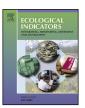
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Original Research paper

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 \sim 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):

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

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

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

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