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Anthropogenic stressors and riverine fish extinctions



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ABSTRACT

Human activities are often implicated in the contemporary extinction of contemporary species. Concerning riverine fishes, the major biotic and abiotic threats widely cited include introduction of non-native species, habitat fragmentation and homogenization in stream flow dynamics due to the damming of rivers, dumping of organic loadings, degradation of the riverine habitat by agricultural practices and water abstraction for human and agricultural consumption. However, few studies have evaluated the role of each of these threats on fish extinction at large spatial scales. Focusing on Western Europe and the USA, two of the most heavily impacted regions on Earth, we quantify fish species loss per river basin and evaluate for the first time to what extent, if any, these threats have been promoting fish extinctions. We show that mean fish extinction rates during the last 110 years in both continents is ~112 times higher than calculated natural extinction rates. However, we identified only weak effects of our selected anthropogenic stressors on fish extinctions. Only river fragmentation by dams and percentage of non-native species seem to be significant, although weak, drivers of fish species extinction. In our opinion, the most probable explanation for the weak effects found here comes from limitations of both biological and threats datasets currently available. Obtaining realistic estimates on both extinctions and anthropogenic threats in individual river basins is thus urgently needed.

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1. Introduction

Humans have modified ecosystems on Earth and have been responsible for the extinction of hundreds of species (Barnosky et al., 2011). Predicting to what extent large-scale anthropogenic alterations have resulted in species loss is thus critical for guiding conservation strategies aiming to maintain biodiversity in altered ecosystems as high losses in biodiversity may compromise the future provisioning of vital ecosystem services. In order to build effective scenarios of future changes in global freshwater biodiversity we have to know how human pressures can influence patterns of species loss. Many recent studies analyzing drivers of species extinction have generally used surrogates of extinction risk (e.g., human population density, economic activity, the extent of agricultural and urban land-area; (Davies et al., 2006; Luck et al., 2004)), or tried to identify the most vulnerable groups of organisms through non-spatial frameworks (i.e., through correlations with species life-

history traits; (Cardillo et al., 2008; Hutchings et al., 2012; Olden et al., 2007; Reynolds et al., 2005)). However, these approaches, mainly applied because of data deficiency on the spatial distribution of extinctions and threats (Joppa et al., 2016), prevent the direct assessment of the specific role of individual anthropogenic stressors in biodiversity loss (Clavero et al., 2010; Vörösmarty et al., 2010).

Riverine ecosystems are extraordinarily diverse (Balian et al., 2008; Tisseuil et al., 2013) and one of the most threatened habitats on Earth (Jenkins, 2003; Vörösmarty et al., 2010). Extinction risk for riverine fishes, for instance, is thought to be higher than that of terrestrial organisms (Ricciardi and Rasmussen, 1999) and recent extinction rate estimates for fish range from 130 to 855 times higher than natural extinction rates (Burkhead, 2012; Tedesco et al., 2013). For terrestrial organisms, estimating geographic variation in species loss is a challenging task mainly due to the lack of discrete boundaries on the landscape, but the extinction of fish populations from distinct river basins (i.e., closed systems; (Hugueny et al., 2010)) provides an opportunity to highlight the underlying drivers of geographical variation in species loss.

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Four major classes of direct anthropogenic drivers of biodiversity and ecosystem change can be distinguished (Millennium Ecosystem Assessment, 2005) and they hold true for riverine systems, affecting fish biodiversity to varying degrees (see reviews (Carpenter et al., 2011; Vörösmarty et al., 2010)). Habitat alteration (e.g., land-use, urbanization, deforestation) may reduce population sizes of resident species by decreasing the size of species natural habitat and increasing *in fine* the risk of species extinction (Giam et al., 2011). Habitat fragmentation (e.g., dams) reduces population sizes and gene flow of resident species and, more importantly, could block migrations of diadromous species, hence increasing their extinction risk (Carpenter et al., 2011; Reidy-Liermann et al., 2012). Introduced non-native species often compete with and/or prey upon native species, alter structure and functioning of riverine ecosystems (Blanchet et al., 2010) and are a key contributor to the ongoing biotic homogenization of these ecosystems occurring at the global level (Clavero et al., 2010; Villéger et al., 2011). Water pollution (e.g. nitrogen, phosphorus, pesticide and heavy metal loadings) leads either to direct mortality or jeopardises animal development and health, particularly in top predators following bioaccumulation within food web (pesticide and heavy metals loadings); besides, nitrogen and phosphorous loading enhance eutrophication and oxygen depletion (Carpenter et al., 2011). There are, however, few studies analyzing the specific role of each of these threats on fish extinction at large grains and extents (Clavero et al., 2010). In this sense, the intercontinental comparison of highly impacted regions containing independent extinction histories may shed light on the main drivers of species loss (Kerr et al., 2007). Moreover, understanding the differential response of fish species to distinct human threats is key to guide new policies concerning the conservation status of aquatic organisms and rivers.

In this study, we use a set of spatially explicit freshwater threats recently developed at the global extent (Vörösmarty et al., 2010), together with a uniquely comprehensive database of freshwater fish extinctions at the river drainage basin grain, to evaluate to what extent each of the main threats have promoted fish extinctions in the United States of America (USA) and western European river basins, two presumably well-studied regions where records of fish extinctions are available. We expect that i) riverine fish species, including resident and diadromous species groups, would present high current extinction rates compared to background rates, as human threats to aquatic biodiversity are pervasive along the studied regions; ii) our extinction metrics would be positively related to many of our selected anthropogenic drivers; iii) diadromous species loss would be more related to anthropogenic drivers linked to water resource development (e.g., river fragmentation), whereas water pollution, catchment disturbance and biotic factors would be the main determinants of resident fish species loss (Table 1).

2. Materials and methods

2.1. Biological data

The occurrence of fish species (both native and introduced species) was assessed based on a comprehensive spatial data set on global freshwater fish distribution at the river basin grain (Brosse et al., 2013). Freshwater fish extinctions were assessed using multiple complementary sources. For Western Europe (i.e., from Portugal to Petchora, Volga and Ural river basins in Russia), we further incorporated registers of fish extinctions per river basin using information from (Kottelat and Freyhof, 2007) completed by data from unpublished reports, scientific papers and Red Lists. For the USA, we used a comprehensive compilation of the extinction status of native freshwater fish data from (NatureServe, 2010) completed by data from (Burkhead, 2012) and (Jelks et al., 2008). Species were

considered extinct from a given basin when only historical records of their presence were reported throughout the hydrological units composing the river basin (see Table S1 in Supplementary Material). False zero extinction values are a potential bias inherent to this kind of data, mainly affecting small river basins that are most often under-studied. In order to minimize this potential bias, river basins having less than five registered species and less than 5000 km² in surface area were withdrawn from our dataset (85 small drainage basins). Lacustrine species were not considered. Because diadromous and resident species may have differential sensitivity to anthropogenic threats, and hence different responses in terms of species extinction, we analyzed separately these two components of fish assemblages. For all species, we therefore compiled information on their diadromous (i.e., anadromous and catadromous species; hereafter, diadromous), resident and body size status based on FishBase (Froese and Pauly, 2011). Fish species body size was based on maximum body length.

2.2. Computing fish extinction ratio

We computed the historical total native, resident and diadromous species richness for each river basin (Brosse et al., 2013; Froese and Pauly, 2011); we further calculated presence/absence, number (i.e., number of extinct species) and percentage of extinction in each river basin. The percentage of extinction was calculated as the number of extinct fish species divided by the total native fish species richness in each river basin. When separating diadromous and resident species, total native richness in each case was calculated accordingly (i.e., richness of diadromous species and richness of resident species).

When analyzing recent human induced extinctions it is important, however, to control first for natural extinction rates. Otherwise, estimates of ongoing natural and anthropogenic extinction rates could be confounded. To circumvent this problem, we also used Observed/Natural Extinction ratios per river basin. To obtain these ratios we relied on a highly accurate empirical riverine fish population extinction–area relationship previously established by (Hugueny et al., 2011) for the Northern Hemisphere to estimate the natural (i.e., background) extinction rates in river basins (see (Tedesco et al., 2013) for an application) and calculate Observed/Natural Extinction ratios during the last 110 years, assuming that human-related extinctions started approximately at this period (Burkhead, 2012; Miller et al., 1989).

The population extinction–area relationship proposed by (Hugueny et al., 2011) allows calculating the expected natural extinction rate per species per year, e , as a function of river drainage surface area, A (in km²):

$$e = f(A) = 1 - [1/\exp(cA^b)] \quad (1)$$

where $c = 0.0073$ and $b = 0.6724$. For a given drainage basin surface A , assuming species are identical with regard to extinction risk and that no colonization occurs from adjacent drainage basins, the expected natural number of extinct species over t years is given by:

$$E = SR_0 - SR_0[1 - e]^t \quad (2)$$

with e given by Eq. (1) and SR_0 being the initial species richness (see (Tedesco et al., 2013) for further details). Applying Eq. (2), we obtained the number of species extinctions expected under natural conditions over the last 110 years for each river basin. Finally, natural extinctions E were used to compute the extinction ratios per river basin by dividing the observed number of extinction by the expected natural extinctions. We then used this ratio as a response variable for testing the effects of our set of anthropogenic predictors. A potential source of underestimation for our background extinction rate could come from the model assumption that all species are identical with regard to extinction risk

(Hugueny et al., 2011). Indeed, species with restricted ranges within a drainage basin should display higher natural extinction rates than more widely distributed species (Saupe et al., 2015). There is no way, however, to include this parameter in the model at this time. Improving the model sensitivity in this regard will certainly refine our predictions.

2.3. Anthropogenic predictors

In a recent analysis of global threats to river biodiversity, (Vörösmarty et al., 2010) developed a set of spatially explicit variables (30 arc-second resolution) grouped in four broad categories (i.e. Catchment Disturbance, Pollution, Water Resource Development and Biotic factors) and reflecting the main stress-

Table 1
Stressors listed in (Vörösmarty et al., 2010) and their effects on river habitat and aquatic biodiversity.

Theme	Driver	Abbrev.	BD Weight ^a	Selected	Overall effects
Catchment disturbance	Croplands	Crop	0.31	X	Degrades and fragments local riparian habitats
	Impervious Surfaces	ImpSurf	0.25		Degrades local riparian and floodplain habitats, increases variability of flow
	Livestock Density	LivDens	0.18	X	Degrades local riparian and floodplain habitats, soil compaction, distorts flow patterns
	Wetland Disconnectivity	WDisc	0.26		Leads to losses of habitat, nutrient processing and retention, and organic matter inputs, distorts flow patterns
Pollution	Soil Salinization	SSalin	0.08		Causes osmoregulatory and ionic stress that can lead to chronic sub-lethal stress or mortality
	Nitrogen Loading	Nitr	0.12		Fosters eutrophication (and oxygen depletion)
	Phosphorus Loading	Phosph	0.13		Fosters eutrophication (and oxygen depletion), causes blooms of N-fixing cyanobacteria that can be toxic to aquatic animals
	Mercury Deposition	Mercur	0.05		Jeopardizes animal development and health, particularly in top predators following bioaccumulation within food web
	Pesticide Loading	Pestic	0.10	X	Imposes acute or chronic toxicity through a variety of mechanisms depending upon specific pesticide and dose, has indirect effects on species interactions and ecosystem processes
	Sediment Loading	Sedim	0.17		Increases water turbidity, alters benthic physical structure, interferes with respiration, breeding and vision of aquatic animals
	Organic Loading	Organ	0.15		Changes trophic state of rivers, fosters oxygen deficits, potentially releases toxic chemicals and nutrients
	Potential Acidification	PotAcid	0.09		Lethal and sub-lethal effects on sensitive taxa, increases solubility of certain toxic chemicals, has indirect effects on food availability for pH-insensitive taxa
	Thermal Alteration	TAlt	0.11		Alters habitat conditions, excludes native species, encourage invasion by non-native species, enhances susceptibility to eutrophication and oxygen depletion
Water Resource Development	Dam Density	DamD	0.25	X	Inundates riparian ecosystems, eliminates turbulent reaches, facilitates invasion by lentic biota, blocks animal movements, retains nutrients and sediment that contribute to downstream river and floodplain productivity
	River Fragmentation	Rfrag	0.30		Reduces population sizes and gene flow of aquatic species, restricts animal migrations. This factor was calculated using the GWSP-GRAND data set of georeferenced large dams and represents the proportion of each drainage basin that is accessible from a given grid cell. This factor thus summarizes the potential impact of river network fragmentation on fish populations.
	Consumptive Water Loss	CWLoss	0.22	X	Decreases contaminant dilution potential, reduces habitat area, distorts flow patterns
	Human Water Stress	HWStr	0.04		Decreases contaminant dilution potential, reduces habitat area, distorts flow patterns
	Agricultural Water Stress	AWStr	0.07		Decreases contaminant dilution potential, reduces habitat area, distorts flow patterns
	Flow Disruption	FlowDis	0.12		Retains nutrients, organic material, and fine particles, alters hydrological and thermal regimes

Table 1 (Continued)

Theme	Driver	Abbrev.	BD Weight ^a	Selected	Overall effects
Biotic Factors	Non-Native Fishes (%)	%Exot	0.26	X ^b	Competes with and/or preys upon native species, alters structure and functioning of ecosystems, may contribute to degradation of water quality
	Non-Native Fishes (#)	#Exot	0.21		Competes with and/or preys upon native species, alters structure and functioning of ecosystems, may contribute to degradation of water quality
	Fishing Pressure	FishPres	0.34		Alters community structure and can give rise to trophic cascades, induces behavioral changes, may contribute to degradation of water quality
	Aquaculture Pressure	AquaPres	0.19		Degrades water quality through concentrated chemical pollution, may alter habitat structure and flow, provides a source of non-native species

^a See Suppl. Inform. from (Vörösmarty et al., 2010).

^b This threat was computed based on our own data set (see Section 2.3. Anthropogenic predictors).

ors for freshwater organisms (Table 1). Based on the expertise of freshwater specialists, these authors also weighted the supposed biological importance of each stressor and aggregate them to obtain a synthetic Incident Biodiversity Threat index (hereafter IBT). We first used the IBT index to evaluate the potential link between overall aquatic threats and the pattern of fish extinction in river basins. In a second step, as our aim here was to assess the specific role of individual anthropogenic stressors in biodiversity loss, we extracted the two most weighted stressors within each category (except for the “Biotic factors” category where only one stressor was selected due to high collinearity between stressors) and computed their mean values for each drainage basin. This procedure selects a parsimonious subset of the most important stressors keeping low collinearity between them. As we extracted stressor values at the sub-drainage scale (Lehner et al., 2006), our mean value for the entire drainage basin was calculated by averaging values of all sub-drainages constituting the drainage basin, weighted by their respective surface area. This surface-related weighting procedure assures better estimates of mean threats per drainage basin when heterogeneity in threat level is important among sub-drainages (e.g., without weighting by sub-drainage surface, a small, highly-impacted sub-drainage would contribute most to the overall drainage threat mean). We relied on the Fish-SPRICH database (Brosse et al., 2013) to compute the invasion threats. Therefore, these stressor values were rescaled to vary between 0 and 1 using the same Cumulative Distribution Function approach adopted by (Vörösmarty et al., 2010) (and Supplementary Information therein). Selected stressors and their putative effects on fish extinctions are listed in Table 1.

2.4. Data analysis

Presence-absence of fish extinction: we assigned “1” to river basins in which the presence of at least one fish extinction has been recorded whereas those without fish extinction records were set to “0”. This qualitative approach is useful because the whole drainage basin is only assigned to “0” if none of its fish species have been recorded as extinct, therefore minimizing the detection failure of fish extinction. We then modeled the presence/absence of fish extinction on river basins by applying Generalized Linear Models (GLMs) with Bernoulli error distribution (*logit* link function). The surface area and total native fish richness of each drainage basin (both \log_{10} -transformed, centered and scaled so that they have zero mean and unit standard deviation) were also included as predictors in the model as the surface area of a drainage basin is supposed to be negatively linked to species extinction rates (Hugueny et al., 2011)

and as extinction probability is supposed to be positively linked to species richness.

Percentage of fish extinction: we modeled the percentage of fish extinction (i.e., number of extinct species divided by the total number of species) against our selected stressors using Generalized Linear Models with Beta-Binomial error distribution (*logit* link function). This model is equivalent to fitting Binomial GLM in which the probability of success and its variance are Beta distributed (Zuur et al., 2015). The Beta-Binomial GLMs are useful here as they allow modeling proportions ranging from 0 to 1 as a function of stressors while controlling for overdispersion (i.e., more variability than expected under the classic Binomial GLM) on the response variable. Total native fish species richness (\log_{10} -transformed, centered and scaled) was also included in the model to control for potential bias in % values of fish extinction due to differences in overall species richness between drainage basins.

Number of fish extinction: we modeled the number of extinction events (i.e., fish extinction count per river basin) by fitting GLMs with Negative-Binomial error distribution (*log* link function). This is equivalent to fitting GLMs with Poisson error distribution, but the Negative-Binomial distribution explicitly integrates data variability and avoids over-dispersion due to high frequencies of small numbers and zeros on the response variable. Additionally, both the (\log_{10} -transformed, centered and scaled) surface area and total fish richness of each basin were included as predictors as large basins tend to display high overall species richness and thus high number of fish extinction events.

Observed/natural extinction ratios: we further modeled the observed/natural extinction ratios against our selected stressors using Ordinary Least Square (OLS) with Gaussian error distribution (*identity* link function). The Observed/Natural extinction ratios were \log_{10} -transformed before modeling. In this case, the surface area of the river basin was not included as it was directly taken into account when calculating extinction ratios (see Section 2.2, and Eq. (1)).

As extinctions were established from the past 110 years and as (Vörösmarty et al., 2010) anthropogenic factors represent a portrait of conditions from the mid-1990s to about 2005, extinctions could be related to events (i.e. anthropogenic disturbances) that had happened back in time. To evaluate this possibility we further introduced in our models a human demographic factor (i.e., the mean annual rate of increase in human population density between 1900 and 2000 per river drainage basin [calculated as the $\log_{10}(\text{density } 2000 - \text{density } 1900)/100$] using data from (Klein Goldewijk et al., 2011)). Although not all types of impact are necessarily associated with the human density, this factor is usually a reliable synthetic

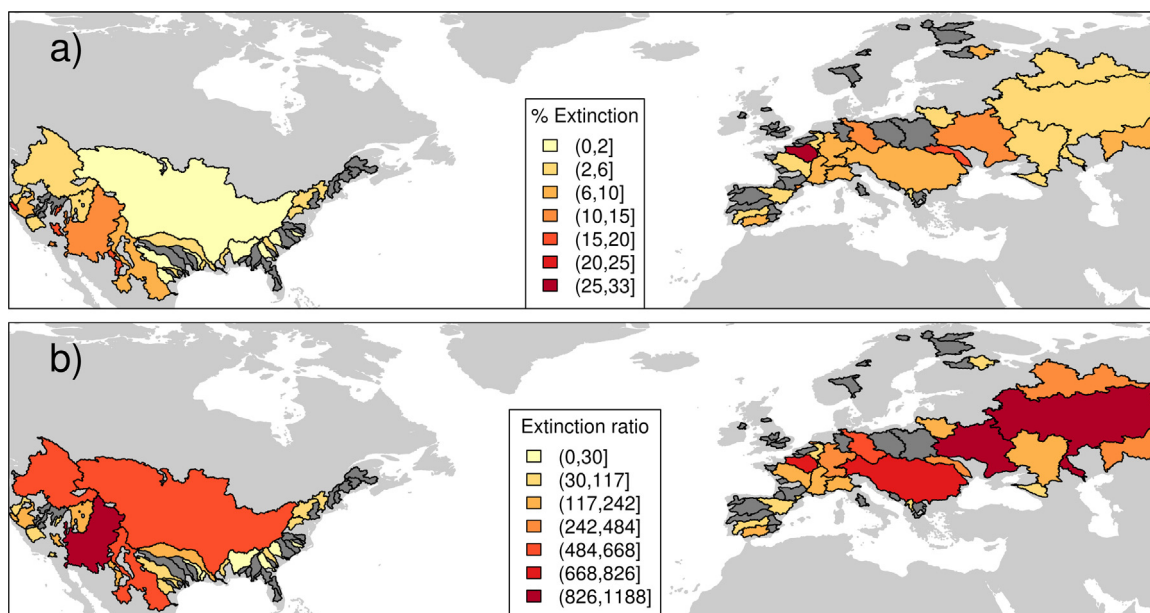


Fig. 1. Percentage of extinction (a) and Observed/Natural extinction ratios (b) of total fish species per river basin for the USA and Western Europe. Dark-gray polygons represent basins where no extinction has been recorded.

proxy for biological threat over broad spatial scales (Cardillo et al., 2004). Two European river basins (Dordogne and Shannon-Ireland) showed a decrease in human population densities during the last century, and have been excluded from the data set.

A binary covariate distinguishing USA (0) and European (1) river basins was included in all models (i.e., presence/absence, count, percentage and extinction ratio) to assess differences in fish species loss among continents. Collinearity among predictors was assessed with the Variance Inflation Factor (VIF) in all models; although there are no canonical rules of thumb, VIF values <10 are acceptable and indicate low collinearity among predictors (Dormann et al., 2012). Models were built considering all species and then separating diadromous from resident species to investigate differences in extinction rates for both groups of species. Finally, we used a Linear Mixed-Effect Model (LMM, (Zuur et al., 2009)) with species as sampling points in order to test for differences in maximum body size between extinct and extant species and explicitly included a random hierarchical effect of Order/Family/Genus. Such random hierarchical structure is useful to control for potential differences in body size related to taxonomic effects (i.e., a proxy for phylogenetic effects) as species from the same genus often share similar body sizes compared to species from distinct genera and families.

The significance of all predictors was determined by dropping individual variables by applying Likelihood Ratio Tests (LRT), and, in order to be conservative, significance was set at $p < 0.01$. We further calculated the pseudo- R^2 using null and residual deviances from GLM models as a measure of model fit (Zuur et al., 2009). All analyses and graphics have been performed under R environment (R Core Team, 2013) using glmmADMB (Skaug et al., 2015) and MASS (Venables and Ripley, 2002) packages.

3. Results

3.1. Overall estimates

A total of 934 species inhabiting 111 river basins were analyzed (see Table S1 in Supporting Material), representing 73% of the total number of species listed in (Brosse et al., 2013) for both Western Europe and the USA. Among all river basins (mean = 1.063 species extinction by river; $sd = 1.66$; range = 0–8), 50 have suf-

fered, at least one species extinction (mean = 2.36 extinctions; $sd = 1.75$; range = 1–8). For USA, the highest numbers of species extinction are found in the Mississippi (8), Grande (6) and Red (5) river basins whereas for Western Europe the highest numbers of species extinction are found in the Dnepr (7), Seine (5), Dnepr (5), and Danube (4) river basins. IBT values vary from 0.15 to 0.98 (mean = 0.79; $sd = 0.18$), showing that all river basins analyzed are somehow disturbed and many of them highly altered by human activities. The mean percentage of species extinction per river basin is 3.4% ($sd = 5.9\%$; range = 0–33%, 1st quartile = 0, 3rd quartile = 4.94, median = 0; Fig. 1a).

The Observed/Natural extinction ratios show that fish species extinctions in the last century are, on average, 112 times ($sd = 238$, median = 0, range = 0–1188; 1st quartile = 0, 3rd quartile = 91) higher than expected under natural conditions, although many river basins have no recorded species extinctions. Among the 50 river basins with non-zero extinction values, the Colorado (1112), Grande (668), and Mississippi (553) river basins in USA and the Dnepr (1188), Volga (1047), and Danube (826) river basins in Europe show the highest Observed/Natural extinction ratios (Fig. 1b).

Finally, no difference in mean body size was found between extant and extinct species (LMM: LRT = 0.13, $p = 0.72$; Fig. 2), after controlling for potential taxonomic effects.

3.2. Model results

Neither the Incident Biodiversity Threat index nor the rates of increase in human population density are significantly related to fish extinctions, whatever the adopted response variable (i.e. presence/absence, count, % of extinctions or Observed/natural extinction ratios) (Table 2a). In turn, the total surface area of the drainage and its total native species richness, when entered in the models, are both and often positively related to fish extinctions. According to the Observed/Natural extinction ratios model, diadromous species loss was higher in Europe compared to USA.

When analyzing individual threats, results vary depending on the response variable (Table 2b). For presence/absence models, both variables total surface area of the drainage and total native species richness are most of times significantly and positively

Table 2

Summary (parameters and standard error) of Presence/Absence (Bernoulli), Proportion (Beta-Binomial), Count (Negative-Binomial) GLMs and Extinction Ratio (Gaussian, Ordinary Least Square) models relating extinction to combined (a)), and individual (b)) anthropogenic threats in the USA and European river basins. Models have been fitted for Total (N = 111 river basins), Diadromous (N = 109) and Resident (N = 102) fish species. Small values of the Variance Inflation Factor (VIF) indicate colinearity is not affecting model results.

a)	P/A			Proportion			Count			Extinction Ratio		
Composed Threats	Total	Diad	Res	Total	Diad	Res	Total	Diad	Res	Total	Diad	Res
(Intercept)	0.31(1.36)	−3.69(1.93)	−2.63(1.52)	−2.77(0.92)	−5.63(1.64)	−2.87(1.09)	−1.39(0.87)	−4.29(1.61)	−2.82(1.09)	0.86(0.55)	0.43(0.6)	0.34(0.47)
HumanDensity.dif (log)	0.15(0.27)	0.48(0.3)	−0.51(0.46)	−0.02(0.17)	0.1(0.19)	−0.53(0.35)	0.05(0.17)	0.34(0.22)	−0.53(0.35)	−0.07(0.12)	0.05(0.12)	−0.16(0.11)
Incbed Threat	−0.72(1.74)	−1.78(1.82)	−1.26(2.1)	−0.56(1.01)	−0.6(1.28)	−1.86(1.48)	0.11(1.06)	−1.35(1.39)	−1.09(1.48)	0.1(0.69)	0.33(0.74)	0.22(0.58)
Continent(USA = 0, EU = 1)	−0.36(0.31)	0.23(0.27)	−0.18(0.43)	0.31(0.2)	0.26(0.19)	0.28(0.3)	−0.05(0.19)	0.06(0.19)	0.09(0.32)	0.03(0.11)	0.3(0.11)**	−0.21(0.09)*
Surface area (log10)	1.53(0.35)**	1.14(0.33)**	0.51(0.3)P	–	–	–	0.61(0.14)**	0.58(0.17)**	0.31(0.17)P	–	–	–
Species richness (log10)	0.02(0.38)	1.71(0.68)**	0.79(0.36)*	−0.14(0.54)	2.79(1.36)*	0.28(0.55)	0.32(0.23)	1.82(0.59)**	0.87(0.26)**	–	–	–
VIF	1.68(0.35)	1.22(0.19)	1.86(0.57)	1.03(0.02)	1.51(0.49)	1.03(0.01)	1.84(0.52)	1.32(0.22)	1.92(0.73)	1.19(0.16)	1.19(0.16)	1.18(0.16)
R ² (%)	23	30	21	2	5	4	29	38	43	0	5	4
Dispersion Parameter	–	–	–	28.45(10.81)	15.53(7.54)	51.39(30.63)	1.63(0.73)	1.38(0.73)	1.49(1.01)	–	–	–
Residual	–	–	–	–	–	–	–	–	–	1.12	1.12	0.93
b)	P/A			Proportion			Count			Extinction Ratio		
Individual Threats	Total	Diad	Res	Total	Diad	Res	Total	Diad	Res	Total	Diad	Res
(intercept)	−2.3(2.15)	−6.07(2.05)	−8.15(2.54)	−4.32(1.06)	−5.14(1.57)	−6.3(0.99)	−1.34(1.29)	−5.21(1.61)	−7.51(1.65)	0.94(0.1)	0.69(0.1)	0.49(0.09)
HumanDensity.dif (log)	0.11(0.34)	0.4(0.39)	−1.03(0.56)*	−0.07(0.19)	0.18(0.25)	−0.77(0.38)*	0.09(0.2)	0.33(0.28)	−0.89(0.4)*	−0.14(0.14)	0.08(0.15)	−0.28(0.13)*
Crop	−0.31(0.63)	−0.57(0.8)	−1.82(0.85)*	−0.03(0.37)	0.49(0.61)	−1.05(0.46)*	0.26(0.36)	0.41(0.6)	−1.1(0.47)*	0.12(0.27)	0.3(0.27)	−0.25(0.23)
Wdisc	−0.13(0.31)	−0.02(0.42)	−0.38(0.36)	−0.13(0.18)	0.07(0.29)	−0.17(0.24)	−0.04(0.17)	−0.23(0.31)	−0.07(0.2)	0.01(0.12)	0.09(0.13)	−0.08(0.11)
Sedim	0.95(0.56)P	1.1(0.68)P	1.3(0.86)P	0.21(0.29)	0.16(0.4)	0.75(0.54)	0.47(0.35)	0.42(0.43)	0.5(0.51)	0(0.22)	−0.06(0.22)	0.23(0.18)
Organ	−1.28(0.88)	−1.02(1.08)	−0.79(1.06)	−0.48(0.46)	−0.92(0.74)	−0.45(0.69)	−0.59(0.49)	−0.89(0.72)	−0.6(0.65)	−0.07(0.36)	−0.08(0.36)	0.08(0.3)
Rfrag	−0.09(0.32)	−0.19(0.38)	0.49(0.43)	0.24(0.18)	0.23(0.22)	0.29(0.26)	0.15(0.19)	−0.19(0.27)	0.28(0.24)	0.35(0.12)**	0.29(0.12)*	0.3(0.11)**
CWLoss	0.56(0.53)	0.37(0.69)	0.49(0.6)	0.1(0.29)	0.16(0.45)	0.16(0.36)	−0.18(0.3)	0.02(0.47)	0.33(0.35)	−0.04(0.19)	−0.22(0.2)	0.02(0.17)
%Exot	0.32(0.34)	0.34(0.37)	0.91(0.51)P	0.56(0.21)**	0.26(0.26)	0.75(0.3)**	0.18(0.2)	0.22(0.25)	0.75(0.31)*	0.22(0.13)P	0.21(0.14)	0.08(0.11)
Continent(USA = 0, EU = 1)	0.06(0.47)	0.43(0.45)	1.38(0.81)P	0.62(0.24)**	0.52(0.29)P	1.07(0.38)**	0.08(0.3)	0.07(0.3)	1.55(0.54)**	0.19(0.14)	0.45(0.14)**	−0.15(0.12)
Surface area (log10)	1.52(0.41)**	1.34(0.4)**	−0.09(0.49)	–	–	–	0.58(0.2)**	0.73(0.22)**	−0.34(0.28)	–	–	–
Species richness (log10)	0.62(0.64)	2.1(0.85)**	2.24(0.82)**	0.5(0.69)	1.75(1.46)	1.54(0.67)*	0.31(0.38)	1.71(0.65)**	2.1(0.52)**	–	–	–
VIF	4.71(3.98)	4.5(4.41)	5.27(3.75)	1.05(0.02)	1.45(0.47)	1.34(0.25)	4.68(3.08)	4.2(3.86)	5.88(4.19)	3.98(3.66)	3.88(3.49)	3.8(3.36)
R ² (%)	28	34	35	9	8	16	34	42	55	8	11	11
Dispersion Parameter	–	–	–	41.32(17.8)	17.67(9.17)	105.01(69.3)	1.83(0.83)	1.43(0.72)	4(4.95)	–	–	–
Residual	–	–	–	–	–	–	–	–	–	1.06	1.08	0.89

P 0.05 < p < 0.10.

** p < 0.01.

* 0.01 < p < 0.05.

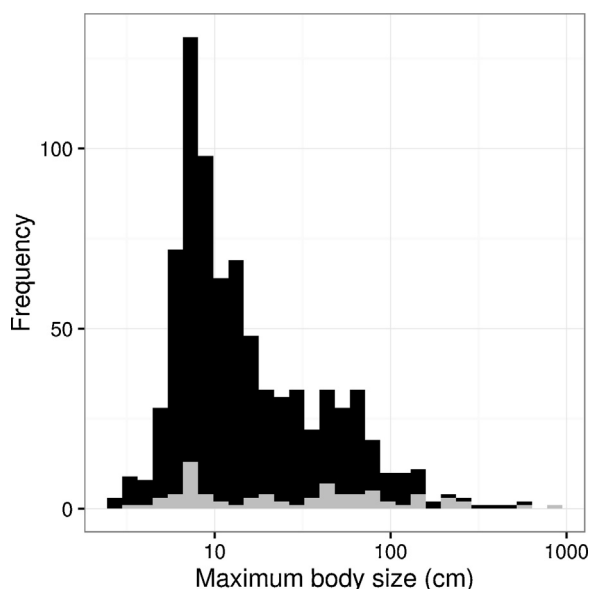


Fig. 2. Maximum body size-frequency (Total length, in cm) distribution of all (black), and extinct (gray) fish species found in both European continent and the USA.

related to extinctions. For proportion models, basins with higher proportion of exotic species have higher total and resident fish extinctions (Fig. 3a). Still, European continent show higher total and resident fish loss compared to USA. For count models, total surface area of the drainage and total species richness are both often significantly and positively related to fish extinctions; still, the number of resident fish extinction in Europe is higher compared to USA. Finally, when using Observed/Natural extinction ratios, river fragmentation is significantly and positively related to total and resident fish extinctions (Fig. 3b); still, Europe has higher diadromous extinction ratios compared to the USA.

4. Discussion

This work provides the first large-scale analysis of the relationships between riverine fish extinction and anthropogenic threats. To do so we focused on river basins from Western Europe and the USA, two of the most heavily impacted regions on Earth and benefiting from documented information on the extinction status of riverine fish species (Burkhead, 2012; Freyhof and Brooks, 2011; Jelks et al., 2008; Kottelat and Freyhof, 2007; NatureServe, 2010). In general, when considering only presence/absence or extinction numbers, almost 50% of the drainage basins analyzed here have suffered extinctions and these extinctions seem to have occurred preferentially in large rivers (i.e., Mississippi, Grande and Red river basins for the USA and Dnestr, Seine, Dnepr and Danube river basins for Western Europe).

When considering extinction rates, Observed/Natural extinction ratios show that fish species extinctions in the last century are, on average, 112 times higher than expected under natural conditions. The average 112-fold increase of extinction rates observed here includes all river basins; i.e., those affected by species extinctions as well as those with no recorded extinction. For this reason, the average increase in extinction rate is lower compared to recent estimates for the Nearctic fish fauna made by (Burkhead, 2012) and (Tedesco et al., 2013) (respectively 855 and 130 times higher than natural extinction rates). Contrary to our study, (Tedesco et al., 2013) considered only river basins affected by species extinctions, while (Burkhead, 2012) did not use river basins as spatial sample units. Our estimated average increase in fish extinction rates is thus clearly conservative compared to the estimates made

by these authors. Indeed, when focusing only on drainage basins impacted by species extinctions in our database, extinction rate estimates increased and reached similar levels as the ones observed by (Burkhead, 2012) (up to 998 times; Fig. 1b). Following these results, there is no doubt that biodiversity of freshwater fish is increasingly threatened (Burkhead, 2012; Dudgeon et al., 2006; Olden et al., 2007; Ricciardi and Rasmussen, 1999; Tedesco et al., 2013).

Our results are, however, somewhat weak when trying to disentangle the role of the most well-known anthropogenic drivers (Dudgeon et al., 2006; Jelks et al., 2008) in driving fish species loss. Indeed, our statistical models lead to several conclusions. First, whatever the response variable used (i.e. presence/absence of extinction, number of extinction, percentage of extinction and Observed/natural extinction ratios), we found no significant link between the Incident Biodiversity Threat (IBT) index developed by (Vörösmarty et al., 2010) and the loss of riverine fish diversity. Hence, our results suggest that the IBT is too coarse to predict fish extinctions at the drainage basin grain.

Second, when individual threats were included in the models, we found a nearly systematic positive relationship with the size of the river drainage basin. This result is unexpected as ecological theory predicts that large areas support more individuals through high habitat diversity and availability, and should thus show lower species extinctions rates (MacArthur and Wilson, 1967; Williamson, 1988). Three explanations can be invoked for this surprising pattern. The size of rivers co-varies with important anthropogenic stressors not accounted for in our study. This explanation seems quite doubtful as we used here, as explanatory factors, the most widely known biotic and abiotic threats to fish biodiversity (reviewed in (Dudgeon et al., 2006; Vörösmarty et al., 2010)). Compared to small rivers, large rivers host higher number of small-sized species (Tedesco et al., 2012). Small-sized species have generally small range size (Pyrön, 1999; Tales et al., 2004) and are thus supposed to be more prone to extinction (Reynolds et al., 2005). If the extinct species analyzed here were preferentially small-bodied species, then a positive relationship between fish extinctions and river size would be expected. However this potential explanation is unlikely as no difference in maximum body size distribution was found between the overall set of species and the set of extinct ones. Another possibility is that only large river basins have well documented fish extinctions. Although we tried to control for this potential bias by only selecting river basins larger than 5000 km², this last explanation, even if likely, remains to be further evaluated.

Third, when accounting for natural extinction rates, which seems, in our opinion, the best way to analyze human driven extinction patterns, only river fragmentation by dams was found to play a significant, yet weak, role in explaining current patterns of fish extinction. Dams act directly on the degree of connectivity between species sub-populations by decreasing the permeability and availability of habitat within drainages (Luttrell et al., 1999; Pelicice et al., 2015; Rahel, 2007). Furthermore, dams eliminate the natural flow dynamics of rivers (Poff et al., 2007) to which freshwater fish assemblages are tightly adapted (Mims and Olden, 2012; Olden et al., 2006). These new conditions affect meta-population dynamics both directly and indirectly by decreasing the size of sub-populations (Alò and Turner, 2005) and the overall genetic pool (Sterling et al., 2012), thus leading to fish species extinction (Hugueny et al., 2011; Perkin and Gido, 2011; Perkin and Gido, 2011). Moreover, our results also suggest an increase in extinction rates only for resident fish species in rivers highly fragmented by dams. Interestingly, this finding challenges the common idea that diadromous rather than resident fish species should be the most affected by dams. Diadromous species may be affected by the creation of physical barriers that make accessing spawning and

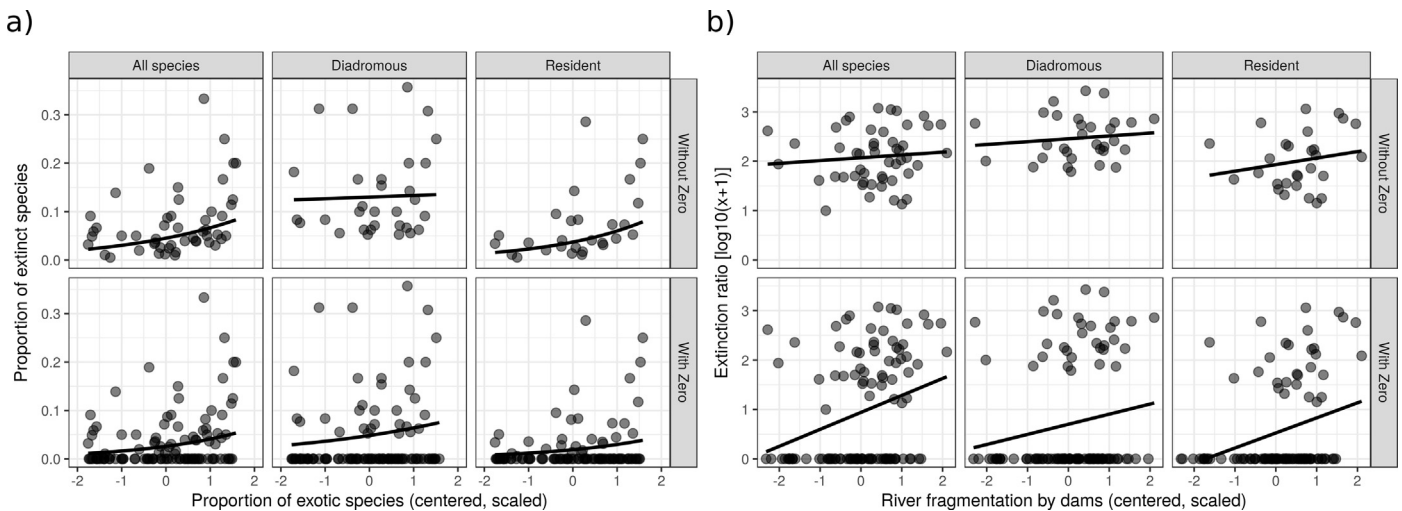


Fig. 3. Relationship between the percentage of fish extinction and the proportion of exotic fish species per basin (a), and between the extinction ratio and the threat river fragmentation by dams (b) for the entire dataset, diadromous and for resident species. We plotted data with and without zero values, and included the trend lines (assuming a) GLM with Binomial, and b) OLS with Gaussian distributions) to improve visualization. Significance of trend lines for data including zero values can be found in models from Table 2b.

feeding grounds difficult (Reidy-Liermann et al., 2012). However, diadromous species might overcome such fragmentation levels by crossing dams through fish passes (but see (Brown et al., 2013)), reproduce in remnant free-flowing river sections (as suggested by theoretical population models (Jager et al., 2001)) and/or benefit from effective conservation efforts undertaken within the two regions (Vörösmarty et al., 2010). On the other hand, resident species, which tend to be more restrictive in their habitat requirements, may be shrinking as a result of damming which creates barriers to movement and isolates populations in different sub-basins (Luttrell et al., 1999). Overall, the negative effects of dams on fish biodiversity highlighted here have important conservation implications as the number of large dam constructions is strongly increasing in tropical regions (Finer and Jenkins, 2012; Lehner et al., 2011; Ziv et al., 2012) where freshwater diversity is concentrated (Oberdorff et al., 2011; Tedesco et al., 2012; Tisseuil et al., 2013).

Fourth, when using extinction descriptors other than Observed/Natural extinction ratios (i.e., presence/absence, number or % of extinctions), none of our selected anthropogenic stressors had significant effects on extinction patterns, except the percentage of non-native species when modeling the % of extinctions. The introduction of non-native species outside their native range is considered one of the potentially leading threats to contemporary biodiversity (Sala et al., 2000), including to riverine fish biodiversity (Clavero et al., 2010; Leprieur et al., 2009, 2008). Nevertheless, the fact that this biotic stressor is no more significant when using extinction ratios rises a doubt on the importance of such a threat in generating significant fish extinctions, at least at the river basin grain.

Finally, we found no link between the rate of increase in human population density and the loss of riverine fish diversity. This last result minimizes the possibility of a mismatch between the temporal ranges of our threats predictors and extinction events in explaining the poor correlations found between our stressors and extinction patterns.

As with any large-scale analysis, the findings of the current study are dependent on both the completeness and the accuracy of the data underpinning it. There are a number of issues with both the biological and the threats datasets that could have weakened our results. Concerning the threat dataset, though the drivers listed in (Vörösmarty et al., 2010) represent a state-of-the-art summary of global scale geospatial data on threats to riverine systems, they

suffer from limitations imposed by uncertainties in some drivers, differences in the spatial scale of the original data (e.g., country versus grid cells), spatial resolution for gridded source data (e.g., 1 km versus 30'), and the basic quality of original data sets (Vörösmarty et al., 2010). Concerning our biological dataset, even if we focused on two well-studied regions where supposedly good quality records of fish extinctions are available, we cannot discard the possibility of having missed fish extinctions.

In our opinion, the most probable explanation for the weak effects found here between human stressors and extinction patterns comes from limitations of both biological and threat datasets currently available. If this is indeed the case, there is then an urgent need to increase regional-scale research and monitoring in order to obtain realistic estimates on extinctions and anthropogenic threats in individual river basins. Without realistic estimates of biodiversity loss and of the major threats to biodiversity we will have difficulties in proposing appropriate actions to avert the current trends in species loss. Filling in biodiversity threat gaps should be a priority (Joppa et al., 2016).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolind.2017.03.053>.

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