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Non-native Fish Occurrence and Biomass in 1943 Western Palearctic Lakes and Reservoirs and their Abiotic and Biotic Correlates

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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 water bodies 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 water bodies (16%). If the average number of occupied water bodies per country was weighted by number of water bodies per country, the grand mean occurrence of non-natives in Western Palearctic water bodies 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 water bodies, 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 water body.

Key words: invasion biology; lake fish communities; translocated species; exotic species; invasion meltdown; trophic similarity.

INTRODUCTION

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

There is a fundamental discrepancy between the analytical levels in worldwide reports of invasions and studies on the consequences of invasions. Elucidation of the global homogenisation of the freshwater fish fauna and the changes of species pools has been based on presence/absence data of fish species in the major catchments of the world and comparison between historical and recent reports (Villeger and others 2011). In contrast, understanding the potential impacts of non-native fish species on genetic, individual, population, community and ecosystem levels (reviewed by Cucherousset and Olden 2011) requires much more comprehensive information than obtained from simple presence/absence records at catchment scale (Fitzgerald and others 2016). The contribution of non-natives to local fish abundance or biomass (Hansen and others 2013) and information on the ecological traits of fish species forming the local community and the resulting biotic interactions (Henriksson and others 2016a) may help to elucidate, which biotic conditions facilitate high biomasses of non-natives and, then, under which conditions strong community and ecosystem effects of non-natives can be expected. Processes related to invasions at local scale are biological resistance or invasion meltdown, and trophic similarity (overview in Catford and others 2009). Biological resistance means that higher richness of native species impedes the establishment of non-native species (Elton 1958). In contrast, invasion meltdown suggests that the establishment of new species makes communities more vulnerable to further invasions (Simberloff and Von Holle 1999). The success of invasions may also depend on the niche similarity between native and non-native species, based on the assumption that invaders with low overlap to native species along several niche axes may become more easily established (MacArthur and Levins 1967). However, detailed information about the contribution of non-native species to local community composition and trophic structure is usually limited to single aquatic systems (but see Henriksson and others 2016b).

Valuable information on non-native fish distribution in aquatic systems can be found in multinational monitoring programmes. In Europe, the Water Framework Directive (WFD) (EU 2000) made monitoring of the ecological quality of large water bodies mandatory for Member States, and standardised fishing has accordingly been con-

ducted in lakes and reservoirs in many European countries (Argillier and others 2013; Brucet and others 2013). Here, we analyse data on the occurrence, richness and contribution to community biomass of non-native fish species in almost 2000 lakes and reservoirs from several countries in the Western Palearctic. The analyses are based on systematic and standardised fishing surveys conducted in all water bodies during the previous 25 years. We explored the following three hypotheses: (1) Average non-native fish occurrence in single lakes would be lower than that suggested from catchment-scale data, according to which non-natives occur in about 60% of the Palearctic catchments (Villeger and others 2011). This is because lakes are relatively isolated ecosystems, and fish usually need hydraulic connections for dispersal (Mehner and others 2014); (2) Occurrence probability and richness of non-native fishes would not be equally distributed across the Western Palearctic, but follow geographical gradients. In particular, we expected that energy availability, habitat heterogeneity, human activities and other anthropogenic effects on lakes facilitate the occurrence of non-native fish species (Oberdorff and others 1995; Garcia-Berthou and others 2005; Leprieur and others 2008). This approach provides a more detailed view on the potential determinants of the occurrence and richness of non-natives than that achievable at catchment scale; (3) Non-natives would have high contributions to community biomass (Hansen and others 2013). We focused explicitly on the contribution of non-native species to fish biomass in individual lakes, because the potential effects of non-natives on community and ecosystem ecology intensify relative to local abundance and biomass (Parker and others 1999; Ricciardi 2003). Furthermore, we expected higher relative biomasses of translocated than exotic species in Western Palearctic lakes (Leprieur and others 2009a; Toussaint and others 2014), because there is a higher similarity of environmental conditions between source and target water bodies for translocated species than for those exotic fish species, which have their natural origin in other realms of the world. We further evaluated whether the richness of native or non-native species (reflecting biotic resistance or invasion meltdown hypotheses, respectively) predicted high biomass contributions (Henriksson and others 2016a, c) and whether trophic similarity, as expressed by trophic levels of non-native and native fish species (Sagouis and others 2015; Fitzgerald and others 2016), was a useful predictor of high biomass contributions of non-native species in certain lakes.

METHODS

Fish Data

We used a fish database including approximately 1900 European natural lakes and reservoirs (artificial lakes created by impounding rivers) compiled for the purpose of intercalibration of national evaluation systems from 12 European countries for the Water Framework Directive 2000/60/EC (Argillier and others 2013; Brucet and others 2013), supplemented with data from Spanish reservoirs (provided by Confederacion Hidrografica del Ebro, Spain) and data from 46 lakes located in Western and Central Turkey (Boll and others 2016). Thus, the final database encompassed 1807 natural lakes and 136 reservoirs (total $n = 1943$) from 14 countries (Mehner and others 2017). Ireland was treated at the whole island level covering the political jurisdictions of the Republic of Ireland and Northern Ireland of UK, with the remainder of the UK presented as its mainland component. The location of the lakes covered a latitudinal gradient between 36.70 and 69.70°N and a longitudinal gradient between −10.18 and 36.16°E. Lake area ranged between 0.001 and 116 km^2, with about 700 lakes having an area less tan 0.5 km^2 (50 ha). Lake maximum depth ranged between 0.2 and 190 m (Appendix S1 in Supporting Information).

The selected lakes were sampled at least once, primarily between June and September during the years 1993–2012. Nordic benthic multi-mesh gillnets were used, which is in accordance with the recommendations made by the European Committee for Standardization (CEN 2015). Benthic gillnets (12 mesh sizes between 5.0 and 55 mm in a geometric series, each panel being 2.5 m long and 1.5 m high) were set in a random stratified sampling design across all depth layers in the benthic habitat, following the recommendations of the standard (CEN 2015). Nets were generally set for 12 to 16 h overnight. The total fishing effort per lake (number of benthic nets) was standardised by lake area and maximum depth according to CEN 14757 (CEN 2015). Pelagic gillnets (11 mesh sizes as above, but excluding 5.0 mm) were set in several of the lakes with a maximum depth of at least 6 m and covered the entire depth range from the surface to the bottom. These nets varied in height between 1.5 and 6.0 m. Fish biomass was expressed as biomass per unit effort (BPUE, wet mass of fish), standardised with respect to number of gillnets set per night per lake (g fish net^{-1} night^{-1}). Pelagic 3-m-high gillnets had a net area about twice as large as that of the benthic nets and were therefore

counted as two nets, and 6-m-high pelagic nets were counted as four nets. In several deeper lakes, sampling using pelagic gillnets was not undertaken; however, the contribution of catches in pelagic gillnets to the lake-wide species richness and fish biomass is relatively low (Diekmann and others 2005; Emmrich and others 2012; Alexander and others 2015). Consequently, we assume that the deviations from the systematic fishing protocols with respect to the pelagic catches have not significantly biased the analyses. The sampling of the German lakes was split into a spring and an autumn campaign (Mehner and others 2005). However, the results were subsequently summed to allow comparison with the other samplings. If several fishing campaigns were carried out in a lake, we used only the data from the most recent one.

Each individual fish caught was determined to species level. All species were classified as native or non-native per country (except for the island of Ireland and the UK mainland, for which information was based on the two physical islands) by local researchers and experts based on information from national databases (Appendix S2 in Supporting Information). A species was considered native if it was present in the country before the sixteenth century (the beginning of globalisation, DAISIE 2009), following the definition by van den Veer and Nentwig (2015). This definition of native status is comparable with the reference to the historical pre-industrial situation used in earlier studies (Villeger and others 2011). Non-native species are either truly exotic to the Western Palearctic or have been translocated among European countries since the sixteenth century (Leprieur and others 2009a; Toussaint and others 2014). Translocations between watersheds or lakes within the same country are therefore not covered, but this level of detail is usually not available in the local records (but see Henriksson and others 2016b). Consequently, in our analyses we assume that a species native in a country is native in all water bodies of this country. We calculated the proportion (%) of sampled Palearctic water bodies in which non-native fish species occurred, and similarly calculated the %occurrence of non-natives in water bodies per country. To take into account uneven sampling efforts in the countries, we weighted the percentage of water bodies with non-natives per country by the number of water bodies larger than 0.1 km^2 per country (Messager and others 2016) and calculated a grand mean proportion of occurrence of non-natives in Western Palearctic water bodies.

Species richness was calculated as the total number of fish species collected in a lake and was split into richness of native and non-native species. For further calculations, we separately calculated the richness of translocated and exotic species per lake. In the same way, total BPUE was split into BPUE of native and non-native fishes, and BPUE was separately calculated for translocated and exotic species. For use in several subsequent analyses, we further calculated %richness and %biomass (%BPUE) of translocated and exotic species. We also assessed the trophic levels (TL) of fish, defined as mean trophic level of all food items +1 (for example, Pauly and Christensen 1995), using the arithmetic mean from all single estimates available per species in FishBase (www.fishbase.org). We calculated the average TL of native, translocated and exotic species, weighted by the biomass proportions per species within the species groups.

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

Predictor Variables

We selected six geographical and lake variables known to influence fish community composition (Brucet and others 2013). Information on lake elevation (m), lake area (km^2) and lake maximum depth (m) was extracted from the national databases. Annual precipitation (mm) and annual average air temperature (°C) were obtained from the climate CRU model as based on geographical coordinates and elevation of the lake (New and others 2002). Air temperature was used as a proxy of epilimnetic lake temperature (Livingstone and Lotter 1998). This was based on the assumption that air temperature presumably provided a better integrated value than snapshot lake temperature data obtained during irregular surveys. Furthermore, we defined the binary variable 'lake type', which was either 'natural lake' or 'impoundment reservoir', assuming that the artificially created reservoirs reflect strongly modified ecosystems under substantial anthropogenic pressure.

Latitude (northings of UTM projection) was strongly correlated with average air temperature (Pearson's $r = -0.88$, $P < 0.0001$), and we therefore did not consider latitude separately in subse-

quent calculations. The year of sampling was a positive predictor of the richness of non-native species (Pearson's $r = 0.32$, $P < 0.0001$). However, there was also a strong interaction between latitude and year of sampling, as many lakes in central and southern Europe have been sampled primarily after 2004. These lakes had higher numbers of non-native fish species, and the richness of non-native species thus seems to have increased over time as an indirect consequence of geographical bias in sampling activity over the years. However, for the 1501 lakes above 620,000 northing (Sweden, Finland, Norway), there was no correlation between year of sampling and number of non-native fish species per lake (Pearson's $r = -0.007$, $P = 0.77$). Therefore, we did not include year of sampling as predictor.

Statistical Analysis

To evaluate the potential abiotic predictors of occurrence or richness of non-native species in the lakes, multiple linear regressions are conventionally used. However, non-native fish species were found in only 304 of the 1943 surveyed lakes, creating a non-normal distribution of occurrences and richness (Shapiro–Wilk test, $P < 0.001$) and a high frequency of zero observations (84%). To account for this 'zero-inflation', we used two-component hurdle models (Zeileis and others 2008), consisting of a hurdle component modelling zero versus larger counts (presence–absence model) using a Bernoulli (that is, binomial) distribution and a count component in which all zeroes were excluded and counts greater than 0 were fitted with a truncated Poisson distribution. Elevation, precipitation, annual average temperature, $\log_{10}$ lake area, $\log_{10}$ lake maximum depth and lake type were the predictors (Irz and others 2004a; Field and others 2009). We first tested whether the interactions between lake type and precipitation or lake type and average temperature were significant and removed non-significant interaction terms from the initial models. Then, we reduced the initial models backwardly in a step-wise manner (see Zeileis and others 2008) and the best and most parsimonious models were selected based on the log-likelihood test. To check for spatial autocorrelation in the residuals of the final hurdle models, we computed Moran's I correlograms over a range of distances (km) between the lakes (Dormann and others 2007).

The database was dominated by Swedish lakes ($n = 1145$, 58.9% of total; Figures 1 and 2), and this geographical bias might influence the results as
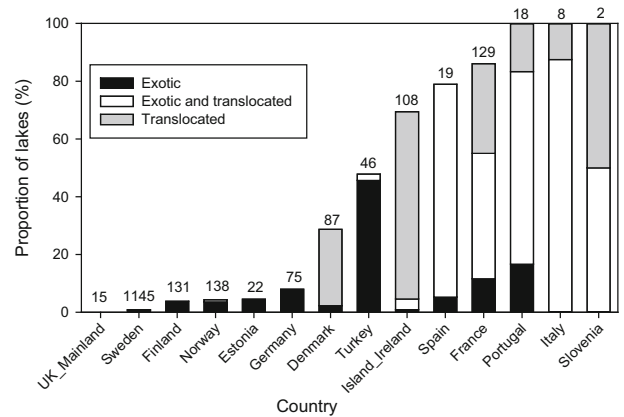

Figure 1. Relative occurrence (%) of translocated and exotic fish species in water bodies of the 14 countries of the Western Palearctic. The numbers above the bars indicate the number of water bodies sampled per country.
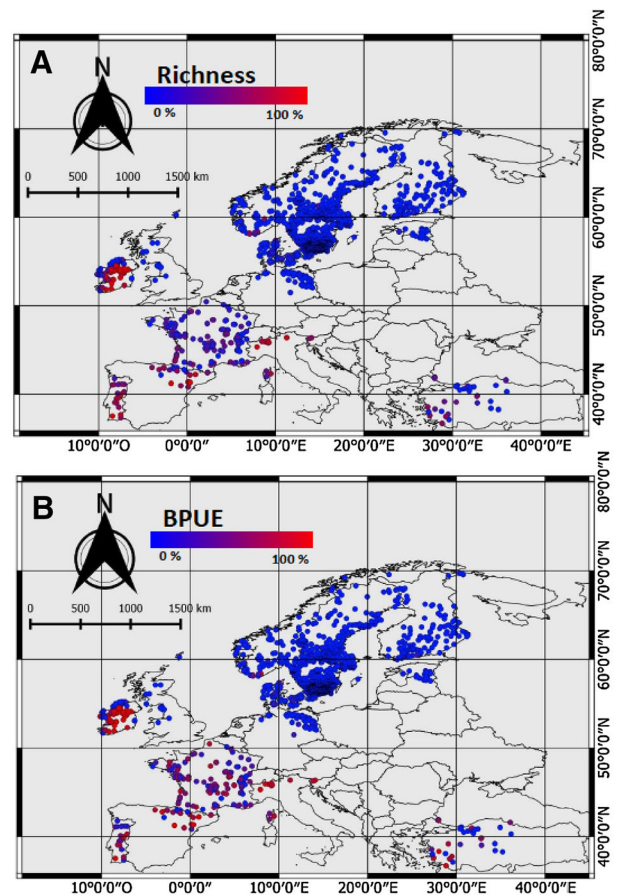

Figure 2. Maps showing the location of the 1943 lakes and reservoirs sampled in the Western Palearctic and **A** the relative richness (%) or **B** the relative biomass (%BPUE) of non-native fish species in the waterbodies.

Swedish lakes have a relatively low species richness and a low number of non-native fish species. Furthermore, lake trophic state has been shown to

modify the composition of fish assemblages in lakes (Mehner and others 2005; Brucet and others 2013); however, information on trophic state was not available for all the 1943 lakes in the database. Accordingly, we split the lakes into three spatial subsamples (regions) based on latitude and four spatial subsamples based on longitude (see geographical distribution of the subset, Appendix S3 in Supporting Information) and checked for which lakes per subsample information on annual mean total phosphorus concentration (TP, mg m^{-3}) were available. From the lake list with TP information, we subsampled about 15% of the lakes from each sub-region using the 'select a random sample' function in the IBM SPSS 20 software (see Brucet and others 2013 for a similar procedure). Next, we re-ran hurdle models using this unbiased data subset (in total 302 lakes) and TP as an approximation of lake trophic state as an additional, seventh predictor.

To evaluate whether translocated species contribute more to local richness and biomass than exotic species, both absolute richness and BPUE could not be used because local richness and biomass respond to confounding variables, such as lake size and productivity. Hence, richness or BPUE of translocated fish in one lake and richness or BPUE of exotic species in another lake cannot be compared directly without a correction for locally differing variables. To facilitate comparison, we compared the slopes of the reduced major axis (RMA) regression of the relative share of translocated species in local richness (%richness) with the relative share of translocated species in local biomass (%BPUE) and the similarly calculated RMA slope for exotic species. We applied RMA, that is, least products regression, because both the predictor and the response variables were measured with error (Legendre and Legendre 2012). Significance tests of RMA regressions were based on 999 permutations. The results of RMA can be interpreted in the same way as those based on ordinary least squares linear regression models; hence, an RMA slope equal to 1 would indicate that local %biomass increases proportionally with %richness. However, we expected an RMA slope substantially larger than 1 and steeper for translocated than for exotic species, which would support the hypothesis that translocated species contribute more to local biomass than exotic species.

We further sought to explain which biotic predictors facilitated a strong local biomass contribution of exotic or translocated species. To achieve normally distributed data, we calculated logit (%biomass) for non-natives per lake ($n = 306$),

separately calculated as % biomass of translocated and exotic species. Because logit (1.0) is not explained, we replaced 1.0 with 0.999 in all cases where non-native species locally reached 100% biomass. We assumed that high biomass contributions can be explained by local processes such as biotic resistance, invasion meltdown and niche similarity and thus can be predicted by four variables characterising the local community composition (richness of native and translocated or exotic species per lake) and food sources (mean trophic level of native and translocated or exotic species per lake). Thus, we ran multiple regressions, with the logit(%biomass) of translocated or exotic species as the dependent variable, and the four biotic predictors. Model complexity was reduced in a stepwise manner based on minimising the Akaike Information Criterion (AIC), and the two 'best' models were compared using ANOVA. To facilitate comparison of effect sizes, we calculated standardised coefficients for the significant predictors.

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

RESULTS

The 1943 lakes and reservoirs in the 14 countries hosted 119 fish species, ecotypes of salmonids and hybrids (Appendix S2). Among these, 15 species were considered exotic for all countries, whereas another 22 species were considered translocated within the Western Palearctic (Appendix S2). Non-native fish species were caught in a total of 304 (15.6%) of the 1943 water bodies (184 natural lakes, 120 reservoirs). Translocated species occurred in 235 (12.1%) of the water bodies, whereas exotic species occurred in 164 (8.4%) of the water bodies. Translocated and exotic species were found together in 95 water bodies (4.9%). The relative proportion of water bodies per country in which translocated species were found was highly variable (Figure 1). UK mainland, Sweden, Finland, Norway and Estonia had very low proportions of lakes with non-natives, whereas non-native fish species occurred in all sampled water bodies in Italy, Slovenia and Portugal (Figure 1). If the average proportion of water bodies with non-native fish species per country was weighted with the number

of water bodies larger than 0.1 km^2 per country, the grand mean relative occurrence across the water bodies in the countries of the Western Palearctic was 10.3%, caused by the low proportion of non-natives in water bodies of the countries with the highest number of lakes (Sweden, Norway and Finland). Turkey was the country with the highest proportion of water bodies with exotic species, whereas France, Italy, Portugal and Spain had the highest proportion with a mix of translocated and exotic species. The Irish lakes (island) were dominated by translocated species (Figure 1).

The %richness and %biomass of non-natives in the 1943 water bodies varied between 0 and 100% with arithmetic mean values of 6.5 and 6.2%, respectively (Figure 2). Non-native %richness was lower than 5% in water bodies from the UK mainland, Sweden, Norway, Germany, Finland, Estonia and Denmark (Figure 2A). Turkey, Italy, Portugal, Spain and Island of Ireland were the locations with the highest %richness of non-native fish ($>$50%, Figure 2A). Turkey, Spain, Ireland and Slovenia showed biomass contributions of non-native fishes above 50% in many of the water bodies (Figure 2B).

The median species-specific contribution of non-native fishes to the total fish biomass per lake was less than 15% for the four most frequently occurring exotic species (*Lepomis gibbosus, Ameiurus melas, Oncorhynchus mykiss, Micropterus salmoides*; Table 1). In contrast, the median species-specific contribution to the total fish biomass per lake was greater than 30% for the translocated *Rutilus rutilus* and *Perca fluviatilis* (Table 1). However, the most frequently occurring translocated species were *Sander lucioperca* and *Cyprinus carpio* whose median %biomass contributions were less than 10% (Table 1).

The presence–absence step of the hurdle model (binomial with logit link) for richness indicated that the probability of non-native fish presence was positively related to annual average temperatures, precipitation and elevation and was higher in reservoirs than in natural lakes (Table 2). These predictors as well as lake area (positive effect) also contributed to the probability of occurrence when considering translocated and exotic species separately (Table 2). For translocated species, the probability of occurrence in response to increasing temperature was higher for reservoirs than for lakes (see significant interaction terms, Table 2). The count part of the hurdle models indicated that richness of translocated species increased with area, while richness of exotic species increased with temperature (Table 2). The Moran's I correlograms of residuals of the hurdle models for richness of

non-native, translocated and exotic species revealed no substantial spatial autocorrelation in the final models (Appendix S4 in Supporting Information).

Additional hurdle models were run using a geographically unbiased data subset with TP information available (that is, subsampling 302 lakes, Appendix S3) and including TP as an additional predictor. The main predictors of occurrence and richness of non-native species (annual precipitation, lake area, average temperature; Appendix S5 in Supporting Information) were essentially similar to those obtained for the complete dataset (1943 lakes, Table 2), suggesting that the strong dominance of Swedish lakes in the entire dataset did not affect the main conclusions. The concentration of TP was a weakly negative predictor of the richness of translocated species but was not included in the models for the sum of non-native or the exotic species (Appendix S5).

The RMA regression between %richness and %biomass of translocated species was significant (Figure 3A; $R^2 = 0.77$, $n = 235$, $P = 0.001$), with a slope estimate slightly higher than 1 (1.25, 95% CI [1.16, 1.34]). The RMA regression of %richness with %biomass of exotic species had a substantially steeper slope (Figure 3B; $R^2 = 0.47$, $n = 164$, $P = 0.001$, slope = 1.58 [1.35, 1.88]).

The multiple regression for logit(%biomass) of translocated species with four biotic predictors testing invasion meltdown, biotic resistance and trophic similarity hypotheses was significant (adj. $R^2 = 0.49$ $F_{3,231} = 151.0$, $P < 0.0001$). There were three significant predictors (richness of native species, standardised coefficient = -0.53, $t = -11.8$, $P < 0.0001$, Figure 4A; richness of translocated species, standardised coefficient = 0.46, $t = 10.7$, $P < 0.0001$, Figure 4B; trophic level of translocated species, standardised coefficient = 0.17, $t = 4.2$, $P < 0.0001$, Figure 4C). The multiple regression for logit (%biomass) of exotic species with the same set of predictors was likewise significant, but with a low proportion of predicted variance (adj. $R^2 = 0.098$, $F_{2,161} = 9.8$, $P < 0.0001$), and had only two significant predictors (richness of native species, standardised coefficient = -0.25, $t = -3.4$, $P = 0.0008$, Figure 5A; richness of exotic species, standardised coefficient = 0.22, $t = 2.9$, $P = 0.0036$, Figure 5B).

DISCUSSION

We demonstrate that the occurrence of non-native fish species in the sampled Western Palearctic lakes and reservoirs is overall low, but there are geo-

Table 1. Arithmetic Mean, Median and Maximum %Biomass per Lake and Number of Western Palearctic water bodies (from a total of $n = 1943$) in Which 15 Exotic and 22 Translocated Fish Species Occurred

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

graphical hotspots (for example, Southern Europe) where non-native species occur frequently. High average temperatures, high precipitation, large ecosystem size and artificially created lakes (that is, reservoirs) are correlated with the occurrence of non-native fish species. However, the majority of non-native species belong to species translocated among European catchments, whereas true exotic species from outside the Western Palearctic occurred in only 8% of the sampled lakes. Our data suggest that exotic species may contribute slightly over-proportionally to local biomass compared with translocated species. However, there were strong positive relationships between %biomass of non-natives and richness of non-natives and strong negative relationships between %biomass of non-natives and richness of natives, suggesting that the local biomass contribution of non-natives increases primarily with the arrival of new non-native species and is high at low native richness. The spread of non-native species across European and Turkish water bodies seems to be assisted strongly by human interventions, such as creation of reservoirs and subsequent intentional stocking of species for fisheries purposes.

The data presented are based on monitoring surveys primarily conducted to evaluate the ecological integrity of lakes (EU 2000) and have been

Table 2. Results of the Hurdle Models (coefficient estimates ± standard error SE, z-statistics) Predicting Total Richness of Non-native (sum of translocated and exotic) Species and Richness of Translocated and Exotic Fish Species in 1943 European Lakes and Reservoirs

Sum of non-native species	Estimate	SE	z-value	Pr(> |z|)
Count model coefficients (truncated Poisson with log link)				
(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)				
(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)				
(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)				
(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)				
(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)				
(Intercept)	−5.7204	0.5884	−9.721	<0.0001
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

Elevation (m a.s.l), area = lake area (km², Precip = annual precipitation (mm year⁻¹), ave_temp = mean annual air temperature (°C), LakeTypeN = lake type Natural lake (vs. LakeTypeA = reservoir). Ave_temp:LakeType reflects significant interaction terms

derived by standardised fish biomass estimates in each lake. Therefore, they provide local occurrences and biomasses of non-native species in the water bodies in contrast to the presence/absence data used in an earlier global analysis (Villeger and others 2011) as the latter were extracted from literature reports at the entire catchment scale. We found non-natives in about 16% of the sampled waterbodies, but this number is biased by the strong contribution of Swedish lakes to the entire dataset. If the average occurrence per country was weighted by the number of water bodies per country, about 10% of water bodies were occupied by non-natives, and this number is substantially lower than the estimate that about 60% of Palearctic catchments would be occupied by non-

native fish species (Villeger and others 2011). We have sampled fish only in 14 European countries, and therefore the average occurrence of non-natives may potentially increase by inclusion of data from the other 24 European countries. However, from the about 80,000 water bodies larger than 0.1 km² in Europe except Russia (Messager and others 2016), 62,000 water bodies are located in the 14 countries from which we have obtained samples. Therefore, it is unlikely that the weighted average occurrence would change substantially by inclusion of water bodies from countries so far not covered. Furthermore, the list of frequently occurring translocated and exotic species in the sampled water bodies is similar to the non-native species documented at the catchment scale (Tous-
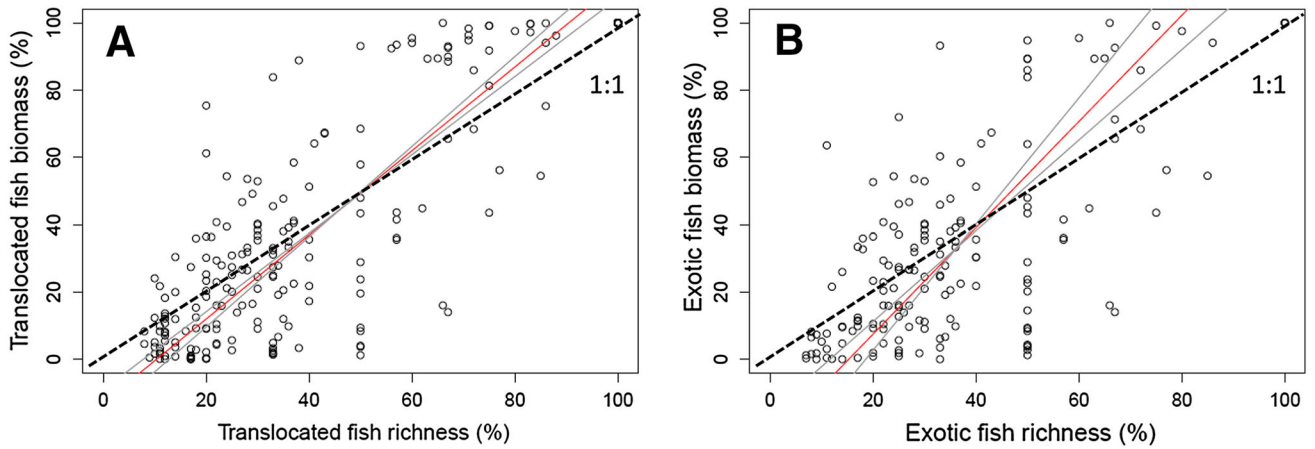
Figure 3. Reduced major axis regressions (regression line and 95% confidence band) between proportion (%) of fish in richness (*x*-axis) and proportion (%) of fish in biomass (*y*-axis) for **A** 22 translocated fish species and **B** 15 exotic fish species in Western Palearctic lakes and reservoirs. The stippled 1:1 line indicates where %richness would equal %biomass.
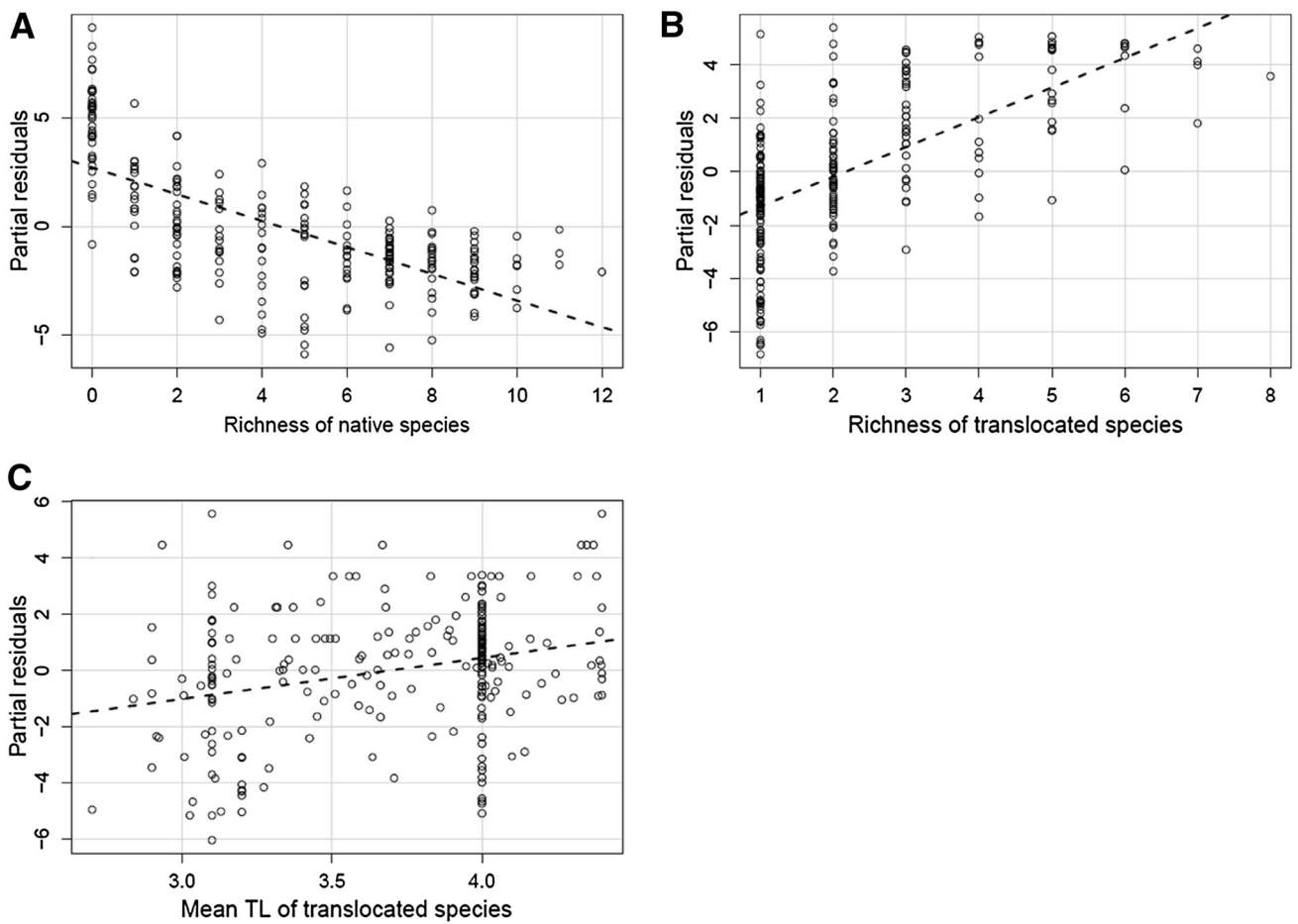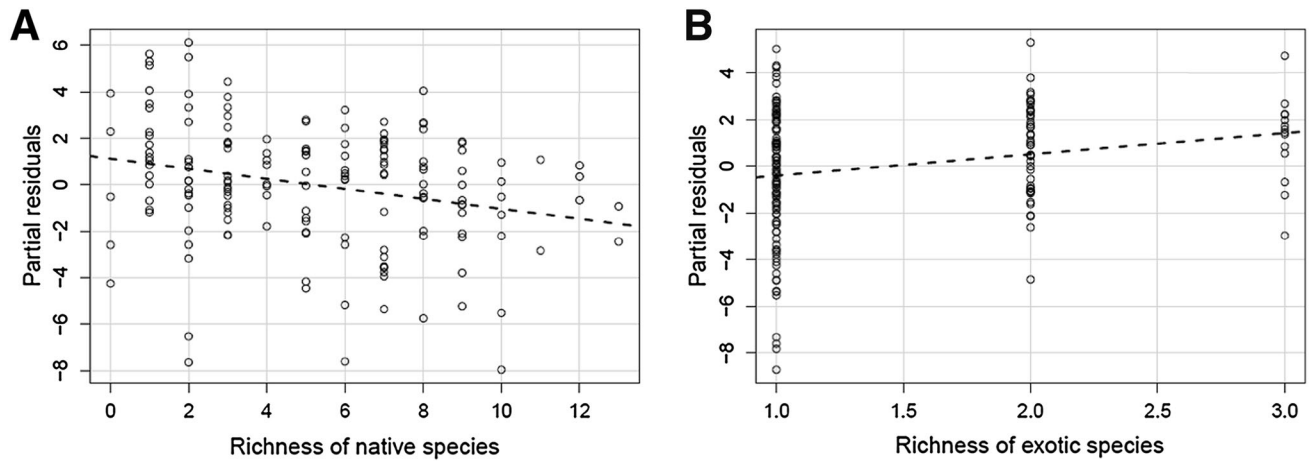

Figure 4. Partial residual plots of significant predictors in a multiple linear regression between logit(%biomass) and biotic predictors for translocated species, predicted by **A** the local richness of native species, **B** the local richness of translocated species, and **C** the mean trophic level (TL) of translocated species in Western Palearctic lakes and reservoirs.

Figure 5. Partial residual plots of significant predictors in a multiple linear regression between logit (%biomass) and biotic predictors for exotic species, predicted by **A** the local richness of native species, **B** the local richness of exotic species in Western Palearctic lakes and reservoirs.

saint and others 2016). Consequently, we conclude that the lower occurrence of non-native species in lakes and reservoirs of the Western Palearctic reflects the hydraulically less connected nature of standing water bodies in comparison with river catchments. Nevertheless, the detailed information obtained by standardised sampling can be used as justification for intensified observation and management, in particular for water bodies with mixed communities of native and non-native fish species (Britton and others 2008). However, so far practical recommendations for such management are limited (Leprieur and others 2009b), in particular with respect to potential interactions among the effects of multiple stressors in aquatic ecosystems in addition to the occurrence of non-natives (Ormerod and others 2010).

The presence of non-native fish species was positively related to precipitation and temperature and accordingly higher in the southern and western parts of the Palearctic than in the northern areas. Furthermore, lake area and artificial origin of the waterbody also facilitated a higher occurrence of non-natives. Climatic similarity between the native and the receiving regions is considered an essential requirement for successful invasions (Ficetola and others 2007; Gallien and others 2010), particularly for translocated species since these have been moved over shorter geographical distances within the Western Palearctic, often between neighbouring watersheds. However, the significant effect of precipitation and temperature as major drivers of invasions throughout the world has been highlighted (for example, Field and others 2009; Feld and others 2016); thus, energy avail-

ability (approximated by high temperature and precipitation) in the receiving habitat may be particularly important, also for the occurrence of exotic species having their origin in warmer realms in Asia or North America. The high contribution of non-native fish species to richness and biomass in lakes and reservoirs in southern Europe and Turkey seems to support this general trend (Godinho and others 1998). In contrast, the absence of native species and often 100% biomass of non-native species in 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, the fact that large lakes are more likely candidates to host non-native fish species could be attributed to a larger spatial heterogeneity, that is, larger lakes generally host more fish species than smaller ones (Brucet and others 2013).

Our results also showed that increased lake productivity (using TP concentration as a proxy, data on which were only available for a subset of lakes) did not predict the presence or richness of non-native fish species. The richness (and hence indirectly also the biomass contribution) of translocated species was even negatively correlated with TP in this subset. Many translocations have presumably been conducted for fisheries purposes, and several species of importance for commercial or recreational fisheries belong to the Salmonidae (Tammi and others 2003) and Percidae families, which thrive better in lakes of lower productivity (Persson and others 1991; Mehner and others 2005). Hence, lakes exposed to high human fisheries or angling activities are not necessarily those

with the highest TP concentrations. Our results confirm that eutrophication has a relatively minor role in shaping biodiversity patterns of European fish assemblages in lakes compared with the strong effect by broad-scale climatic drivers (Brucet and others 2013). In contrast to low occurrence of non-natives in natural lakes, 120 of the 136 reservoirs hosted non-native fish species. Non-native species are favoured in reservoirs because the hydrology and temperature are substantially altered when rivers and streams are impounded, and many native fishes often cannot cope with these changes (Moyle and Light 1996; Irz and others 2004b). Furthermore, in many Southern regions, reservoirs do not have native lacustrine systems to provide fauna colonizers. Accordingly, non-native species in these reservoirs are often introduced to satisfy anglers and fisheries demands because the original riverine fish fauna disappears when rivers are dammed (Argillier and others 2002). In addition, fish stocking is frequently conducted to balance the consequences of water level fluctuations, which may affect native fish population dynamics (Kahl and others 2008).

The information on the biomasses of non-native fish species offered additional insight into the composition of lake fish communities. As indicated by the slope of the reduced major axis regression, translocated and in particular exotic species seem to reach slightly higher relative biomasses in the local communities than reflected by their relative shares of local richness. For example, the biomass of non-native fish species was close to 100% in some lakes, despite that these species represented only 60–70% of the local richness. These results support a recent study in which the abundance distributions of native and non-native aquatic species were compared across numerous lakes or rivers (Hansen and others 2013). Both native and non-native species occurred in low densities in most of the sampling sites (that is, exhibited right-skewed abundance distributions), but non-native species generally reached significantly higher densities than native species (Hansen and others 2013). The high biomass contributions of non-native species in several locations support the overall hypothesis that invasive species often perform better in their new range (Parker and others 2013) due to the novel ecological and evolutionary dynamics in the introduced locations. Evidence of high biomass or abundance contributions of non-natives despite lower contribution to richness in single lakes is of great importance for biodiversity management in these waterbodies, since the ecological impact of invasive species is positively correlated with their abundance (Parker and others 1999;

Ricciardi 2003). However, in the majority of lakes occupied by non-natives, the biomass contributions of exotic species did not exceed 15%, whereas higher local biomass contributions of non-natives were found primarily by translocated common species, such as *Perca fluviatilis* and *Rutilus rutilus*.

The local richness of native or non-native fish species was the strongest predictors of the %biomass of both translocated and exotic species. The highest biomass contributions of non-natives tended to occur in water bodies with low numbers of natives and already high numbers of non-natives. This pattern supports the invasion meltdown hypothesis, suggesting that successful invaders have negative effects on resistance, that is, that positive feedback makes the success of each subsequent invasion or introduction more likely (Simberloff and Von Holle 1999). In turn, the negative correlation between %biomass of non-natives and local richness of native fish species may reflect some biotic resistance in the sense that a high diversity of native fish species prevents the biomass dominance of invaders. A recent meta-analysis of biotic resistance mechanisms suggested that consumptive resistance was much stronger than competitive resistance, at least in freshwater ecosystems (Alofs and Jackson 2014). This would mean that the feeding modes and trophic levels of native and non-native species are important for the invasion as stated by the trophic similarity hypothesis. However, we found no evidence that the TL of native or non-native fish species modified the %biomass of exotic species and only a weak positive contribution of the mean TL of translocated species to %biomass of translocated species in the water bodies was calculated. Among the most frequently translocated fishes, many species are piscivores (*Sander lucioperca*, *Esox lucius*, *Perca fluviatilis*, *Silurus glanis*), supporting the idea that certain lakes have received a high load from human-assisted translocations (Garcia-Berthou and others 2005), most likely for fisheries purposes. Strong piscivory may reduce the biomass of prey species, and the %biomass of translocated piscivores may therefore reach higher relative levels than if translocated species were omnivores. However, overall, there was surprisingly little evidence that feeding interactions and trophic similarity between native and non-native species contributed to the biomass dominance of non-native fish species.

CONCLUSIONS

In general, our results showed that the large majority of lakes in the Western Palearctic sampled

for this study do not yet host exotic fish species, in particular those in northern Europe. This result in part contrasts the broad-scale distribution of non-natives assessed from their presence in the major river catchments. However, the Iberian Peninsula, parts of France and Italy, Turkey and Ireland are geographical hotspots where non-native fish species occur in almost every lake and reservoir. Translocation of species between the major watersheds seems to be the dominant mechanism behind the increasing number of non-native fish species in lakes, and it is certainly an important reason for the high richness of non-natives in reservoirs. Translocations between neighbouring lakes might be even more frequent but could not be evaluated here due to the absence of data. Therefore, the local richness of translocated (but not exotic) species may be underestimated. Although large-scale climatic drivers are primary determinants of fish species richness and community composition, local species richness of natives and non-natives may determine the local biomass contribution of non-natives and hence predict the strength of community and ecosystem effects exerted by non-native species. Large-scale monitoring programmes, for example the European Water Framework Directive, may help to generate the data needed to evaluate the status of lakes and reservoirs with respect to the richness of non-native species. In contrast, the biomass contributions of non-natives were strongly correlated with richness contributions, suggesting that local presence/absence records of non-natives alone can already strongly support large-scale biodiversity management at moderate costs. The occurrence of a fish community including a mix of native and non-native fish species calls for the development of management plans that are much more detailed than those existing today in a cooperation between water managers and conservationists (see for example http://easin.jrc.ec.europa.eu).

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