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5 2 **Non-native fish occurrence and biomass in 1943 Western Palearctic lakes and**
6 3 **reservoirs and their abiotic and biotic correlates**
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25 46 **Key words:** invasion biology, lake fish communities, translocated species, exotic species,
26 47 invasion meltdown, trophic similarity

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29 48 **Running title:** Non-native fish species in lakes and reservoirs

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35 51 **Author contributions:** SB and TM conceived of study; CT and TM analysed the major dataset;
36 52 SB, CA, IA, MB, LB, TF, TH, KH, EJ, FK, TK, MR, PV, IJW and TM performed research and
37 53 analysed local data; CT and TM wrote the paper; all authors commented on and approved
38 54 the final manuscript

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Abstract

Invasion of non-native species is considered a major threat to global biodiversity. Here we present a comprehensive overview of the occurrence, richness and biomass contribution of non-native fish species in 1943 standing waterbodies from 14 countries of the Western Palearctic, based on standardised fish catches by multi-mesh gillnetting. We expected strong geographical gradients to emerge in the occurrence of non-natives. We further hypothesised that the contribution by non-natives to the local fish community biomass was correlated with local richness and the trophic level of native and non-native species. Non-native fish species occurred in 304 of 1943 waterbodies (16%). If the average number of occupied waterbodies per country was weighted by number of waterbodies per country, the grand mean occurrence of non-natives in Western Palearctic waterbodies was 10%. Exotic (non-native to the Palearctic) and translocated (non-native only to parts of the Palearctic) species were found in 164 (8.4%) or 235 (12.1%) of the waterbodies, respectively. The occurrence and local richness of non-native fish species increased with temperature, precipitation and lake area and were substantially higher in reservoirs than in natural lakes. High local biomass contributions of non-native species were strongly correlated with low richness of native species and high richness of non-native species, whereas the trophic level of the fish species had only a weak effect. Single non-native species rarely dominated community biomass, but high biomass contributions and thus strong community and ecosystem impacts can be expected if several non-native species accumulate in a waterbody.

76 Introduction

77 Invasion of non-native species is considered a major threat to global biodiversity
78 (Butchart et al., 2010; McGeoch et al., 2010) and has therefore stimulated numerous
79 empirical (e.g., Lowry et al., 2013) and conceptual (Catford et al., 2009; Jeschke, 2014)
80 studies. Among the vertebrates, fishes are the most numerous taxon and their invasion
81 biology is therefore relatively well covered in the scientific literature (reviewed by Copp et
82 al., 2005; Gozlan et al., 2010; Cucherousset and Olden, 2011). For freshwater fishes,
83 continental and global records indicate that several bioregions are particularly threatened by
84 taxonomic homogenisation, i.e. an increased similarity of fish faunas caused by invasion of
85 the same fish species into many regional species pools (Rahel, 2000; Vileger et al., 2011).
86 The Palearctic and Nearctic realms have experienced the most drastic changes in faunal
87 composition relative to former times (Vileger et al., 2011). Homogenisation has been caused
88 primarily by translocation of widespread species native to the realms into previously
89 unoccupied watersheds, whereas invasion of exotic species from outside the realms has
90 occurred less frequently (Leprieur et al., 2009a; Toussaint et al., 2014). Nonetheless, in
91 Southern Europe where natural lakes are rare, dominance of exotic fish species in artificially
92 created lakes (reservoirs) is a widespread phenomenon (Godinho et al., 1998).

93 There is a fundamental discrepancy between the analytical levels in worldwide
94 reports of invasions and studies on the consequences of invasions. Elucidation of the global
95 homogenisation of the freshwater fish fauna and the changes of species pools has been
96 based on presence/absence data of fish species in the major catchments of the world and
97 comparison between historical and recent reports (Vileger et al., 2011). In contrast,
98 understanding the potential impacts of non-native fish species on genetic, individual,
99 population, community and ecosystem levels (reviewed by Cucherousset and Olden, 2011)
100 requires much more comprehensive information than obtained from simple
101 presence/absence records at catchment scale (Fitzgerald et al., 2016). The contribution of
102 non-natives to local fish abundance or biomass (Hansen et al., 2013) and information on the
103 ecological traits of fish species forming the local community and the resulting biotic
104 interactions (Henriksson et al., 2016a) may help to elucidate, which biotic conditions
105 facilitate high biomasses of non-natives and, then, under which conditions strong
106 community and ecosystem effects of non-natives can be expected. Processes related to

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3 107 invasions at local scale are biological resistance or invasion meltdown, and trophic similarity
4 108 (overview in Catford et al., 2009). Biological resistance means that higher richness of native
5 109 species impedes the establishment of non-native species (Elton, 1958). In contrast, invasion
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7 110 meltdown suggests that the establishment of new species makes communities more
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9 111 vulnerable to further invasions (Simberloff and Von Holle, 1999). The success of invasions
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11 112 may also depend on the niche similarity between native and non-native species, based on
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13 113 the assumption that invaders with low overlap to native species along several niche axes
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15 114 may become more easily established (MacArthur and Levins, 1967). However, detailed
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17 115 information about the contribution of non-native species to local community composition
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19 116 and trophic structure is usually limited to single aquatic systems (but see Henriksson et al.,
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21 117 2016b).

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23 118 Valuable information on non-native fish distribution in aquatic systems can be found
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25 119 in multi-national monitoring programs. In Europe, the Water Framework Directive (WFD)
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27 120 (EU, 2000) made monitoring of the ecological quality of large waterbodies mandatory for
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29 121 Member States, and standardised fishing has accordingly been conducted in lakes and
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31 122 reservoirs in many European countries (Argillier et al., 2013; Bruce et al., 2013). Here, we
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33 123 analyse data on the occurrence, richness and contribution to community biomass of non-
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35 124 native fish species in almost 2000 lakes and reservoirs from several countries in the Western
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37 125 Palearctic. The analyses are based on systematic and standardised fishing surveys conducted
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39 126 in all waterbodies during the previous 25 years. We explored the following three
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41 127 hypotheses: 1) Average non-native fish occurrence in single lakes would be lower than that
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43 128 suggested from catchment-scale data, according to which non-natives occur in about 60% of
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45 129 the Palearctic catchments (Villegier et al., 2011). This is because lakes are relatively isolated
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47 130 ecosystems, and fish usually need hydraulic connections for dispersal (Mehner et al., 2014);
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49 131 2) Occurrence probability and richness of non-native fishes would not be equally distributed
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51 132 across the Western Palearctic, but follow geographical gradients. In particular, we expected
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53 133 that energy availability, habitat heterogeneity, human activities and other anthropogenic
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55 134 effects on lakes facilitate the occurrence of non-native fish species (Oberdorff et al., 1995;
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57 135 Garcia-Berthou et al., 2005; Leprieur et al., 2008). This approach provides a more detailed
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59 136 view on the potential determinants of the occurrence and richness of non-natives than that
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137 achievable at catchment scale; 3) Non-natives would have high contributions to community
138 biomass (Hansen et al., 2013). We focused explicitly on the contribution of non-native

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3 139 species to fish biomass in individual lakes, because the potential effects of non-natives on
4 140 community and ecosystem ecology intensify relative to local abundance and biomass (Parker
5 141 et al., 1999; Ricciardi, 2003). Furthermore, we expected higher relative biomasses of
6 142 translocated than exotic species in Western Palearctic lakes (Leprieur et al., 2009a; Toussaint
7 143 et al., 2014), since there is a higher similarity of environmental conditions between source
8 144 and target waterbodies for translocated species than for those exotic fish species, which
9 145 have their natural origin in other realms of the world. We further evaluated whether the
10 146 richness of native or non-native species (reflecting biotic resistance or invasion meltdown
11 147 hypotheses, respectively) predicted high biomass contributions (Henriksson et al., 2016a;
12 148 Henriksson et al., 2016c) and whether trophic similarity, as expressed by trophic levels of
13 149 non-native and native fish species (Sagouis et al., 2015; Fitzgerald et al., 2016), was a useful
14 150 predictor of high biomass contributions of non-native species in certain lakes.
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152 **Methods**

153 Fish data

154 We used a fish database including approximately 1900 European natural lakes and
155 reservoirs (artificial lakes created by impounding rivers) compiled for the purpose of
156 intercalibration of national evaluation systems from 12 European countries for the Water
157 Framework Directive 2000/60/EC (Argillier et al., 2013; Brucet et al., 2013), supplemented
158 with data from Spanish reservoirs (provided by Confederacion Hidrografica del Ebro, Spain)
159 and data from 46 lakes located in Western and Central Turkey (Boll et al., 2016). Thus, the
160 final database encompassed 1807 natural lakes and 136 reservoirs (total n=1943) from 14
161 countries (Mehner et al., 2017). Ireland was treated at whole island level covering the
162 political jurisdictions of the Republic of Ireland and Northern Ireland of U.K., with the
163 remainder of the U.K. presented as its mainland component. The location of the lakes
164 covered a latitudinal gradient between 36.70 and 69.70°N and a longitudinal gradient
165 between -10.18 and 36.16°E. Lake area ranged between 0.001 and 116 km², with about 700
166 lakes having an area <0.5 km² (50 ha). Lake maximum depth ranged between 0.2 and 190 m
167 (Appendix S1 in Supporting Information).

168 The selected lakes were sampled at least once, primarily between June and
169 September during the years 1993 to 2012. Nordic benthic multi-mesh gillnets were used,

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3 170 which is in accordance with the recommendations made by the European Committee for
4 171 Standardization (CEN, 2015). Benthic gillnets (12 mesh sizes between 5.0 and 55 mm in a
5 172 geometric series, each panel being 2.5 m long and 1.5 m high) were set in a random
6 173 stratified sampling design across all depth layers in the benthic habitat, following the
7 174 recommendations of the standard (CEN, 2015). Nets were generally set for 12 to 16 hours
8 175 overnight. The total fishing effort per lake (number of benthic nets) was standardised by lake
9 176 area and maximum depth according to CEN 14757 (CEN, 2015). Pelagic gillnets (11 mesh
10 177 sizes as above, but excluding 5.0 mm) were set in several of the lakes with a maximum depth
11 178 of at least 6 m and covered the entire depth range from the surface to the bottom. These
12 179 nets varied in height between 1.5 and 6.0 m. Fish biomass was expressed as biomass per unit
13 180 effort (BPUE, wet mass of fish), standardised with respect to number of gillnets set per night
14 181 per lake ($\text{g fish net}^{-1} \text{night}^{-1}$). Pelagic 3 m high gillnets had a net area about twice as large as
15 182 that of the benthic nets and were therefore counted as two nets, and 6 m high pelagic nets
16 183 were counted as four nets. In several deeper lakes, sampling using pelagic gillnets was not
17 184 undertaken; however, the contribution of catches in pelagic gillnets to the lake-wide species
18 185 richness and fish biomass is relatively low (Diekmann et al., 2005; Emmrich et al., 2012;
19 186 Alexander et al., 2015). Consequently, we assume that the deviations from the systematic
20 187 fishing protocols with respect to the pelagic catches have not significantly biased the
21 188 analyses. The sampling of the German lakes was split into a spring and an autumn campaign
22 189 (Mehner et al., 2005). However, the results were subsequently summed to allow comparison
23 190 with the other samplings. If several fishing campaigns were carried out in a lake, we used
24 191 only the data from the most recent one.

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41 192 Each individual fish caught was determined to species level. All species were
42 193 classified as native or non-native per country (except for the island of Ireland and the UK
43 194 mainland, for which information was based on the two physical islands) by local researchers
44 195 and experts based on information from national databases (Appendix S2 in Supporting
45 196 Information). A species was considered native if it was present in the country before the
46 197 16th century (the beginning of globalization, DAISIE, 2009), following the definition by van
47 198 den Veer and Nentwig (2015). This definition of native status is comparable with the
48 199 reference to the historical pre-industrial situation used in earlier studies (Villeger et al.,
49 200 2011). Non-native species are either truly exotic to the Western Palearctic or have been
50 201 translocated among European countries since the 16th century (Leprieur et al., 2009a;

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3 202 Toussaint et al., 2014). Translocations between watersheds or lakes within the same country
4 203 are therefore not covered, but this level of detail is usually not available in the local records
5 204 (but see Henriksson et al., 2016b). Consequently, in our analyses we assume that a species
6 205 native in a country is native in all waterbodies of this country. We calculated the proportion
7 206 (%) of sampled Palearctic waterbodies in which non-native fish species occurred, and
8 207 similarly calculated the %occurrence of non-natives in waterbodies per country. To take into
9 208 account uneven sampling efforts in the countries, we weighted the percentage of
10 209 waterbodies with non-natives per country by the number of waterbodies $>0.1 \text{ km}^2$ per
11 210 country (Messenger et al., 2016) and calculated a grand mean proportion of occurrence of
12 211 non-natives in Western Palearctic waterbodies.

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15 212 Species richness was calculated as the total number of fish species collected in a lake
16 213 and was split into richness of native and non-native species. For further calculations, we
17 214 separately calculated the richness of translocated and exotic species per lake. In the same
18 215 way, total BPUE was split into BPUE of native and non-native fishes, and BPUE was
19 216 separately calculated for translocated and exotic species. For use in several subsequent
20 217 analyses, we further calculated %richness and %biomass (%BPUE) of translocated and exotic
21 218 species. We also assessed the trophic levels (TL) of fish, defined as mean trophic level of all
22 219 food items +1 (e.g., Pauly and Christensen, 1995), using the arithmetic mean from all single
23 220 estimates available per species in FishBase (www.fishbase.org). We calculated the average
24 221 TL of native, translocated and exotic species, weighted by the biomass proportions per
25 222 species within the species groups.

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28 223 For a species-specific analysis of the contribution of non-native species to the fish
29 224 biomass per lake, we aggregated the %biomass per non-native species for all lakes in which a
30 225 single non-native species was found. From these lists, we calculated the number of lakes
31 226 occupied by this species, as well as the arithmetic mean, the median and the maximum
32 227 %biomass per lake for each species.

33 228 34 229 Predictor variables

35 230 We selected six geographical and lake variables known to influence fish community
36 231 composition (Brucet et al., 2013). Information on lake elevation (m), lake area (km^2) and lake
37 232 maximum depth (m) was extracted from the national databases. Annual precipitation (mm)
38 233 and annual average air temperature ($^{\circ}\text{C}$) were obtained from the climate CRU model as

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3 234 based on geographical coordinates and elevation of the lake (New et al., 2002). Air
4 235 temperature was used as a proxy of epilimnetic lake temperature (Livingstone and Lotter,
5 236 1998). This was based on the assumption that air temperature presumably provided a better
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7 237 integrated value than snapshot lake temperature data obtained during irregular surveys.
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9 238 Furthermore, we defined the binary variable 'lake type', which was either 'natural lake' or
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11 239 'impoundment reservoir', assuming that the artificially created reservoirs reflect strongly
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13 240 modified ecosystems under substantial anthropogenic pressure.

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15 241 Latitude (northings of UTM projection) was strongly correlated with average air
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17 242 temperature (Pearson's $r=-0.88$, $P<0.0001$) and we therefore did not consider latitude
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19 243 separately in subsequent calculations. The year of sampling was a positive predictor of the
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21 244 richness of non-native species (Pearson's $r=0.32$, $P<0.0001$). However, there was also a
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23 245 strong interaction between latitude and year of sampling, as many lakes in central and
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25 246 southern Europe have been sampled primarily after 2004. These lakes had higher numbers
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27 247 of non-native fish species and the richness of non-native species thus seems to have
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29 248 increased over time as an indirect consequence of geographical bias in sampling activity over
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31 250 the years. However, for the 1501 lakes >620000 northing (Sweden, Finland, Norway), there
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33 251 was no correlation between year of sampling and number of non-native fish species per lake
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35 252 (Pearson's $r=-0.007$, $P=0.77$). Therefore, we did not include year of sampling as predictor.

35 253 Statistical analysis

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37 254 To evaluate the potential abiotic predictors of occurrence or richness of non-native
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39 255 species in the lakes, multiple linear regressions are conventionally used. However, non-
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41 256 native fish species were found in only 306 of the 1943 surveyed lakes, creating a non-normal
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43 257 distribution of occurrences and richness (Shapiro–Wilk test, $P<0.001$) and a high frequency
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45 258 of zero observations (84%). To account for this 'zero-inflation', we used two-component
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47 259 hurdle models (Zeileis et al., 2008), consisting of a hurdle component modelling zero vs.
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49 260 larger counts (presence–absence model) using a Bernoulli (i.e. binomial) distribution and a
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51 261 count component in which all zeroes were excluded and counts >0 were fitted with a
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53 262 truncated Poisson distribution. Elevation, precipitation, annual average temperature, \log_{10}
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55 263 lake area, \log_{10} lake maximum depth and lake type were the predictors (Irz et al., 2004a;
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57 264 Field et al., 2009). We first tested whether the interactions between lake type and
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59 265 precipitation or lake type and average temperature were significant and removed non-

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3 266 significant interaction terms from the initial models. Then, we reduced the initial models
4 267 backwardly in a step-wise manner (see Zeileis et al., 2008) and the best and most
5 268 parsimonious models were selected based on the log-likelihood test. To check for spatial
6 269 autocorrelation in the residuals of the final hurdle models, we computed Moran's I
7 270 correlograms over a range of distances (km) between the lakes (Dormann et al., 2007).

11 271 The database was dominated by Swedish lakes (n=1145, 58.9% of total; Figs. 1 & 2),
12 272 and this geographical bias might influence the results as Swedish lakes have a relatively low
13 273 species richness and a low number of non-native fish species. Furthermore, lake trophic
14 274 state has been shown to modify the composition of fish assemblages in lakes (Mehner et al.,
15 275 2005; Bruçet et al., 2013); however, information on trophic state was not available for all the
16 276 1943 lakes in the database. Accordingly, we split the lakes into three spatial subsamples
17 277 (regions) based on latitude and four spatial subsamples based on longitude (see
18 278 geographical distribution of the subset, Appendix S3 in Supporting Information) and checked
19 279 for which lakes per subsample information on annual mean total phosphorus concentration
20 280 (TP, mg m⁻³) were available. From the lake list with TP information, we subsampled about
21 281 15% of the lakes from each sub-region using the 'select a random sample' function in the
22 282 IBM SPSS 20 software (see Bruçet et al., 2013 for a similar procedure). Next, we re-ran
23 283 hurdle models using this unbiased data subset (in total 302 lakes) and TP as an
24 284 approximation of lake trophic state as an additional, seventh predictor.

25 285 To evaluate whether translocated species contribute more to local richness and
26 286 biomass than exotic species, both absolute richness and BPUE could not be used because
27 287 local richness and biomass respond to confounding variables, such as lake size and
28 288 productivity. Hence, richness or BPUE of translocated fish in one lake and richness or BPUE
29 289 of exotic species in another lake cannot be compared directly without a correction for locally
30 290 differing variables. To facilitate comparison, we compared the slopes of the reduced major
31 291 axis (RMA) regression of the relative share of translocated species in local richness
32 292 (%richness) with the relative share of translocated species in local biomass (%BPUE) and the
33 293 similarly calculated RMA slope for exotic species. We applied RMA, a.k.a. least products
34 294 regression, because both the predictor and the response variables were measured with error
35 295 (Legendre and Legendre, 2012). Significance tests of RMA regressions were based on 999
36 296 permutations. The results of RMA can be interpreted in the same way as those based on
37 297 ordinary least squares linear regression models; hence, an RMA slope=1 would indicate that

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3 298 local %biomass increases proportionally with %richness. However, we expected an RMA
4 299 slope substantially larger than 1 and steeper for translocated than for exotic species, which
5 300 would support the hypothesis that translocated species contribute more to local biomass
6 301 than exotic species.

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9 302 We further sought to explain which biotic predictors facilitated a strong local biomass
10 303 contribution of exotic or translocated species. To achieve normally distributed data, we
11 304 calculated $\text{logit}(\% \text{biomass})$ for non-natives per lake ($n=306$), separately calculated as
12 305 %biomass of translocated and exotic species. Because $\text{logit}(1.0)$ is not explained, we
13 306 replaced 1.0 with 0.999 in all cases where non-native species locally reached 100% biomass.
14 307 We assumed that high biomass contributions can be explained by local processes such as
15 308 biotic resistance, invasion meltdown and niche similarity and thus can be predicted by four
16 309 variables characterising the local community composition (richness of native and
17 310 translocated or exotic species per lake) and food sources (mean trophic level of native and
18 311 translocated or exotic species per lake). Thus, we ran multiple regressions, with the
19 312 $\text{logit}(\% \text{biomass})$ of translocated or exotic species as the dependent variable, and the four
20 313 biotic predictors. Model complexity was reduced in a step-wise manner based on minimising
21 314 the Akaike Information Criterion (AIC), and the two 'best' models were compared using
22 315 ANOVA. To facilitate comparison of effect sizes, we calculated standardised coefficients for
23 316 the significant predictors.

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26 317 Data manipulation and analyses of linear regression, reduced major axis regression,
27 318 hurdle models and Moran's I were performed in 'R' version 3.2.2 (Development Core Team,
28 319 2015) using the packages dplyr (Wickham and Francois, 2016), reshape2 (Wickham, 2007),
29 320 lmodel2 (Legendre, 2014), pscl (Zeileis et al., 2008), car (Fox and Weisberg, 2011) and letsR,
30 321 respectively (Vilela and Villalobos, 2015).

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34 323 **Results**

35
36 324 The 1943 lakes and reservoirs in the 14 countries hosted 119 fish species, ecotypes of
37 325 salmonids and hybrids (Appendix S2). Among these, 15 species were considered exotic for all
38 326 countries, while another 22 species were considered translocated within the Western
39 327 Palearctic (Appendix S2). Non-native fish species were caught in a total of 304 (15.6%) of the
40 328 1943 waterbodies (184 natural lakes, 120 reservoirs). Translocated species occurred in 235
41 329 (12.1%) of the waterbodies, whereas exotic species occurred in 164 (8.4%) of the

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3 330 waterbodies. Translocated and exotic species were found together in 95 waterbodies (4.9%).
4 331 The relative proportion of waterbodies per country in which translocated species were
5 332 found was highly variable (Fig. 1). UK mainland, Sweden, Finland, Norway and Estonia had
6 333 very low proportions of lakes with non-natives, whereas non-native fish species occurred in
7 334 all sampled waterbodies in Italy, Slovenia and Portugal (Fig. 1). If the average proportion of
8 335 waterbodies with non-native fish species per country was weighted with the number of
9 336 waterbodies >0.1 km² per country, the grand mean relative occurrence across the
10 337 waterbodies in the countries of the Western Palearctic was 10.3%, caused by the low
11 338 proportion of non-natives in waterbodies of the countries with the highest number of lakes
12 339 (Sweden, Norway and Finland). Turkey was the country with the highest proportion of
13 340 waterbodies with exotic species, whereas France, Italy, Portugal and Spain had the highest
14 341 proportion with a mix of translocated and exotic species. The Irish lakes (island) were
15 342 dominated by translocated species (Fig. 1).

16 343 The %richness and %biomass of non-natives in the 1943 waterbodies varied between
17 344 0 and 100% with arithmetic mean values of 6.5% and 6.2%, respectively (Fig. 2). Non-native
18 345 %richness was lower than 5% in waterbodies from the UK mainland, Sweden, Norway,
19 346 Germany, Finland, Estonia and Denmark (Fig. 2a). Turkey, Italy, Portugal, Spain and Island of
20 347 Ireland were the locations with the highest %richness of non-native fish (>50%, Fig. 2a).
21 348 Turkey, Spain, Ireland and Slovenia showed biomass contributions of non-native fishes >50%
22 349 in many of the waterbodies (Fig. 2b).

23 350 The median species-specific contribution of non-native fishes to the total fish
24 351 biomass per lake was <15% for the four most frequently occurring exotic species (*Lepomis*
25 352 *gibbosus*, *Ameiurus melas*, *Oncorhynchus mykiss*, *Micropterus salmoides*; Table 1). In
26 353 contrast, the median species-specific contribution to the total fish biomass per lake was
27 354 >30% for the translocated *Rutilus rutilus* and *Perca fluviatilis* (Table 1). However, the most
28 355 frequently occurring translocated species were *Sander lucioperca* and *Cyprinus carpio* whose
29 356 median %biomass contributions were <10% (Table 1).

30 357 The presence-absence step of the hurdle model (binomial with logit link) for richness
31 358 indicated that the probability of non-native fish presence was positively related to annual
32 359 average temperatures, precipitation and elevation, and was higher in reservoirs than in
33 360 natural lakes (Table 2). These predictors as well as lake area (positive effect) also contributed
34 361 to the probability of occurrence when considering translocated and exotic species separately

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3 362 (Table 2). For translocated species, the probability of occurrence in response to increasing
4 363 temperature was higher for reservoirs than for lakes (see significant interaction terms, Table
5 364 2). The count part of the hurdle models indicated that richness of translocated species
6 365 increased with area, while richness of exotic species increased with temperature (Table 2).
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8 366 The Moran's I correlograms of residuals of the hurdle models for richness of non-native,
9 367 translocated and exotic species revealed no substantial spatial autocorrelation in the final
10 368 models (Appendix S4 in Supporting Information).

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13 369 Additional hurdle models were run using a geographically unbiased data subset with
14 370 TP information available (i.e. subsampling 302 lakes, Appendix S3) and including TP as an
15 371 additional predictor. The main predictors of occurrence and richness of non-native species
16 372 (annual precipitation, lake area, average temperature; Appendix S5 in Supporting
17 373 Information) were essentially similar to those obtained for the complete dataset (1943 lakes,
18 374 Table 2), suggesting that the strong dominance of Swedish lakes in the entire dataset did not
19 375 affect the main conclusions. The concentration of TP was a weakly negative predictor of the
20 376 richness of translocated species but was not included in the models for the sum of non-
21 377 native or the exotic species (Appendix S5).

22 378 The RMA regression between %richness and %biomass of translocated species was
23 379 significant (Fig. 3a; $R^2=0.77$, $n=235$, $P=0.001$), with a slope estimate slightly higher than 1
24 380 (1.25, 95% CI: [1.16, 1.34]). The RMA regression of %richness with %biomass of exotic
25 381 species had a substantially steeper slope (Fig. 3b; $R^2=0.47$, $n=164$, $P=0.001$, slope=1.58 [1.35,
26 382 1.88]).

27 383 The multiple regression for $\text{logit}(\% \text{biomass})$ of translocated species with four biotic
28 384 predictors testing invasion meltdown, biotic resistance and trophic similarity hypotheses was
29 385 significant (adj. $R^2=0.49$, $F_{3,191}=63.4$, $P<0.0001$). There were three significant predictors
30 386 (richness of translocated species, standardised coefficient =0.57, $t=10.6$, $P<0.0001$, Fig. 4a;
31 387 richness of native species, standardised coefficient =-0.31, $t=-5.4$, $P<0.0001$, Fig. 4b; trophic
32 388 level of translocated species, standardised coefficient =0.11, $t=2.0$, $P=0.044$, Fig. 4c). The
33 389 multiple regression for $\text{logit}(\% \text{biomass})$ of exotic species with the same set of predictors was
34 390 likewise significant, but with a low proportion of predicted variance (adj. $R^2=0.112$,
35 391 $F_{2,156}=11.0$, $P<0.0001$), and had only two significant predictors (richness of exotic species,
36 392 standardised coefficient =0.23, $t=3.0$, $P=0.003$, Fig. 5a; richness of native species,
37 393 standardised coefficient =-0.27, $t=-3.7$, $P=0.0003$, Fig. 5b).

394

395 **Discussion**

396 We demonstrate that the occurrence of non-native fish species in the sampled
397 Western Palearctic lakes and reservoirs is overall low, but there are geographical hotspots
398 (e.g., Southern Europe) where non-native species occur frequently. High average
399 temperatures, high precipitation, large ecosystem size and artificially created lakes (i.e.,
400 reservoirs) are correlated with the occurrence of non-native fish species. However, the
401 majority of non-native species belong to species translocated among European catchments,
402 whereas true exotic species from outside the Western Palearctic occurred in only 8% of the
403 sampled lakes. Our data suggest that exotic species may contribute slightly over-
404 proportionally to local biomass compared with translocated species. However, there were
405 strong positive relationships between %biomass of non-natives and richness of non-natives
406 and strong negative relationships between %biomass of non-natives and richness of natives,
407 suggesting that the local biomass contribution of non-natives increases primarily with the
408 arrival of new non-native species and is high at low native richness. The spread of non-native
409 species across European and Turkish waterbodies seems to be assisted strongly by human
410 interventions, such as creation of reservoirs and subsequent intentional stocking of species
411 for fisheries purposes.

412 The data presented are based on monitoring surveys primarily conducted to evaluate
413 the ecological integrity of lakes (EU, 2000) and have been derived by standardised fish
414 biomass estimates in each lake. Therefore, they provide local occurrences and biomasses of
415 non-native species in the waterbodies in contrast to the presence/absence data used in an
416 earlier global analysis (Villegger et al., 2011) as the latter were extracted from literature
417 reports at the entire catchment scale. We found non-natives in about 16% of the sampled
418 waterbodies, but this number is biased by the strong contribution of Swedish lakes to the
419 entire dataset. If the average occurrence per country was weighted by the number of
420 waterbodies per country, about 10% of waterbodies were occupied by non-natives, and this
421 number is substantially lower than the estimate that about 60% of Palearctic catchments
422 would be occupied by non-native fish species (Villegger et al., 2011). We have sampled fish
423 only in 14 European countries, and therefore the average occurrence of non-natives may
424 potentially increase by inclusion of data from the other 24 European countries. However,

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3 425 from the about 80,000 waterbodies $>0.1 \text{ km}^2$ in Europe except Russia (Messenger et al.,
4 426 2016), 62,000 waterbodies are located in the 14 countries from which we have obtained
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6 427 samples. Therefore, it is unlikely that the weighted average occurrence would change
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8 428 substantially by inclusion of waterbodies from countries so far not covered. Furthermore,
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10 429 the list of frequently occurring translocated and exotic species in the sampled waterbodies is
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12 430 similar to the non-native species documented at the catchment scale (Toussaint et al., 2016).
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14 431 Consequently, we conclude that the lower occurrence of non-native species in lakes and
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16 432 reservoirs of the Western Palearctic reflects the hydraulically less connected nature of
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18 433 standing waterbodies in comparison with river catchments. Nevertheless, the detailed
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20 434 information obtained by standardised sampling can be used as justification for intensified
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22 435 observation and management, in particular for waterbodies with mixed communities of
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24 436 native and non-native fish species (Britton et al., 2008). However, so far practical
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26 437 recommendations for such management are limited (Leprieur et al., 2009b), in particular
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28 438 with respect to potential interactions among the effects of multiple stressors in aquatic
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30 439 ecosystems in addition to the occurrence of non-natives (Ormerod et al., 2010).

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32 440 The presence of non-native fish species was positively related to precipitation and
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34 441 temperature and accordingly higher in the southern and western parts of the Palearctic than
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36 442 in the northern areas. Furthermore, lake area and artificial origin of the waterbody also
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38 443 facilitated a higher occurrence of non-natives. Climatic similarity between the native and the
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40 444 receiving regions is considered an essential requirement for successful invasions (Ficetola et
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42 445 al., 2007; Gallien et al., 2010), particularly for translocated species since these have been
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44 446 moved over shorter geographical distances within the Western Palearctic, often between
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46 447 neighbouring watersheds. However, the significant effect of precipitation and temperature
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48 448 as major drivers of invasions throughout the world has been highlighted (e.g., Field et al.,
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50 449 2009; Feld et al., 2016); thus, energy availability (approximated by high temperature and
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52 450 precipitation) in the receiving habitat may be particularly important, also for the occurrence
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54 451 of exotic species having their origin in warmer realms in Asia or North America. The high
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56 452 contribution of non-native fish species to richness and biomass in lakes and reservoirs in
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58 453 southern Europe and Turkey seems to support this general trend (Godinho et al., 1998). In
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60 454 contrast, the absence of native species and often 100% biomass of non-native species in
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456 some lakes on the island of Ireland may be explained by the biogeographical isolation of
islands, which in general are more susceptible to invasion (Drake and Mooney, 1989). Finally,

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3 457 the fact that large lakes are more likely candidates to host non-native fish species could be
4 458 attributed to a larger spatial heterogeneity, i.e. larger lakes generally host more fish species
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6 459 than smaller ones (Brucet et al., 2013).
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9 460 Our results also showed that increased lake productivity (using TP concentration as a
10 461 proxy, data on which were only available for a subset of lakes) did not predict the presence
11 462 or richness of non-native fish species. The richness (and hence indirectly also the biomass
12 463 contribution) of translocated species was even negatively correlated with TP in this subset.
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14 464 Many translocations have presumably been conducted for fisheries purposes, and several
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16 465 species of importance for commercial or recreational fisheries belong to the Salmonidae
17 466 (Tammi et al., 2003) and Percidae families, which thrive better in lakes of lower productivity
18 467 (Persson et al., 1991; Mehner et al., 2005). Hence, lakes exposed to high human fisheries or
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20 468 angling activities are not necessarily those with the highest TP concentrations. Our results
21 469 confirm that eutrophication has a relatively minor role in shaping biodiversity patterns of
22 470 European fish assemblages in lakes compared with the strong effect by broad-scale climatic
23 471 drivers (Brucet et al., 2013). In contrast to low occurrence of non-natives in natural lakes,
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25 472 120 of the 136 reservoirs hosted non-native fish species. Non-native species are favoured in
26 473 reservoirs because the hydrology and temperature are substantially altered when rivers and
27 474 streams are impounded, and many native fishes often cannot cope with these changes
28 475 (Moyle and Light, 1996; Irz et al., 2004b). Furthermore, in many Southern regions, reservoirs
29 476 do not have native lacustrine systems to provide fauna colonizers. Accordingly, non-native
30 477 species in these reservoirs are often introduced to satisfy anglers and fisheries demands
31 478 because the original riverine fish fauna disappears when rivers are dammed (Argillier et al.,
32 479 2002). In addition, fish stocking is frequently conducted in order to balance the
33 480 consequences of water level fluctuations, which may affect native fish population dynamics
34 481 (Kahl et al., 2008).
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47 482 The information on the biomasses of non-native fish species offered additional
48 483 insight into the composition of lake fish communities. As indicated by the slope of the
49 484 reduced major axis regression, translocated and in particular exotic species seem to reach
50 485 slightly higher relative biomasses in the local communities than reflected by their relative
51 486 shares of local richness. For example, the biomass of non-native fish species was close to
52 487 100% in some lakes, despite that these species represented only 60-70% of the local
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3 488 richness. These results support a recent study in which the abundance distributions of native
4 489 and non-native aquatic species were compared across numerous lakes or rivers (Hansen et
5 490 al., 2013). Both native and non-native species occurred in low densities in most of the
6 491 sampling sites (i.e., exhibited right-skewed abundance distributions), but non-native species
7 492 generally reached significantly higher densities than native species (Hansen et al., 2013). The
8 493 high biomass contributions of non-native species in several locations support the overall
9 494 hypothesis that invasive species often perform better in their new range (Parker et al., 2013)
10 495 due to the novel ecological and evolutionary dynamics in the introduced locations. Evidence
11 496 of high biomass or abundance contributions of non-natives despite lower contribution to
12 497 richness in single lakes is of great importance for biodiversity management in these
13 498 waterbodies, since the ecological impact of invasive species is positively correlated with their
14 499 abundance (Parker et al., 1999; Ricciardi, 2003). However, in the majority of lakes occupied
15 500 by non-natives, the biomass contributions of exotic species did not exceed 15%, whereas
16 501 higher local biomass contributions of non-natives were found primarily by translocated
17 502 common species, such as *Perca fluviatilis* and *Rutilus rutilus*.

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30 503 The local richness of native or non-native fish species were the strongest predictors
31 504 of the %biomass of both translocated and exotic species. The highest biomass contributions
32 505 of non-natives tended to occur in waterbodies with low numbers of natives and already high
33 506 numbers of non-natives. This pattern supports the invasion meltdown hypothesis,
34 507 suggesting that successful invaders have negative effects on resistance, i.e. that positive
35 508 feedback makes the success of each subsequent invasion or introduction more likely
36 509 (Simberloff and Von Holle, 1999). In turn, the negative correlation between %biomass of
37 510 non-natives and local richness of native fish species may reflect some biotic resistance in the
38 511 sense that a high diversity of native fish species prevents the biomass dominance of
39 512 invaders. A recent meta-analysis of biotic resistance mechanisms suggested that
40 513 consumptive resistance was much stronger than competitive resistance, at least in
41 514 freshwater ecosystems (Alofs and Jackson, 2014). This would mean that the feeding modes
42 515 and trophic levels of native and non-native species are important for the invasion as stated
43 516 by the trophic similarity hypothesis. However, we found no evidence that the TL of native or
44 517 non-native fish species modified the %biomass of exotic species and only a weak positive
45 518 contribution of the mean TL of translocated species to %biomass of translocated species in
46 519 the waterbodies was calculated. Among the most frequently translocated fishes, many

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3 520 species are piscivores (*Sander lucioperca*, *Esox lucius*, *Perca fluviatilis*, *Silurus glanis*),
4 521 supporting the idea that certain lakes have received a high load from human-assisted
5 522 translocations (Garcia-Berthou et al., 2005), most likely for fisheries purposes. Strong
6 523 piscivory may reduce the biomass of prey species, and the %biomass of translocated
7 524 piscivores may therefore reach higher relative levels than if translocated species were
8 525 omnivores. However, overall, there was surprisingly little evidence that feeding interactions
9 526 and trophic similarity between native and non-native species contributed to the biomass
10 527 dominance of non-native fish species.

17 528 **Conclusions**

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20 529 In general, our results showed that the large majority of lakes in the Western
21 530 Palearctic sampled for this study do not yet host exotic fish species, in particular those in
22 531 northern Europe. This result in part contrasts the broad-scale distribution of non-natives
23 532 assessed from their presence in the major river catchments. However, the Iberian Peninsula,
24 533 parts of France and Italy, Turkey and Ireland are geographical hotspots where non-native fish
25 534 species occur in almost every lake and reservoir. Translocation of species between the major
26 535 watersheds seems to be the dominant mechanism behind the increasing number of non-
27 536 native fish species in lakes, and it is certainly an important reason for the high richness of
28 537 non-natives in reservoirs. Translocations between neighbouring lakes might be even more
29 538 frequent but could not be evaluated here due to absence of data. Therefore, the local
30 539 richness of translocated (but not exotic) species may be underestimated. While large-scale
31 540 climatic drivers are primary determinants of fish species richness and community
32 541 composition, local species richness of natives and non-natives may determine the local
33 542 biomass contribution of non-natives and hence predict the strength of community and
34 543 ecosystem effects exerted by non-native species. Large-scale monitoring programs, for
35 544 example the European Water Framework Directive, may help to generate the data needed
36 545 to evaluate the status of lakes and reservoirs with respect to the richness of non-native
37 546 species. In contrast, the biomass contributions of non-natives were strongly correlated with
38 547 richness contributions, suggesting that local presence/absence records of non-natives alone
39 548 can already strongly support large-scale biodiversity management at moderate costs. The
40 549 occurrence of a fish community including a mix of native and non-native fish species calls for
41 550 the development of management plans that are much more detailed than those existing

551 today in a cooperation between water managers and conservationists (see for example
552 <http://easin.jrc.ec.europa.eu>).

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567 **List of brief titles of items in the supplementary material**

568 Appendix S1: Overview on abiotic, geographical and trophic predictors for the 1943 Western
569 Palearctic lakes and reservoirs.

570 Appendix S2: List of 119 fish species, ecological forms and hybrids caught in the 1943
571 Western Palearctic lakes and reservoirs and their country-specific status.

572 Appendix S3: Geographical map showing the location of the subset of 302 lakes with
573 information on total phosphorus concentration.

574 Appendix S4: Moran's I correlograms of residuals across geographical distance (km) for the
575 Hurdle models of species richness predicted by six abiotic correlates.

576 Appendix S5: Results of the Hurdle models predicting total richness of non-native
577 (translocated + exotic) species in a geographically stratified subset of 302 European lakes

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771 Table 1: Arithmetic mean, median and maximum %biomass per lake and number of Western
 772 Palearctic waterbodies (from a total of n=1943) in which 15 exotic and 22 translocated fish
 773 species occurred.

% Biomass per lake	mean	median	maximum	Number of lakes
Exotic species				
<i>Lepomis gibbosus</i>	1.2%	0.3%	10.8%	70
<i>Ameiurus melas</i>	15.4%	14.5%	43.2%	38
<i>Oncorhynchus mykiss</i>	17.1%	9.7%	89.4%	38
<i>Micropterus salmoides</i>	3.3%	1.2%	40.7%	28
<i>Carassius gibelio</i>	27.3%	13.0%	93.2%	20
<i>Salvelinus fontinalis</i>	2.5%	2.0%	6.1%	10
<i>Hypophthalmichthys molitrix</i>	30.1%	9.1%	86.0%	7
<i>Pseudorasbora parva</i>	16.3%	7.0%	63.5%	6
<i>Gambusia holbrooki</i>	14.2%	8.0%	37.1%	6
<i>Salvelinus namaycush</i>	0.3%	0.3%	0.6%	4
<i>Coregonus peled</i>	46.9%	48.9%	72.0%	3
<i>Hypophthalmichthys nobilis</i>	7.1%	7.1%	7.7%	2
<i>Carassius auratus</i>	7.8%	7.8%	8.2%	2
<i>Gambusia affinis</i>	<0.01%	<0.01%	<0.01%	1
<i>Coptodon zillii</i>	5.9%	5.9%	5.9%	1
Translocated species				
<i>Sander lucioperca</i>	12.3%	9.5%	51.6%	122
<i>Cyprinus carpio</i>	20.5%	8.1%	100.0%	65
<i>Perca fluviatilis</i>	42.5%	34.8%	100.0%	62
<i>Esox lucius</i>	10.4%	8.0%	43.8%	53
<i>Rutilus rutilus</i>	34.7%	38.5%	87.1%	48
<i>Scardinius erythrophthalmus</i>	23.1%	15.5%	97.2%	32
Hybrids cyprinid	16.8%	15.6%	45.3%	28
<i>Abramis brama</i>	14.1%	9.0%	69.7%	27
<i>Silurus glanis</i>	2.3%	1.3%	10.1%	25
<i>Alburnus alburnus</i>	9.0%	4.1%	26.3%	10
<i>Phoxinus phoxinus</i>	3.3%	1.4%	19.6%	9
<i>Gobio gobio</i>	0.3%	0.1%	0.7%	7
<i>Tinca tinca</i>	8.4%	2.7%	31.1%	5
<i>Carassius carassius</i>	2.6%	2.7%	4.9%	4
<i>Leucaspis delineatus</i>	0.5%	<0.01%	1.4%	3
<i>Blicca bjoerkna</i>	24.6%	24.6%	48.8%	2
<i>Coregonus</i> sp	2.4%	2.4%	4.1%	2
<i>Gymnocephalus cernua</i>	2.6%	2.6%	3.0%	2
<i>Rhodeus amarus</i>	<0.01%	<0.01%	<0.01%	2
<i>Salvelinus umbla</i>	28.4%	28.4%	28.4%	1
<i>Squalius cephalus</i>	3.6%	3.6%	3.6%	1

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2
3 776 Table 2: Results of the Hurdle models (coefficient estimates \pm standard error SE, z-statistics)
4 777 predicting total richness of non-native (sum of translocated and exotic) species and richness
5 778 of translocated and exotic fish species in 1943 European lakes and reservoirs. Elevation (m
6 a.s.l), area=lake area (km²), Precip=annual precipitation (mm year⁻¹), ave_temp=mean
7 779 annual air temperature (°C), LakeTypeN=lake type Natural lake (vs. LakeTypeA=reservoir).
8 780 Ave_temp:LakeType reflects significant interaction terms.
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Sum of non-native species

Count model coefficients (truncated Poisson with log link)

	Estimate	SE	z-value	Pr(> z)
(Intercept)	-0.2749	0.2772	-0.992	0.3213
Elevation	-0.0004	0.0002	-2.721	0.0065
log10(area)	0.3273	0.0621	5.266	<0.0001
Precip	0.0004	0.0001	3.789	0.0001
ave_temp	0.0651	0.0177	3.673	0.0002

Zero hurdle model coefficients (binomial with logit link)

	Estimate	SE	z-value	Pr(> z)
(Intercept)	-6.1776	0.5967	-10.353	<0.0001
Elevation	0.0007	0.0003	2.194	0.0282
Precip	0.0016	0.0002	7.577	<0.0001
ave_temp	0.6739	0.0462	14.506	<0.0001
Lake_TypeN	-2.1682	0.3249	-6.673	<0.0001

Translocated species

Count model coefficients (truncated Poisson with log link)

	Estimate	SE	z-value	Pr(> z)
(Intercept)	0.5248	0.0609	8.621	<0.0001
log10(area)	0.2946	0.0763	3.861	0.0001

Zero hurdle model coefficients (binomial with logit link)

	Estimate	SE	z-value	Pr(> z)
(Intercept)	-8.1908	0.4875	-16.801	<0.0001
log10(area)	0.4323	0.1444	2.993	0.0027
Precip	0.0021	0.0002	9.008	<0.0001
ave_temp:Lake_TypeA	0.7496	0.0456	16.431	<0.0001
ave_temp:Lake_TypeN	0.5548	0.0444	12.503	<0.0001

Exotic species

Count model coefficients (truncated Poisson with log link)

	Estimate	SE	z-value	Pr(> z)
(Intercept)	-2.1281	0.4591	-4.635	<0.0001
ave_temp	0.1596	0.0348	4.585	<0.0001

Zero hurdle model coefficients (binomial with logit link)

	Estimate	SE	z-value	Pr(> z)
(Intercept)	-5.7204	0.5884	-9.721	<0.0001

Ecosystems

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Elevation	0.0017	0.0003	5.333	<0.0001
Precip	0.0006	0.0002	2.638	0.0080
ave_temp	0.4745	0.0416	11.400	<0.0001
Lake_TypeN	-1.5868	0.2538	-6.252	<0.0001

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3 785 **Figure legends:**

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5 786 Fig. 1: Relative occurrence (%) of translocated and exotic fish species in waterbodies of
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7 787 the 14 countries of the Western Palearctic. The numbers above the bars indicate the number
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9 788 of waterbodies sampled per country.

10 789 Fig. 2: Maps showing the location of the 1943 lakes and reservoirs sampled in the
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12 790 Western Palearctic and a) the relative richness (%) or b) the relative biomass (%BPUE) of
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14 791 non-native fish species in the waterbodies.

15 792 Fig. 3: Reduced major axis regressions (regression line and 95% confidence band)
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17 793 between proportion (%) of fish in richness (x-axis) and proportion (%) of fish in biomass (y-
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19 794 axis) for a) 22 translocated fish species and b) 15 exotic fish species in Western Palearctic
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21 795 lakes and reservoirs. The stippled 1:1 line indicates where %richness would equal %biomass.

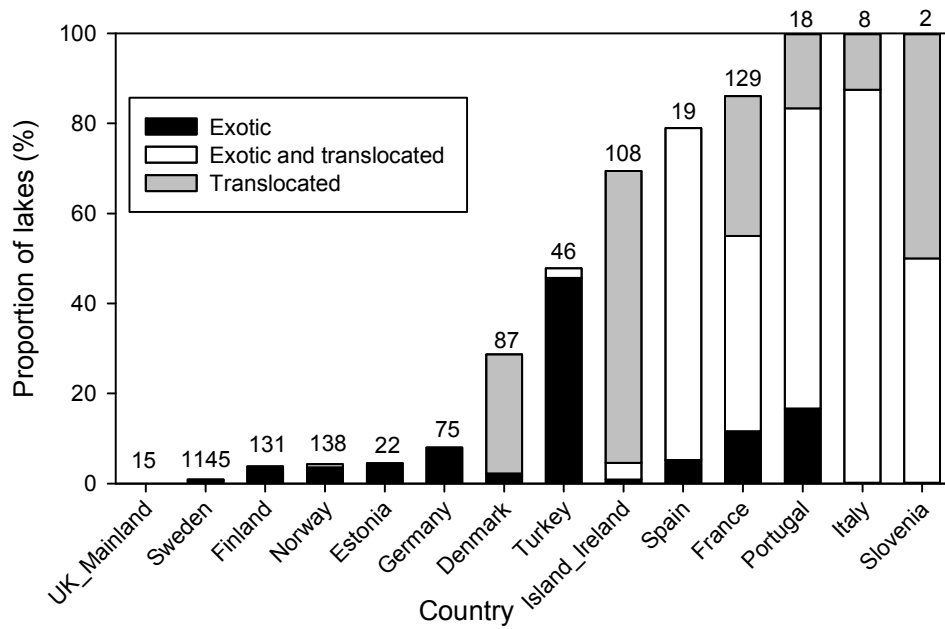
22 796 Fig. 4: Partial residual plots of significant predictors in a multiple linear regression
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24 797 between logit(%biomass) and biotic predictors for translocated species, predicted by a) the
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26 798 local richness of native species, b) the local richness of translocated species, and c) the mean
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28 799 trophic level (TL) of translocated species in Western Palearctic lakes and reservoirs.

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30 800 Fig. 5: Partial residual plots of significant predictors in a multiple linear regression
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32 801 between logit(%biomass) and biotic predictors for exotic species, predicted by a) the local
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34 802 richness of native species, b) the local richness of exotic species in Western Palearctic lakes
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36 803 and reservoirs.

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806 Fig. 1: Relative occurrence (%) of translocated and exotic fish species in waterbodies of
 807 the 14 countries of the Western Palearctic. The numbers above the bars indicate the number
 808 of waterbodies sampled per country.



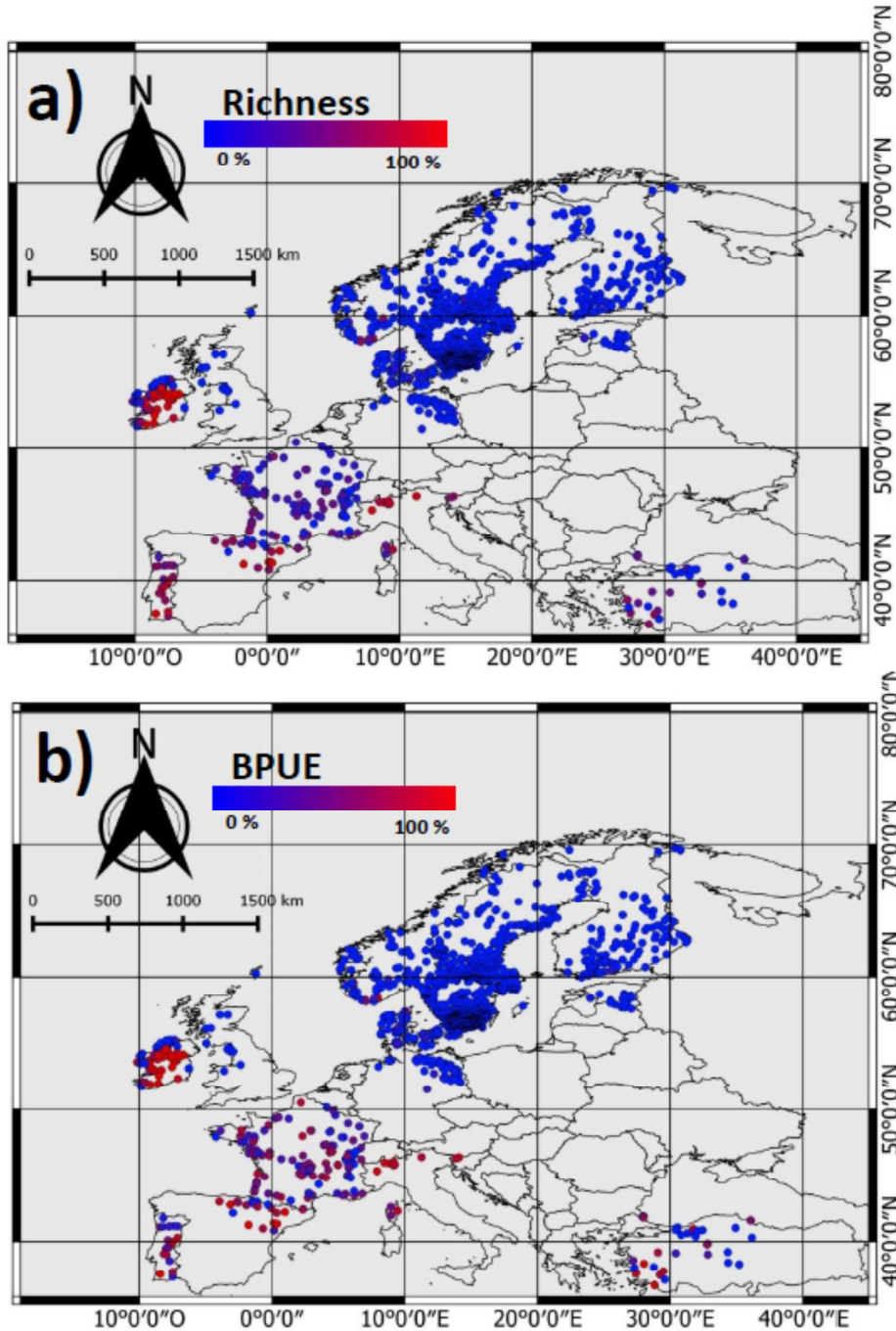
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3 814 Fig. 2: Maps showing the location of the 1943 lakes and reservoirs sampled in the
4 815 Western Palearctic and a) the relative richness (%) or b) the relative biomass (%BPUE) of
5 816 non-native fish species in the waterbodies.
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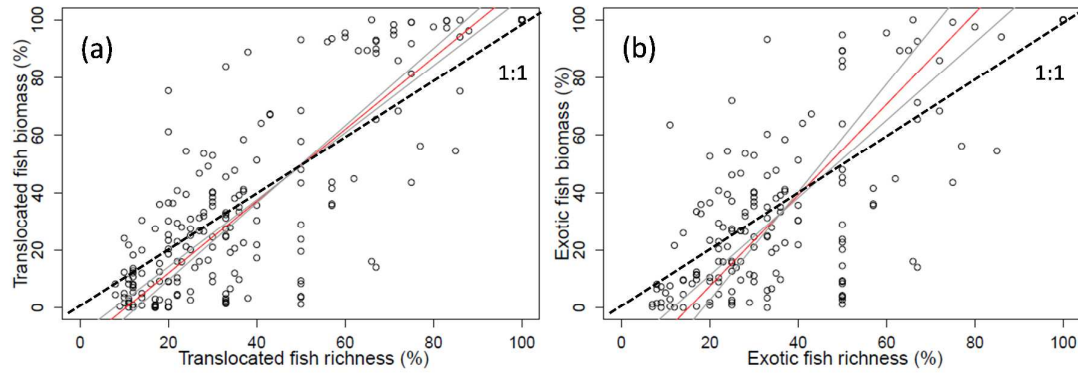
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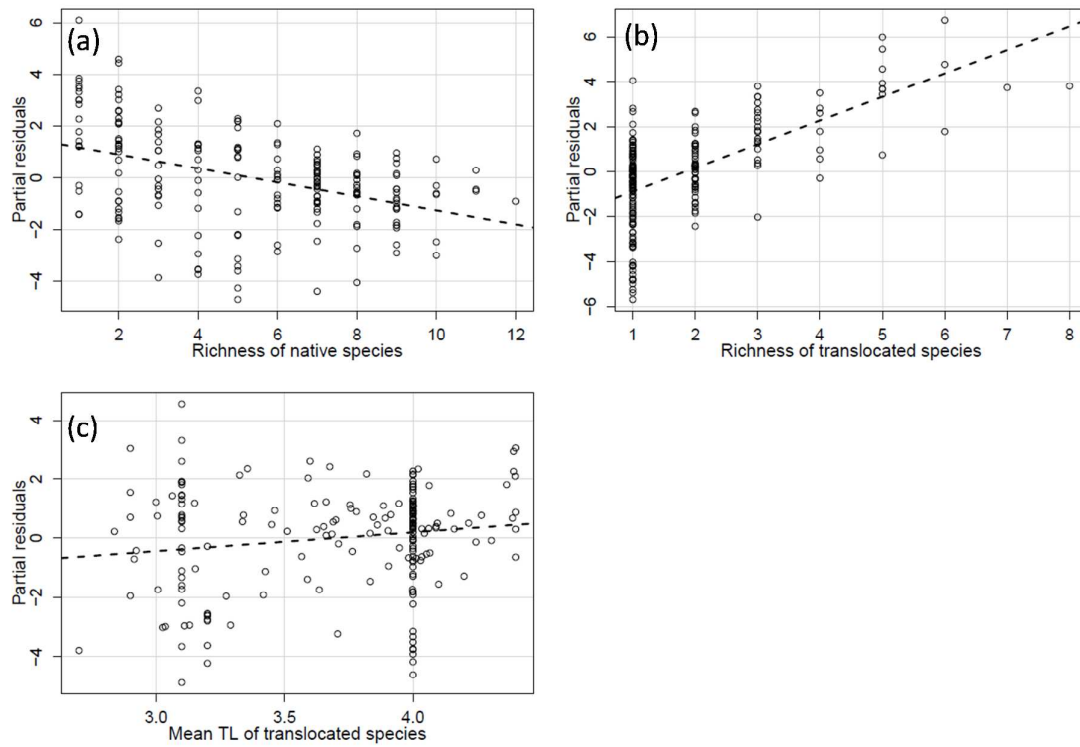
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3 819 Fig. 3: Reduced major axis regressions (regression line and 95% confidence band) between
4 820 proportion (%) of fish in richness (x-axis) and proportion (%) of fish in biomass (y-axis) for a)
5 821 22 translocated fish species and b) 15 exotic fish species in Western Palearctic lakes and
6 822 reservoirs. The stippled 1:1 line indicates where %richness would equal %biomass.
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3 826 Fig. 4: Partial residual plots of significant predictors in a multiple linear regression
4 827 between logit(%biomass) and biotic predictors for translocated species, predicted by a) the
5 828 local richness of native species, b) the local richness of translocated species, and c) the mean
6 829 trophic level (TL) of translocated species in Western Palearctic lakes and reservoirs.

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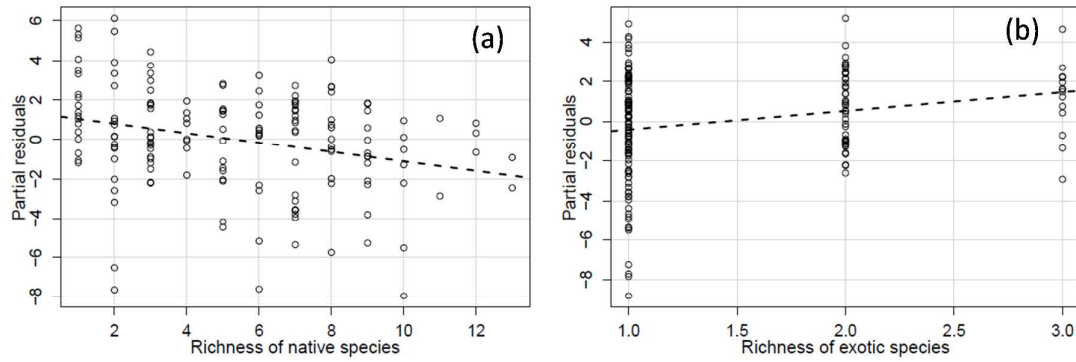
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3 834 Fig. 5: Partial residual plots of significant predictors in a multiple linear regression
4 835 between logit(%biomass) and biotic predictors for exotic species, predicted by a) the local
5 836 richness of native species, b) the local richness of exotic species in Western Palearctic lakes
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7 837 and reservoirs.
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841 **Supplementary Material**

842 Appendix S1: Overview on the mean, median and range of geographical, abiotic and trophic
 843 predictors in the 1943 Western Palearctic lakes and reservoirs.

	Mean	Median	Std. deviation	Minimum	Maximum	<i>n</i>
Location						
Latitude (°)	56.7223	57.2603	5.5364	36.6954	69.6972	1943
Longitude (°)	12.9774	14.1906	8.3402	-10.1763	36.1569	1943
Elevation (m)	212	145	238	-1.0	1739	1943
Climate						
Precipitation (mm)	751	657	321	6.4	3231	1943
Average temperature (°C)	5.9	6.0	3.2	-3.8	21.4	1943
Lake parameters						
Area (Km ²)	2.59	0.60	8.29	0.001	116.50	1943
Maximum depth (m)	14.9	10.3	15.6	0.2	190	1943
Total phosphorus (µg L ⁻¹)	38.2	15.1	114.8	<0.001	3333.6	1171
Total phosphorus (µg L ⁻¹) subset	37.9	15.9	74.6	1.0	932	302

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846 Appendix S2: List of 119 fish species and hybrids caught in the 1943 Western Palearctic lakes
 847 and reservoirs, and their country-specific status (N= native to the country; T= translocated
 848 from other countries of Western Palearctic, but non-native to the country; E= exotic to entire
 849 Western Palearctic) in the 14 countries (Ireland is treated at the whole island level covering
 850 the political jurisdictions of Republic of Ireland and Northern Ireland, with U.K. presented as
 851 only its mainland component).

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Fish name	Denmark	Estonia	Finland	France	Germany	Island of Ireland	Italy	Norway	Portugal	Slovenia	Spain	Sweden	Turkey	U.K. mainland
<i>Abramis</i> sp.				N										
<i>Abramis brama</i> (L.)	N	N	N	N	N	T	T	N				N	N	N
<i>Acipenser ruthenus</i> L.				T										
<i>Alburnoides bipunctatus</i> (Bloch)				N										
<i>Alburnoides</i> cf. <i>smyrnaeus</i> (Boulenger)													N	
<i>Alburnus alburnus</i> (L.)	N	N	N	N	N		T		T		T	N	N	
<i>Alburnus demiri</i> Özuluc & Freyhof														N
<i>Alburnus derjugini</i> (Berg)														N
<i>Alburnus escherichii</i> (Steindachner)														N
<i>Alburnus istanbulensis</i> (Battalgil)														N
<i>Alosa agone</i> (Scopoli)								N						
<i>Alosa fallax killarzensis</i> (Regan 1916)							N							
<i>Ameiurus melas</i> (Rafinesque)				E			E		E					
<i>Anguilla anguilla</i> (L.)	N			N	N	N					N	N		N
<i>Aphanius anatoliae</i> (Leidenfrost)														N
<i>Aphanius danfordii</i> (Boulenger)														N
<i>Leuciscus aspilus</i> (L.)		N	N		N							N		
<i>Atherina boyeri</i> Risso														N
<i>Ballerus ballerus</i> (L.)				N								N		
<i>Barbatula barbatula</i> (L.)					N	N								
<i>Barbus barbus</i> (L.)				N										
<i>Barbus escherichii</i> Steindachner														N
<i>Barbus graellsii</i> Steindachner												N		
<i>Barbus haasi</i> Mertens												N		
<i>Blicca bjoerkna</i> (L.)	N	N	N	N	N						T	N	N	
<i>Capoeta baliki</i> Turan, Kottelat, Ekmekçi & Imamoglu														N
<i>Carassius auratus</i> (L.)	E			E					E		E		E	
<i>Carassius carassius</i> (L.)	N		N	N	N		T	N				N	T	
<i>Carassius gibelio</i> (Bloch)		E			E						E		E	
<i>Chondrostoma meandrense</i> Elvira														N
<i>Chondrostoma nasus</i> (L.)				N										
<i>Clupea sprattus</i> L.	N													
<i>Cobitis kurui</i> Erk'akan, Atalay-Ekmekçi & Nalbant														N
<i>Cobitis simplicispina</i> Hankó														N
<i>Cobitis taenia</i> L.	N	N		N	N							N		

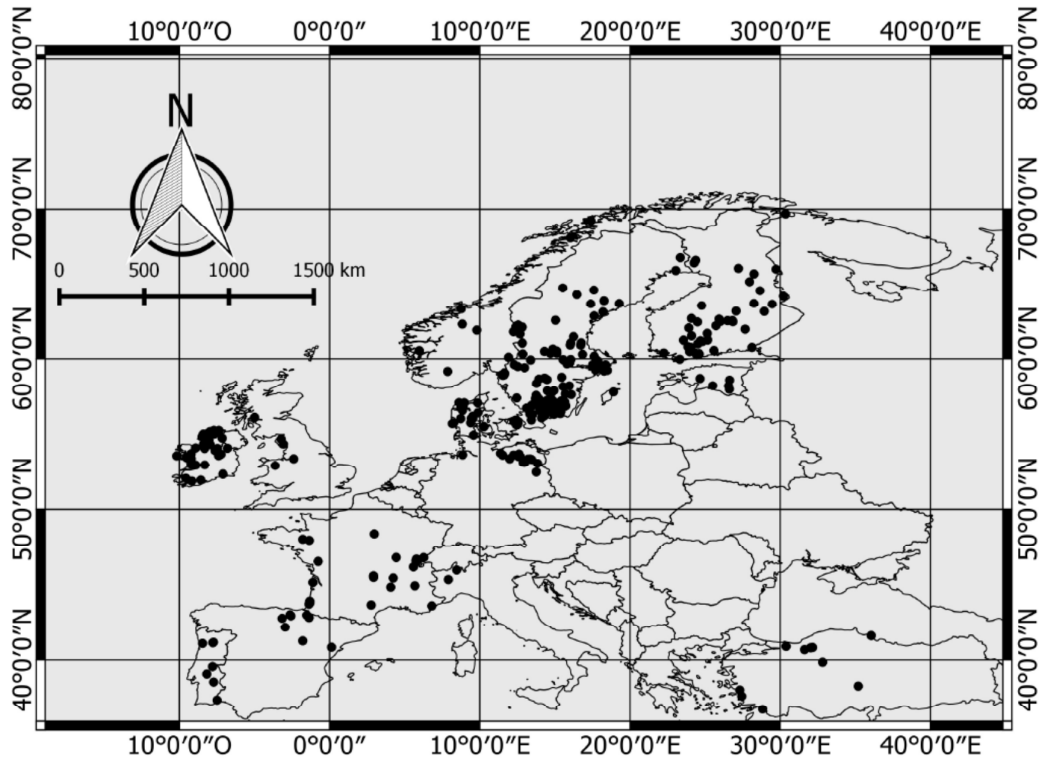
Ecosystems

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3	<i>Pseudochondrostoma duriense</i> (Coelho) N
4	<i>Pseudochondrostoma polylepis</i> (Steindachner) N
5	<i>Pseudochondrostoma wilkommii</i> (Steindachner) N
6	<i>Pseudophoxinus crassus</i> (Ladiges) N
7	<i>Pseudophoxinus elizavetae</i> Bogutskaya, Küçük & Atalay N
8	<i>Pseudorasbora parva</i> (Temminck & Schlegel) E E
9	<i>Pungitius pungitius</i> (L.) N N N N N N N
10	<i>Rhodeus amarus</i> (Bloch) N N T N
11	<i>Rutilus aula</i> (Bonaparte) N
12	<i>Rutilus rutilus</i> (L.) N N N N N T T N T T N N N
13	<i>Salmo abanticus</i> Tortonese N
14	<i>Salmo ferox</i> Jardine N
15	<i>Salmo nigripinnis</i> Günther N
16	<i>Salmo salar</i> L. N N
17	<i>Salmo stomachicus</i> Günther N
18	<i>Salmo trutta</i> (lake form) L. N N N N N N N N
19	<i>Salmo trutta</i> (resident) L. N N N
20	<i>Salmo trutta</i> (anadromous) L. N N
21	<i>Salvelinus fontinalis</i> (Mitchill) E E
22	<i>Salvelinus namaycush</i> (Walbaum) E
23	<i>Salvelinus</i> spp N N N N N T N N
24	<i>Sander lucioperca</i> (L.) T N N T N T T T T N N
25	<i>Scardinius erythrophthalmus</i> (L.) N N N N N T T T T N N
26	<i>Seminemacheilus lendlii</i> (Hankó) N
27	<i>Silurus glanis</i> L. T N T T N
28	<i>Squalius carolitertii</i> (Doadrio) N
29	<i>Squalius cephalus</i> (L.) N N N N
30	<i>Squalius fellowesi</i> (Günther) N
31	<i>Squalius pursakensis</i> (Hankó) N
32	<i>Squalius pyrenaicus</i> (Günther) N
33	<i>Telestes souffia</i> (Risso) N N
34	<i>Thymallus thymallus</i> (L.) N N N N
35	<i>Tinca tinca</i> (L.) N N N N N T N T N N N
36	<i>Trigloporus quadricornis</i> (L.) N
37	<i>Vimba vimba</i> (L.) N

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3 855 Appendix S3: Geographical map, showing the location of the subset of 302 lakes and
4 856 reservoirs with information on total phosphorus concentration sampled in Western
5 857 Palearctic (Europe and Turkey).

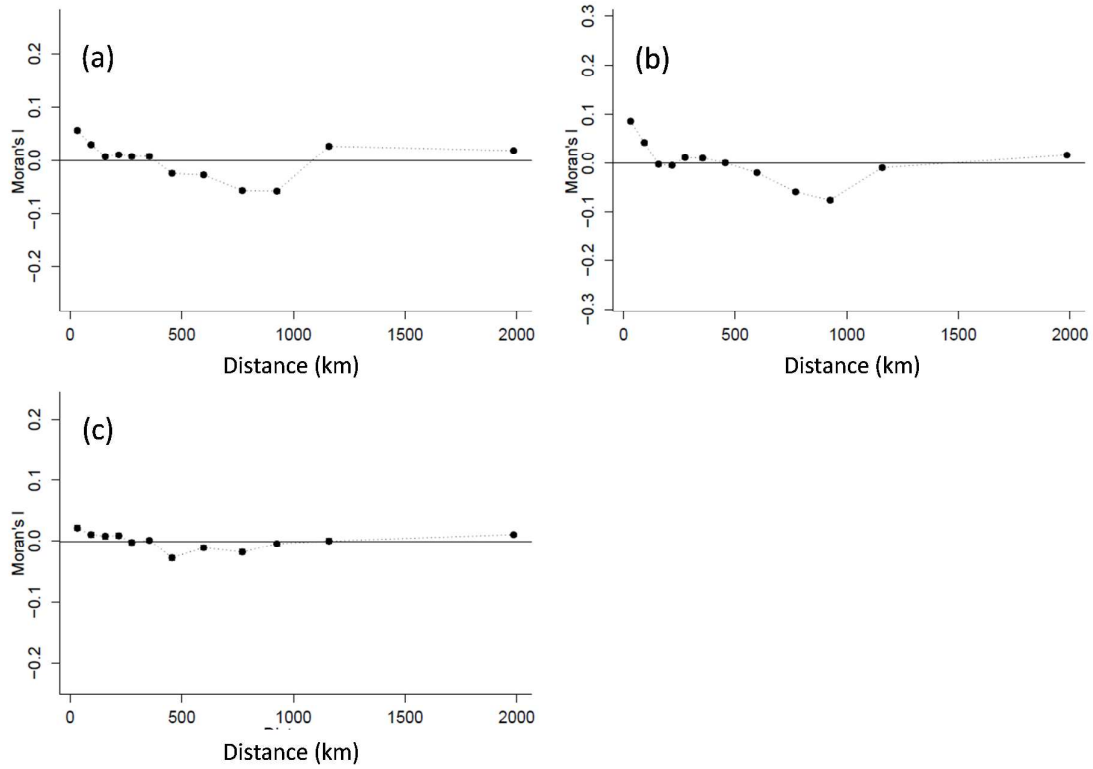


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3 861 Appendix S4: Moran's I correlograms of residuals across geographical distance (km) for the
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5 862 Hurdle models of species richness predicted by six abiotic correlates, for a) all non-native fish
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7 863 species, b) translocated fish species, and c) exotic fish species.
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866 Appendix S5: Results of the Hurdle models (coefficient estimates \pm standard error SE, z-
 867 statistics) to predict total richness of non-native (translocated + exotic) species, and
 868 separately calculated for translocated and exotic fish species in a geographically stratified
 869 subset of 302 European lakes and reservoirs for which information on total phosphorus
 870 concentration was available. area=lake area (km²), Precip=annual precipitation (mm),
 871 ave_temp=mean annual air temperature (°C), TP=total phosphorus concentration (mg m⁻³),
 872 LakeTypeN=lake type Natural lake (vs. LakeTypeA=reservoir).

Sum of non-native species

Count model coefficients (truncated Poisson with log link)

	Estimate	SE	z-value	Pr(> z)
(Intercept)	0.663	0.109	6.068	<0.0001
log10(area)	0.491	0.123	3.977	<0.0001

Zero hurdle model coefficients (binomial with logit link)

	Estimate	SE	z-value	Pr(> z)
(Intercept)	-9.298	1.233	-7.540	<0.0001
log10(area)	0.694	0.288	2.414	0.0158
Precip	0.001	0.0004	2.686	0.0072
ave_temp	0.890	0.131	6.773	<0.0001

Translocated species

Count model coefficients (truncated Poisson with log link)

	Estimate	SE	z-value	Pr(> z)
(Intercept)	0.775	0.184	4.201	<0.0001
log10(area)	0.461	0.150	3.062	0.0022
TP	-0.012	0.004	-2.613	0.0090

Zero hurdle model coefficients (binomial with logit link)

	Estimate	SE	z-value	Pr(> z)
(Intercept)	-8.560	1.040	-8.243	<0.0001
Precip	0.002	0.0004	4.794	<0.0001
ave_temp	0.646	0.093	6.924	<0.0001

Exotic species

Count model coefficients (truncated Poisson with log link)

	Estimate	SE	z-value	Pr(> z)
(Intercept)	0.0522	0.204	0.2568	0.798

Zero hurdle model coefficients (binomial with logit link)

	Estimate	SE	z-value	Pr(> z)
(Intercept)	-6.848	1.360	-5.033	<0.0001
Lake_TypeN	-1.535	0.598	-2.567	0.0103
ave_temp	0.674	0.119	5.638	<0.0001

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