# Taxonomic rarity and functional originality of freshwater fishes and their responses to anthropogenic habitat alterations 

Rita Tóth ${ }^{1}$ | István Czeglédi $^{1}$ | Péter Takács ${ }^{1}$ | Pablo A. Tedesco ${ }^{2}$ | Tibor Erős ${ }^{1}$ ©

${ }^{1}$ Balaton Limnological Research Institute, Eötvös Loránd Research Network (ELKH), Tihany, Hungary
${ }^{2}$ Laboratoire Évolution et Diversité Biologique (EDB), Université Toulouse 3 Paul Sabatier, Toulouse, France

## Correspondence

Tibor Erős, Balaton Limnological Research Institute, Eötvös Loránd Research Network (ELKH), Klebelsberg K. u. 3, H-8237 Tihany, Hungary.
Email: eros.tibor@blki.hu

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#### Abstract

1. The human alteration of habitats is a major driver in the decline of biodiversity worldwide. However, the relationships between different forms of rarity, including both taxonomic and functional aspects, are poorly known. Two relationships were examined in this study: (i) between the different forms of taxonomic rarity and functional originality of lotic fishes; and (ii) between rarity indices and the degree of human alterations. 2. Stream fish communities at 429 stream and river sites were sampled between 2013 and 2018. The taxonomic rarity of fishes was characterized based on their local rarity, habitat specificity and geographical restrictedness. The functional originality of each species was also quantified by using ecomorphological traits, and the relationships between the different indices and their responses to human habitat degradation were explored. 3. Only weak or medium level correlations were found among the indices of taxonomic rarity. A combined taxonomic rarity index showed that overall taxonomic rarity was determined most strongly by local rarity, followed by habitat specificity, and finally, geographical restrictedness. Functional originality was not related either to individual rarity indices or the combined taxonomic rarity index. Mean taxonomic rarity of species was correlated with the degree of habitat degradation of the sites. Contrary to taxonomic rarity, mean functional originality of species increased with the degree of human alteration. 4. This study shows that a more exact characterization of species rarity requires multiple metrics, including functional ones, because these indices respond differently to human alterations. Combined indices of rarity can help to prioritize species level conservation actions, although single rarity metrics are still needed to adapt these actions to species attributes (e.g. endemism or unique functions). Species level conservation would benefit from including the evaluation of functional rarity into conservation policy.


## KEYWORDS

functional rarity, functional uniqueness, rare species, species level conservation, stream fish, taxonomic rarity

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## 1 | INTRODUCTION

The decline in biodiversity is accelerating, threatening the functioning of ecosystems, ecosystem services and human well-being (Ceballos et al., 2015). Several underlying mechanisms facilitate the disappearance of species (Davies, Margules \& Lawrence, 2004; Giam \& Olden, 2018). For example, species with low local abundance are more exposed to environmental and demographic stochasticity, which increases local extinction risk at a given site (Pimm, Jones \& Diamond, 1988). Geographically restricted species have a greater susceptibility to the disturbance and loss of their habitats (Purvis et al., 2000; Runge et al., 2015). Species with narrow habitat and unique environmental requirements have populations that are less resilient to environmental stresses (Kotiaho et al., 2005; Pandit, Kolasa \& Cottenie, 2009; Runge et al., 2015; Mykrä \& Heino, 2017). Indeed, species that are rare with respect to several forms of rarity (i.e. local abundance, geographical range and habitat breadth) face multiple jeopardy from human pressures (Pritt \& Frimpong, 2010; Harnik, Simpson \& Payne, 2012).

The importance of species to biodiversity and conservation cannot be determined using only the rarity of species (hereafter 'taxonomic rarity'), but also the rarity of functions (hereafter 'functional originality'; Violle et al., 2017; Kondratyeva, Grandcolas \& Pavoine, 2019). If taxonomically rare species have unique functional roles, their extinction could severely influence ecosystem functioning (Leitão et al., 2016; Violle et al., 2017). On the contrary, the disappearance of functionally redundant species within local or regional assemblages may have minimal consequences on the maintenance of ecosystem processes. Species combining both taxonomic rarity and functional originality may be essential to conserve in order to maintain biodiversity and ecosystem structure and functioning, especially if these species are susceptible to the effects of human alterations (Violle et al., 2017; Griffin et al., 2020). However, few empirical studies (e.g. Leitão et al., 2016) have examined the relationships between taxonomic rarity and functional originality, and ranked species based on multiple rarity facets.

Freshwater habitats, and the biodiversity they support, are especially vulnerable to human activities, with rates of biodiversity loss in streams and rivers exceeding those of any other ecosystem (e.g. Ricciardi \& Rasmussen, 1999; Dudgeon et al., 2006; Vörösmarty et al., 2010; Reid et al., 2019;). Fishes play a key role in the functioning of lotic ecosystems and provide essential contributions to freshwater ecosystem services (Villéger et al., 2017), yet previous studies evaluating the rarity of species have not considered how taxonomic rarity is correlated with functional originality or how human activities influence patterns of rarity and originality. For example, Pritt \& Frimpong (2010) categorized fishes based on different forms of taxonomic rarity, and Giam \& Olden (2018) showed how life history, ecological attributes and biogeography influence interrelationships among different dimensions of taxonomic rarity in fishes of the USA. In tropical rainforest streams, Leitão et al. (2016) found that species with low local abundance (i.e. one of the three forms of taxonomic rarity) were also functionally original based on
ecomorphological traits. However, neither of these studies explored the relationships of different taxonomic and functional rarity indices with the degree of habitat alterations in a single study. To fill this knowledge gap, this study examined the relationships between different forms of taxonomic rarity and functional originality in lotic fish assemblages in the Pannon Biogeographical Region (Hungary, Central Europe), and related them to the degree of local anthropogenic habitat degradation.

Following previous classic and more recent studies combining the different forms of taxonomic rarity (based on local abundance, geographical range and habitat breadth) (Brown, 1984; Tales, Keith \& Oberdorff, 2004; Faulks et al., 2015; Leitão et al., 2016), we expected a positive relationship among the different forms, indicating that a double or even triple jeopardy of extinction threatens freshwater fishes in the biogeographical region studied. Three scenarios were established to inform species-specific conservation actions: (i) A positive relationship between taxonomic rarity and functional originality calls for urgent conservation actions, because the higher risk of species extirpation would result not only in species loss but also in reduced ecological functions. In this case, the lower probability of substituting the lost ecological functions by the remaining species may result in a sharp decline in both biodiversity and ecosystem functioning. (ii) A negative association may indicate that rare species do not possess unique ecological functions. The higher risk of extirpation of taxonomically rare but functionally redundant species would not compromise ecosystem integrity. (iii) A lack of a relationship between rarity and originality indicates that both rare and common species can provide unique ecological functions, suggesting that effective conservation actions should consider both. The association among the three forms of taxonomic rarity (based on local abundance, geographical restrictedness, habitat breadth) and functional originality with the degree of anthropogenic degradation was explored to provide guidance for prioritizing conservation or restoration actions to mitigate further loss of species and ecological functions.

## 2 | MATERIALS AND METHODS

## 2.1 | Study area

The study area was located in the Pannon Biogeographical Region, Hungary where all streams and rivers are tributaries of the River Danube, the second largest river in Europe (catchment area $796,250 \mathrm{~km}^{2}$; length $2,847 \mathrm{~km}$ ). The majority of the country's $93,030 \mathrm{~km}^{2}$ are lowland areas (i.e. situated below 300 m a.s.l.), with only a very small proportion located in submontane regions (the highest mountain attaining $1,014 \mathrm{~m}$ ). Consequently, lowland (mainly silty-sand substrate) and highland (mainly gravel and sand substrate) streams and rivers form the majority of watercourses in this region (Erős, 2007; see Figure 1 for the map of the stream network). Largescale river regulations that began in the second half of the 19th century, paralleled by massive agricultural industrialization, have

FIGURE 1 (a) Distribution of the sampling sites in the Pannon Biogeographical region, Hungary, and the degree of degradation at each site.
(b) Frequency distribution of sites along the habitat degradation gradient

substantially changed the landscape in the Hungarian lowlands which formerly functioned as the floodplain area of the River Tisza (the second largest tributary of the Danube). Watercourses in the highlands, however, were mainly affected locally by small-scale canalization, reservoir construction and, in the past, industrial activities. Submontane streams remained relatively unimpaired, although some of them are now exposed to local influences such as intensive tourism, forestry and organic pollution from villages. The dominant land use in the catchments is arable fields, with vineyards, orchards, pastures and managed deciduous forest forming a smaller proportion (Tóth et al., 2019).

## 2.2 | Fish sampling

An institutional database (Erős et al., 2020) provided data on fish assemblages and environmental variables for 429 stream and river sites (Figure 1). The database was created from the data collected during country-wide fish and habitat surveys between 2013 and 2018. Fish were generally collected during the summer or early autumn base flow period (Erős et al., 2020). Two types of electrofishing methods were used (Erős et al., 2017), which were consistent with widely used electrofishing protocols (Oberdorff
et al., 2001; Pont et al., 2006). For streams (drainage basin area $<1,000 \mathrm{~km}^{2}$ ), a battery-powered electrofishing device was used (Hans-Grassl IG 200/2B device, PDC). The crew sampled a 150 m long reach, slowly walking upstream and with single-pass fishing of the whole stream width. For non-wadeable rivers, boat electrofishing was used with a generator driven device (Hans-Grassl EL64 II GI device, max $7,000 \mathrm{~W}, \mathrm{DC}$ ), slowly moving downstream and fishing 500 or $1,000 \mathrm{~m}$ long reaches in near-shore areas, respectively, for rivers (drainage basin area from $1,000-10,000 \mathrm{~km}^{2}$ ) and large rivers ( $>10,000 \mathrm{~km}^{2}$ ). This division in sampling length for streams, rivers and large rivers was necessary to optimize sampling effort and to sample fish assemblages representatively and in proportion to the size of the water body (Erős, 2007; Erős et al., 2020). After identification and counting, fish were released into the water at the site of capture (Table 1).

## 2.3 | Rarity indices

The taxonomic rarity of 42 exclusively native species (including Gobio sp. that may comprise a few cryptic species only distinguishable with genetic analyses; Table 1) was characterized by three continuous variables related to the three forms of rarity commonly studied: the

|  | Common name | Abbreviation | No. Ind. |
| :---: | :---: | :---: | :---: |
| Abramis brama | Common bream | abrbra | 459 |
| Alburnoides bipunctatus | Spirlin | albbip | 4,153 |
| Alburnus alburnus | Common bleak | albalb | 27,606 |
| Ballerus ballerus | Zope | balbal | 4 |
| Ballerus sapa | White-eye bream | balsap | 23 |
| Barbatula barbatula | Stone loach | ortbar | 6,441 |
| Barbus barbus | Common barbel | barbar | 1881 |
| Barbus charpaticus | Carpathian barbel | barpel | 957 |
| Blicca bjoerkna | White bream | blibjo | 1,305 |
| Carassius carassius | Golden carp | carcar | 18 |
| Chondrostoma nasus | Common nase | chonas | 745 |
| Cobitis elongatoides | Spined loach | cobelo | 3,534 |
| Cyprinus carpio | Common carp | cypcar | 322 |
| Esox lucius | Northern pike | esoluc | 541 |
| Gobio sp. | Gudgeon | gobgob | 9,505 |
| Gymnocephalus baloni | Danube ruffe/Balon's ruffe | gymbal | 52 |
| Gymnocephalus cernua | Ruffe | gymcer | 47 |
| Gymnocephalus schraetser | Schraetzer | gymsch | 17 |
| Leuciscus aspius | Asp | leuasp | 175 |
| Leucaspius delineatus | Sunbleak | leudel | 159 |
| Leuciscus idus | Ide | leuidu | 381 |
| Leuciscus leuciscus | Common dace | leuleu | 788 |
| Lota lota | Burbot | lotlot | 60 |
| Misgurnus fossilis | Weatherfish | misfos | 388 |
| Perca fluviatilis | European perch | perflu | 1,122 |
| Phoxinus phoxinus | Eurasian minnow | phopho | 2,201 |
| Rhodeus amarus | Bitterling | rhoser | 24,850 |
| Romanogobio kesslerii | Kessler's gudgeon | romkes | 46 |
| Romanogobio vladykovi | Danube whitefinned gudgeon | romvla | 1,318 |
| Rutilus pigus virgo | Danube roach | rutpig | 9 |
| Rutilus rutilus | Roach | rutrut | 18,005 |
| Sabanejewia aurata | Golden loach | sabaur | 85 |
| Salmo trutta morpha fario | Brown trout | saltru | 159 |
| Sander lucioperca | Pike-perch | sanluc | 225 |
| Scardinius erythrophthalmus | Common rudd | scaery | 1,293 |
| Silurus glanis | Wels catfish | silgla | 67 |
| Squalius cephalus | Chub | squcep | 17,486 |
| Tinca tinca | Tench | tintin | 38 |
| Umbra krameri | European mudminnow | umbkra | 214 |
| Vimba vimba | Vimba bream | vimvim | 185 |
| Zingel streber | Danube streber | zinstr | 105 |
| Zingel zingel | Zingel | zinzin | 37 |

TABLE 1 Species list, fish code abbreviations and the total number of individuals for each species
local relative abundance (hereafter called local rarity), the geographical range size (geographical restrictedness) and the habitat breadth (habitat specificity). Local rarity was quantified using the mean relative abundance of each species across all sites. Values of species
geographical restrictedness were extracted from the global database of geographical distribution of freshwater fishes built by CarvajalQuintero et al. (2019), providing the geographical range size of species in $\mathrm{km}^{2}$. Habitat specificity was calculated using the outlying
mean index analysis (Dolédec, Chessel \& Gimaret-Carpentier, 2000). This analysis calculates the habitat breadth of each species from an ordination plane of the environmental characteristics of the sites as the ratio of the polygon area occupied by a given species to the total polygon area of all sampled sites. Outlying mean index analysis was conducted using the following environmental variables, which were collected based on visual estimation and measurements at every transect point (Tóth et al., 2019): mean wet width, mean water depth, mean current velocity, bottom substrate (\% of marl or silt, sand, gravel, stone, rock, and concrete), vegetation coverage (\% of emergent, submerged, floating plant, and filamentous algae), and bank coverage (\% of arboreal vegetation, herbaceous vegetation, and concrete). These three rarity indices were transformed to equal scale (between 0 and 1), so that higher values represent rarer species.

For an integrative measure of rarity, a combined taxonomic rarity index was also established from the above-mentioned three indices following Leitão et al. (2016). Here, the three taxonomic rarity indices were weighted by their degree of independence to each other:

$$
\mathrm{CR}_{\mathrm{i}}=\frac{\left(\mathrm{Ir}_{\mathrm{i}} \times \omega_{\mathrm{lr}}\right)}{\omega_{\mathrm{lr}}+\omega_{\mathrm{gr}}+\omega_{\mathrm{hs}}}+\frac{\left(\mathrm{gr}_{\mathrm{i}} \times \omega_{\mathrm{gr}}\right)}{\omega_{\mathrm{lr}}+\omega_{\mathrm{gr}}+\omega_{\mathrm{hs}}}+\frac{\left(\mathrm{hs}_{\mathrm{i}} \times \omega_{\mathrm{hs}}\right)}{\omega_{\mathrm{lr}}+\omega_{\mathrm{gr}}+\omega_{\mathrm{hs}}}
$$

where $\mathrm{Ir}_{\mathrm{i}}$, $\mathrm{gr}_{\mathrm{i}}$ and $\mathrm{hs}_{\mathrm{i}}$ refer to local rarity, geographical restrictedness and habitat specificity of each species. The weighting parameters were calculated as follows:

$$
\omega_{\mathrm{lr}}=\frac{1}{2}+\frac{1-\left|\rho_{\mathrm{lr}-\mathrm{gr}}\right|}{2}+\frac{1-\left|\rho_{\mathrm{lr}-\mathrm{hs}}\right|}{2}
$$

where $\rho_{\mathrm{rl} \text {-gd }}$ and $\rho_{\mathrm{rl} \text {-hs }}$ are the Spearman correlation coefficients between local rarity and geographical restrictedness, and between local rarity and habitat specificity, respectively (Leitão et al., 2016).

Functional originality was based on the ecomorphological characteristics of the species, which provide information on key functions, such as food acquisition, nutrient processing, vertical position in the water column and locomotion types (Villéger et al., 2010; Leitão et al., 2016) (see Table S1 and Figure S1). Mean values from five individuals of each species were used for 20 continuous morphometric measures (Takács et al., 2021). From these measures, 15 functional traits were computed (Table S2) following Villéger et al. (2010). The local functional distinctiveness index of Violle et al. (2017) and Grenié et al. (2017) was used to define the species functional originality. This index quantifies functional originality of species as the mean distance in the functional trait space to all other species that occur in a given assemblage:

$$
F O_{i}=\frac{\sum_{j=1, j=i *}^{N} d_{i j}}{N-1}
$$

where $d_{i j}$ is the functional distance between species $i$ and $j$. This distance is standardized by dividing it by the maximum value of functional distances. $N$ is the number of species at the site (Violle
et al., 2017). Therefore, the index provides a good proxy of the uniqueness of the ecological roles delivered by a species in the assemblages it occupies (Violle et al., 2017).

## 2.4 | Habitat degradation index

A composite habitat degradation index was used to quantify the overall human alteration of the sites (see also Erős, O'Hanley \& Czeglédi, 2018; Erős et al., 2020). Five different indicators of habitat condition were used to compute the index: (i) state of the catchment; (ii) chemical degradation of the study reach; (iii) pressure of nonnative fishes; (iv) degradation of the riparian zone; and (v) instream hydromorphological degradation.

The state of the catchment (i) was characterized by the land use index (LUI) of Böhmer et al. (2004), which describes land use intensity and impact within a catchment along a gradient from natural forest cover to agricultural and urban use (Ligeiro et al., 2013; Erős, O'Hanley \& Czeglédi, 2018): LUI $=\%$ pasture $+2 \times \%$ arable land $+4 \times \%$ urban area.

The percentages of land use categories in each site (i.e. its corresponding catchment) were determined by GIS imagery using the Corine Land Cover database.

To characterize chemical degradation (ii), conductivity, dissolved oxygen content and pH were measured with an OAKTON Waterproof PCD 650 portable handheld meter, and the content of nitrogen forms (i.e. nitrite, nitrate, ammonium) and phosphate were measured using field kits (Visocolor ECO, Macherey-Nagel 158 GmbH \& Co. KG., Germany). These parameters were transformed if necessary (using square-root, double square-root or log-transformation), and analysed in a standardized principal component analysis. The first principal component (explaining about $50 \%$ of the total variability and related to nitrogen forms and phosphate; (see Figure S2) was used as an index of chemical degradation.

The biotic pressure from non-native species (iii) was measured as their relative abundance (\%), with higher values hence depicting higher biotic pressures (Erős et al., 2020). Non-native species were defined as those species that were non-native within the whole study area. Invasion by non-native species can adversely influence the structure of native assemblages, for example by direct predation or competition for space or food (Cucherousset \& Olden, 2011; Sagouis et al., 2015).

The riparian degradation (RIPD; (iv) of the stream margins (i.e. along a $\sim 10 \mathrm{~m}$ wide strip on both sides) was characterized by visually estimating the percentage of vegetation cover (herbaceous and arboreal) and concrete (Erős et al., 2017), following the formula from Erős et al. (2020): RIPD $=\%$ arboreal $+2 \times \%$ herbaceous $+4 \times \%$ concrete cover.

Decreasing arboreal vegetation and increasing concrete cover can influence assemblage structure and integrity of the biota in streams and rivers (Moore \& Palmer, 2005; Dala-Corte et al., 2016; Tóth et al., 2019). Therefore, higher RIPD values show higher riparian degradation. The percentage of instream concrete covered surface
was used as a coarse measure of hydromorphological degradation (v). These five degradation indices were scaled between 0 and 1 and summed to form the 'composite' habitat degradation index, with 0 indicating the most natural condition and 1 the most degraded (Figure 1).

## 2.5 | Statistical analysis

Associations between taxonomic rarity and functional originality indices were quantified using Spearman rank correlation coefficients.

The relationship between habitat degradation and the rarity of fish assemblages was examined using general linear models, previously excluding any spatial dependency potentially affecting the rarity forms and habitat degradation index using Moran's I spatial autocorrelation coefficients (Pebesma \& Bivand, 2005).

R 3.5.2 software was used to analyse the data ( R Core Team, 2018) using the following $R$ packages: ade4 (Dray \& Dufour, 2007), car (Fox \& Weisberg, 2011), funrar (Grenié et al., 2017), ggplot2 (Wickham, 2016), sp (Bivand, Pebesma \& Gómez-Rubio, 2013), spdep (R: Bivand \& Piras, 2015), splancs (Rowlingson \& Diggle, 2017), tmaptools (Tennekes, 2018) and vegan (Oksanen et al., 2019).

## 3 | RESULTS

Relatively large differences were found in the order of rarity of the 42 native fish species when comparing the different taxonomic rarity indices (Table S3). For example, the European mudminnow (Umbra krameri) was among the most common species based on local abundance, but was among the rarest based on habitat specificity and geographical restrictedness. Another example is the European perch (Perca fluviatilis) which was relatively rare locally, but was among the most common species based on geographical restrictedness and habitat specificity. Accordingly, Spearman correlations revealed only weak positive relationships between local rarity and geographical restrictedness, and local rarity and habitat specificity, although the latter did not prove to be statistically significant (Table 2). Geographical restrictedness and habitat specificity showed a moderately strong positive correlation (Table 2). The combined

TABLE 2 Correlation matrix (Spearman's $r$ and $P$ values, in the upper and lower diagonals, respectively) between the different rarity forms. LR: local rarity, GR: geographical restrictedness, HS: habitat specificity, CR: combined taxonomic rarity, FO: functional originality

|  | LR | GR | HS | CR | FO |
| :--- | :---: | :---: | :---: | :--- | ---: |
| LR |  | 0.3114 | 0.2548 | 0.7320 | 0.1114 |
| GR | 0.0451 |  | 0.4514 | 0.6349 | -0.0228 |
| HS | 0.1035 | 0.0026 |  | 0.6736 | 0.0758 |
| CR | $<0.001$ | $<0.001$ | $<0.001$ |  | 0.0348 |
| FO | 0.4811 | 0.8861 | 0.6334 | 0.8266 |  |

taxonomic rarity index was mostly determined by local rarity, followed by habitat specificity and finally geographical restrictedness (Table 2). Functional originality did not show any correlation either with the individual rarity indices or with the combined taxonomic rarity index (Table 2). According to the combined taxonomic rarity index, the Danube roach (Rutilus pigus virgo), the zope (Abramis ballerus), the Danube streber (Zingel streber), the schraetzer (Gymnocephalus schraetzer) and the zingel (Zingel zingel) were the five rarest species, whereas the functionally most original five species were the sunbleak (Leucaspius delineatus), bitterling (Rhodeus amarus), wels catfish (Silurus glanis), burbot (Lota lota) and Eurasian minnow (Phoxinus phoxinus). The distribution of species along the axes formed by the combined taxonomic rarity and the functional originality indices showed that most species were taxonomically rather rare, but functionally rather common (Figure 2).

The habitat degradation index indicated that most sites were only moderately degraded (Figure 1). Although the ratio of extremely degraded and highly natural sites was relatively low, the sites covered a long gradient of human alteration (Figure 1; Table 3) which was ideal for testing the relationship between rarity and habitat degradation. The linear models showed that the different forms of taxonomic rarity and functional originality changed in a different way along the degradation gradient: local rarity ( $\beta=-0.111$, adjusted $P=0.001$ ), habitat specificity ( $\beta=-0.178$, adjusted $P<0.001$ ) and combined taxonomic rarity ( $\beta=-0.218$, adjusted $P<0.001$ ) were lower in more degraded places; and functional originality increased towards higher values of the degradation index ( $\beta=0.207$, adjusted $P<0.001$; Table 4).

## 4 | DISCUSSION

Only weak or medium level correlations were found among the indices of taxonomic rarity, and no relationships were found between taxonomic rarity and functional originality. These results show that considering different facets of rarity is important for a more exact evaluation of species vulnerability to extinction. The positive correlations between local rarity and geographical restrictedness, and geographical restrictedness and habitat specificity suggest that fish species face a double jeopardy of extinction in the Pannon Biogeographical region.

The combined taxonomic rarity index showed that among the species examined, large river fishes are in general the most vulnerable. This is unsurprising because the dendritic structure of river networks constrains the amount of large downstream habitats, restricting the occupancy of large river specialists compared with those species living in smaller streams and rivers. Furthermore, the rarest large river specialists (e.g. Danube roach, the zope; the Danube streber; the schraetzer; the zingel, Erős, 2007) are species endemic to the Danube basin, hence being also biogeographically rare. Note that the local abundance of populations of very large river fishes is probably underestimated in conventional fish monitoring surveys, owing to the difficulty of sampling fishes representatively offshore in these large systems. Nevertheless, as these species are generally rare in all facets

FIGURE 2 The combined taxonomic rarity and functional originality of species (axis $X$ and $Y$ respectively). Marginal boxplots show the distributions of index values. Fish codes with red letters indicate species protected by law in Hungary. See Table 1 for fish code abbreviations


TABLE 3 Mean, minimum and maximum values of environmental stressor variables of the examined sites ( $\mathrm{n}=429$ )

| Variable | Min. | Mean | Max. |
| :--- | ---: | ---: | ---: |
| Land use index (LUI, \%) | 0.000 | 145.000 | 308.900 |
| Ammonium ( $\mathrm{mg} \mathrm{L}^{-1}$ ) | 0.014 | 0.450 | 8.860 |
| Nitrate $\left(\mu \mathrm{g} \mathrm{L}^{-1}\right)$ | 0.125 | 2.762 | 14.170 |
| Nitrite $\left(\mu \mathrm{g} \mathrm{L}^{-1}\right)$ | 0.005 | 0.070 | 0.505 |
| Phosphate ( $\mu \mathrm{g} \mathrm{L}^{-1}$ ) | 66.960 | 864.120 | 6528.970 |
| pH | 6.620 | 8.015 | 8.550 |
| Conductivity $\left(\mu \mathrm{S} \mathrm{cm}^{-1}\right)$ | 145.000 | 798.900 | 2177.300 |
| Dissolved oxygen (mg L-1) | 2.038 | 8.973 | 13.552 |
| Hydromorphological degradation (\%) | 0.000 | 2.522 | 94.000 |
| Riparian degradation (RIPD, \%) | 25.000 | 46.640 | 100.000 |
| Relative abundance of non-native fishes (\%) | 0.000 | 15.901 | 99.594 |

TABLE 4 Relationships between anthropogenic habitat degradation and the different rarity indices based on GLMs. $P$-values are Bonferroni-Holm corrected

| Dependent variable | Estimate | SE | t-value | Adjusted $P$-value |
| :--- | :--- | :--- | :--- | :---: |
| Local rarity (LR) | -0.111 | 0.032 | -3.421 | 0.001 |
| Geographical restrictedness (GR) | -0.017 | 0.018 | -0.981 | 0.327 |
| Habitat specificity (HS) | -0.178 | 0.039 | -4.502 | $<0.001$ |
| Combined rarity (CR) | -0.218 | 0.043 | -5.105 | $<0.001$ |
| Functional originality (FO) | 0.207 | 0.037 | 5.622 | $<0.001$ |

of taxonomic rarity they need urgent protection from further human impacts. In this regard, maintaining natural hydromorphological conditions in large rivers should be a priority in this region (Hein et al., 2019; Szalóky et al., 2021). Protection of Danubian endemic
species can only be effectively attained with transboundary collaboration, involving several small countries that share the river and catchment of the Danube basin (Sommerwerk et al., 2010; Dolezsai et al., 2015).

Interestingly, some species considered as top priority for conservation in Hungary and strictly protected, were not among the rarest species identified based on the combined taxonomic rarity index. For example, the European mudminnow (U. krameri) was one of the most abundant species locally but one of the rarest based on its habitat specificity and geographical distribution (see Table S3). Nevertheless, we believe that protecting these species is extremely important, because the destruction of only a few sites or habitats can shift the whole species close to extinction (Purvis et al., 2000; Harnik, Simpson \& Payne, 2012). Indeed, it can be more urgent to conserve species restricted to a few places but with high abundance than those widely distributed but locally rare, especially in Hungary where habitat destruction (e.g. dredging) or serious chemical pollution can still be a reality (Erős et al., 2015).

The lack of a relationship between taxonomic rarity indices and functional originality shows that both rare and common species can provide unique ecological functions in this region. Thus, it is essential to determine the vulnerability of both common and rare species to human impacts for maximizing the effectiveness of conservation actions. In addition, the fact that taxonomic rarity cannot be used as a proxy for functional originality calls for a more systematic incorporation of functional rarity indices into conservation policy, although this requires a more widespread characterization of functional rarity across biogeographical regions. Extinction of taxonomically and functionally rare species may severely undermine the integrity of ecological processes (Mouillot et al., 2013; Leitão et al., 2016). Therefore, a more detailed understanding of the effect that the disappearance of taxonomically and functionally rare species has on ecosystem functioning should be a priority of species level, evidence-based conservation.

This study provided evidence that the combined taxonomic rarity index is correlated with the degree of degradation of rivers and streams. This is an important finding for evidence-based conservation, as it shows how human impacts at a regional scale can cause the disappearance of fish populations, despite the variability and noise that are inherent in snapshot, regional scale surveys. Proving the effect of human alterations on the disappearance of species can be difficult (Rose, 2000; Luck \& Smallbone, 2010; Tóth et al., 2019), owing to time lags in their effects, to interactions among environmental variables, and to metapopulation processes such as source-sink dynamics (Schlosser \& Angermeier, 1995; Rose, 2000). Community level species richness can even increase as a result of the introduction of non-native species, which may proliferate in modified habitats (Villéger et al., 2010; Tóth et al., 2019). However, this study emphasizes that because of the sensitivity of taxonomically rare species to habitat alteration, detailed investigations of their metapopulation dynamics are needed urgently on which to base management actions. Unfortunately, such analyses are still uncommon in conservation practice owing to many practical difficulties (Fullerton et al., 2016; Cid et al., 2020).

In contrast to taxonomic rarity, mean functional originality of species increased with the degree of human alteration. This result
might suggest that in general functionally rather common species were more affected by the effects of degradation than those with more uncommon functional traits. Although disentangling the exact mechanism behind this pattern still requires further investigation, we speculate that simple neutral effects may be involved, because most species were functionally relatively common. As functionally common species were more frequent in the studied communities, these species may disappear more often than functionally rare ones, especially if functionally common and rare species respond to habitat alterations in a similar way.

A limitation of this study was that only ecomorphological traits were used for characterizing functional originality. Although ecomorphological traits mirror evolutionary processes and can be used as a proxy of functional niche and ecological functions, we believe that a more direct quantification of species functions is warranted (Villéger et al., 2017; Svozil et al., 2020). In fact, the exact relationships between ecomorphological traits and ecosystem functions have been studied in detail only for a few traits and taxa (Wainwright, 1991; Higham, 2007a; Higham, 2007b; CochranBiederman \& Winemiller, 2010; Villéger et al., 2017; Svozil et al., 2020;). Nevertheless, such trait-based analyses can be useful at large spatial scales and for multi-species comparisons, since the exact quantification of the role of species in multiple (or all) ecological functions is hardly feasible at the community level (Liu, Comte \& Olden, 2017).

In conclusion, the results of this study have shown that a more exact characterization of species rarity requires multiple metrics, including functional ones, because these indices respond differently to anthropogenic alterations. Combined indices of rarity can help to prioritize species-level conservation actions, although single rarity metrics are still needed to adapt these actions to species attributes (e.g. endemism or unique functions). Species-level conservation would benefit from integrating the evaluation of functional rarity within conservation policy in the face of increasing global changes.

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## CONFLICT OF INTEREST

The authors have no conflict of interest to declare in regard to this research or its funding.

## DATA AVAILABILITY STATEMENT

Data available on request from the authors.

## ORCID

Tibor Erös (D) https://orcid.org/0000-0002-2252-3115

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