

1 **The original published PDF available in this website:**

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5 **Land use effects in riverscapes: diversity and environmental drivers of stream fish**
6 **communities in protected, agricultural and urban landscapes**

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34 **Abstract**

35 Increasing agriculture and urbanization inevitably lead to changes in the biodiversity of
36 stream ecosystems. However, few studies examined comprehensively how biodiversity is
37 distributed within and among protected, agricultural and urban land use types in streams. We
38 studied environmental characteristics of streams and patterns of species richness and other
39 community attributes of stream fish communities in these three characteristic land use types in
40 the catchment of the Danube River, Hungary. Land use separated streams to some degree
41 based on their environmental characteristics. However, both between stream environmental
42 and fish community variability were high in most types, and comparable to land use type level
43 differences in case of many streams. A variety of environmental gradients influenced fish
44 community structure rather independently of land use type, which was also influenced by
45 spatial drivers. Non-native fishes modified the structure of native fish communities, especially
46 in agricultural streams, although their modification effect varied more among individual
47 streams than among land use types. In conclusion, land use type proved to be a poor predictor
48 of fish communities in this human modified landscape. We found that even intensively
49 managed areas (i.e. agricultural and urban) can contribute to the maintenance of fish diversity
50 in this biogeographic region, or at least their potential can be comparable to those streams
51 which flow in protected areas. Thus, conservation management should focus on maintaining
52 streams in more natural condition in protected areas and/or use the potential of non-protected
53 agricultural and urban streams in maintaining fish diversity in human modified landscapes.

54 key words: land use type, within and between type variability, environmental gradients,
55 agriculture, urbanization, conservation, biodiversity

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57

58 **Introduction**

59 The alteration of natural landscapes caused by human activity is one of the leading factors
60 driving the decline of biodiversity worldwide (Sala et al., 2000; Foley et al., 2005). The
61 conversion of natural habitats to agricultural or urban uses not only affects terrestrial
62 ecosystems but can also substantially influence the biodiversity and biological integrity of
63 streams and rivers flowing through these terrain (Paul and Meyer, 2001; Allan, 2004). In fact,
64 streams and rivers are among the most threatened ecosystems on Earth, and their biodiversity
65 is declining at a much faster rate than that of any other ecosystem (Dudgeon et al., 2006).
66 However, the mechanisms by which changes in land use change influence stream
67 communities are still poorly understood (Johnson and Angeler, 2014; Barnum et al., 2017),
68 which can impede the implementation of effective management practices (Rose, 2000; Palmer
69 et al., 2005; Roy et al., 2016).

70 Disentangling the effects of land use on stream systems is difficult because they are complex,
71 scale dependent, and, in most cases, non-linear (Allan, 2004; Urban et al., 2006; Dala-Corte et
72 al., 2016). Although these factors are widely recognised, most studies have only examined
73 responses at the local scale, and justified the negative influence of urban or agricultural
74 development on local (i.e. alpha) diversity using land cover gradients. For a more complete
75 understanding of the response of stream biota to modifications in land use, local (alpha) and
76 between-site (beta) diversity should be jointly examined (Johnson and Angeler, 2014; Edge et
77 al., 2017). However, the study of how local and between site diversity varies within and
78 between land use types is largely neglected in stream ecosystems.

79 Invasions by non-native (exotic) species can further reinforce the negative effect of land use
80 changes on stream communities. In many cases, the detrimental effects of non-natives have
81 been found to be related to landscape-level habitat change (e.g. urban development, water
82 diversion and stream flow modification for agriculture; Marchetti et al., 2004; Kennard et al.,
83 2005; Light and Marchetti, 2007; Hermoso et al., 2011). Non-natives can also modify the
84 homogenisation or heterogenisation effect of land use on biodiversity at regional scales
85 (Olden and Poff, 2003; Marchetti et al., 2006; Hermoso et al., 2012). However, the scale
86 dependent effect of non-natives on the biodiversity of native communities in different land
87 use types remains largely unknown (e.g. agricultural, urban). It is likely that patterns in their
88 invasion may substantially influence among type differences in stream fish biodiversity.

89 In this study we examined the effect of land use and associated changes in stream habitat
90 characteristics on the biodiversity and community structure of fish communities in the Pannon
91 Biogeographic Region, Hungary. We were especially interested in quantifying to what extent
92 the *a priori* categorisation of land use can explain the diversity of stream fish communities.
93 Our questions were as follows. 1) Do the environmental characteristics of streams differ
94 among protected, agricultural, and urban stream habitats, and if so, what are the most
95 important environmental variables that differentiate land use types? 2) How do alpha and beta
96 diversity of fishes differ within and between land use types? 3) How non-native fishes
97 influence patterns in alpha and beta diversity within and between land use types? 4) Which
98 environmental variables are likely to be most responsible for shaping the biodiversity and
99 community structure of fishes in this landscape?

100 We predicted that differences in land use would induce changes in the environmental
101 characteristics of streams, which would subsequently lead to differences in the diversity and
102 structure of fish communities. We expected that both the alpha and beta diversity of native
103 fishes would be highest in protected, relatively natural sites, intermediate in agricultural sites,
104 and lowest in urban sites (Kennard et al., 2005; Scott, 2006; Trautwein et al., 2012), due to
105 increasing perturbation effects and, consequently, homogenisation of habitat structure (Scott,
106 2006; Hermoso et al., 2012). We also expected that natural stream conditions would make the
107 habitat more resistant to invasion (Marchetti and Moyle, 2001), and that protected status
108 would ensure the preservation of natural stream habitats to some degree. Water storage
109 reservoirs and fishponds are common in this region and are utilized in agriculture; they have
110 been found to be most highly associated with the proliferation of non-natives in this (Erős et
111 al., 2012; Takács et al., 2017) and other biogeographic regions (Havel et al., 2005; Clavero
112 and Hermoso, 2011). Therefore, we predicted that the influence of non-native fishes on
113 community structure would be highest in agricultural areas, show intermediate level influence
114 in perturbed urban sites, and be lowest in protected sites. Taken together, these predictions
115 should yield a variety of outcomes for the diversity and community structure of fishes among
116 land use types, which we wanted to disentangle and quantify in this study.

117

118 **Materials and methods**

119 Study sites

120 The study area was located in Hungary where all the streams and rivers are tributaries of the
121 River Danube, the second largest river in Europe (catchment area 796 250 km²; length 2847
122 km). The majority of the country's 93,000 km² are relatively lowland areas (i.e. situated
123 below 300 m a.s.l.), with only a very small proportion being located in submontane regions
124 (highest mountain peak is only 1014 m). The dominant land use type in the catchments is
125 arable fields, with vineyards, orchards, pastures, and managed deciduous forest forming a
126 smaller proportion.

127 We selected 75 sampling sites in total for this study, using geoinformatic maps. In selecting
128 the sites we applied the following criteria: (i) all stream sites should be wadeable (2nd and 3rd
129 order streams), and be situated below 300 m a.s.l. to decrease the effect of natural
130 environmental variability as much as possible; (ii) the 25 sites selected as samples of
131 protected land use type should be part of the protected area network of Hungary (i.e. either
132 belong to national parks and/or form part of the NATURA 2000 network); (iii) the 25 sites
133 selected for the agricultural land use type should be situated in catchments where agricultural
134 land use exceeds 70%; (iv) the 25 sites selected for the urban land use type should be situated
135 close to the centre of settlements (villages and cities with less than 250,000 inhabitants); (v)
136 all sites should be located within a reasonable distance from the nearest road for accessibility.
137 Of the 75 selected sites we actually sampled 62 stream sites. Of these, 21, 20, and 21 sites
138 represented protected, agricultural, and urban land use categories, respectively, the remainder
139 could not be sampled due to desiccation, problems with accessibility, or other logistical
140 constraints.

141

142 Environmental variables

143 Basically, we followed the methodology of Erős et al (2012, 2017) for characterising the
144 environmental features of the sites, which will be reiterated here briefly. Altogether 10
145 transects were placed perpendicular to the main channel at each sampling site (150 m long
146 each, see below) to characterise physical features of the environment (see Appendix I).

147 Wetted width was measured along each transect. Water depth and current velocity (at 60%
148 depth) were measured at five equally spaced points along each transect. Visual estimates of
149 percentage substratum cover were made at every transect point as well (see Appendix I for
150 categories). Percentage substratum data of the transect points were later pooled and overall
151 percentage of substrate categories were calculated for each site. Macrovegetation (emergent,

152 submerged, floating) and periphyton coverage (macrophyte types) was also estimated visually
153 for each transect points and later pooled, and overall percentage of macrophyte categories
154 were calculated for each site. Water temperature, conductivity, dissolved oxygen content,
155 TDS, and pH were measured with an YSI EXO2 multiparameter water quality sonde (Xylem
156 Inc. NY, USA) before fish sampling, and the content of nitrogen forms (i.e., nitrite, nitrate,
157 ammonium) and phosphate were measured using field kits (Visocolor ECO, Macherey-Nagel
158 GmbH & Co. KG., Germany). Percentage coverage of vegetation at the stream margin (i.e.
159 along a ~ 10 m wide strip in both sides) was estimated visually distinguishing herbaceous and
160 arboreal categories. Altitude was measured in the field using a GPS device (Garmin Montana
161 650). The coefficient of variation (CV) of depth, velocity, and width data were also calculated
162 to characterise instream habitat heterogeneity. Finally, we calculated both substrate and
163 macrophyte diversity as the Shannon diversity of the proportion of different substrate and
164 macrophyte types, respectively. We used these variables as these provide meaningful
165 information on both catchment and instream level characteristics of the habitat, including
166 possible human effects (Wang et al., 2003; Hoeinghaus et al., 2007; Erős et al., 2012).

167

168 Fish sampling

169 Fish were collected during the summer months (July-August) of 2017. At each site, we
170 surveyed a 150 m long reach by wading, single pass electrofishing using a backpack
171 electrofishing gear (IG200/2B, PDC, 50-100 Hz, 350-650 V, max. 10 kW; Hans Grassl
172 GmbH, Germany). This amount of sampling effort was found to yield representative samples
173 of fish communities in this study area for between-site community comparisons (Sály et al.,
174 2009) and is also comparable with those routinely used elsewhere for the sampling of fish in
175 wadeable streams (Magalhães, Batalda & Collares-Pereira, 2002; Hughes & Peck, 2008). Fish
176 were identified to species level (Appendix II), counted and released back to the stream.

177

178 Data analysis

179 We used Constrained Analysis of Principal Coordinates (CAP, Anderson and Willis 2003),
180 complemented with a permutation based ANOVA (Oksanen et al. 2018) to test whether land
181 use type influenced the environmental characteristics of the streams. The Euclidean distance
182 was used to compare the environmental similarity of the sites. Prior to calculations, the

183 environmental variables were divided by their maximum values to standardise them to equal
184 (0-1) scale. K-means analysis was also performed to check the differences between *a priori*
185 and *a posteriori* classifications of the sites to land use types and for the quantification of
186 classification error (%). In this manner, we could further quantify the discriminative power of
187 land use type on the environmental characteristics of the streams.

188 General linear models (LM) were used to test the effects of land use (categorical predictor)
189 and the measured environmental variables (continuous predictors) on species richness.
190 Variables that showed strong correlation with other variables in pairwise comparisons
191 (Pearson correlation value > 0.7) and had a high variance inflation factor value (VIF > 5)
192 were omitted before the analysis. Model selection was started by fitting the full model (i.e.
193 using all the selected environmental variables for the analysis) and the Akaike's information
194 criterion (AIC) was used to find the minimum adequate model.

195 Similarly to abiotic data, CAP (Anderson and Willis 2003) and k-means analyses were used to
196 quantify the separation of fish communities among the land use types and to visually examine
197 the relative role of within- and between-type variability (i.e. beta diversity). We used the
198 Sorensen and the Bray and Curtis indices for composition (presence-absence) and Hellinger
199 transformed abundance data (Legendre & Gallagher, 2001), respectively for these analyses.

200 Finally, we applied variance partitioning in redundancy analysis (RDA) to examine the
201 contribution of environmental effects and spatial positioning of the streams in the landscape to
202 variation in fish community structure. For obtaining spatial variables, we ran principal
203 coordinates of neighbour matrix analysis (PCNM or also called Moran eigenvector map)
204 based on Euclidean watercourse distance among the sites (Borcard et al., 2011; Legendre and
205 Legendre, 2012). We retained the PCNM eigenvectors with positive eigenvalues as spatial
206 explanatory variables in the RDA analyses. For partitioning the variation in community
207 structure (i.e. Hellinger transformed abundance data) between local environmental variables
208 and spatial location, each group of explanatory variables was first screened using forward
209 selection with Monte Carlo randomization test (1000 runs) in separate RDA analyses. Only
210 variables significantly related to community variability were retained in the final RDA
211 models. Variation in community structure was subsequently partitioned into shared
212 environmental and spatial position, pure environmental, pure spatial, and unexplained
213 proportions using adjusted R^2 values (Borcard et al., 2011; Legendre and Legendre, 2012).
214 We performed the analyses at the whole landscape level, and for each land use type
215 separately. All statistical analyses were performed in R (R Development Core team, 2015)

216 using packages vegan (Oksanen et al., 2018), car (Fox & Weisberg, 2011) and MASS
217 (Venables & Ripley, 2002).

218

219 Results

220 *Land use effects on stream environment*

221 CAP revealed that the environmental characteristics of the streams differed among the land
222 use types (Fig. 1, ANOVA like permutation $F= 4.397$, $p<0.001$). Streams in protected areas
223 had generally more natural bank vegetation (i.e. higher percentage of trees along the bank),
224 and, consequently, lower amount of instream vegetation. Protected stream sites generally
225 situated at higher altitudes (albeit all below 300 m) and could also be characterised by higher
226 flow velocity. Streams in agricultural areas had higher percentage of silt, emergent
227 macrovegetation (mainly reed *Phragmites australis*), and herbaceous bank vegetation. Not
228 surprisingly, typical urban streams contained higher percentage of concrete both as instream
229 substrate and along the bank. Nevertheless, k-means analysis showed that consistency
230 between the *a priori* and the *a posteriori* land use classification schemes was only moderate.
231 The percentage of correct allocations was 52.4%, 70.0%, and 33.3% for the protected,
232 agricultural, and urban classes, respectively. Overall, these results indicate that land use
233 separate streams to some degree based on their environmental characteristics. However,
234 between-stream variability is high, and it can be comparable to land use type level differences
235 in case of many streams.

236

237 *Land use effects on fish communities*

238 Species richness was highest in protected sites and lowest in urban areas (Fig. 2). This pattern
239 did not change with the removal of non-native species from the community (i.e. at the native
240 community level). However, as predicted, the absence of non-natives caused the largest
241 change in the species richness in agricultural areas compared with the richness at the entire
242 community level. The general linear models showed that the relative abundance of non-
243 natives ($p<0.001$), altitude ($p=0.001$), agricultural land use ($p=0.004$), pH ($p=0.020$), water
244 velocity ($p=0.027$), and, albeit marginally, the number of non-native species ($p=0.041$) were
245 the most important variables determining the number of native species in the studied land type
246 studied (Table 1).

247 CAPs showed that the structure of fish communities both in terms of composition (Fig. 3a;
248 $F=2.439$, $p=0.008$) and relative abundance (Fig. 3b; $F=1.763$, $p=0.013$) differed significantly
249 among land use types. However, visual examination of the results and the F and p values
250 indicated that overall difference in community structure was low. In general, streams in
251 protected areas could be characterised mainly by native fishes (e.g. chub *Squalius cephalus*,
252 spirlin *Alburnoides bipunctatus*) while the abundance of the non-native gibel carp (*Carassius*
253 *gibelio*) and stone morocco (*Pseudorasbora parva*) increased in both urban, and, especially
254 agricultural areas. Calculations based on k-means analysis showed that the percentage of
255 correct allocations was 52.4%, 50.0%, and 38.1% for protected, agricultural, and urban land
256 types, respectively, for composition (presence/absence) data. The corresponding values were
257 52.4%, 40.0%, and 47.6% for relative abundance. These results on patterns in beta diversity
258 supported the findings of stream environmental data and showed that between-stream level
259 variability in a single land use type can be comparable to that among type level differences in
260 the case of most streams.

261 Variance partitioning analysis in RDA indicated a relatively low level of predictability of fish
262 community structure based on environmental and spatial data. The pure environmental (adj
263 $R^2=0.238$ $p<0.001$), pure spatial adj $R^2=0.061$ $p=0.131$), and shared environmental and spatial
264 variables adj $R^2=0.034$ $p=0.013$) explained 23.8%, 6.1%, and 3.4% of the variance in the data,
265 respectively, whereas 66.7% of the variation remained unexplained. The first axis of the
266 environmental RDA was influenced by altitude, substrate composition (especially, the ratio of
267 stone or silt), and the percentage of total plant coverage (i.e. plant free space), whereas the
268 coefficient of variation in water velocity and the percentage of emergent macrophyte coverage
269 were the main determinants of community structure along the second axis (Fig. 4). Variance
270 partitioning analysis conducted separately for each land use type suggested approximately the
271 same amount of explained variation in case of each land use type (Table 2). However, the
272 relative role of environmental (E) and spatial (S) variables differed (Table 2). The ratio of E/S
273 was the largest in protected (7.0), intermediate in agricultural (2.2) and the lowest (0.9) in
274 urban areas.

275

276 Discussion

277 The diversity and community structure of stream fishes varied largely within the *a priori*
278 established land use types. In fact, within-type level differences in environmental

279 characteristics and fish community structure were comparable to between-type level changes
280 in the case of many streams. These results show that markedly different land use categories
281 (i.e. protected, agricultural, urban) are not a reliable indicator of fish community structure in
282 streams. Rather, a more in-depth analysis of the environmental characteristics of streams is
283 needed to disentangle changes in stream fish diversity in modified landscapes.

284 As expected, streams in protected areas generally contained more native fishes and were less
285 affected by non-natives than agricultural and urban streams. Streams in protected areas also
286 showed some differences in the composition and relative abundance of species. These
287 differences could be attributed to differences in the environmental characteristics of the
288 streams among the land use types. For example, Erős et al (2012) showed that even subtle
289 differences in altitude could induce changes in fish community structure that are comparable
290 to human alteration effects. Streams running through protected areas were more common at
291 higher altitudes, and species that are more common in highland streams (e.g. chub, spirlin; see
292 Erős, 2007) were more abundant in these streams than in agricultural and urban landscapes
293 (Fig. 3b). Nevertheless, CAP and k-means analyses indicated that many streams in protected
294 areas had similar environmental features to those of agricultural or urban streams, and
295 correspondingly, their fish communities were also relatively similar. The results of the k-
296 means analysis are especially interesting since they showed that only half of the streams
297 (52.4%) were allocated to the protected type appropriately, based on environmental or fish
298 community characteristics of the streams. These results deserve the attention of conservation
299 management in that (i) the land's protected status is only a very crude indicator of the
300 naturalness of its streams and (ii) the potential of agricultural and urban streams to maintain
301 fish diversity can be comparable to those of protected areas. Our results, coupled with those
302 from other biogeographic regions, thus emphasise the need for a more thorough consideration
303 of even intensively managed areas in conservation design in human dominated landscapes
304 (Heino et al., 2009; Durán et al., 2014).

305 Several studies examined how landscape-level proxy variables, such as the proportion of
306 urban and agricultural areas in the catchment, influence the structure of stream fish
307 communities (e.g. Scott, 2006; Trautwein et al., 2012). However, studies which directly
308 compare within- and between-stream environmental heterogeneity and beta diversity of fish
309 communities in protected, agricultural, and urban land use types are lacking. The CAP
310 analysis indicated that between-stream environmental variability and, consequently, fish
311 community variability in urban streams was comparable to that of protected streams. In fact,

312 streams in urban areas were ordered along a long environmental gradient (Fig. 1). They
313 ranged from typical urban sites (i.e. with almost complete coverage of concrete in both
314 instream and along the bank) to stream sites which showed the features of typical agricultural
315 and, albeit in lower portion, of protected streams.

316 Conversely, agricultural streams were more homogenous than urban and protected streams, at
317 least based on their environmental characteristics. Streams in agricultural landscapes were
318 similar to those in other regions of the world, with canal-like construction, and agricultural
319 use close to the stream margin. Such land management encourages channel incision and
320 excessive sedimentation and allows only relatively low environmental heterogeneity, both
321 within streams and along the banks (Roth et al., 1996; Lester and Boulton, 2008). Land use
322 type thus proved to be a relatively good determinant of agricultural streams, at least compared
323 with protected and urban streams and based only on environmental variables (70% of correct
324 allocations in this type).

325 Despite displaying lower environmental variability, between-stream community variability of
326 agricultural streams was comparable to other stream types. This variability cannot only be
327 attributed to the relatively high abundance of non-native species in this stream type (see also
328 Erős et al, 2012), but also to between-stream variability in the native community.

329 Nevertheless, non-native fishes were important in separating agricultural and urban streams
330 from protected streams to some extent, especially based on relative abundance. Previous
331 studies found a strong relationship between the distribution of fishponds and other water
332 storage reservoirs in the landscape and the proliferation of non-native fishes (Moyle &
333 Marchetti, 2006; Johnson *et al.*, 2008). These artificial lentic habitats are especially abundant
334 in the vicinity of urban and agricultural areas (Erős et al., 2012; Takács et al., 2017). Thus, it
335 is not surprising that non-native invasive fishes were more abundant in these stream types
336 than in streams which run in relatively remote protected areas.

337 Variance partitioning in RDA showed the overarching role of environmental gradients over
338 spatial effects in shaping fish community structure, both in global analysis (Fig. 4) and when
339 the relative role of environmental and spatial effects were examined separately for each land
340 use type, with the exception of urban streams (Table 2). Interestingly, fish community and
341 environmental variable correlations were almost completely independent of land use type,
342 which is well indicated by the dispersion of stream types in the ordination diagram (Fig. 4).
343 Specifically, while agricultural and protected streams separated along the first RDA axis to
344 some extent, urban stream sites were completely mixed among the different types of sites.

345 These results further corroborate the heterogeneity of streams within land use types and
346 emphasise that a mixture of environmental variables shapes fish community patterns
347 relatively independently of land use management. Case studies show that natural
348 environmental gradients can affect stream communities more than land use management (e.g.
349 Erős et al., 2012; Tolkkinen et al., 2016), and that the effects of natural and anthropogenic
350 gradients are often interrelated (Herlihy et al., 2005. Hein et al., 2011). Our study found
351 differences in altitude, albeit relatively small, and a gradient in riparian and instream
352 vegetation, and its associated siltation effect, was the most influential gradient (Fig. 1 and 4).

353 Our results thus support former studies that emphasised the strong coupling between riparian
354 vegetation, instream habitat, and community level properties (Cruz et al., 2013; Dala-Corte et
355 al., 2016). Removal of trees along the stream margin can enhance the proliferation of
356 emergent macrovegetation, which can negatively influence the stream biota (Dala-Corte et al.,
357 2016 and reference herein). Note that homogenised riparian and instream macrovegetation
358 was most prevalent in agricultural streams, although it occurred in other land use types, too.
359 Maintenance of riparian woody vegetation (i.e. native trees along the stream margin) would
360 thus be critically important to keep stream ecosystems in a more natural condition,
361 independent of land use type (see also Lester and Boulton, 2008).

362 Overall, these results seemingly contradict some former studies that found a relatively strong
363 effect of land use on stream biodiversity (Hardling et al., 1999; Allan, 2004; Weijters et al.,
364 2009). However, we would like to emphasise that only the rough scale categorisation of land
365 use (e.g. to agricultural or urban types) in itself proved to be inadequate for predicting stream
366 (fish) biodiversity. Land use clearly had a fingerprint in the studied system, too. In fact,
367 streams may undergo a variety of land use effects while flowing through the landscape and
368 such effects cannot necessarily be directly connected to any single land use type. For
369 example, streams located in protected areas may exhibit different levels of degradation or
370 urban streams may have different levels of agricultural influences or riparian and within-
371 stream habitat structure. This within-type variability may explain why quantitative
372 environmental gradients explained some patterns better, seemingly independently of land use
373 type; this is in contrast to terrestrial systems, where even the rough scale categorisation of
374 land use proved to be a good predictor of biodiversity (Batáry et al., 2007; Ernst et al., 2017).

375 Besides environmental effects spatial variables also influenced fish communities to some
376 degree. In fact, spatial variables were more predictive for urban communities than
377 environmental ones. This result is surprising since urban sites were not closer to each other

378 than site distances within agricultural or urban stream types. This finding thus warrants
379 further, more detailed elucidation of coupled stream network structure and land use effects.

380 In conclusion, a variety of environmental gradients influence fish community structure in a
381 complex manner in this landscape, which is also influenced by spatial drivers. Non-native
382 fishes modify the structure of native fish communities, although the effect of their
383 modification varies more among individual streams than among land use types. Results
384 suggest that even intensively used areas (i.e. agricultural and urban streams) can contribute to
385 the maintenance of fish diversity in this biogeographic region, or at least their potential can be
386 comparable to those streams which flow in protected areas. Thus, conservation management
387 should focus on maintaining streams in more natural condition in protected areas and/or use
388 the potential of non-protected agricultural and urban streams in maintaining fish diversity in
389 human-modified landscapes.

390

391 **Acknowledgements**

392 This work was supported by the grants OTKA K128496 and GINOP 2.3.3-15-2016-00019.
393 We would like to express our thanks to the anonymous referees for their comments on the
394 manuscript.

395

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544

545 Table 1.

546 Top ranked multiple general linear regression models based on Akaike's information criterion
547 (AIC) to predict the number of native stream fishes.

548

Model and variables	AIC	K	delta_AIC	w _i	R ²
LU (agr), altitude, ln(velocity +1), pH, no nn species, relab nn species	113.35	15	0.00	0.03	0.55
Water temperature	114.53	16	1.18	0.05	0.55
C.V. velocity	116.00	17	1.47	0.10	0.54
Coverage (%) of emerse plants	117.77	18	1.77	0.24	0.54
TDS	119.56	19	1.79	0.59	0.53

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551 Notes: K is the number of variables including the intercept; delta_AIC is the difference in the
552 Akaike's information criterion between each model and the top- ranked model; w_i is the
553 Akaike weight; Model variable abbreviations are as follows. LU (agr), agricultural land use;
554 no nn species, number of non-native species; relab nn species, relative abundance of non-
555 native species; C.V. velocity, Coefficient of variation of flow velocity; TDS, total dissolved
556 solids.

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564 Table 2. Results of the variance partitioning analyses (% explained and residual variance) for
565 protected, agricultural, and urban streams.

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	environmental	spatial	env+spa	residual
protected	18.1	2.6	18.6	60.7
agricultural	13.2	5.9	11.8	69.8
urban	13.0	15.1	13.4	58.5

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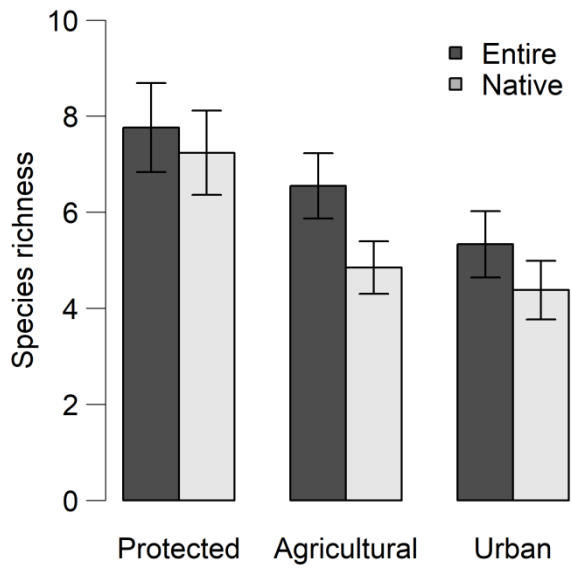
570 **Captions to figures**

571 Fig. 1. Ordination plot of the Canonical Analysis of Principal Coordinates (CAP) of the
572 studied stream sites based on environmental variables. Protected, agricultural and urban
573 streams are indicated with dark grey circles, light grey squares and white triangles,
574 respectively.

575 Fig. 2. Mean (\pm SEM) fish species richness of protected, agricultural and urban stream sites at
576 the entire community level (Entire) and at the level of the native community (Native), i.e.
577 when non-native species were excluded from the analysis.

578 Fig. 3. Ordination plot of the Canonical Analysis of Principal Coordinates (CAP) of the
579 studied stream sites based on compositional (presence/absence) (a) and relative abundance
580 data (b) of the fish communities. Protected, agricultural and urban streams are indicated with
581 dark grey circles, light grey squares and white triangles, respectively. Fish code abbreviations
582 are as follows (see also Appendix II). albbip: *Alburnoides bipunctatus*; ortbar: *Barbatula*
583 *barbatula*; cargib: *Carassius gibelio*; cobelo: *Cobitis elongatoides*; gobgob: *Gobio*
584 *obtusirostris*; psepar: *Pseudorasbora parva*; rhoser: *Rhodeus sericeus*; rutrut: *Rutilus rutilus*;
585 squence: *Squalius cephalus*.

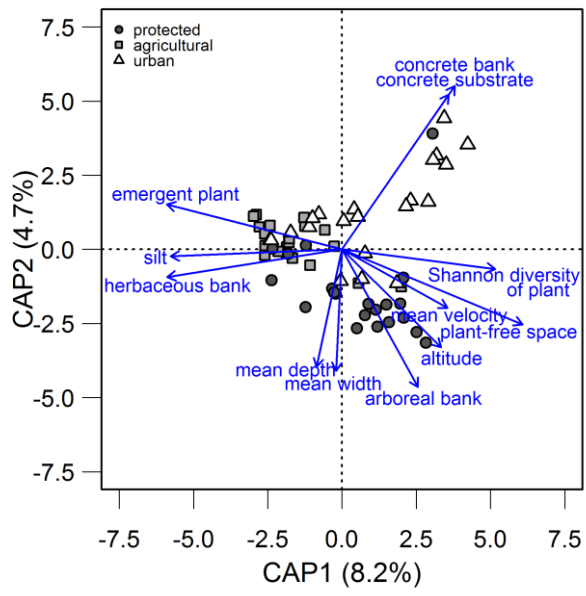
586 Fig. 4. Redundancy analysis diagram showing the relationship between environmental
587 variables and the sampling sites in protected, agricultural and urban stream types. Fish code
588 abbreviations are as follows (see also Appendix II). abrbra: *Abramis brama*; albbip:
589 *Alburnoides bipunctatus*; albalb: *Alburnus alburnus*; amemel: *Ameiurus melas*; ortbar:
590 *Barbatula barbatula*; barbar: *Barbus barbus*; barpel: *Barbus charpaticus*; blibjo: *Blicca*
591 *bjoerkna*; carcar: *Carassius carassius*; cargib: *Carassius gibelio*; chonas: *Chondrostoma*
592 *nasus*; cobelo: *Cobitis elongatoides*; cypcar: *Cyprinus carpio*; esoluc: *Esox lucius*; eudmar:
593 *Eudontomyzon mariae*; gobgob: *Gobio obtusirostris*; gymcer: *Gymnocephalus cernua*; lepgib:
594 *Lepomis gibbosus*; leuasp: *Leuciscus aspius*; leuidu: *Leuciscus idus*; leuleu: *Leuciscus*
595 *leuciscus*; misfos: *Misgurnus fossilis*; neoflu: *Neogobius fluviatilis*; neomel: *Neogobius*
596 *melanostomus*; oncmyk: *Oncorhynchus mykiss*; perflu: *Perca fluviatilis*; pergle: *Perccottus*
597 *glenii*; phopho: *Phoxinus phoxinus*; prosem: *Proterorhinus semilunaris*; psepar:
598 *Pseudorasbora parva*; rhoser: *Rhodeus sericeus*; romvla: *Romanogobio vladkovi*; rutrut:
599 *Rutilus rutilus*; Sabaur: *Sabanejewia aurata*; saltru: *Salmo trutta morpha fario*; sanluc: *Sander*
600 *lucioperca*; scaery: *Scardinius erythrophthalmus*; squence: *Squalius cephalus*; umbkra: *Umbra*
601 *krameri*; vimvim: *Vimba vimba*.



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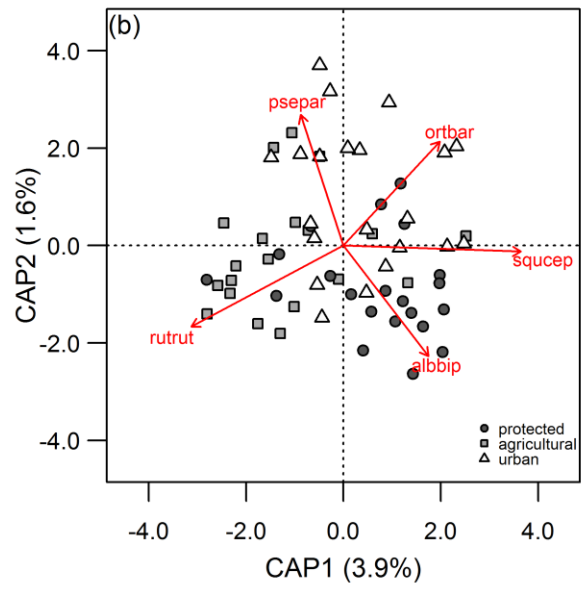
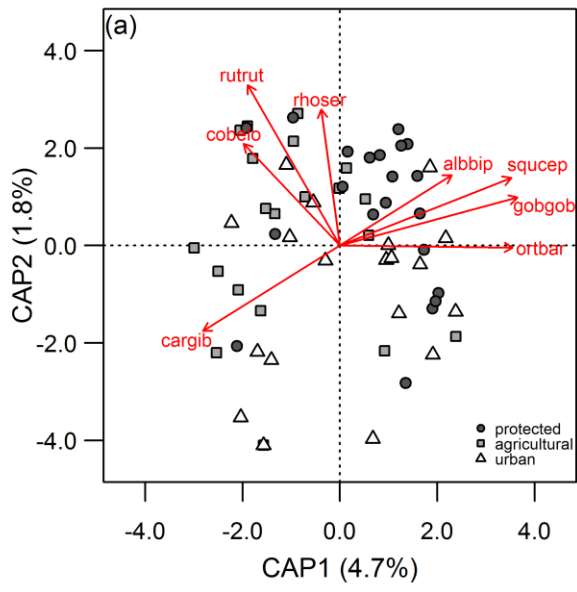
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