



Cross-continental evaluation of landscape-scale drivers and their impacts to fluvial fishes: Understanding frequency and severity to improve fish conservation in Europe and the United States



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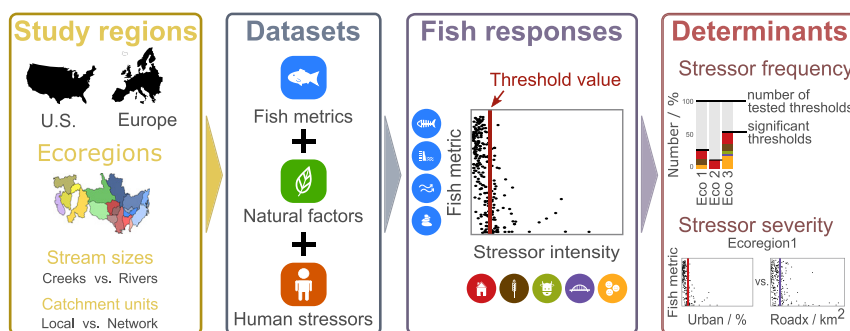
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HIGHLIGHTS

- Cross-continental analysis of more than 30,000 fish sampling sites
- Hundreds of negative fish responses to human stressors were identified in the U.S and Europe.
- Urbanization was one of the most pervasive human landscape stressors.
- Fish metrics most sensitive to human landscape stressors were identified.

GRAPHICAL ABSTRACT



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ABSTRACT

Fluvial fishes are threatened globally from intensive human landscape stressors degrading aquatic ecosystems. However, impacts vary regionally, as stressors and natural environmental factors differ between ecoregions and continents. To date, a comparison of fish responses to landscape stressors over continents is lacking, limiting understanding of consistency of impacts and hampering efficiencies in conserving fishes over large regions. This study addresses these shortcomings through a novel, integrative assessment of fluvial fishes throughout Europe and the conterminous United States. Using large-scale datasets, including information on fish assemblages from more than 30,000 locations on both continents, we identified threshold responses of fishes summarized by functional traits to landscape stressors including agriculture, pasture, urban area, road crossings, and human population density. After summarizing stressors by catchment unit (local and network) and constraining analyses by stream size (creeks vs. rivers), we analyzed stressor frequency (number of significant thresholds) and stressor severity (value of identified thresholds) within ecoregions across Europe and the United States. We document hundreds of responses of fish metrics to multi-scale stressors in ecoregions across two continents, providing rich findings to aid in understanding and comparing threats to fishes across the study regions. Collectively, we found that lithophilic species and, as expected, intolerant species are most sensitive to stressors in both continents, while migratory and rheophilic species are similarly strongly affected in the United States. Also, urban land use and human population density were most frequently associated with declines in

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fish assemblages, underscoring the pervasiveness of these stressors in both continents. This study offers an unprecedented comparison of landscape stressor effects on fluvial fishes in a consistent and comparable manner, supporting conservation of freshwater habitats in both continents and worldwide.

1. Introduction

Nearly all of the world's landscapes are drained by rivers, and riverine ecosystems are a complex product of the landscapes which they drain (Hynes, 1975). Rivers are formed by intricate networks incorporating vast ranges of habitats with tremendous potential to support biodiversity and represent essential sources of environmental health, economic wealth, and human well-being (Allan et al., 1997; Grill et al., 2019). In spite of the prevalence of rivers globally and their role in supporting numerous ecosystem services (Grizzetti et al., 2016; Millennium Ecosystem Assessment, 2005; Vollmer et al., 2018), freshwater biodiversity is poorly studied relative to marine and terrestrial biota (van Rees et al., 2020). This contributes to a greater problem as riverine ecosystems have experienced the largest decline in biodiversity globally in recent decades, leading to disproportionate threats to rivers (Abell et al., 2017; Dias et al., 2017; Maasri et al., 2021). As a consequence, freshwater biodiversity decline and the increasingly imperiled status of river fishes have turned into a global crisis (Reid et al., 2019; Su et al., 2021; Tickner et al., 2020).

Human-mediated drivers and pressures (Friberg, 2010; Hering et al., 2015; Perujo et al., 2021), often operating throughout river catchments, are most often responsible for declines in fluvial fishes (Allan, 2004; Schinegger et al., 2016a). Main drivers relate primarily to agriculture or urbanization, resulting in pressures as in-stream, riparian, and floodplain habitat degradation and fragmentation; altered hydrology and thermal regimes; migration barriers; and water quality problems in streams and rivers. All these pressures impact the inhabiting fish assemblages (Allan, 2004; Blevins et al., 2013; Dudgeon, 2019; Wang et al., 2001). Declines in fishes resulting from such pressures can lead to changes in assemblage structure including loss of fishes with particular functional traits, such as specific habitat preferences, unique reproductive strategies, and/or low tolerances to pressures. Consequently, evaluating changes in fish assemblages represented by functional traits can yield specific insights into outcomes of degradation from drivers and pressures (Hughes et al., 1998; Su et al., 2021), which we from here on call “human stressors” in this manuscript.

Recently, many studies assessing changes in fluvial fish assemblages with human stressors have been undertaken in different regions of the world, for example Europe (Mueller et al., 2020; Schinegger et al., 2016a), the United States (Cooper et al., 2017; Esselman et al., 2011), China (Xiong et al., 2021), South America (Leal et al., 2017) and Australia (Mantyka-Pringle et al., 2014). These regional studies broadly underscore the fact that increasing types and intensities of human stressors can lead to losses in numbers of fishes and specific functional traits. However, their results typically cannot be directly compared. Regional studies have generally been conducted with different analytical approaches to test for fish responses to stressors; also, in some cases, studies assess fish response to stressors summarized in different spatial units (i.e., river catchments vs. buffers). An additional factor confounding the comparison of results from these studies stems from the fact that influences of natural landscape factors such as geology and climate can mediate or exacerbate stressor effects on fluvial fishes (Utz et al., 2010). This lack of comparability leaves a major gap in understanding large-scale influences of landscape stressors on fluvial fishes, limiting efforts to identify and apply effective conservation actions over large regions.

In recent years, multiple large-scale efforts have occurred to assess the condition of freshwaters globally (e.g., Dias et al., 2017; Feio et al., 2021; Grill et al., 2019; Mulligan et al., 2020) with the major advantage of identifying general patterns in frequency and intensity of stressors affecting freshwaters and the organisms they support. While such studies have been supported by advances in the availability of geospatial data and in

computational power, the coarse resolution of data used for these efforts lacks the specificity needed to identify fine-scale patterns in freshwater stressors occurring over continental and especially global scales. In contrast to the regional studies described above, quantitative data-driven approaches for evaluating fish responses to stressors across broad scales are largely lacking. Chen and Olden (2020) analyzed threshold responses of fluvial fish communities to land use conversion across regions of the world. This study identified differences in threshold responses to urban and agricultural land use across large regions and demonstrated the need to assess fish-human stressors relationships at broad spatial extents. However, the continued absence of fine-scale information from such studies prevents the ability to identify specific mechanisms leading to impairment of freshwater habitats and to understand regional differences in fish responses to various stressor impacts. Su et al. (2021) investigated human impacts on global freshwater fish biodiversity by assessing the extent to which six key indicators – taxonomic, functional, and phylogenetic richness, plus the dissimilarity in each of these categories across river basins – have changed over the past two centuries in 2456 river basins, covering almost the entire continental surface of Earth and hosting >14,000 species. However, that study was conducted at basin-scale and while it identified changes in fish richness, it did not identify the drivers of these changes. Overall, the limitations of these prior regional and large-scale studies collectively underscore the need for efforts that more directly characterize stressor effects on freshwaters at cross-continental scales. Further, they show the need to expand the focus from simple loss of species to integrate changes in facets of biodiversity, including which organisms are most sensitive to stressors, which stressors are most limiting, and how sensitivity might vary by region.

To address limitations related to comparability of regional studies and by taking advantage of comparable datasets at large-scales, our study's goal was to assess the impacts of human stressors on fluvial fish assemblages in a consistent, comparable manner across Europe and the conterminous United States. According to Dias et al. (2017), understanding how humans can influence fish assemblages, including how they may reduce abundances or lead to eventual species or trait loss, is essential to mitigate those changes and develop effective scenarios of future changes in global freshwater biodiversity. We contribute to this need by considering responses of fishes as summarized by key functional traits which we theorized should result into similar mechanistic responses of fish assemblages to stressors in both continents. We consider two determinants to quantify the impact of human landscape stressors in our investigation. The first is stressor frequency, reflecting how commonly a given landscape stressor yields a detectable, negative response in stream fish assemblages. The second is stressor severity, which reflects the intensity at which a given human stressor causes a negative response in fish assemblages. We analyzed these determinants using fish data assembled from over 30,000 locations across the continent of Europe and the conterminous United States. We constrained our analyses by the Freshwater Ecoregions of the World (Abell et al., 2008) and stream size (creeks and rivers based on the network catchment area) to account for a large amount of variation in natural landscape influences which are expected to affect fishes across our study regions. Controlling for these factors allows us to more rigorously detect how human stressors lead to changes in fish assemblages. Further, we tested stressors aggregated by different catchment units (local and network catchment) to account for impacts of stressors operating over different scales. These steps allowed us to test our hypotheses that stressor frequency and stressor severity vary between biogeographical zones (continent, ecoregion, and stream size) and spatial dimensions (catchment unit). Such information can contribute to our understanding of fish response to

stressors for large spatial extents and can aid in efforts to inform the protection and restoration of freshwater biodiversity and to conserve freshwater fishes globally.

2. Methods

2.1. Defining a spatial framework

The study regions extend over the conterminous United States (U.S.) in North America and the European continent (Figs. 1 and 2). For analyses, these study regions were subdivided into freshwater ecoregions (Freshwater Ecoregions of the World) to better account for natural differences in the distributions of fish assemblages across the U.S. and Europe (see supplementary information (Supp.)). Within ecoregions, stream reaches represent the smallest spatial units of analysis and were defined as stream sections between two confluences (Supp.; Wang et al., 2011). We used two different catchment units (Fig. 1) to summarize natural landscape and human stressor characteristics (Appendix A Table A.1) for our analyses. The local catchment (LC) was defined as the area draining directly into the stream

reach, and the network catchment (NC) is defined as the entire area draining into the stream network upstream of and directly into the stream reach (Wang et al., 2011). We used the National Hydrography Dataset Plus V1 (NHDPlusV1; U.S. EPA and USGS, 2010) for the U.S. and the Catchment Characterisation and Modelling River and Catchment Database, Version 2.0 (CCM2; Vogt et al., 2007) for Europe to define stream reaches and to delineate local and network catchments. For our analyses, only stream reaches with a fish sampling site were considered. To aid in accounting for the known influence of stream size on numbers and types of fishes (Goldstein and Meador, 2004), stream reaches were classified into two size groups based on network catchment area (Lyche Solheim et al., 2019; Wang et al., 2011): creeks (C; $\leq 100 \text{ km}^2$) and rivers (R; $>100 \text{ km}^2$; Fig. 1). Analyses within ecoregions were conducted by strata, defined by combining stream size and catchment units (Fig. 1).

2.2. Compiling the datasets for analyses

For our analyses, we used 25,580 fish sampling sites located across the U.S. and 5646 fish sampling sites across Europe (Fig. 2). Fish assemblage

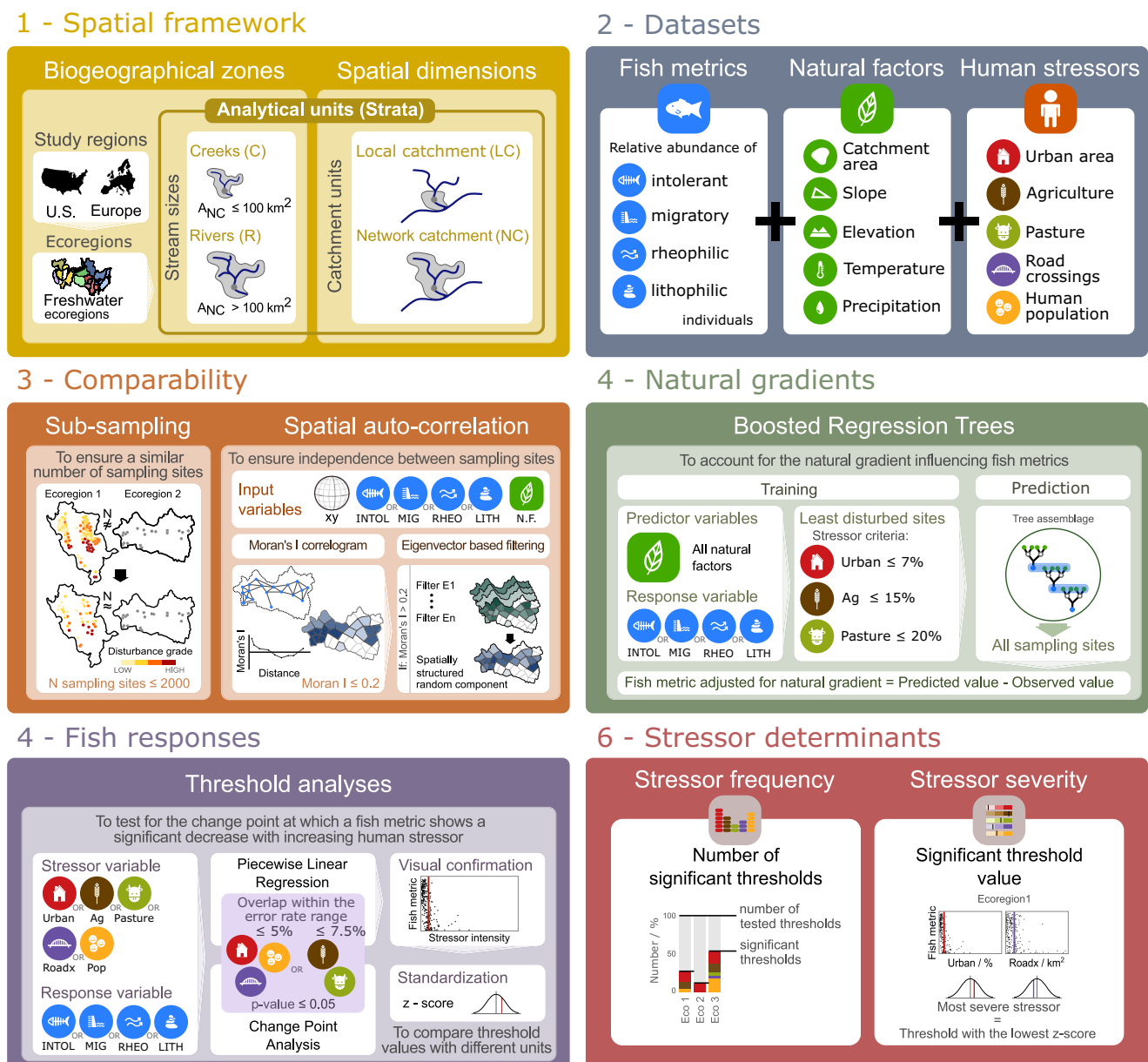


Fig. 1. Overview of the methodical approach.

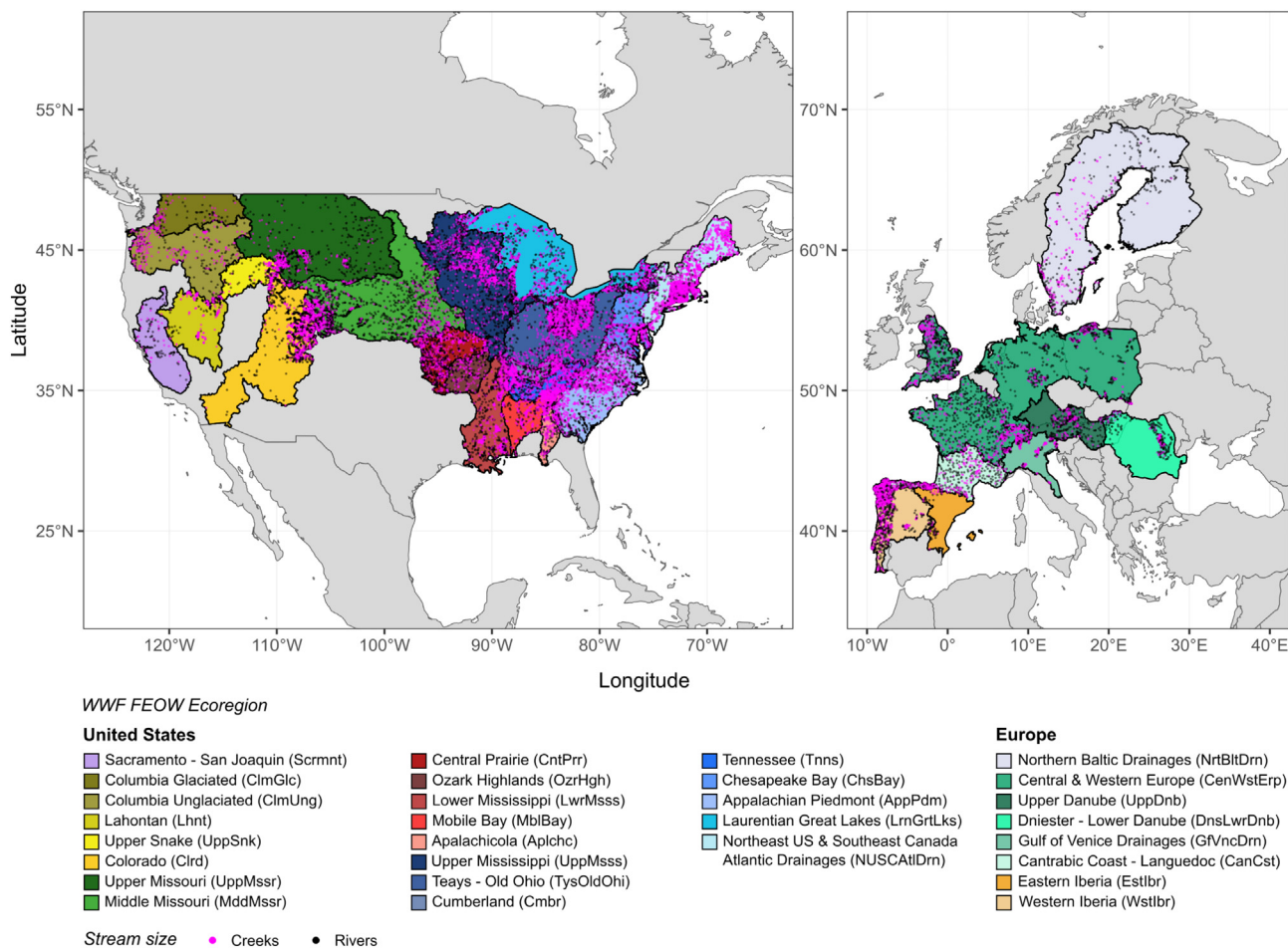


Fig. 2. Study regions including ecoregions and fish sampling sites.

data for the U.S. were acquired from a database integrating fish survey data collected by state agencies, universities, and federal programs (Daniel et al., 2015). European fish assemblage data were extracted from an extensive database (EFI+ Consortium, 2009; Schinegger et al., 2016b) containing fish surveys conducted by several academic institutions and environmental

agencies across Europe (Supp.). Fish data were collected using single-pass boat or backpack electrofishing surveys during low flow periods between 1990 and 2013 in the U.S. and between 1990 and 2007 in Europe (CEN, 2003; Crawford et al., 2016; Schinegger et al., 2016a; Schinegger et al., 2013). To prepare these data for analysis, multiple analytical steps were

Table 1

Descriptions and references of the fish metrics in the U.S. and Europe. Fish metrics (relative abundance values) were selected by their representation of various ecological factors and management considerations for both continents.

Fish metric	Abbreviation	Description (U.S.)	Description (Europe)	Reference (U.S./Europe)
<i>Intolerance</i> % individuals of intolerant species	INTOL	Species listed in the U.S. EPA's list of fish indicator species with the majority of designations as intolerant.	Species that are in general intolerant to the usual national water quality parameters and hydromorphological degradation.	Grabarkiewicz and Davis, 2008; Whittier et al., 2007; EFI+ Consortium, 2009; Holzer, 2008
<i>Migration</i> % individuals of migratory species	MIG	Potamodromous or anadromous species; Species that exhibit significant movement related to spawning. Species moving within freshwater from large river, reservoirs, or lakes to tributary streams (potamodromous) or between marine and freshwater (anadromous).	Potamodromous or anadromous species; Species that migrate between river zones or reaches (potamodromous) or live in the sea and migrate into the river to spawn (anadromous).	Frimpong and Angermeier, 2009; EFI+ Consortium, 2009; Holzer, 2008
<i>Habitat preference</i> % individuals of rheophilic species	RHEO	Species that prefer fast flow conditions.	Species that prefer to live in a habitat with fast flow conditions and clear water.	Frimpong and Angermeier, 2009; EFI+ Consortium, 2009; Holzer, 2008
<i>Reproductive ecology</i> % individuals of lithophilic species	LITH	Species that spawn on gravel and rocks.	Species that spawn exclusively on gravel, rocks, stones, rubble or pebbles. Hatchlings are photophobic.	Frimpong and Angermeier, 2009; EFI+ Consortium, 2009; Holzer, 2008

taken to ensure comparability and independence of fish sampling sites (Fig. 1 and Supp.). We reduced the number of fish sampling sites in ecoregions with more than 2000 sites by conducting a systematic random selection to harmonize site densities between ecoregions and thus assure a more comparable threshold response across ecoregions. To ensure the independence of the analyzed stream reaches, each fish metric was tested for spatial autocorrelation among fish sampling sites in each ecoregion by conducting Moran's I correlograms (Cooper et al., 2017; Daniel et al., 2015). If positive spatial autocorrelation of a Moran's I coefficient >0.2 was detected among sites within an ecoregion, we applied a set of eigenvector-based spatial filters. Fish assemblages were classified into four trait-based metrics including intolerant, migratory, rheophilic, and lithophilic species (Table 1 and Fig. 1; Supp.), summarized for each sampling site and metric by the relative abundance of individuals assigned to each trait. These fish metrics have been reported in the literature as responsive to disturbances in both the U.S. and Europe (e.g., 171 Hughes et al., 1998; Pont et al., 2007; Schinegger et al., 2016a; Whittier et al., 2007). These are functional traits, which are defined as morpho-physiophenological traits that impact fitness indirectly via their effects on growth, reproduction and survival, the three components of individual performance (Violle et al., 2007). Overall, we summarized seven natural environmental factors and five human stressors for stream reaches to characterize landscapes draining into stream reaches. Natural factors include network catchment area, stream reach slope, mean elevation of the local catchment, and local and network catchment summaries of mean annual air temperature and mean annual precipitation (Fig. 1 and Appendix A Table A.1). Human stressors include percentage of three land use classes (urban area, agriculture, and pasture) as well as human population density and road crossing density within the two catchment units. Beside these large-scale drivers, we did not consider dams or other direct stressors, as data availability and resolution would not allow for a comparable analysis across continents. Harmonization of datasets yielded comparable variables for the U.S. and Europe and is described in more detail in the supplementary information and a list of data sources is found in Appendix A.

2.3. Modeling the natural gradient by ecoregions

For large regions with substantial natural variation, it is critical to account for the influence of natural landscape factors known to affect distributions and abundances of stream fishes to effectively characterize their stressor response. Thus, we used Boosted Regression Tree (BRT) analysis (Elith et al., 2008) to quantify variance in fish assemblages explained by natural factors (Fig. 1; Supp.). Models were trained with sampling sites classified as 'least disturbed' based on low percentages of human land use within the network catchment (Daniel et al., 2015; Esselman et al., 2013), using the natural factors as predictor variables. Then, BRT models were used to predict fish metric values under least disturbed conditions for all fish sampling sites within an ecoregion. Our resulting analyses were conducted on residuals, which are the fish metric values considering natural landscape conditions (Esselman et al., 2013).

2.4. Assessing fish response to stressors

According to Allan (2004), severe anthropogenic disturbances may lead to a substantial, typically non-linear decrease in biological condition. Because of that, we chose to test for threshold responses (as opposed to linear responses) in fish assemblages to stressors, following Daniel et al. (2015). To identify thresholds where fish metrics change substantially and negatively with increasing human stressor intensity, threshold analyses were performed using piecewise linear regression (Muggeo, 2003). Models were fit to the data using the R package 'segmented' (Muggeo, 2003, 2008). We verified all significant thresholds by conducting a nonparametric change-point analysis (Baker and King, 2010). To perform this, we used the R package 'TITAN2' (Baker et al., 2015). Threshold values were standardized by determining the z-score to compare thresholds identified for human stressors with different units (Fig. 1; Supp.).

2.5. Determinants of stressors

We analyzed human stressors in the U.S. and Europe for stressor frequency by counting significant thresholds per ecoregion and strata and determining the percentage of tested thresholds that resulted in significant thresholds. Stressor severity is characterized by the value of the stressor beyond which the fish metric experiences a sudden negative decrease (threshold value). With this we evaluated the most severe stressor for each ecoregion and strata by selecting the stressor that yielded the lowest z-score.

We used R version 3.4.4 (R Core Team, 2018) and R studio version 1.1.442 (RStudio Team, 2018) for all analyses. A list of all applied R packages is provided in the supplementary information.

3. Results

3.1. Stressor frequency: how commonly does a stressor yield a significant response?

3.1.1. Continental comparison

We tested 1540 thresholds for five human stressors in two continents, 29 ecoregions (21 in the U.S. and 8 in Europe) and across four strata using four fish metrics (Appendix A Table A.2). Using our conservative analytical approach of verifying thresholds with two different methods, we identified 195 significant thresholds (hereafter called "thresholds") in 25 ecoregions (135 in the U.S. and 60 in Europe), which is a similar overall percentage of about 13 % of tested thresholds for each continent. Generally, thresholds were more often associated with human population density and urban area than with agriculture, pasture, or road crossing density (Fig. 3 and Supp. Table S.6), underscoring their pervasive threat to fishes in both continents. Despite these broad findings, results varied by stressor and by fish metric across continents. In the U.S., 28 % and 24 % of thresholds were identified for urban area and human population density, and in Europe, 38 % and 37 % of thresholds were identified, respectively. Further, in Europe, for intolerant species, 43 % of thresholds were detected, and for lithophilic species, 38 % of thresholds were detected (Fig. 3 and Supp. Table S.6). Numbers in the U.S. were lower, with 32 % for intolerant species and 24 % for lithophilic species. In the U.S. we found similar results for rheophilic (23 %) and migratory species (21 %), while in Europe only 7 % and 12 % of thresholds were detected, respectively.

3.1.2. Ecoregional comparison

Stressor frequency also varies between ecoregions (Fig. 4). By far, the most thresholds were identified in the Middle Missouri ecoregion in the U.S., where 42 % of tested thresholds were significant. Overall, thresholds for human population density and urban area were identified in most of the ecoregions, 19 in the U.S. and 17 in Europe. Also, we identified the highest frequency of thresholds for agriculture in the Appalachian Piedmont ecoregion, in which 20 % of the tested thresholds were significant. This is followed by human population density in the Central Prairie ecoregion (15 %), urban area in the Middle Missouri ecoregion (12 %), and the Central and Western Europe ecoregion (12 %). In terms of fish metrics, we detected thresholds for lithophilic species in most ecoregions (11 in the U.S., 5 in Europe). Whereas, for intolerant and rheophilic species, we identified thresholds in 15 ecoregions (10 and 13 in the U.S., and 5 and 2 in Europe, respectively; Fig. 4 and Supp. Fig. S.7). For migratory species, we only identified significant thresholds in 7 ecoregions (5 in the U.S. and 2 in Europe), with a comparatively high frequency in the U.S. ecoregions Middle Missouri with 17 %, Northeast U.S. and Southeast Canada Atlantic Drainages with 13 % and Laurentian Great Lakes with 9 % of the tested thresholds.

3.1.3. Comparison by strata

Stressor frequency varied by strata, with a higher percentage of thresholds identified for the network catchments, with 60 % in the U.S. and 67 % in Europe, compared to thresholds found for the local catchments with

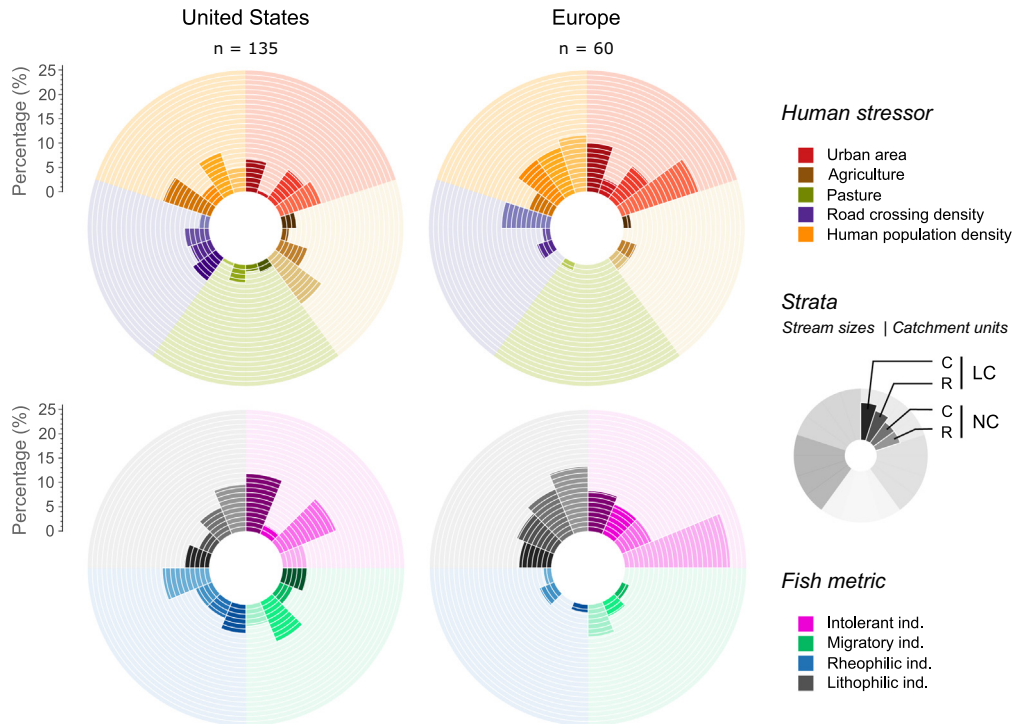


Fig. 3. Distribution of significant thresholds for human stressors per strata (top) and fish metrics per strata as a percentage (bottom) of total significant thresholds per continent, i.e. 135 (U.S.) and 60 (Europe).

40 % in the U.S. and 33 % in Europe (Supp. Fig. S.4). In contrast, in the U.S., we detected more thresholds for creeks (59 %) vs. rivers (41 %), but the opposite occurred in Europe (C 40 %; R 60 %). Stressor frequency for the three

land use classes shows similar trends for different strata in the U.S. and Europe (Fig. 3). In both continents, thresholds for urban area were rarely identified for the local catchments of rivers and were most often identified

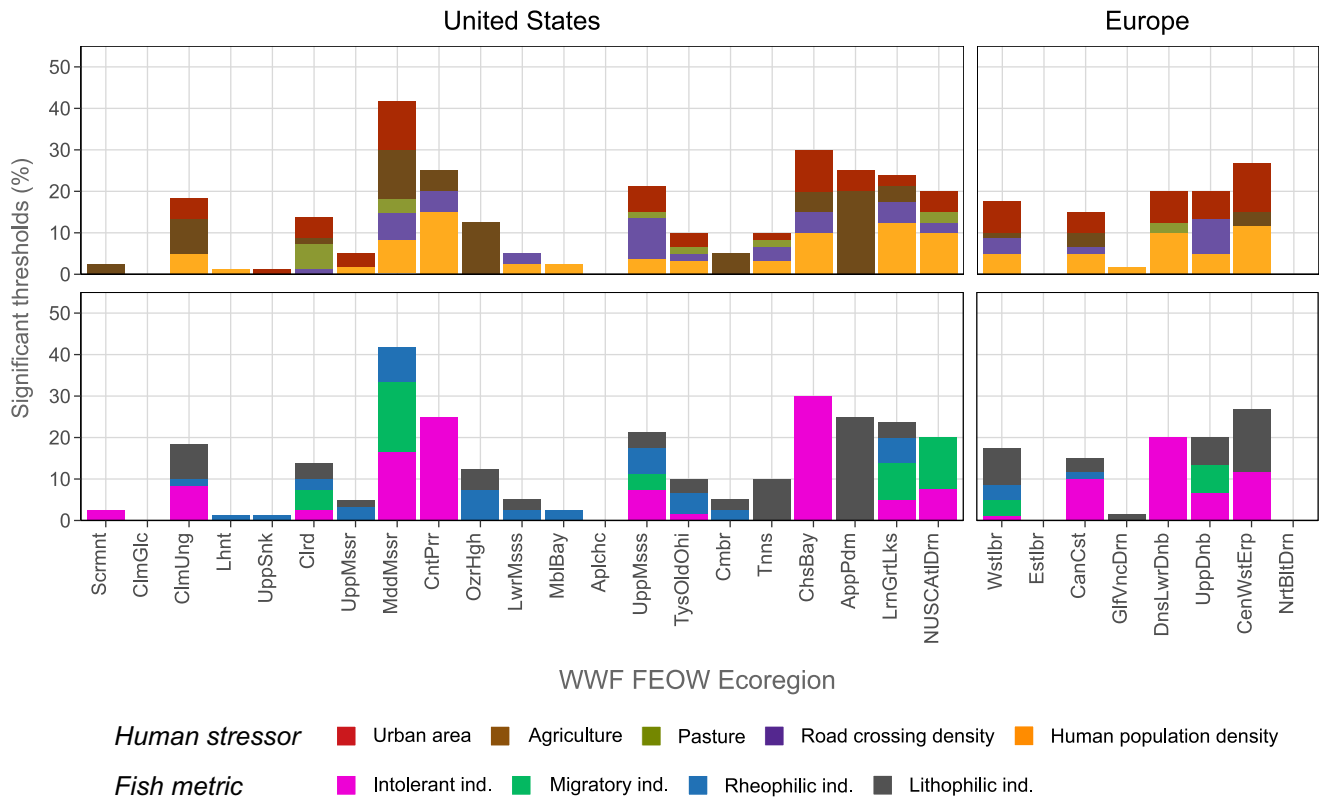


Fig. 4. Stressor frequency, showing how often human stressors (top) and fish metrics (bottom) yield a significant threshold as a percentage of overall tested thresholds per ecoregion.

for the network catchments of rivers (9 % in the U.S. and 17 % in Europe). Further, for agriculture and pasture, the frequency of significant thresholds is generally higher for the network catchments than for the local catchments. In the U.S., we identified the highest percentage of thresholds by far for agriculture in the network catchments of rivers (12 %). Stressor frequency for road crossing and human population density was more variable in both continents. In the U.S., thresholds for road crossing density were most frequently identified for the local catchments of creeks (6 %), while in Europe, most significant thresholds were detected for the network catchments of rivers (10 %). In the U.S., thresholds for human population density were less frequently found for rivers (9 %) compared to creeks (19 %), while in Europe, thresholds were slightly more frequent for rivers (17 %) than for creeks (15 %) and considerably less frequent for the local catchments of creeks (5 %). Overall, for all four fish metrics, we found thresholds more frequently for the network catchments than for the local catchments (Fig. 3). For lithophilic species, we detected 10 % (U.S.) and 13 % (Europe) of thresholds for the network catchments of rivers, which was the highest percentage. This trend was also identified for rheophilic species in the U.S. (10 % of thresholds) and intolerant and migratory species (22 % and 7 % of thresholds, respectively) in Europe. In contrast, for migratory species in the U.S. and for rheophilic species in Europe, for the network catchments of creeks, we detected 9 % and 3 % of all thresholds, respectively.

3.2. Stressor severity: at which intensity does a human stressor yield a significant threshold?

3.2.1. Continental comparison

Overall, across continents, the range of threshold values is larger for the land use classes agriculture and pasture than for urban area, which only ranges from 0.6 to 16.2 % in the U.S. and from 0.08 to 8.6 % in Europe (Fig. 5). However, we detected threshold values for agriculture and pasture up to 78.3 % and 25.5 % in the U.S. and 57.3 % and 7.3 % in Europe,

respectively. Threshold values identified for road crossing density range from 0.001 to 1.08 road crossings/km² for both continents. In terms of human population density, threshold values range between 14 and 400 people/km² in Europe, whereas in the U.S., all values are below 100 people/km². Overall, in the U.S., agriculture was identified most frequently (15 times; Figs. 6 and 7) as the most severe stressor, followed by human population density (14). In Europe, urban area (7) and human population density (7) were detected most frequently as the most severe stressor. In contrast, in the U.S., the stressor urban area was least often identified as the most severe one (4). In terms of tested fish metrics, the most severe stressor was often identified for intolerant (24) and lithophilic species (21).

3.2.2. Ecoregional comparison

By comparing ecoregions in which the same stressor was detected as the most severe, we identified differences between continents (Figs. 6 and 7). In ecoregions where urban area was the most severe stressor, threshold values are generally lower in Europe compared to the U.S., with the lowest value of 0.08 % urban area within the network catchments of rivers in West Iberia. In contrast, in ecoregions where agriculture, pasture, road crossing density or human population density were the most severe stressor, threshold values are generally lower in the U.S. compared to Europe. We identified the lowest value for road crossing density (0.001 road crossings/km² within the network catchments of creeks) and human population density (0.19 people/km² within the local catchments of rivers) in the Laurentian Great Lakes. However, we found the lowest threshold value for agriculture in Middle Missouri at 0.10 % agricultural land use within the network catchments of rivers and in Upper Mississippi at 1.52 % for pasture within the network catchments of creeks.

3.2.3. Comparison by strata

Further, differences between strata occur for the most severe stressor both within and between the two continents. Overall, for the local

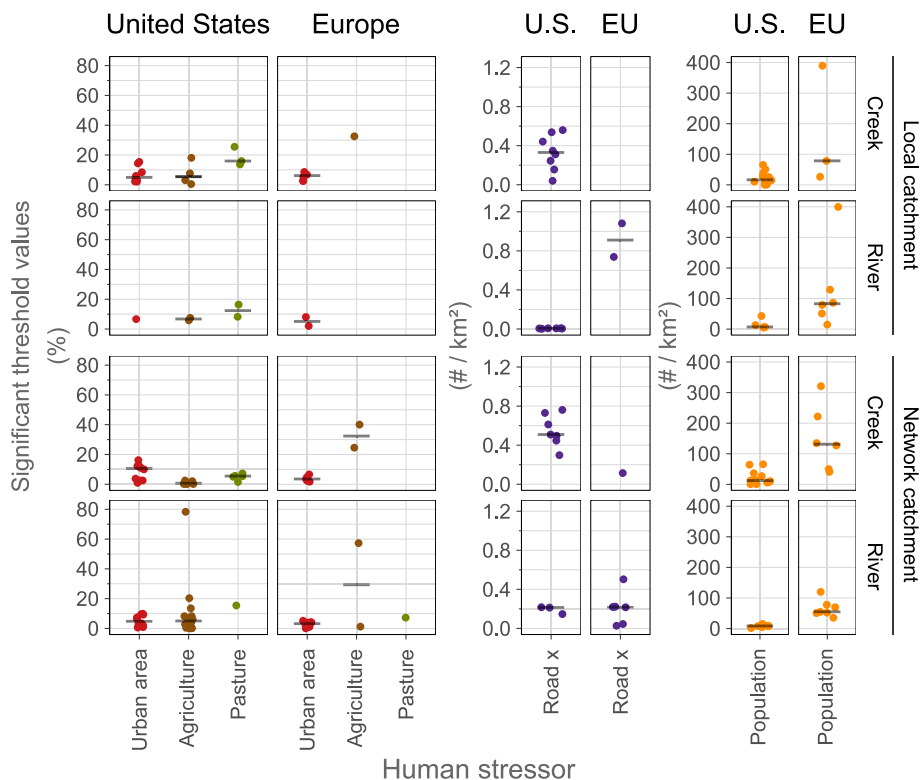


Fig. 5. Stressor severity expressed by significant threshold values identified for urban area, agriculture, pasture, road crossing density, and human population density in the United States (U.S.) and Europe (EU). Panels show results for strata, i.e. fish sampling sites in creeks and rivers for the local and network catchments. The gray line indicates the median value. No median was calculated in cases where zero or one threshold was identified.

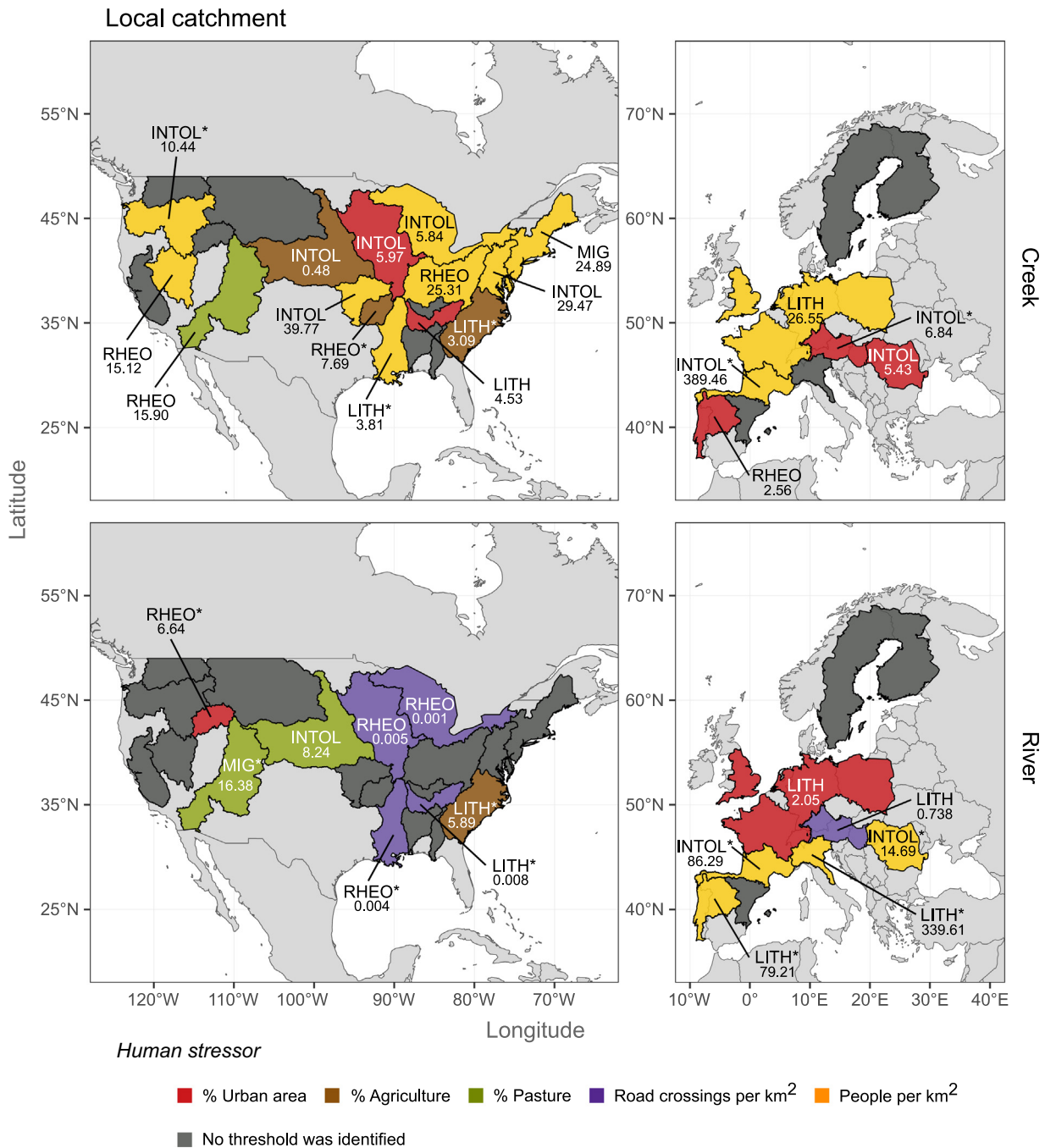


Fig. 6. Most severe human stressor of the local catchment identified for each ecoregion in the U.S. and Europe. Labeling within ecoregions indicates the fish metric for which the significant threshold was identified, i.e. lithophilic (LITH), rheophilic (RHEO), intolerant (INTOL) and migratory (MIG) as well as the identified threshold value. *Only one significant threshold was identified for this ecoregion and stratum.

catchments, human population density was the most severe stressor for creeks (10 out of 29 tested ecoregions; Fig. 6), while for rivers, road crossing density was more often the most severe stressor (5 ecoregions). However, for the network catchments of both stream sizes, agriculture was the most severe stressor in 5 ecoregions for creeks and 8 ecoregions for rivers. Further, the network catchment results show a clear difference between continents, with agriculture identified as the most severe stressor in the U.S. and urban area in Europe. When comparing the results of creeks and rivers, it is noteworthy that road crossing density was identified more often as the most severe stressor for rivers (8 times) than for creeks (3 times; Fig. 7). In addition, in the U.S., the range of threshold values detected for road crossing density is much smaller for rivers than for creeks (Fig. 5),

indicating a potential threat of roads to fish. However, thresholds were generally more frequently identified for creeks than for rivers (Fig. 3).

4. Discussion

By establishing a harmonized dataset, which characterizes distributions of fluvial fishes in more than 30,000 locations, we were able to document the impacts of five human landscape stressors on fluvial fishes in two continents. This study is unprecedented in the rigor of methodology and analyses conducted over such a large spatial extent and by steps to account for natural factors and stressor variables important to fishes summarized within stream catchments. We identified fish metrics most sensitive to

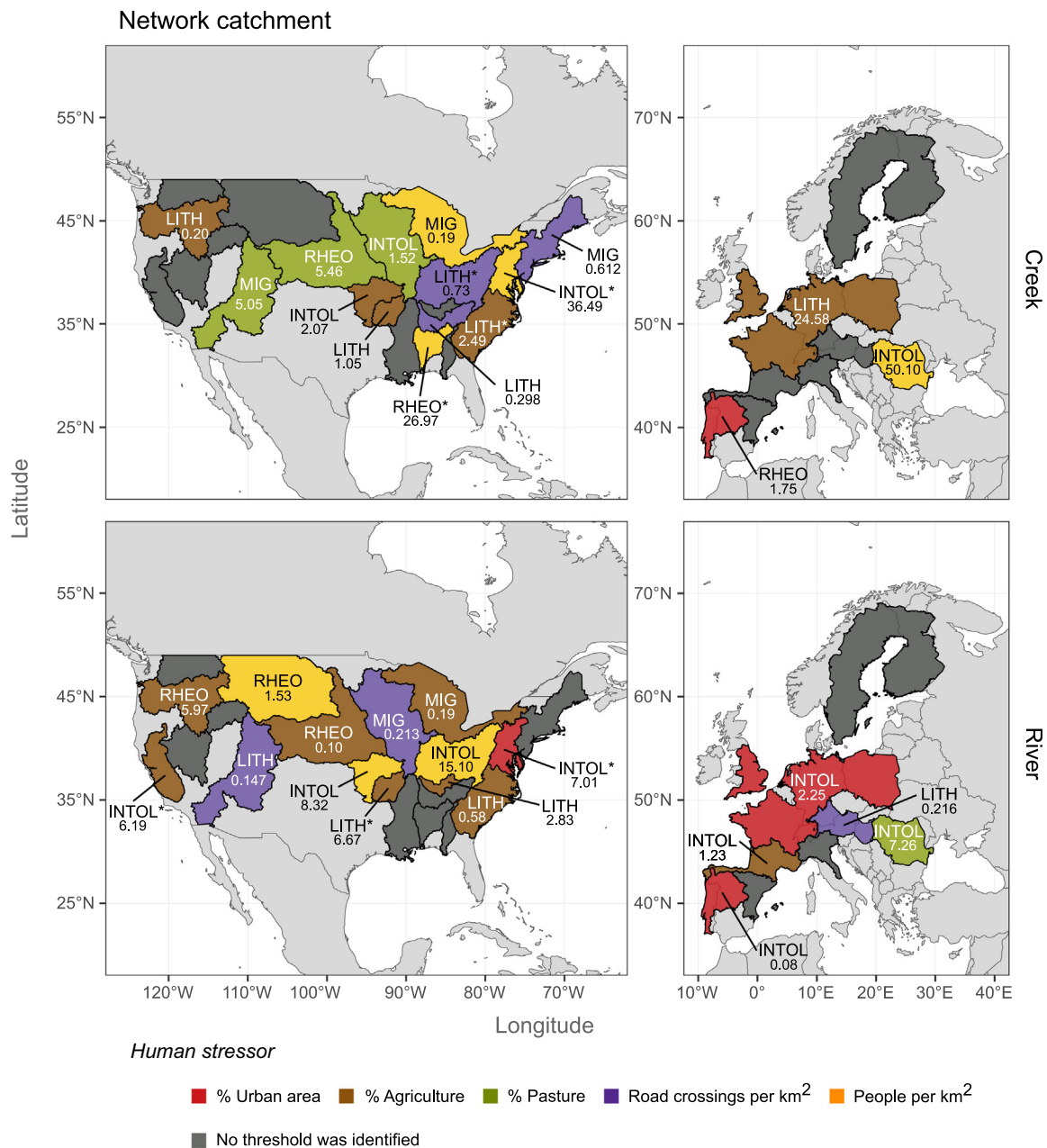


Fig. 7. Most severe human stressor of the network catchment identified for each ecoregion in the U.S. and Europe. Labeling within ecoregions indicates the fish metric for which the significant threshold was identified, i.e. lithophilic (LITH), rheophilic (RHEO), intolerant (INTOL) and migratory (MIG) as well as the identified threshold value. *Only one significant threshold was identified for this ecoregion and stratum.

landscape stressors in both continents and quantified levels at which fishes respond to stressors including identification of most severe stressors by region and stream size. Collectively, our results provide novel understanding of fish responses to landscape stressors and provide critical information for freshwater conservation over large spatial extents to assess and compare conditions across systems, providing managers and decision-makers with important insights into the status of resources within a region of interest.

4.1. The distinction between the human landscape stressor determinants is important

Our results showed that urbanization and human population density are linked to most thresholds in both continents. This is in line with the findings of Grizzetti et al. (2016), who demonstrated that better ecological status is

associated with natural areas in floodplains while urbanization and nutrient pollution are essential predictors of ecological degradation in European waterbodies. In the U.S., urbanization is also one of the most pervasive landscape stressors for fishes limiting habitat quality in ecoregions (Esselman et al., 2013).

Also, our identification of the most severe stressors by continent and region provides additional, critical information to managers who can invest in developing conservation strategies, including policy, specifically in response to severe stressors. In the United States, agriculture at the network catchment was most often identified as the most severe stressor, while urbanization was for Europe. In ecoregions where urban land use was identified as most severe, threshold values of the stressor were generally lower in Europe than in the U.S. Moreover, threshold value ranges were larger for agricultural- than for urban land use. This is also confirmed by Chen and Olden (2020), who found that freshwater fishes are sensitive to even low

levels of watershed urbanization (range of threshold values: 1 %–12 %), but consistently higher (and more variable) levels of agricultural development (2 %–37 %). However, our analyses were much more comprehensive, including additional stressors and spatial scales (i.e., local and network catchments).

4.2. Multiple traits show the sensitivity of fishes to stressors

As expected, fish assemblages in both continents responded significantly to human stressors. Thus, considering multiple traits to understand fish assemblages' response to stressors in large-scale studies is key (Hughes et al., 1998). Our results show that the percentage of intolerant and lithophilic species are the most responsive and sensitive traits over a wide range of ecoregions and across continents. Intolerant species were specifically selected due to their sensitivity to habitat degradation in general, including water quality impairments and hydromorphological changes (Grabarkiewicz and Davis, 2008; Schmutz et al., 2016). Previous studies determined that intolerant species show responses to stressors over a broad range of different ecoregions (e.g., Cooper et al., 2017; Esselman et al., 2013; Schinegger et al., 2016a). Our results for lithophilic species also agree with those of former studies, showing that they are sensitive to hydromorphological alterations, which are threatening their spawning grounds and subsequently, their reproductive success (e.g., Schmutz et al., 2016). Therefore, the use of intolerant species for large-scale comparisons of fish habitat conditions is promising and could serve as a useful indicator worldwide, for example to support the Freshwater Health Index (Vollmer et al., 2018) and its implementation.

While in Europe, detected thresholds were mainly identified for intolerant and lithophilic species, in the U.S. the responsiveness of all analyzed metrics (i.e. rheophilic, migratory, intolerant and lithophilic) was similar. This is underscored by the facts that fish species diversity is much higher in the U.S. than in Europe, and that diversity varies by ecoregion (Abell et al., 2008; Griffiths, 2018). Further, we found that threshold values detected for human population density are often higher in Europe compared to the U.S. This might be linked to the history of human settlement, as humans had a close tie to rivers since the beginning of modern human life, especially in Europe (Haidvogel, 2018). This leads to the assumption that some sensitive species are already extinct or were able to adapt to a certain degree of human stressors over the past centuries. Chen and Olden (2020) investigated threshold responses of riverine fish communities to land use conversion across regions of the world by using relative species abundance and species richness. In contrast, our study has a more precise and robust level of information, incorporating information on specific traits, albeit for Europe and the U.S. only.

4.3. Regionalization and stratification are critical in large-scale analyses

Our results showed that the determinants of stressor and the response of fish assemblages vary between continents and ecoregions. This is in line with multiple other studies which have shown that metrics indicating the ecological condition of streams can vary regionally (e.g., Daniel et al., 2015; Stoddard et al., 2008) and that stream fishes may respond differently to human stressors based on regional differences in natural environmental factors and by differences in mechanisms by which stressors affect fishes (e.g., Schinegger et al., 2016a; Thornbrough and Infante, 2019; Utz et al., 2010). These studies collectively confirm that the selected ecoregional-approach for constraining our analysis following Abell et al. (2008) is essential to effectively detect influences of stressors to fishes across large regions.

Moreover, fishes are responding differently to landscape stressors based on stream size and catchment unit. We detected more significant thresholds for creeks in the U.S. than for rivers (59 % vs. 41 %), but found the opposite result for Europe (40 % for creeks; 60 % for rivers). This may be due to differences in the configuration of stressors in small creeks in the U.S. vs. Europe, as well as differences in how creeks may be managed. In terms of the catchment unit, thresholds were more frequently identified for the

network catchments (60 % in the U.S. and 67 % in Europe) than the local catchments (40 % in the U.S. and 33 % in Europe). This could result from the fact that landscape-scale stressors accumulate downstream, as the network catchment is the scale over which stressors have substantial effects on fish, for example, in terms of hydrological alterations (Allan, 2004; Schmutz et al., 2016). As expected, fish assemblages were significantly responding to human stressors at all four strata in both continents. Generally, for the local catchments, human population density was identified in most ecoregions as the most severe stressor, while for the network catchments agricultural and pastoral land use became more relevant.

Thus, our findings highlight the importance of regionalization and stratification for stressor management, as already targeted by the EU Water Framework Directive and related River Basin Management Plans through catchment-based approaches.

4.4. Uncertainties & limitations of our study

One limitation of our study is that it did not fully capture information for large rivers, as fish-sampling data collected in a comparable manner were mainly available for wadeable streams across continents (Daniel et al., 2015; Schinegger et al., 2016b). Fish data for large rivers remain a limitation globally and deserve attention to understand conditions of and threats to fishes and fisheries in our largest rivers (Zajicek and Wolter, 2018). As a second limitation, trait assignments of fish species along with definitions of specific traits can differ between databases (Cano-Barbacid et al., 2020). We also discovered these differences and therefore restricted our selection of fish metrics with matching trait definitions to ensure their compatibility across continents. To expand this analysis to other regions of the world and to investigate the responsiveness of a greater variety of fish traits, globally consistent trait assignments for fish are needed. As an additional limitation, our study neither accounts for direct human stressors such as dams or channelization (Stendera et al., 2012) nor for the cumulative effects of multiple human stressors (Schinegger et al., 2016a). A consistent dataset of barriers and dams was unavailable and was therefore not considered in this large scale analysis. Cooper et al. (2017) implemented the U.S. inventory in their work and showed that dams act as a significant landscape-scale stressor to stream fishes. Thus, the establishment of a comprehensive and consistent dam inventory for Europe would be key for future large scale analyses. Additionally, it is important to understand potential effects of other stressors, such as climate change and introductions of invasive species. The evaluation of these would be an important next step in order to gain a deeper understanding about the mechanisms behind stressor-response relationships and the whole DPSIR (Driver-Pressure-State-Impact-Response) cascade. While our rigorous analytical approach does an effective job of characterizing changes in numbers of fishes with ranges in landscape stressors, we acknowledge that in regions where a given stressor (such as agriculture) may be widespread and intensive, we may not be able to detect a significant change in numbers of fishes, especially if that stressor has been on the landscape for many years. This is an important caveat to our results and suggests the importance of understanding landscape context to apply our outcomes for conservation actions.

4.5. Future directions & management implications

Global trends in freshwater fish biodiversity loss indicate that current conservation strategies are not sufficient, requiring the development of new strategies and approaches to protect fishes (Su et al., 2021; van Rees et al., 2020). Our study provides a new approach that elucidates how large-scale human stressors have altered fish assemblages in two continents. This valuable ecological context is key to conservation and management, as is the understanding of interactions among organisms and their environment that determine their responses to global change (Maasri et al., 2021). Our identified thresholds thus can be a critical benchmark for management, by guiding decisions within ecoregions to maintain freshwater fish biodiversity in altered ecosystems (Dias et al., 2017; Su et al.,

2021), as they are based on rigorous analyses. Given the fact that agriculture is such a prominent land use in Europe and the U.S., it is critical to better understand the stressor characteristics of different agricultural practices as well as the underlying mechanisms by which they may affect fish assemblages. Such knowledge can support the development of effective landscape-scale solutions to mitigate agricultural effects on stream habitats. Further, it can provide insights into management, i.e. activities needed in terms of river restoration and fish conservation, specifically when nature-based solutions are targeted (Abell et al., 2019).

Moreover, given the global freshwater biodiversity crisis (Su et al., 2021; Tickner et al., 2020) more work is required to understand why fishes are imperiled. Here, knowledge about stressor factors generated in this study could assist multi-stressor assessments and regionalization of analyses and thus support strategic planning in catchment management to balance human and wildlife needs (van Rees et al., 2020). Finally, this study helps to draw general conclusions for future freshwater ecosystem assessment and management around the world (Vollmer et al., 2018), which also requires an integration of freshwater- and terrestrial conservation planning (Leal et al., 2020).

CRedit authorship contribution statement

Maria M. Üblacker: Conceptualization, Formal analysis, Visualization, Data curation, Methodology, Writing - original draft. **Dana M. Infante:** Supervision, Conceptualization, Writing - original draft. **Arthur R. Cooper:** Methodology, Writing - review & editing. **Wesley M. Daniel:** Methodology, Writing - review & editing. **Stefan Schmutz:** Writing - review & editing. **Rafaela Schinegger:** Supervision, Conceptualization, Investigation, Methodology, Project administration, Writing - original draft.

Data availability

Fish assemblage data that support the findings of this study were provided by the NFHP in the U.S. and the EFI+ Consortium in Europe. As we are not

the owners of these data, we do not have the permission to share them. Metadata of the European fish assemblage data can be downloaded at http://freshwaterjournal.eu/issues/FMJ_2016_17.pdf. Metadata for a subset of fish data used for the conterminous U.S. can be downloaded at <https://www.sciencebase.gov/catalog/item/5005aa08e4b052a0c18e3461>. Fish assemblage data can be requested directly by the leading data owners to discuss possible conditions for access.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A

Table A.1

Description and data source of the natural factors and human stressor variables in the U.S. and Europe.

Variable	Description	Unit	Source ¹ (U.S./Europe)	Dataset ² (U.S./Europe)	Scale (U.S./Europe)
Natural factors					
top_nc_area	Network catchment area	km ²	U.S. EPA & USGS/EC-JRC	2006 NHDPlusV1/2007 CCM2	1:100,000/1:250,000
top_lc_slope	Slope of the stream reach	%	U.S. EPA & USGS/EC-JRC	2006 NHDPlusV1/2007 CCM2	30 m/100 m
top_lc_elev	Local catchment mean elevation	m a.s.l.	U.S. EPA & USGS/EC-JRC	2006 NHDPlusV1/2007 CCM2	30 m/100 m
cli_lc_prec	Local catchment mean annual precipitation	mm	OCS/EC-JRC	2013 PRISM 1990–2010/2007 CCM2 1950–2000	4 km/1 km
cli_nc_prec	network catchment mean annual precipitation	mm	OCS/EC-JRC	2013 PRISM 1990–2010/2007 CCM2 1950–2000	4 km/1 km
cli_lc_temp	local catchment mean annual air temperature	°C	OCS/EC-JRC	2013 PRISM 1990–2010/2007 CCM2 1950–2000	4 km/1 km
cli_nc_temp	Network catchment mean annual air temperature	°C	OCS/EC-JRC	2013 PRISM 1990–2010/2007 CCM2 1950–2000	4 km/1 km
Human stressors					
hs_lc_urban	Local catchment urban area: developed low, medium, and high intensity	%	USGS & MRLC/EEA	2006 NLCD/2006 CLC	30 m/100 m
hs_nc_urban	Network catchment urban area: developed low, medium, and high intensity	%	USGS & MRLC/EEA	2006 NLCD/2006 CLC	30 m/100 m
hs_lc_ag	Local catchment agriculture: cultivated crops	%	USGS & MRLC/EEA	2006 NLCD/2006 CLC	30 m/100 m
hs_nc_ag	Network catchment agriculture: cultivated crops	%	USGS & MRLC/EEA	2006 NLCD/2006 CLC	30 m/100 m
hs_lc_pasture	Local catchment pasture: pasture/hay	%	USGS & MRLC/EEA	2006 NLCD/2006 CLC	30 m/100 m
hs_nc_pasture	Network catchment pasture: pasture/hay	%	USGS & MRLC/EEA	2006 NLCD/2006 CLC	30 m/100 m
hs_lc_pop	Local catchment human population density	#/km ²	U.S. Census/EEA	2010 Census Population Count/2009 Population density grid.	1:100,000/1:100,000
hs_nc_pop	Network catchment human population density	#/km ²	U.S. Census/EEA	2010 Census Population Count/2009 Population density grid.	1:100,000/1:100,000
hs_lc_roadx	Local catchment road crossing density	#/km	U.S. Census/OSMF	2010 TIGER Roads SE/2014 OSM	1:100,000/multiscale
hs_nc_roadx	Network catchment road crossing density	#/km ²	U.S. Census/OSMF	2010 TIGER Roads SE/2014 OSM	1:100,000/multiscale

¹ U.S. source: United States Environmental Protection Agency (U.S. EPA); Oregon

Climate Service (OCS); U.S. Geological Survey (USGS); Multi-Resolution Land Characteristics Consortium (MRLC); Europe source: European Commission — Joint Research Center (EC-JRC); European Environmental Agency (EEA); OpenStreetMap Community Foundation (OSMF).

² U.S. dataset: National Hydrography Dataset Plus V1 (NHDPlusV1); National

Elevation Dataset (NED); National Land Cover (NLC); Europe dataset: Catchment Characterisation and Modelling River and Catchment Database; Version 2.0 (CCM2); Coordination of Information on the Environment (CORINE) Land Cover (CLC); OpenStreetMap (OSM).

Table A.2

Overview of Freshwater Ecoregions of the World (Abell et al., 2008) in the U.S. and Europe indicating the minimum and maximum value of the catchment area, the mean elevation, and the stream reach slope as well as the mean annual temperature and the mean annual precipitation. Variables are given for the local (LC) and/or network catchment (NC). Further, it gives information about the total number of fish sampling sites (Total), the number of creeks (C) and rivers (R), the number of least disturbed sites (LD), the number of tested fish metrics (FM), and the number of identified (tested) thresholds (TH).

ID	Ecoregion	Abbreviation	NC area	LC elev	Slope	LC T	NC T	LC P	NC P	Total	C	R	LD	FM	TH
			km ²	m a.s.l.	‰	°C	°C	mm	mm						
United States															
155	Apalachicola	Aplchc	1.89	1.21	0	17.35	17.16	1288.71	1297	268	187	81	36	1	0
			50,500.84	472.35	34.21										(20)
157	Appalachian Piedmont	AppPdm	0.16	0.35	0	15.7	15.45	1170.55	1179.34	1476	1027	449	80	1	5
			40,851.8	956.09	163.37										(20)
146	Central Prairie	CntPrr	0.98	120.77	0	13.76	13.59	1081.47	1072.23	1060	574	486	54	1	5
			1,280,974.16	470.17	59.9										(20)
158	Chesapeake Bay	ChsBay	0.82	2.52	0	10.85	10.64	1069.62	1085.2	831	548	283	51	1	6
			50,792.67	1050.68	120.99										(20)
130	Colorado	Clrd	0.31	97.72	0	4.83	3.5	559.53	689.56	1998	1065	933	674	4	11
			427,954.02	3821.64	491.07										(80)
120	Columbia glaciated	ClmGlc	2.57	237.09	0	6.83	5.71	885.92	1145.57	132	73	59	40	2	0
			191,371.88	1998.96	225.29										(40)
121	Columbia unglaciated	ClmUng	1.21	1.18	0	8.47	7.42	1046.49	1221.68	374	230	144	140	3	11
			613,891.15	2550.71	248.55										(60)
151	Cumberland	Cmbr	1.08	105.5	0	13.52	13.44	1305.9	1322.02	584	431	153	50	2	2
			32,307.44	741.86	109.93										(40)
126	Lahontan	Lhnt	2.3	1236.17	0	7.14	6.53	411.36	494.82	348	223	125	279	4	1
			21,447.8	2881.03	859.33										(80)
116	Laurentian Great Lakes	LrnGrLks	0.52	75.15	0	8.38	8.23	927.48	939.3	2000	1235	765	119	4	19
			20,874.53	654.82	15,690										(80)
149	Lower Mississippi	LwrMsss	0.72	0.18	0	16.93	16.26	1417.48	1374.07	1064	646	418	115	2	2
			3,090,911.62	177.63	39.81										(40)
143	Middle Missouri	MddMssr	1.2	195.32	0	8.64	7.8	617.36	646.43	1999	841	1158	205	3	25
			1,016,384.2	3726.48	199.71										(60)
153	Mobile Bay	MblBay	0.88	2.14	0	16.07	15.95	1376.61	1392.58	502	415	87	53	2	1
			58,617.78	631.97	91.17										(40)
118	Northeast US Atlantic drainages	NUSCAtlDrm	0.57	4.16	0	8.1	7.96	1226.63	1239.18	2001	1736	265	293	2	8
			27,587.18	835.05	255.7										(40)
147	Ozark highlands	OzrHgh	2.18	55.31	0	14.22	14.08	1189.47	1193.61	271	150	121	40	2	5
			373,219.31	476.09	25.35										(40)
125	Sacramento-San Joaquin	Scrmnt	4.36	7.36	0	14.11	11.13	883.29	1174.68	94	33	61	38	2	1
			32,906.11	2432.88	146.72										(40)
150	Teays – Old Ohio	TysOldOhi	0.34	95.31	0	11.26	11.12	1076.38	1079	2001	1351	650	101	3	6
			416,953.35	1100.11	528.89										(60)
152	Tennessee	Tnns	1.1	101.21	0	13.77	13.57	1372.03	1409.39	1261	964	297	68	3	6
			55,794.28	1531.84	1138.95										(60)
148	Upper Mississippi	UppMsss	0.62	107.25	0	8	7.81	877.52	873.65	2001	1165	836	107	4	17
			1,746,898.76	542.47	202.41										(80)
142	Upper Missouri	UppMssr	0.17	449.24	0	4.7	3.68	512.58	603.8	911	480	431	124	3	3
			461,703.9	3218.28	364.75										(60)
122	Upper Snake	UppSnk	0.24	913.4	0	3.94	2.82	617.86	777.08	160	74	86	64	4	1
			56,579.97	3173.28	216.91										(80)
Europe															
	Cantabric Coast - Languedoc	CanCst	0.72	9.34	0	12.19	11.02	1026.67	1075.28	917	570	347	186	3	9
			95,761.24	2040.12	154										(60)
	Central & Western Europe	CenWstErp	0.81	-0.45	0	8.7	8.14	800.92	857.45	1896	760	1136	170	3	16
			193,725.26	2465.48	371.82										(60)
	Dniester – Lower Danube	DnsLwrDnb	5.01	9.03	0.02	8.17	6.9	605.38	669.46	272	75	197	50	2	8
			43,412.55	1252.68	75										(40)
	Eastern Iberia	EstIbr	5.32	341.49	0	10.9	9.36	673.25	749.43	85	26	59	45	2	0
			3580.04	1643.68	56.73										(40)
	Gulf of Venice drainages	GlFVncDrm	0.54	-2.95	0.01	7.9	5.14	1138.84	1268.1	300	202	98	181	3	1
			12,748.82	2305.35	481.91										(60)
	Northern Baltic drainages	NrtBltdrm	4.22	7.5	0.05	3.62	3.23	635.97	651.23	409	181	228	253	4	0
			39,955.63	979	79.37										(80)
	Upper Danube	UppDnb	1.65	88.83	0.11	7.71	6	918.48	1008.06	397	131	266	93	3	12
			207,423.61	2360.77	168.12										(60)
	Western Iberia	WstIbr	1.86	7.3	0	13.25	12.21	946.26	1018.2	923	503	420	178	4	14
			96,608.08	1930.99	164.4										(80)

Appendix B. Supplementary information

Supplementary information to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2023.165101>.

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