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

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Abstract

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

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

Introduction

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

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

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

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

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

Materials and methods

Study sites

The study area was located in Hungary where all the streams and rivers are tributaries of the River Danube, the second largest river in Europe (catchment area 796 250 km^2; length 2847 km). The majority of the country's 93,000 km^2 are relatively lowland areas (i.e. situated below 300 m a.s.l.), with only a very small proportion being located in submontane regions (highest mountain peak is only 1014 m). The dominant land use type in the catchments is arable fields, with vineyards, orchards, pastures, and managed deciduous forest forming a smaller proportion.

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

Environmental variables

Basically, we followed the methodology of Erős et al (2012, 2017) for characterising the environmental features of the sites, which will be reiterated here briefly. Altogether 10 transects were placed perpendicular to the main channel at each sampling site (150 m long each, see below) to characterise physical features of the environment (see Appendix I). Wetted width was measured along each transect. Water depth and current velocity (at 60% depth) were measured at five equally spaced points along each transect. Visual estimates of percentage substratum cover were made at every transect point as well (see Appendix I for categories). Percentage substratum data of the transect points were later pooled and overall percentage of substrate categories were calculated for each site. Macrovegetation (emergent, submerged, floating) and periphyton coverage (macrophyte types) was also estimated visually for each transect points and later pooled, and overall percentage of macrophyte categories were calculated for each site. Water temperature, conductivity, dissolved oxygen content, TDS, and pH were measured with an YSI EXO2 multiparameter water quality sonde (Xylem Inc. NY, USA) before fish sampling, and the content of nitrogen forms (i.e., nitrite, nitrate, ammonium) and phosphate were measured using field kits (Visocolor ECO, Macherey-Nagel GmbH & Co. KG., Germany). Percentage coverage of vegetation at the stream margin (i.e. along a ~ 10 m wide strip in both sides) was estimated visually distinguishing herbaceous and arboreal categories. Altitude was measured in the field using a GPS device (Garmin Montana 650). The coefficient of variation (CV) of depth, velocity, and width data were also calculated to characterise instream habitat heterogeneity. Finally, we calculated both substrate and macrophyte diversity as the Shannon diversity of the proportion of different substrate and macrophyte types, respectively. We used these variables as these provide meaningful information on both catchment and instream level characteristics of the habitat, including possible human effects (Wang et al., 2003; Hoeinghaus et al., 2007; Erős et al., 2012).

Fish sampling

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

Data analysis

We used Constrained Analysis of Principal Coordinates (CAP, Anderson and Willis 2003), complemented with a permutation based ANOVA (Oksanen et al. 2018) to test whether land use type influenced the environmental characteristics of the streams. The Euclidean distance was used to compare the environmental similarity of the sites. Prior to calculations, the environmental variables were divided by their maximum values to standardise them to equal (0-1) scale. K-means analysis was also performed to check the differences between *a priori* and *a posteriori* classifications of the sites to land use types and for the quantification of classification error (%). In this manner, we could further quantify the discriminative power of land use type on the environmental characteristics of the streams.

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

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

Finally, we applied variance partitioning in redundancy analysis (RDA) to examine the contribution of environmental effects and spatial positioning of the streams in the landscape to variation in fish community structure. For obtaining spatial variables, we ran principal coordinates of neighbour matrix analysis (PCNM or also called Moran eigenvector map) based on Euclidean watercourse distance among the sites (Borcard et al., 2011; Legendre and Legendre, 2012). We retained the PCNM eigenvectors with positive eigenvalues as spatial explanatory variables in the RDA analyses. For partitioning the variation in community structure (i.e. Hellinger transformed abundance data) between local environmental variables and spatial location, each group of explanatory variables was first screened using forward selection with Monte Carlo randomization test (1000 runs) in separate RDA analyses. Only variables significantly related to community variability were retained in the final RDA models. Variation in community structure was subsequently partitioned into shared environmental and spatial position, pure environmental, pure spatial, and unexplained proportions using adjusted R^2 values (Borcard et al., 2011; Legendre and Legendre, 2012). We performed the analyses at the whole landscape level, and for each land use type separately. All statistical analyses were performed in R (R Development Core team, 2015) using packages vegan (Oksanen et al., 2018), car (Fox & Weisberg, 2011) and MASS (Venables & Ripley, 2002).

Results

Land use effects on stream environment

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

Land use effects on fish communities

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

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

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

Discussion

The diversity and community structure of stream fishes varied largely within the *a priori* established land use types. In fact, within-type level differences in environmental characteristics and fish community structure were comparable to between-type level changes in the case of many streams. These results show that markedly different land use categories (i.e. protected, agricultural, urban) are not a reliable indicator of fish community structure in streams. Rather, a more in-depth analysis of the environmental characteristics of streams is needed to disentangle changes in stream fish diversity in modified landscapes.

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

Several studies examined how landscape-level proxy variables, such as the proportion of urban and agricultural areas in the catchment, influence the structure of stream fish communities (e.g. Scott, 2006; Trautwein et al., 2012). However, studies which directly compare within- and between-stream environmental heterogeneity and beta diversity of fish communities in protected, agricultural, and urban land use types are lacking. The CAP analysis indicated that between-stream environmental variability and, consequently, fish community variability in urban streams was comparable to that of protected streams. In fact, streams in urban areas were ordered along a long environmental gradient (Fig. 1). They ranged from typical urban sites (i.e. with almost complete coverage of concrete in both instream and along the bank) to stream sites which showed the features of typical agricultural and, albeit in lower portion, of protected streams.

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

Despite displaying lower environmental variability, between-stream community variability of agricultural streams was comparable to other stream types. This variability cannot only be attributed to the relatively high abundance of non-native species in this stream type (see also Erős et al, 2012), but also to between-stream variability in the native community. Nevertheless, non-native fishes were important in separating agricultural and urban streams from protected streams to some extent, especially based on relative abundance. Previous studies found a strong relationship between the distribution of fishponds and other water storage reservoirs in the landscape and the proliferation of non-native fishes (Moyle & Marchetti, 2006; Johnson *et al.,* 2008). These artificial lentic habitats are especially abundant in the vicinity of urban and agricultural areas (Erős et al., 2012; Takács et al., 2017). Thus, it is not surprising that non-native invasive fishes were more abundant in these stream types than in streams which run in relatively remote protected areas.

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

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

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

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

Besides environmental effects spatial variables also influenced fish communities to some degree. In fact, spatial variables were more predictive for urban communities than environmental ones. This result is surprising since urban sites were not closer to each other than site distances within agricultural or urban stream types. This finding thus warrants further, more detailed elucidation of coupled stream network structure and land use effects.

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

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Table 1.

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

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

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

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

	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

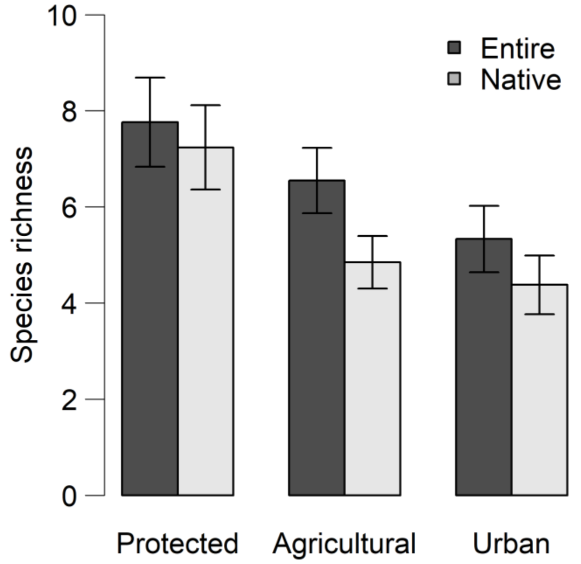
Captions to figures

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

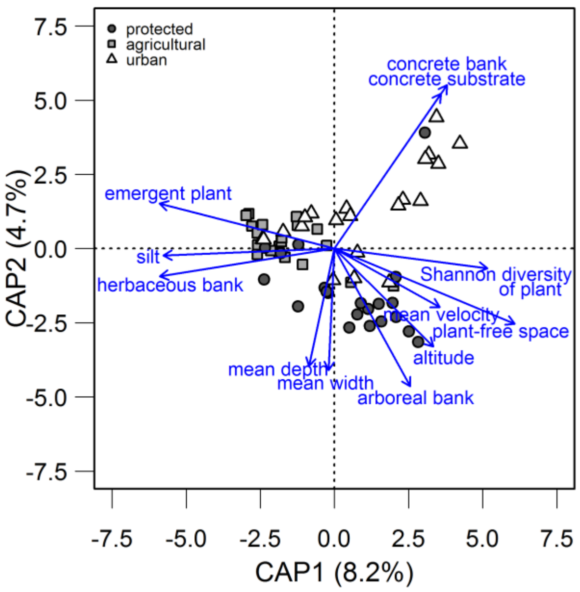
Fig. 2. Mean (±SEM) fish species richness of protected, agricultural and urban stream sites at the entire community level (Entire) and at the level of the native community (Native), i.e. when non-native species were excluded from the analysis.

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

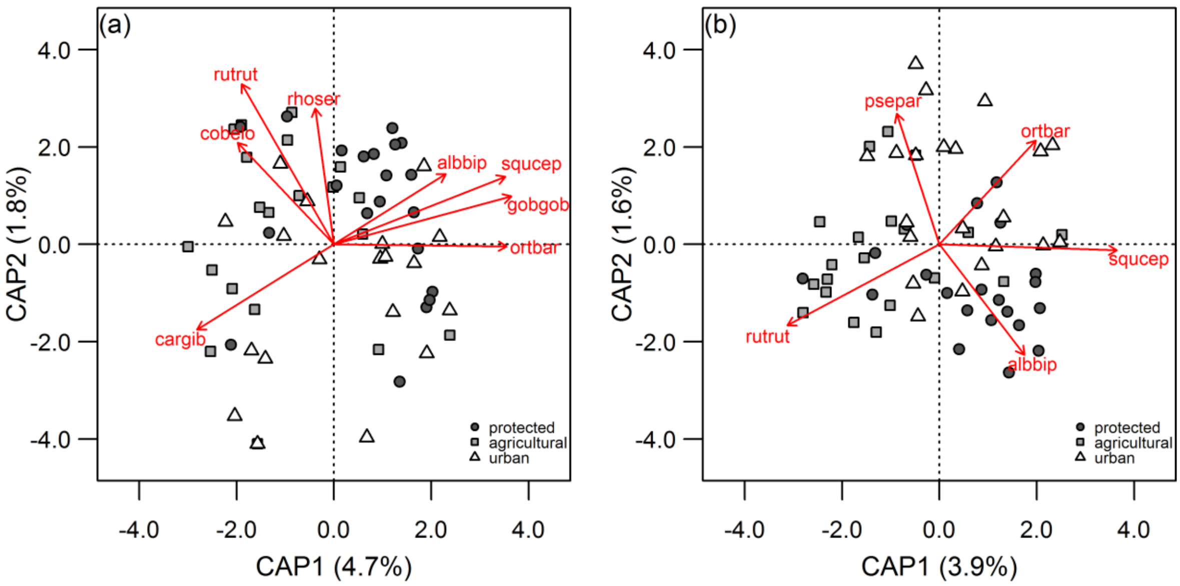
Fig. 4. Redundancy analysis diagram showing the relationship between environmental variables and the sampling sites in protected, agricultural and urban stream types. Fish code abbreviations are as follows (see also Appendix II). abrbra: *Abramis brama*; albbip: *Alburnoides bipunctatus*; albalb: *Alburnus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

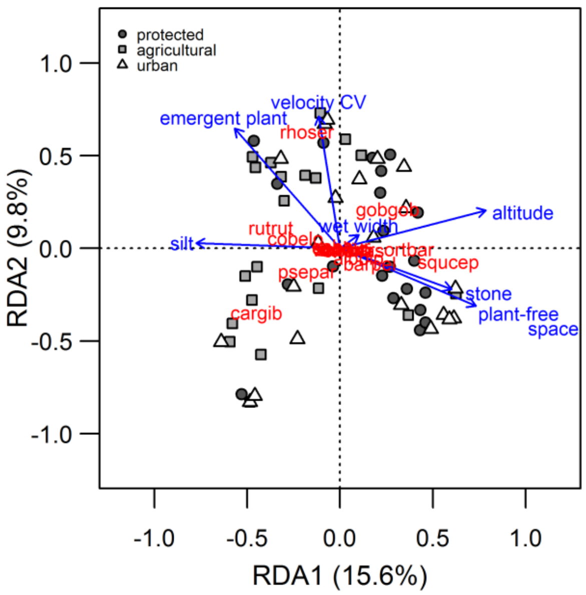


Entire
Native
Species richness
10
8
6
4
2
0
Protected
Agricultural
Urban



protected
agricultural
urban
concrete bank
concrete substrate
emergent plant
silt
herbaceous bank
Shannon diversity
of plant
mean velocity
plant-free space
altitude
mean depth
mean width
arboreal bank
7.5
5.0
2.5
0.0
-2.5
-5.0
-7.5
CAP2 (4.7%)
CAP1 (8.2%)


(a)
rutrut
rhoser
cobelo
albbip
squcep
gobgob
ortbar
cargib
protected
agricultural
urban
CAP1 (4.7%)
CAP2 (1.8%)
(b)
psepar
ortbar
squcep
rutrut
albbip
protected
agricultural
urban
CAP1 (3.9%)
CAP2 (1.6%)


protected
agricultural
urban
velocity CV
emergent plant
rhoser
gobgob
altitude
rutrut
wet width
silt
squcep
psepar
stone
plant-free
space
cargib
1.0
0.5
0.0
-0.5
-1.0
RDA2 (9.8%)
-1.0
-0.5
0.0
0.5
1.0
RDA1 (15.6%)