cakiroglu for database and
26
27 490 statistical support, respectively; two anonymous reviewers for constructive comments; and
28
29 491 Prof. Hildrew for manuscript edition.
30
31
32
33
34

35 492

36
37
38 493 **References**39
40
41 494

- 42
43 495 Abell R., Thieme M.L., Revenga C., Bryer M., Kottelat M., Bogutskaya N., *et al.* (2008)
44
45 496 Freshwater ecoregions of the world: a new map of biogeographic units for freshwater
46
47 497 biodiversity conservation. *Bioscience*, **58**, 403-414.
48
49
50
51 498 Abramovitz, J. (1996). *Imperiled waters, impoverished future: The decline of freshwater*
52
53 499 *ecosystems*. Worldwatch Paper No. 128. Worldwatch Institute, Washington, DC
54
55
56
57
58
59
60

- 1 500 Allan D.J., Abell R., Hogan Z., Revenga C., Taylor B.W., Welcomme R.L. & Winemiller K.
2
3
4 501 (2005) Overfishing of Inland Waters. *BioScience*, **55**, 1041-1051.
5
6
7 502 Allen A.P., Whittier T.R., Kaufmann P.R., Larsen D.P., O'Connor R.J., Hughes R.M., *et al.*
8
9 503 (1999) Concordance of taxonomic richness patterns across multiple assemblages in
10
11 504 lakes of the northeastern United States. *Canadian Journal of Fisheries and Aquatic*
12
13 505 *Sciences*, **56**, 739-747.
14
15
16 506 Allen A.P., Brown J.H., Gillooly J.F. (2002) Global biodiversity, biochemical kinetics, and
17
18 507 the energetic-equivalence rule. *Science*, **297**, 1545-1548.
19
20
21 508 Abramovitz J. (1996) Imperiled waters, impoverished future: The decline of freshwater
22
23 509 ecosystems. World Watch Paper 128, Worldwatch Institute, Washington, DC.
24
25
26
27 510 Appelberg M., Berger H.M., Hesthagen T., Kleiven E., Kurkilahti M., Raitaniemi J. & Rask
28
29 511 M. (1995) Development and intercalibration of methods in Nordic freshwater fish
30
31 512 monitoring. *Water, Air and Soil Pollution*, **85**, 401-406.
32
33
34
35 513 Argillier C., Caussé S., Gevrey M., Pédrón S., De Bortoli J., Brucet S., *et al.* (2013)
36
37 514 Development of a fish-based index to assess the eutrophication status of European lakes.
38
39 515 *Hydrobiologia*, **704**, 193-211.
40
41
42 516 Bahn V. & McGill B.J. (2007) Can niche-based distribution models outperform spatial
43
44 517 interpolation? *Global Ecology and Biogeography*, **16**, 733-742.
45
46
47 518 Barbour C.D. & Brown J.H. (1974) Fish species diversity in lakes. *American Naturalist*, **108**,
48
49 519 473-489.
50
51
52
53 520 Blanck A. & Lamouroux N. (2007) Large-scale intraspecific variation in life-history traits of
54
55 521 European freshwater fish. *Journal of Biogeography*, **34**, 862-875.
56
57
58
59
60

- 1 522 Breiman L., Friedman J.H., Olshen R.A. & Stone C.J. (1984) *Classification and Regression*
2
3
4 523 *Trees*. Wadsworth International Group, Belmont, CA, USA.
- 5
6
7 524 Brown J.H., Gilloly J.F., Allen A.P., Savage V.M. & West G.B. (2004) Toward a metabolic
8
9 525 theory of ecology. *Ecology*, **85**, 1771-1789.
- 10
11
12 526 Carlson S.M., Olsen E.M. & Vøllestad L.A. (2008) Seasonal mortality and the effect of body
13
14 527 size: a review and an empirical test using individual data on brown trout. *Functional*
15
16 528 *Ecology*, **22**, 663-673.
- 17
18
19 529 CEN 14757 Water quality – Sampling of fish with multi-mesh gillnets. European Standard
20
21 530 (2005) European Committee for Standardization Ref. No. EN 14757:2005.
- 22
23
24
25 531 Crawley M.J. (2002) *Statistical computing. An introduction to data analysis using S-Plus*.
26
27 532 Wiley, Chichester.
- 28
29
30 533 Currie D.J. (1991) Energy and Large-Scale Patterns of Animal- and Plant-Species Richness.
31
32 534 *The American Naturalist*, 137, 27-49.
- 33
34
35 535 De'ath G. & Fabricius K.E. (2000) Classification and regression trees: a powerful yet simple
36
37 536 technique for ecological data analysis. *Ecology*, **81**, 3178–3192.
- 38
39
40 537 Diekmann M., Brämick U., Lemcke R., Mehner T. (2005) Habitat-specific fishing revealed
41
42 538 distinct indicator species in German lowland lake fish communities. *Journal of Applied*
43
44 539 *Ecology*, **42**, 901–909.
- 45
46
47
48 540 Dudgeon D., Arthington A.H., Gessner M.O., Kawabata Z., Knowler D.J., Lévêque C., *et al.*
49
50 541 (2006) Freshwater biodiversity: importance, threats, status and conservation challenges,
51
52 542 *Biological Reviews*, **81**, 163-182.
- 53
54
55
56 543 EEA (2010) Assessing biodiversity in Europe. EEA Technical Report No 5/2010. European
57
58 544 Environment Agency, Copenhagen.
- 59
60

- 1 545 European Commission (2010) *Guidance Document on the Intercalibration Process 2008–*
2
3
4 546 *2011*. Guidance Document No. 14. Implementation Strategy for the Water Framework
5
6 547 Directive (2000/60/EC). Office for Official publications of the European Communities,
7
8 548 Luxembourg.
- 10
11 549 Erős T., Specziár A. & Bíró P (2009) Assessing fish assemblages in reed habitats of a large
12
13 550 shallow lake—A comparison between gillnetting and electric fishing. *Fisheries*
14
15 551 *Research* **96**, 70-76.
- 16
17
18
19 552 Gaston K. J. (2000) Global patterns in biodiversity. *Nature*, **405**, 220–227.
- 20
21
22 553 Gillooly J.F. & Dodson S.I. (2000) Latitudinal patterns in the size distribution and seasonal
23
24 554 dynamics of new world, freshwater cladocerans. *Limnology & Oceanography*, **45**, 22-
25
26 555 30.
- 27
28
29 556 Graham M.H. (2003). Confronting multicollinearity in ecological multiple regression.
30
31 557 *Ecology*, 84, 2809–2815.
- 32
33
34 558 Griffiths D. (2006) Pattern and process in the ecological biogeography of European
35
36 559 freshwater fish. *Journal of Animal Ecology*, **75**, 734-751.
- 37
38
39 560 Gyllström M., Hansson L.A., Jeppesen E., García-Criado F., Gross E., Irvine K., *et al.*
40
41 561 (2005) The role of climate in shaping zooplankton communities of shallow lakes.
42
43 562 *Limnology & Oceanography*, **50**, 2008-2021.
- 44
45
46
47 563 Heino J. (2011) A macroecological perspective of diversity patterns in the freshwater realm
48
49 564 *Freshwater Biology*, **56**, 1703-1722
- 50
51
52
53 565 Heino J. (2013) The importance of metacommunity ecology for environmental assessment
54
55 566 research in the freshwater realm. *Biological Reviews*, **88**, 166-178
56
57
58
59
60

- 1 567 Irz P., Argillier C. & Oberdorff T. (2004) Native and introduced fish species richness in
2
3
4 568 French lakes: local and regional influences. *Global Ecology and Biogeography*, **13**, 335-
5
6 569 344.
7
8
9 570 Irz P., De Bortoli J., Michonneau F., Whittier T.R., Oberdorff T. & Argillier C. (2007).
10
11 571 Controlling for natural variability in assessing the response of fish metrics to
12
13 572 anthropogenic pressures for Northeast U.S.A. lakes. *Aquatic Conservation: Marine and*
14
15 573 *Freshwater Ecosystems*, **18**, 633-646.
16
17
18
19 574 Jennings M.J., Bozek M.A., Hatzenbeler G.R., Emmons E.E. & Staggs M.D. (1999)
20
21 575 Cumulative effects of incremental shoreline habitat modification on fish assemblages in
22
23 576 north temperate lakes. *North American Journal of Fisheries Management*, **19**, 18-27.
24
25
26
27 577 Jeppesen E., Jensen J.P., Søndergaard M., Lauridsen T. & Landkildehus F. (2000) Trophic
28
29 578 structure, species richness and biodiversity in Danish lakes: changes along a phosphorus
30
31 579 gradient. *Freshwater Biology*, **45**, 201-218.
32
33
34 580 Jeppesen E., Meerhoff M., Holmgren K., Gonzalez-Bergonzoni I., Teixeira-de Mello F.,
35
36 581 Declerck A.A.J., *et al.* (2010) Impacts of climate warming on lake fish community
37
38 582 structure and potential effects on ecosystem function. *Hydrobiologia*, **646**, 73-90.
39
40
41
42 583 Johnson N., Revenga C. & Echeverria J. (2001) Managing water for people and nature.
43
44 584 *Science*, **292**, 1071-1072.
45
46
47 585 Kerr J.T., Kharouba H.K. & Currie D.J. (2007) The macroecological contribution to global
48
49 586 change solutions. *Science*, **316**, 1581-1584.
50
51
52 587 La Sorte F.A. (2006) Geographical expansion and increased prevalence of common species in
53
54 588 avian assemblages: implications for large-scale patterns of species richness. *Journal of*
55
56 589 *Biogeography*, **33**, 1183-1191.
57
58
59
60

- 1
2 590 MacArthur R.H. & Wilson E.O. (1967) *The theory of island biogeography*. Princeton
3
4 591 University Press, Princeton, NJ.
5
6
7 592 Magurran A.E. (2004) *Measuring biological diversity*. Blackwell Publishing, Oxford, 256 pp.
8
9
10 593 McCullagh P. & Nelder J.A. (1989) *Generalized linear models*. Chapman and Hall/CRC.
11
12 594 Mehner T., Diekmann M., Brämick U. & Lemcke R. (2005) Composition of fish communities
13
14 595 in German lakes as related to lake morphology, trophic state, shore structure and human
15
16 596 use intensity. *Freshwater Biology*, **50**, 70-85.
17
18
19
20 597 Mehner T., Holmgren K., Lauridsen T.L., Jeppesen E. & Diekmann M. (2007) Lake depth
21
22 598 and geographical position modify lake fish assemblages of the European ‘Central
23
24 599 Plains’ ecoregion. *Freshwater Biology*, **52**, 2285-2297.
25
26
27
28 600 Muniz I.P. (1984) The effects of acidification on Scandinavian freshwater fish fauna.
29
30 601 *Philosophical Transactions of the Royal Society B*, **305**, 517-528.
31
32
33 602 New M., Lister D., Hulme M. & Makin I. (2002) A high resolution data set of surface climate
34
35 603 over global land areas. *Climate Research*, **21**, 1-25.
36
37
38 604 Olin M., Rask M., Ruuhijarvi J., Kurkilahti M., Ala-Opas P. & Ylonen O. (2002) Fish
39
40 605 community structure in mesotrophic and eutrophic lakes of southern Finland: the
41
42 606 relative abundances of percids and cyprinids along a trophic gradient. *Journal of Fish*
43
44 607 *Biology*, **60**, 593-612.
45
46
47
48 608 Pielou E.C. (1969) *An introduction to mathematical ecology*. Wiley-Interscience, New York.
49
50
51 609 Reyjol Y., Hugueny B., Pont D., Bianco P.J., Beier U., Caiola N., *et al.* (2007) Patterns in
52
53 610 species richness and endemism of European freshwater fish. *Global Ecology and*
54
55 611 *Biogeography*, **16**, 65-75.
56
57
58
59
60

- 1 612 Rowan J.S., Carwardine J., Duck R.W., Bragg O.M., Black A.R., Cutler M.E.J., Soutar I. &
2
3
4 613 Boon P.J. (2006) Development of a technique for Lake habitat survey (LHS) with
5
6 614 applications for the European Union Water Framework Directive. *Aquatic*
7
8 615 *Conservation-Marine and Freshwater Ecosystems*, **16**, 637-657.
- 9
10
11 616 Sala O.E., Chapin III F.S., Armesto J.J., Berlow E., Bloomfield J., Dirzo R., *et al.* (2000)
12
13 617 Global biodiversity scenarios for the year 2100. *Science*, **287**, 1770-1774.
- 14
15
16
17 618 Schindler D.E., Geib S.I. & Williams M.R. (2000) Patterns of fish growth along a residential
18
19 619 development gradient in North temperate lakes. *Ecosystems*, **3**, 229-237.
- 20
21
22 620 Tabachnick B.G. & Fidell L.S. (2000) *Using Multivariate Statistics*. Harper Collins, New
23
24 621 York.
- 25
26
27 622 Teixeira-de Mello F., Meerhoff M., Pekcan-Hekim Z. & Jeppesen E. (2009) Littoral fish
28
29 623 community structure and dynamics differ substantially in shallow lakes under
30
31 624 contrasting climates. *Freshwater Biology*, **54**, 1202-1215.
- 32
33
34
35 625 Tonn W.M., Magnuson J.J., Rask M. & Toivonen J. (1990) Intercontinental comparison of
36
37 626 small-lake fish assemblages: The balance between local and regional processes.
38
39 627 *American Naturalist* **136**, 345-375.
- 40
41
42 628 Vamosi J.C. & Vamosi S.M. (2007) Body size, rarity, and phylogenetic community structure:
43
44 629 insights from diving beetle assemblages of Alberta. *Diversity and Distributions* **13**, 1-
45
46 630 10.
- 47
48
49
50 631 Volta P., Oggioni A., Bettinetti R. & Jeppesen E. (2011) Assessing lake typologies and
51
52 632 indicator fish species for Italian natural lakes using past fish richness and assemblages.
53
54 633 *Hydrobiologia*, **671**: 227-240.
- 55
56
57
58
59
60

- 1 634 Vörösmarty C.J., McIntyre P.B., Gessner M.O., Dudgeon D., Prusevich A., Green P., *et al.*
2
3
4 635 (2010) Global threats to human water security and river biodiversity. *Nature*, **467**, 555-
5
6 636 561.
7
8
9 637 Zhao S., Fang J., Peng C., Tang Z. & Piao S. (2006) Patterns of fish species richness in
10
11 638 China's lakes. *Global Ecology and Biogeography*, **15**, 386-394.
12
13
14 639
15
16
17 640
18
19
20 641
21
22
23 642
24
25
26 643
27
28
29 644
30
31
32 645
33
34
35 646
36
37
38 647
39
40
41 648
42
43
44 649
45
46
47 650
48
49
50 651
51
52
53 652
54
55
56 653
57
58
59 654
60

655 Table 1. Fish descriptors and explanatory variables analysed, their minima, means and
 656 maxima. The percentage of lakes for each level of the categorical variables is also shown
 657 (from 1, less pressure to 5, more pressure). n, number of lakes; H_{NPUE} , diversity based on fish
 658 number ; H_{BPUE} , diversity based on fish biomass.

659

	Mean	Minimum	Maximum	Std. deviation	n	
Fish descriptors						
Fish number (number fish net m ⁻² h ⁻¹)	0.09	<0.01	1.69	0.13	1632	
Fish biomass (g fish net m ⁻² h ⁻¹)	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 (µg 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)	36.9	2.0	0.6	0.3	1.3	668

60

1
2 bank modification)

3
4 660
5 661
6 662
7 663
8 664
9 665
10 666
11 667
12 668
13 669
14 670
15 671
16 672
17 673
18 674
19 675
20 676
21 677
22 678
23 679
24 680
25 681
26 682
27 683
28 684
29 685
30 686
31 687
32 688
33 689
34 690
35 691
36 692
37 693
38 694
39 695
40 696
41 697
42 698
43 699
44 700
45 701
46 702
47 703
48 704
49 705
50 706
51
52
53
54
55
56
57
58
59
60

707 Table 2. Correlation matrix of the environmental and anthropogenic pressure variables.
 708 Spearman's r_s values above the diagonal and the corresponding P -values below the diagonal.
 709 Values over 0.7 and variables not included in the detailed regression tree analysis with all
 710 pressures are given in grey background. Lat (Latitude), Long (Longitude), T_{\max} (maximum
 711 temperature), T_{\min} (minimum temperature), T_{mean} (mean temperature), T_{amp} (amplitude of
 712 temperature), Precip (Precipitation), Altit (Altitude), TP (total phosphorus), Z_{\max} (maximum
 713 depth), %agric (percentage of agricultural land cover), %nat (percentage of agricultural land
 714 cover).
 715

	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	--

716
 717
 718
 719
 720
 721
 722
 723
 724
 725
 726

727 Table 3. Results of regression tree analysis (n = 1632 lakes) for each fish assemblage
 728 descriptor. Main variables, thresholds defining each node and percentage of variance
 729 explained are listed. For each node main surrogate variables (i.e. those with maximum
 730 agreement) are shown in brackets (first two main surrogates for the node explaining the
 731 highest variance and the first one for the rest of the nodes). Fish number (NPUE), fish
 732 biomass (BPUE), diversity based on fish number (H_{NPUE}), diversity based on fish biomass
 733 (H_{BPUE}), and body size. TP (total phosphorus), T_{max} (maximum temperature), T_{amp} (amplitude of
 734 temperature), Z_{max} (maximum depth).

735

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	0.68km ²	15.7°C	15.7°C	484.2m	23.7µgL ⁻¹	20.0µgL ⁻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	0.67km ²	13.6°C	16.4°C	15.3°C	6.9m
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	0.31km 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	248.3m	0.67km ²	--	12.4°C	--

1							
2	Variance						
3	explained	4%	3%	3%		2%	--
4							
5	Node 5					(-)Z _{max}	
6		--	--	--	--	(area)	--
7							
8	Threshold	--	--	--	--	14.8m	--
9							
10	Variance						
11	explained					2%	

-
- 14 736
 - 15 737
 - 16 738
 - 17 739
 - 18 740
 - 19 741
 - 20 742
 - 21 743
 - 22 744
 - 23 745
 - 24 746
 - 25 747
 - 26 748
 - 27 749
 - 28 750
 - 29 751
 - 30 752
 - 31 753
 - 32 754
 - 33 755
 - 34 756
 - 35 757
 - 36 758
 - 37 759
 - 38 760
 - 39 761
 - 40 762
 - 41 763
 - 42 764
 - 43 765
 - 44 766
 - 45 767
 - 46 768
 - 47 769
 - 48 770
 - 49 771

772 Table 4. Results of regression tree analysis for each fish assemblage descriptor using a
 773 reduced dataset where lakes were evenly distributed among three latitude and four longitude
 774 categories (n = 272 lakes). The variables defining the first node and their thresholds are listed.
 775 Main surrogate variable is given in brackets. Fish number (NPUE), fish biomass (BPUE),
 776 diversity based on fish number (H_{NPUE}), diversity based on fish biomass (H_{BPUE}), and body
 777 size. TP (total phosphorus), T_{max} (maximum temperature), T_{amp} (amplitude of temperature), Z_{max}
 778 (maximum depth).
 779

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	20.1µgL ⁻¹	17.6µgL ⁻¹

780
781
782
783
784
785
786
787
788
789
790
791
792
793
794
795
796
797

798 Table 5. Results of Generalized Linear Models on the effect of anthropogenic factors on fish
 799 diversity. Each fish descriptor variable was split into two data sets following the first node of
 800 the regression tree analysis (see Table 3). Each data set was tested for one (TP or percentage
 801 of agricultural land cover) or both anthropogenic factors together. The top-ranked models
 802 (lowest AICc) are highlighted in bold. Richness (species number), diversity based on fish
 803 number (H_{NPUE}), diversity based on fish biomass (H_{BPUE}), TP (total phosphorus), %
 804 agriculture (percentage of agricultural land cover).

Variable	data set	Factor	AICc	P value
Richness	small lakes < 0.68 km ²	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 km ²	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	lg TP	902.08	<0.001
> 484.2 m a.s.l.	lg % agriculture	566.88	<0.001
	lg TP		<0.001
	lg % agriculture		<0.001
	lg TP * lg % agriculture		<0.001

806

807

808

809

810

811 **FIGURE LEGENDS**

812

813 Figure 1. Geographical distribution of the 1632 lakes across 11 European countries (black
814 circles) and balanced dataset with 272 lakes (white triangles).

815

816 Figure 2. Regression trees of fish assemblage descriptors for 1632 European lakes. The higher
817 a variable in the tree, the more important it is for differentiating fish assemblage descriptors.

818 Each node of the tree is described by the splitting variable. The longer the line, the higher the
819 variance explained by the splitting variable. Each leaf is labelled with the mean rating and the

820 number of observations in the group (in parentheses). For surrogate variables and explained

821 variance see Table 3. Fish number (NPUE; number fish net m⁻² h⁻¹), fish biomass (BPUE; g

822 fish net m⁻² h⁻¹), diversity based on fish number (H_{NPUE}), diversity based on fish biomass

823 (H_{BPUE}), and body size (BPUE:NPUE ratio; g wet weight). TP (total phosphorus), T_{max}

824 (maximum temperature), T_{amp} (amplitude of temperature), Z_{max} (maximum depth).

825

826 Figure 3. Box-plot showing the abundance of fish (NPUE) in different TP (total phosphorus)

827 classes (µg L⁻¹) for two lake categories defined by the regression tree in Table 3: cold lakes

828 (T_{max} < 15°C) and warm lakes (T_{max} > 15°C). Minimum and maximum number of lakes within

829 box-plots are one and 91, respectively for cold lakes, and 26 and 166, respectively for warm

830 lakes. T_{max} (maximum temperature).

1 831

2
3
4 832 Figure 4. Effects of total phosphorus and agricultural land cover on fish descriptors (see Table

5
6 833 5 for statistical results). Estimated marginal means (Generalized linear models) for each fish

7
8
9 834 descriptor are shown. Fish diversity based on fish number (H_{NPUE}), diversity based on fish

10
11 835 biomass (H_{BPUE}).

12
13 836

14
15
16 837 Figure 5. Scheme showing changes (increase and decrease) for each fish assemblage

17
18 838 descriptor in European lakes. Main variables driving changes in each descriptor are given in

19
20 839 bold.

21
22
23 840

24
25 841

26
27 842

28
29
30 843

31
32 844

33
34 845

35
36
37 846

38
39 847

40
41
42 848

43
44 849

45
46 850

47
48
49
50
51
52
53
54
55
56
57
58
59
60

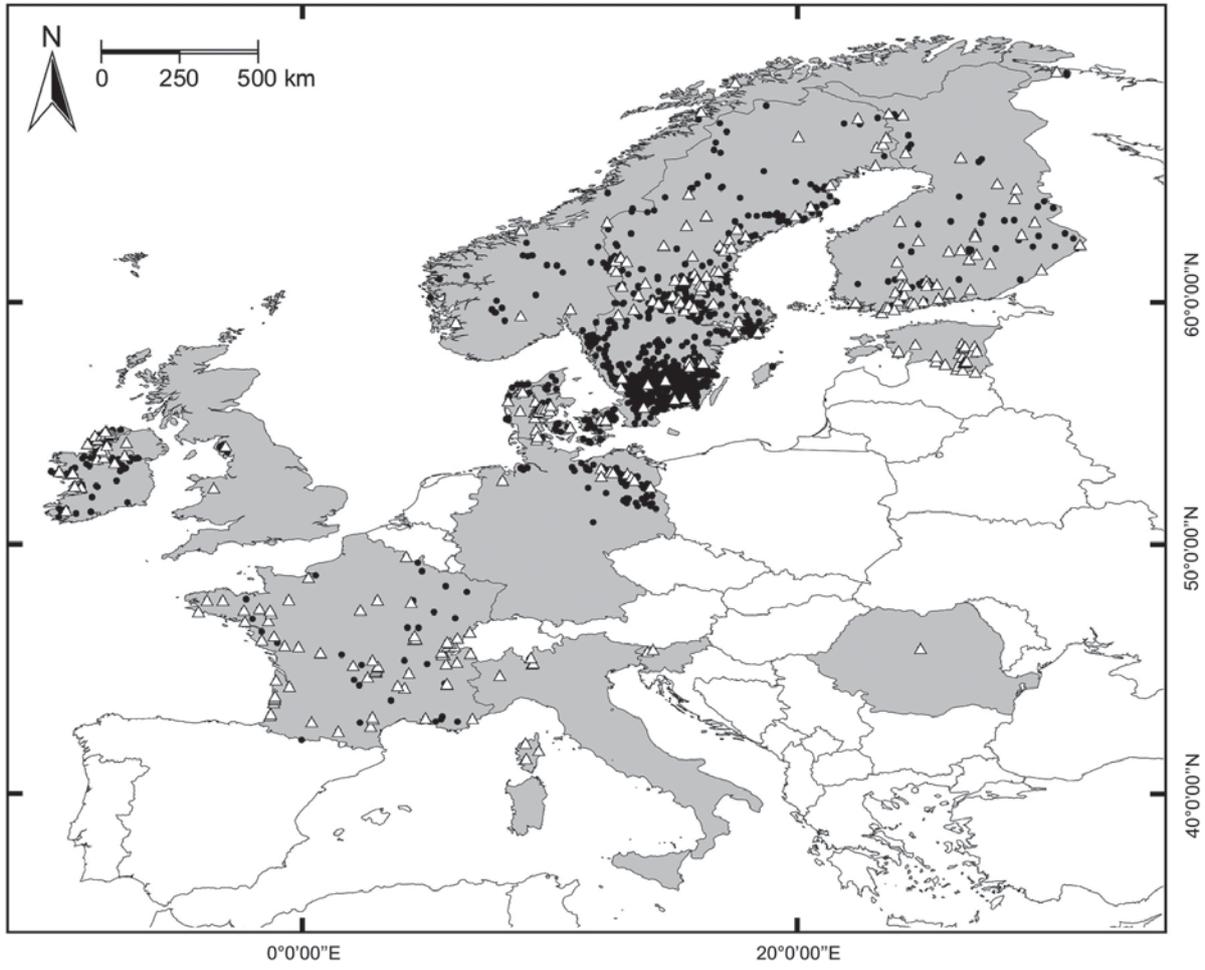
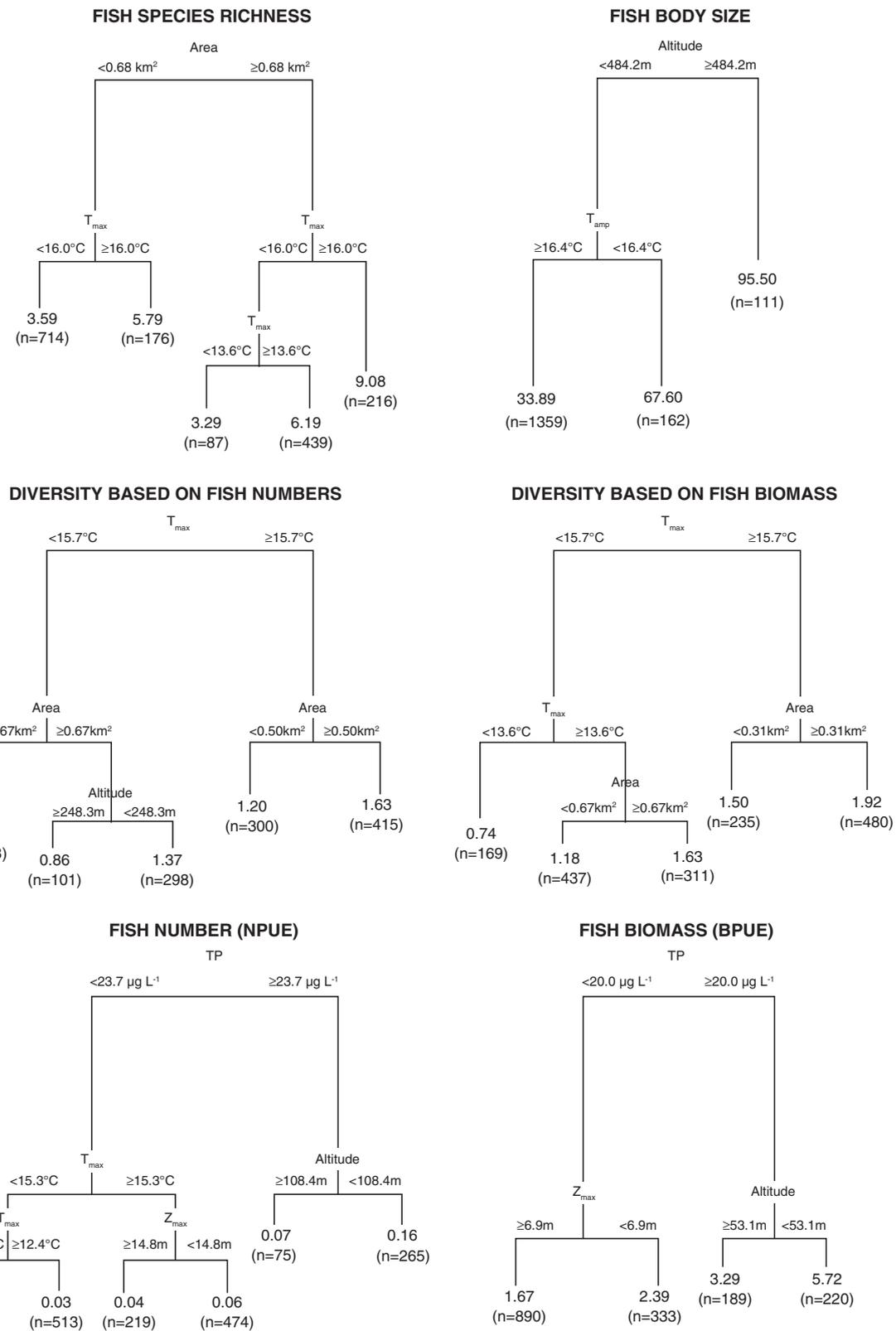


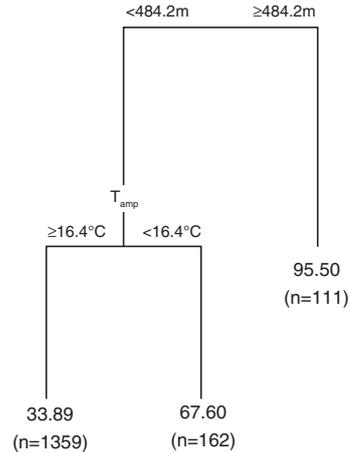
Figure 1

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60



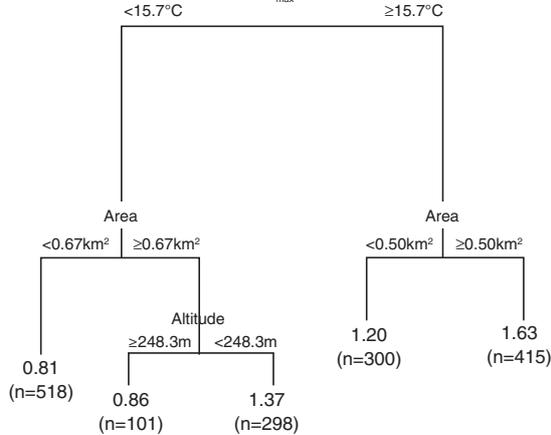
FISH BODY SIZE

Altitude



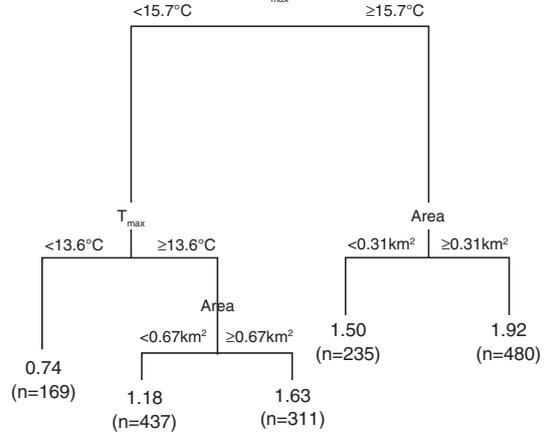
DIVERSITY BASED ON FISH NUMBERS

T_{max}



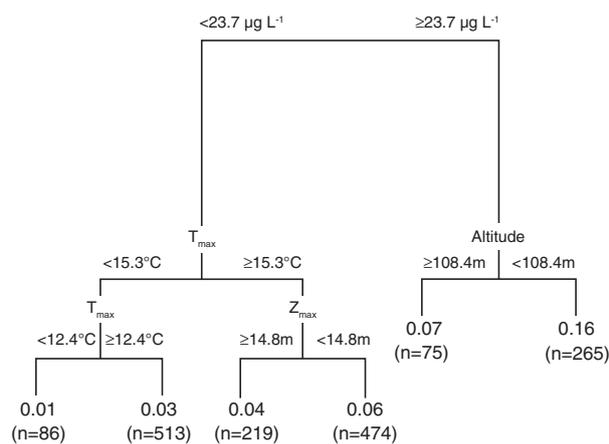
DIVERSITY BASED ON FISH BIOMASS

T_{max}



FISH NUMBER (NPUE)

TP



FISH BIOMASS (BPUE)

TP

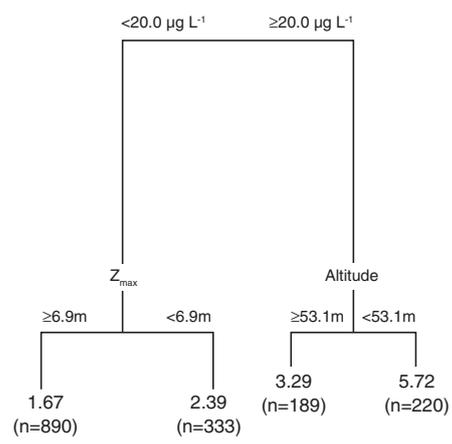


Figure 2

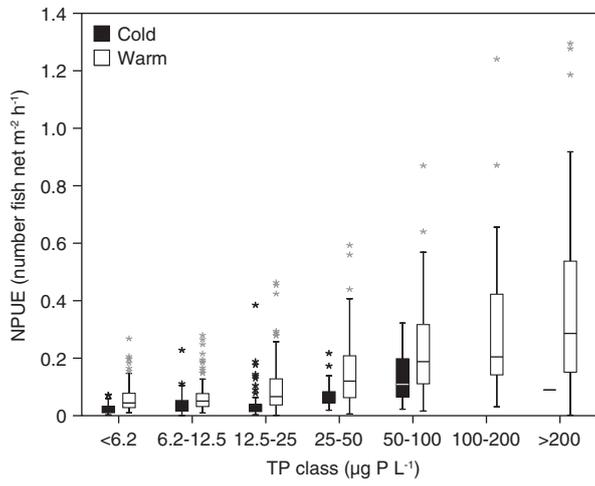


Figure 3

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

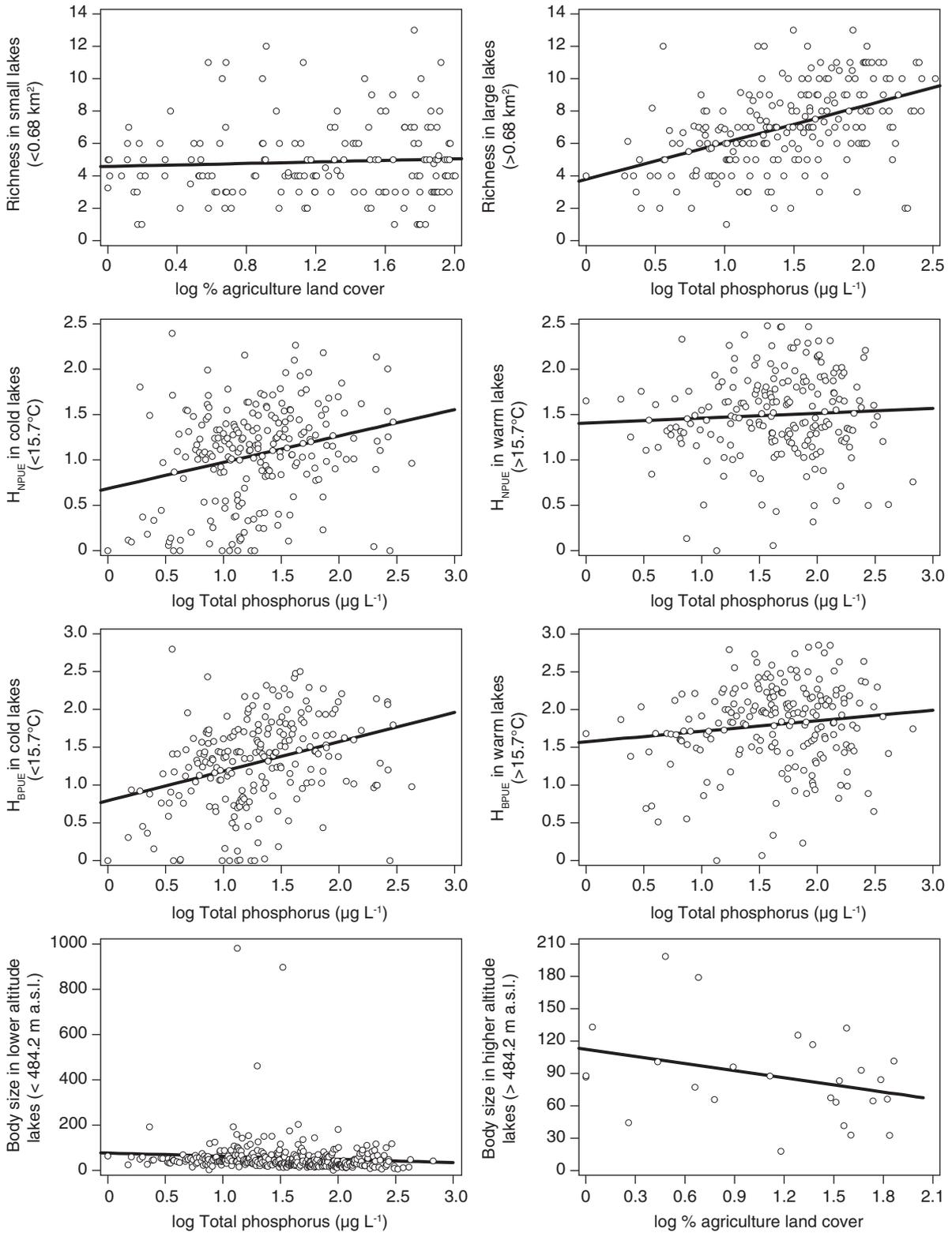


Figure 4

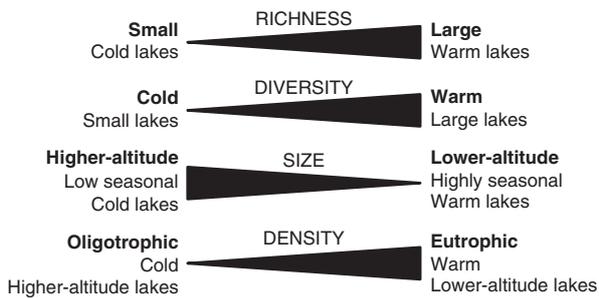
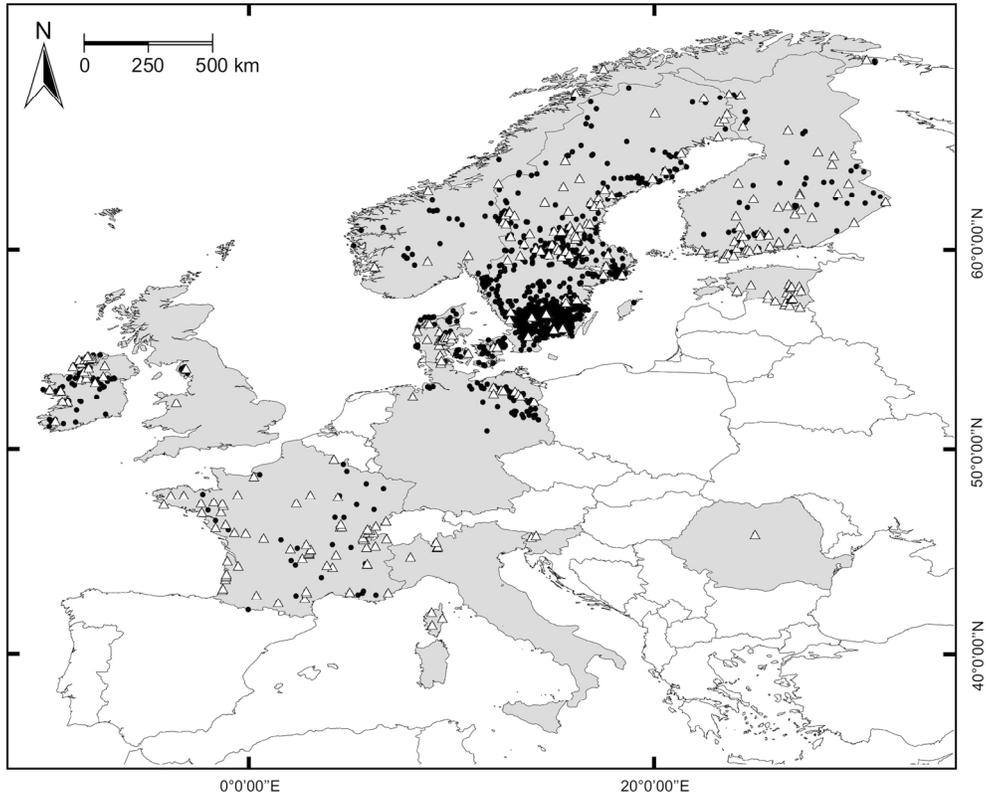


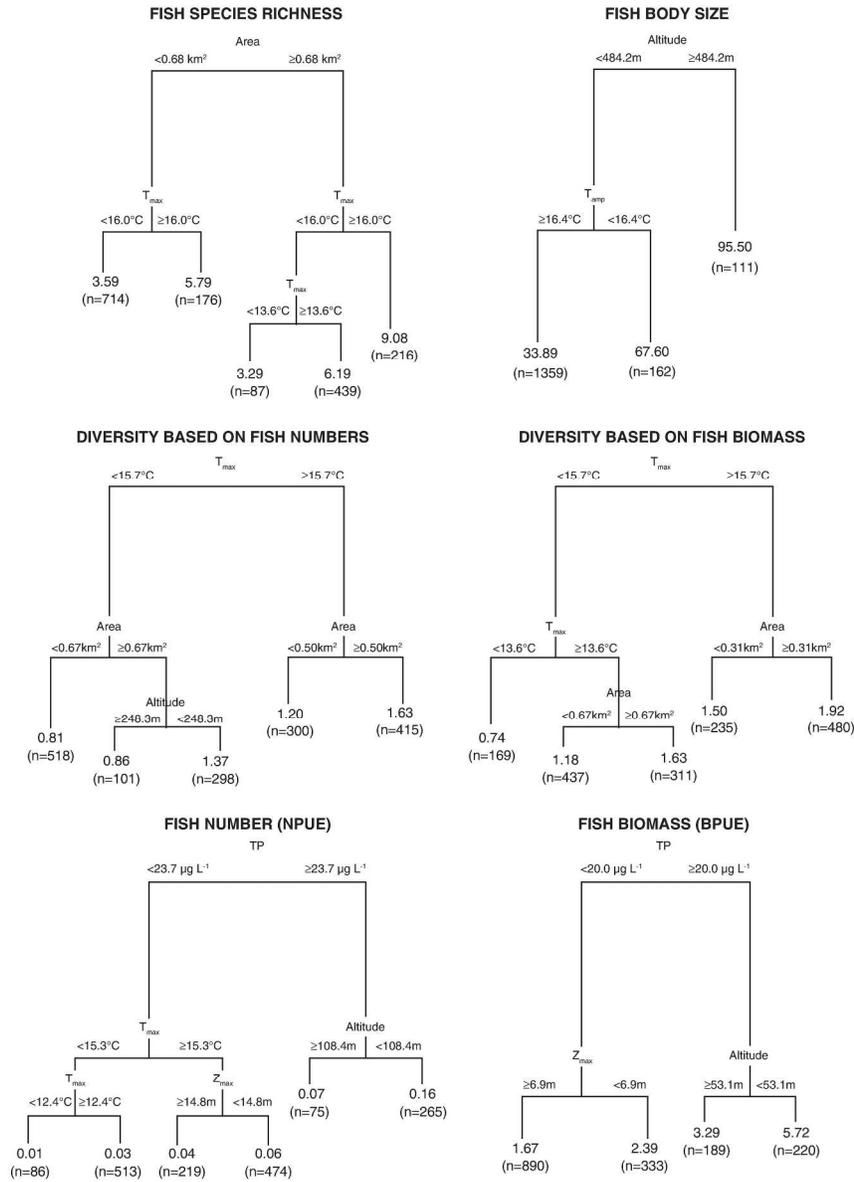
Figure 5



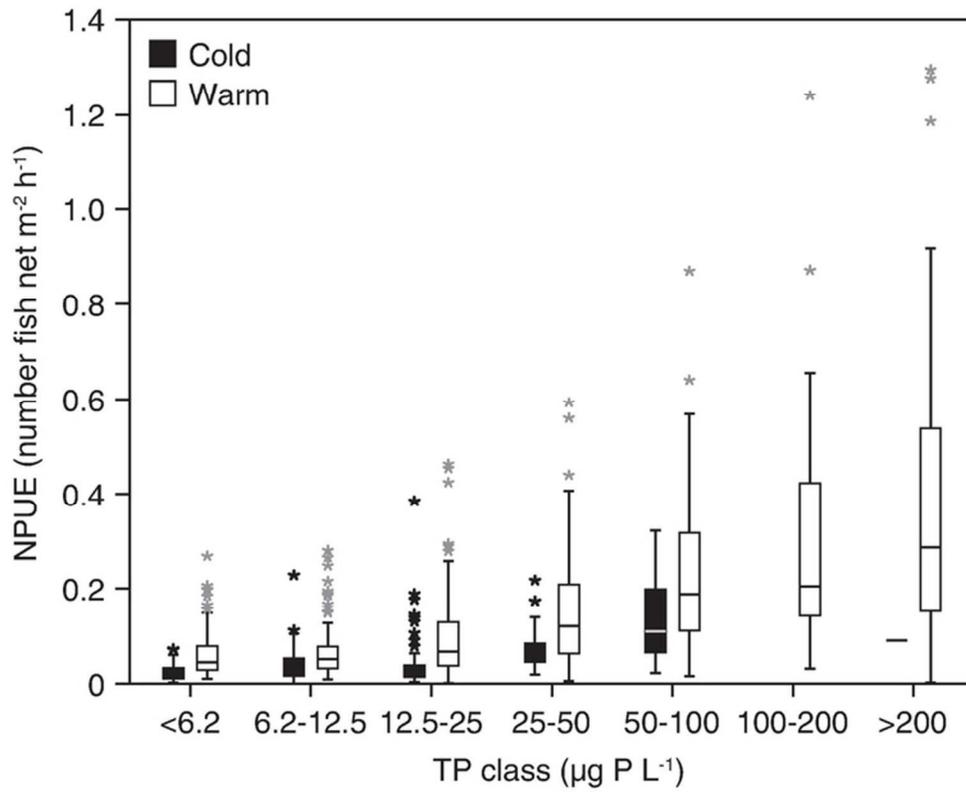
160x129mm (287 x 287 DPI)

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

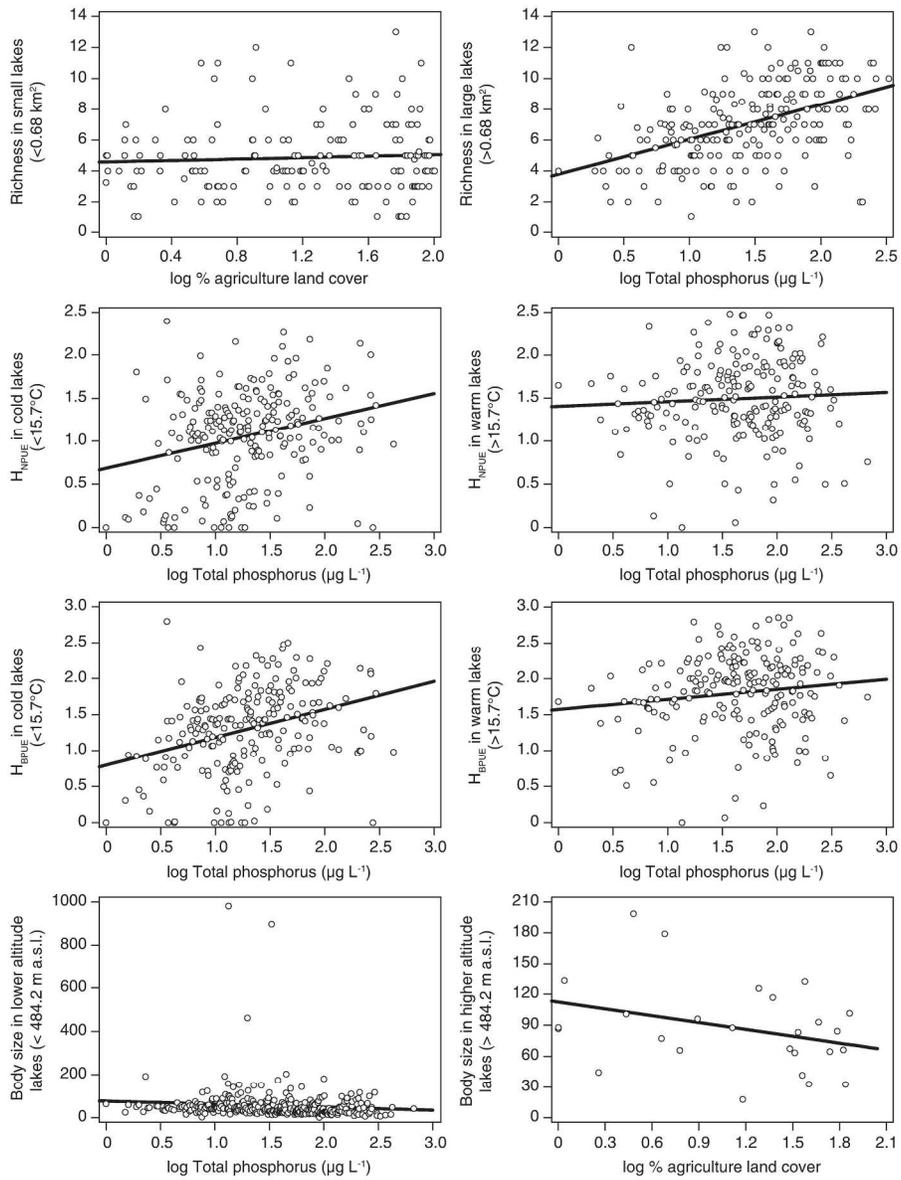


215x290mm (300 x 300 DPI)



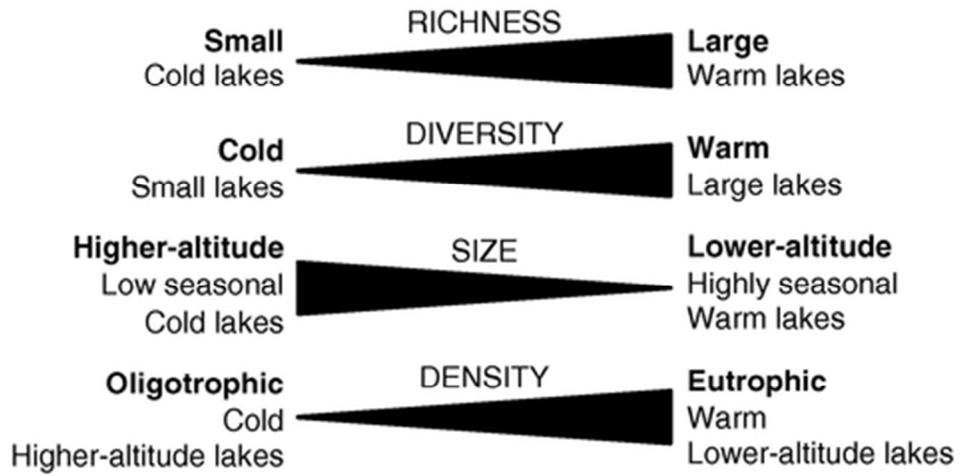
65x54mm (300 x 300 DPI)

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60



210x276mm (300 x 300 DPI)

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60



41x21mm (300 x 300 DPI)