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Non-native fish species in Hungarian waters: historical overview, potential sources and recent trends in their distribution

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Abstract

Due to its central position in the Danube basin and its considerable fishery sector, Hungary plays a key role in the spread of non-native fish species in Europe. Nevertheless, the status of non-native fish has not yet been reviewed for Hungary. Therefore, our aims were 1) to give a comprehensive historical overview regarding the occurrence of non-native fish species of Hungary, 2) to show their recent distribution patterns using GIS, and 3) to evaluate the importance of the possible drivers in their spread. Literature data show 59 non-native fish species from Hungary. The appearance of new species – mostly due to aquarium fish releases – shows an accelerating trend nowadays. Although non-native fish have appeared at 78.7% of the studied 767 sites during our recent countrywide survey, their distribution was uneven. Lowland streams, lowland rivers, and the River Danube were the most affected by non-native fish, particularly the gibel carp, topmouth gudgeon and pumpkinseed escaped from fish/angling ponds, and the recent invasion of Ponto-Caspian gobies. Our results indicated that in order to reduce the effects and intensity of further invasions, more rigorous control of aquarium trade, angling pond stockings, and inter-watershed fish transports are necessary.

keywords: invasion, invasive species, fisheries, aquarium trade, ecological risks, Carpathian basin

Introduction

Although human-assisted species translocations between remote regions (e.g. continents, catchments) had been evidenced from as early as the antiquity through the Middle Ages (Balon, 1995; Hughes, 2003; Perry-Gal et al., 2015), this process has been accelerated greatly in the 20th century (Welcomme, 1992; Gozlan, 2008). Thus, besides climate change and habitat degradation, the expansion of non-native species is considered to be the third most acute problem which threatens native biota, integrity and functioning of ecosystems on global scale (Gurevitch & Padilla, 2004; Casal, 2006; Didham et al., 2007; Ficetola et al., 2007). Freshwater fish are among the most frequently introduced aquatic organisms in Europe and all around the world (Vitule et al., 2009; Gozlan et al., 2010). Intentional human-induced spread of fish species is primarily motivated by economic (i.e. to improve and "diversify" fishing yields) (Holčík, 1991; Pelicice et al., 2014; Ortega et al., 2015), recreational (i.e. angling) (see: Hickley & Chare, 2004) and ornamental (i.e. aquarists) reasons (Magalhães & Vitule, 2013). Human-induced climate change effects and activities that modify natural migration barriers can also influence the distribution of fish species (e.g. Keller et al., 2011; Roche et al., 2013; Rahel & Olden, 2008). Due to the processes mentioned above, nowadays the vast majority of freshwater ecosystems are more or less impacted by non-native fish species (Leprieur et al., 2008; Thomsen et al., 2014).

The significance of the non-native threat is well addressed (Canonico et al., 2005; Britton & Orsi, 2012), and there is great effort worldwide to control their further spread and even to confine invasive populations (Taylor et al., 2002; Hinterthuer, 2012; McColl et al., 2014). In order to prevent or mitigate the further spread of non-native species, evaluation of their status and impacts in the already invaded geographical areas is a prerequisite (Pimentel et al., 2005; DeGrandchamp et al., 2008; Daga et al., 2016). Furthermore, literature provides important information on the historical processes that took place in the studied area. For example, checklists of non-native fish species which are accessible at many areas (e.g. Elvira & Almodóvar, 2001; Povž & Šumer, 2005; Gollasch & Nehring, 2006) may indicate the first appearances and localizations of certain non-native species. Moreover, international databases (e.g. DIAS, GBIF or BIOCASE) provide comprehensive distribution data of the non-native species. However, due to the presented static and unweighted information (e.g. presence-absence data or date of first appearance), which hinders the effective determination of the threat caused by non-native species, their utility is limited. Moreover, for the effective status assessment, reliable information regarding the regional and/or habitat specific abundances of non-native fishes is needed, whereas these features are rarely provided in the above mentioned sources. Obtaining reliable and comparable recent faunistic or abundance information is often a quite difficult task. Monitoring systems established strictly for tracing the invasions/spread of non-native species (Lee et al., 2008; Irons et al., 2011), or even national scale survey campaigns (Erős, 2007) may provide appropriate information on the actual distribution of non-native species. The most important requisite for these surveys is the representative and well-standardized sampling methodology, which results in good quality, reliable and comparable datasets regarding all studied sites. The datasets obtained can be a valuable basis for River Basin Management Plans (Panov et al., 2009) or Species Management Plans (Tatár et al. 2016). Beyond the adequate quantity and quality of historic and recent information, the appropriate interpretation of distribution data (e.g. using Geographic Information System) may facilitate understanding of the recent status and ongoing process for decision makers, who generally have no specific knowledge on the certain research field (Ehlers et al., 2003; Joyce, 2009; Beisel et al., 2017).

Based on the above mentioned criteria, distributions and relative abundance of non-native fishes were studied in the territory of Hungary (Carpathian Basin, Central Europe). Hungary belongs to the catchment area of the River Danube, which is one of the most important freshwater migration routes in Europe (Hewitt, 1999). Therefore, Hungarian waters – with c.a. 60 native fish species –have considerable species diversity (Halasi-Kovács & Harka, 2012; Kottelat & Freyhof, 2007; Sály, 2007). This geographic position, which facilitated the colonization of diverse native fish assemblages through historical ages, is also one of the most important drivers of the "spontaneous" expansion of many non-native species (Copp et al., 2005; Halasi-Kovács & Harka, 2012). Additionally, since the second half of the 20th century due to the extensive relationships of the Hungarian aquaculture (Dobrai, 1974, 1979; Tahy, 1975) numerous non-indigenous species have been introduced to Hungary from different areas for aquaculture purposes (Pintér, 1980). And these species were often introduced intentionally to other European countries from Hungary. Moreover, these non-native species were often introduced into natural waters of Hungary – because it was not banned by law for ages. So through the Danubian hydrosystem these species might easily got into the territory of adjacent countries and beyond. These features made Hungary to be one of the "key" source areas in the spread of non-native fishes in Europe (García-Berthou et al., 2005). Notwithstanding the importance of this area in the spread of non-native fishes in Europe, up to now there were only some specific notes available about the distribution and abundance of non-native fish species of Hungary. In addition, evaluation of the status of non-natives were available only for specific regions or catchments (see: Bódis et al., 2012; Weiperth et al., 2013, Ferincz et al. 2016a). The sole comprehensive study which evaluated the habitat specific distribution of non-natives in lotic systems was published a decade ago (Erős, 2007). Since then the appearance of a great number of new species as well as important assemblage level changes have been reported (Halasi-Kovács et al., 2011; Szalóky et al., 2015).

Therefore, the objectives of our work were: i) to provide an updated list and historical overview on the non-native fish species introduced to Hungarian natural lotic and lentic ecosystems; ii) to present the recent distribution patterns and relative abundances of the non-native fish species in

Hungarian lotic systems using GIS, and iii) to evaluate the possible role of fishing and angling ponds in the local dynamics of non-native fish species.

Materials and methods

Study area

Hungary is situated in the Carpathian Basin and it is surrounded by the Alps and the Carpathian mountains from North and East. The whole area (93 030 km^2) of the country belongs to the catchment of River Danube, the second largest river in Europe (catchment area 796 250 km^2; length 2847 km). Since cca. 70% of the country's area is lowland, lowland streams and rivers constitute the majority of the river network. Moreover, from the middle of the 19th century, parallel with the river regulation works conduced mostly on the Tisza river network (which is the largest tributary of the Danube with its 157 000 km^2 catchment area), an extensive system of draining and irrigation canals was established, with the total length exceeding 40 000 km (Martonné Erdős, 2004). Therefore, the lowland situated and mostly canalised small watercourses are the most frequent lotic habitat type in this area.

From the beginning of the 20th century, numerous fish farms were established mostly on the flood-protected lowland areas, operating on an approximately 25,000 hectares area, and their annual yield is the fourth largest in the European Union (Halasi-Kovács et al., 2012). Fish farms apply mostly similar technology, namely, common-carp (*Cyprinus carpio* Linnaeus 1758) dominated semi-intensive polyculture production (Békefi & Váradi, 2007). Stocking of non-native fish species into Hungarian natural waters is banned by the Act LIII of 1996 on Nature Conservation.

Literature overview of non-native fish appearances

The list of non-native species that had ever been recorded in natural waters of Hungary was assembled using all accessible literature data published in scientific journals and books from the second half of the 19th century. The 'Hungarian Periodicals Table of Contents Database' (accessible at: www.matarka.hu) was used to collect the possible sources in Hungarian language using the keywords: new fish species, non-native fish, and invasive fish. Most of these notes are simple faunistic notes (e.g. Kreisch, 1872; Sterbetz, 1957) published in Hungarian language, but similarly some comprehensive works (e.g. (Pintér, 1989; Harka & Sallai, 2004)) were overviewed to build the database. Moreover, we reviewed the literature notes published in the last five years as well, to collect information on the recent status of the non-native species. From the database, we recorded the scientific name of the species, the taxonomic position (Order and Family), the first date of appearance and the native range. We also recorded the reason of their occurrence (sensu Sály, 2007): accidentally introduced (AI), intentionally introduced (II), directly facilitated settler (DFS), indirectly facilitated settler (IFS), occasional (O). Finally, we determined the probable reason for introduction (vector) i.e. dispersion (active expansion), stocking (intended stocking into natural waters), accidental (unintended stocking), aquaculture (escape from fish ponds) and ornamental (release by aquarists). A certain non-native species was regarded to have "recent data" if it has occurrence data published in the last five years. In order to reveal the possible temporal trends, the cumulative number of the non-native species and reasons of introductions were analyzed in fifty-year periods. We used the nomenclature after fishbase.org (date: 03. 02. 2016).

Field surveys

To evaluate the recent distribution and abundance of non-native fishes we used the data of countrywide fish surveys, which were executed in summer between 2011 and 2015 using standardized electrofishing protocol (URL1). Based on the typology of Erős (2007), we discriminated six running water types: i) submontane streams (SS) with high gradient and small to medium-sized (<1000 km^2) catchment area; ii) highland streams (HS) with moderate gradient and small to medium-sized catchment area; iii) highland rivers (HR) with moderate gradient and large (>1000 km^2) to very large (>10,000 km^2) catchment area; iv) lowland streams and canals (LS) with small to medium-sized catchment area; v) lowland rivers (LR) with large to very large catchment area; and vi) the main channel of the River Danube. In wadeable watercourses (i.e. most of SS, HS, and LS), a 12V battery-powered electrofishing device was used to sample a 150-m long reach at each site by slowly wading upstream and single pass fishing the whole stream width (for more details see: Sály et al., 2009). Non-wadeable HR and LR habitats and the Danubian sites were sampled by boat electrofishing using engine powered devices, slowly moving downstream and electrofishing one (in HR and LR sites) to three (in Danube sites) 500 m long near shore sections (Fig. 1). Comprehensive recent surveys provided relative abundance data for 767 sampling sites of 381 watercourses. Due to the geographic conditions of Hungary most sites belonged to LS (n=335), followed by HS (228), LR (100), HR (48) and SS (45), while the Danube was represented by 11 sites.

Data analysis

Representativeness of field data in function of sampling effort was checked by individual based rarefaction analyses using Ecosim software (Gotelli & Entsminger, 2001). This approach also enabled to compare species richness across habitat types (i.e. SS, HS, HR, LS, LR and the River Danube) with different sampling efforts. Patterns of species number and relative abundance of non-native species as well as relative abundances of the eight most frequent non-native species were displayed on the map of Hungary using QGIS software (QGIS Development Team, 2016) and Inverse Distance Weighting (IDW) method of interpolation (Mitas et al., 1999) with 300×300 longitudinal and vertical resolution.

In order to identify trends in the distribution of non-native species, their species number, proportional species number and relative abundances were correlated with the altitude using Spearman Rank correlations. Mann-Whitney pairwise comparisons ($p<0.05$) were used to indicate the differences of these features between habitat types. Also Mann-Whitney pairwise comparisons were used to analyse these attributes between sites with- and without fish ponds within 10 km distance either upstream or downstream in the concerning catchment. Occurrence and distance data of fish ponds were derived from GIS shape files of the Hungarian hydrosystem and the Google Earth database.

Results

Literature overview

Until 2016, 59 non-native fish species and hybrids classified into 8 orders and 17 families have been reported from the natural waters of Hungary (see: Table 1). The most important group of non-native fishes with 21 species (+1 hybrid) is the order *Perciformes*, followed by *Cypriniformes*, *Siluriformes* and *Cyprinodontiformes*, which were represented by 10 (+1 hybrid), seven and six species, respectively. Twenty-six of the 59 non-native taxa have American origin. Specifically, 12 species have their native ranges in North, nine in Central and five in South America. Twenty-two species originated from Eurasia, of which seven species are Ponto-Caspian. Another six species came from the Far East. In addition, nine thermophilic species are of African origin. According to the classification of Sály (2007), most of the non-native species and hybrids (43) observed in Hungarian natural waters were intentionally introduced, eight species are indirectly and two are directly facilitated settlers, whereas other two species are known to have been introduced accidentally into natural waters. Until the end of the 19th century, only five non-native fish species were observed from Hungary, and only further five species appeared until 1950. Then the number of non-native species increased remarkably during the second half of the 20th century. During the last 15 years, the arrival of new species has accelerated and further 24 non-native species appeared (Table 1). Thus the cumulated number of non-native fish species show exponential growth (Fig. 2a) in the last one and a half century. Moreover, the ornamental fish releases become the most important reason of new species occurrences in the last decades (Fig. 2b).

Species number and abundance of non-native fishes in stream habitats

Altogether 66 fish species were found on the 767 sites surveyed during our countrywide survey (see: Supplementary Table 1), and 28.8% of this species pool (19 species) were non-native. Out of the 200,938 total captured individuals, 36,714 (18.3%) were non-native ones. Eight species comprised 93% of the total catch of non-native individuals. Individual based rarefaction curves seemed to approximate an asymptote in LS, LR and HS habitats regarding the total species number (Fig. 3). However, further sampling in other habitat types would have probably yielded more non-native species. Rarefied total and non-native species richness increased across the habitat types in the following order: SS, HR, River Danube, HS, LR, LS. The occurrence (presence or absence) of non-native species as well as their interpolated species number and relative abundances are shown in the hydrological map of Hungary (Fig. 4 and 5). Total species richness ranged between 1 and 25 (mean±S.D.: 8.9±5.0) species per site and 0 to 6 (1.8±1.5) of them were non-native (Fig. 4). The relative abundance of non-native species ranged between 0 and 100% and had a mean±S.D. of 23.0%±21.1.

Although non-native species occurred in 78.7% of the sites, their occurrence showed great variability across the habitat types. For instance, non-native species occurred in all Danubian sites, whereas only in 29% of SS sites. Similarly, the mean number of non-native species per site was highest in River Danube (4.4±0.7) and lowest in SS (0.4±0.8) sites. The relative abundance of non-natives in the total catch was also highly variable across habitat types and it ranged between 0 and 100% (19.7%±2.8) (Fig. 5). Mean cumulated relative abundances of non-native species were lowest in HR (2.4%) and SS (4.0%) sites, whereas it was highest in the Danube (25.6%) and LS habitats (29.9%) (Table 2). In general, lowland sites hosted more non-native fish than those in the highland or submontane zones. Significant negative correlation was found between the altitude (a.s.l.) and the number ($R=-0.51$, $p<0.05$) and proportion ($R=-0.44$, $p<0.01$) of the non-native species, as well as their relative abundances ($R=-0.46$, $p<0.01$). The relative abundance of non-natives showed a remarkable decrease above 150-160 m a.s.l. (Fig. 5b).

Presence-absence data and interpolated country-wide relative abundances of the eight most frequent non-native species were plotted individually on Fig. 6. The most widely distributed and abundant non-native species was the gibel carp (*Carassius gibelio*, Bloch 1782), which species occurred in 52.3% of all sites surveyed and constituted 8.6% of the total and 46.9% of the non-native catch (see: Supplementary Table 1). Other subdominant species were the topmouth gudgeon (*Pseudorasbora parva,* Temminck and Schlegel, 1842) and the pumpkinseed (*Lepomis gibbosus* Linnaeus, 1758) with 34.0% and 30.1% frequency of occurrence, and with 3.1% and 1.5% relative abundances, respectively.

Actively expanding Ponto-Caspian gobies also become important members of the fish assemblages in Hungary. They were found in all habitat types, but both their cumulative frequency of occurrence and cumulative relative abundance were highest in the River Danube (Table 2). Five species of these gobies, the tubenose goby (*Proterorhinus semilunaris,* Heckel, 1837), the monkey goby (*Neogobius fluviatilis,* Pallas, 1814), the Kessler's goby (*Ponticola kessleri,* Günther, 1861), the round goby (*Neogobius melanostomus,* Pallas, 1814), and the racer goby (*Babka gymnotrachelus,* Kessler, 1857) were found in the River Danube with relatively high abundance. Another species, the Caucasian dwarf goby (*Knipowitschia caucasica,* Berg, 1916) was found in the River Tisza and in two of its tributaries (Nagykunsági-főcsatorna canal, Hármas-Körös River). In terms of frequency of occurrence, the tubenose goby (20.6%) and the monkey goby (13.2%) were the two most widely distributed species (Fig. 6). In addition, the latter species were found in all six habitat types (Table 2).

Fish ponds' role in spread of non-native species

Our analysis revealed that the probability of non-native fish occurrence, their species number, relative species number and the relative abundance of non-native fish in watercourse sections close to fish/angling ponds tended to be higher than in watercourse sections which are not in the vicinity of ponds, although the differences were not always significant (Table 3). The presence and relative abundance of gibel carp, topmouth gudgeon, pumpkinseed, black bullhead (*Ameiurus melas,* Rafinesque, 1820) and amur sleeper (*Percottus glenii,* Dybowski, 1877) related mostly to fish/angling ponds. On the other hand, presence and relative abundance of actively expanding Ponto-Caspian gobies did not show any obvious relationship with the distribution of ponds.

Further analyses showed that the occurrence and relative abundance of some non-native fishes may also be affected by the position of the nearest pond(s) from the sampling site (i.e. upstream, downstream or both), although the strength of this relationship varied among the habitat types (see: Supplementary Table 2). For instance, the downstream positioned sites were more likely charged by non-natives than the upstream situated sites in smaller watercourses (i.e. HS, LS). Sites which were sandwiched between fish ponds were the most infected by non-native species. Finally, the proportion of non-native species (S_R: $R=-0.18$, $p<0.01$) and their relative abundances ($R=-0.19$, $p<0.01$) decreased with distance from the nearest fish pond in the LS habitat type.

Discussion

Historic and recent trends in non-native species distribution

During the last one and a half century, 59 non-native fish species and hybrids were observed in Hungarian natural waters. This figure is especially warning as it approximates the number of native species (ca. 60) known from the country (see: Halasi-Kovács & Harka, 2012). This number indicates that Hungarian waters are particularly exposed to non-native fish introductions compared to other Central-European countries. For example, the documented number of non-native fishes is 41 in the Czech Republic, 36 in Poland, 35 in Slovakia and 16 in Slovenia (see: Lusk et al., 2008; Grabowska, 2010; Koščo et al., 2010; Povž & Šumer, 2005). The ratio of non-natives seems to be remarkably high at global level as well. For example, if the number of non-native fish species ever recorded in Hungary is standardized to area, the result is even higher for Hungary than it is observed in China, which country is the "world recorder" with the occurrence of 439 non-native fish species (Xiong et al., 2015). The cumulative number of non-native species showed exponential growth (see: Fig. 2a) in the last decades, similarly to the findings of Beisel et al. (2017) from French freshwaters. Recent (i.e. not older than five years) publications (e.g. Halasi-Kovács & Harka, 2012; Weiperth et al., 2013, 2015; Takács et al., 2015; etc.) mentioned 46 (77.9% of ever recorded) non-native taxa from Hungary, which feature verifies the increasing trend of non-native appearances.

The reason of introductions show highly similar trend to what was experienced in the neighbouring countries (e.g. Koščo et al., 2010; Rabitsch et al., 2013). Namely, primarily (from app. 1860) some popular North-American sport fishes (e.g. brook trout - *Salvelinus fontinalis* (Mitchill, 1814)) were introduced to diversify angling facilities. In the 1960s and 1970s, introductions were motivated mainly by the purpose of improving fishery yields both in aquaculture and natural waters. Beside some sport (e.g. hybrid striped bass - *Morone saxatilis x M. chrysops*) and cultured species and hybrids (American paddlefish - *Polyodon spathula*

(Walbaum, 1792), or hybrid sturgeon - *Acipenser naccarii* x *A. baerii*), the most recent incomers were dominantly tropical and subtropical ornamental fishes which were released illegally mostly to unique thermal habitats (see: Fig. 2b). However, recently only four of these species (eastern mosquitofish - *Gambusia holbrooki* (Girard, 1859), rainbow cichlid - *Archocentrus multispinosus* (Günther, 1867), jewel cichlid - *Hemichromis guttatus* (Günther, 1862) and common molly - *Poecilia sphenops* Valenciennes, 1846) have self-sustaining populations in these unique habitat types (see: Harka et al., 2014; Takács et al., 2015a). During our countrywide surveys, 19 non-native fish species were caught (see: Table 3); therefore, together with the four above mentioned thermophilic ones, 23 species can be considered as "established" non-native fish species in Hungarian natural lotic systems.

Potential sources of new non-native species

Three main sources of non-native introductions can be identified in the area (see also Sály 2007). The first source is the River Danube, which is the most important aquatic migratory route in Europe (Hewitt, 1999). For example, the upstream expansion of Ponto-Caspian gobies in the River Danube started in the 1800s, with the spread of tubenose goby, which process has intensified from the 1990s (Harka & Bíró, 2007). The fast spread of gobies in the Danube River was connected to intensified shipping, which may explain why these species were found first in the vicinity of urbanised areas, sometimes even some hundreds of kilometres away from their original range limit (Roche et al., 2013; Keller et al., 2011). Although small crevices can provide an ideal spawning place for these speleophil species, which could explain the vector role of ships in their dispersal, other factors, such as bank stabilization by big rocks and boulders (i.e. rip-rap shoreline) or even increasing mean water temperature of the river have been also related to their fast spread and invasion (Harka & Bíró, 2007; Szalóky et al., 2015). Accordingly, upstream expansion of further species, and probably not only of gobies, is expected from the Danube delta (see: Borza et al., 2015; Paunović et al., 2015; Bănăduc et al., 2016).

The second important source of non-native species, in correspondence with the findings of Ortega et al. (2015) and Britton & Orsi (2012), is fish escapes from fish farms and angling ponds. However, it seems that the importance of aquaculture as a source of non-native introductions is declining nowadays, since in the last decades, new fish species used strictly for fishery purposes were introduced solely into isolated recirculating aquaculture systems (e.g. Feledi et al., 2011), from where practically there is no chance to escape into natural waters. Moreover, the semi-intensive fish ponds rather have a specific role in the redistribution and local dynamics of the already established species (this feature will be discussed below). Nevertheless, nowadays the private angling ponds, which were established in large numbers in Hungary to satisfy the needs of about 300,000 registered anglers, facilitate the spread of non-native species into natural waters (Specziár & Erős, 2015), because several new alien species (e.g.: sturgeons, hybrid striped bass) are also stocked into these habitats illegally to make them more attractive. Whereas the angling ponds are mostly connected to natural waters, these species can still escape to the recipient watercourses.

The third main source of new non-native fish species is the release of ornamental fish by aquarists; 35.6% (21 species) of the reported non-native species in Hungarian waters are tropical and subtropical ornamental fishes. The growing number of ornamental species corresponds well with the global trend, because recently the trade of (mostly Percid) ornamental species exceeds the trade of species used for aquaculture purposes, as observed in distant geographic regions such as South-Africa or China (Ellender & Weyl, 2014; Xiong et al., 2015). The recent increase of such species in the checklist is probably also a consequence of the intensified survey of unique thermal habitats in Hungary (Harka et al., 2014; Weiperth et al., 2015; Takács et al., 2015a). The occurrence of many species is however not restricted only to warmwater habitats, because certain species may acclimatize and spread beyond their native thermal ranges. For instance, Eastern mosquitofish, which was unintentionally introduced to Lake Hévíz in the 1920s seems to be acclimatized by now and is able to overwinter even in the cold water of Kis-Balaton wetland area. Moreover, this species was also found recently in substantial quantity in a stream without a close connection to any thermal habitats (Szepesi & Harka, 2015). Due to increasing winter temperatures in the region (Lovász, 2012; Nováky & Bálint, 2013), which is an attendant effect of the global climate change, the risk of invasion of thermophilic species increases, especially in the vicinity of warmwater springs and in watercourses where power-plants discharge their cooling water (Andrews, 1990; Szolnoky & Raum, 1991; Klotz et al., 2013).

Recent distribution of non-native fish in Hungarian lotic systems

In accordance with the earlier observations of Erős (2007), our extensive field surveys revealed the uneven distribution of non-native species in Hungarian watercourses regarding both the number of species and their relative abundances. Nevertheless, results show that by now, non-native fish distributed across the whole area of the country. Only a few sites with specific environmental characteristics, belonging mainly to the submontane stream (SS) habitat type, have remained free from non-native species (see: Sály et al., 2012). Distribution data outline the relevance of three following major trends and underlying processes.

First is the "spontaneous" expansion of certain species in the Danubian river network. As it has already been mentioned, the distribution of Ponto-Caspian gobies seems to be strongly linked to larger rivers. Of these, the Danube provides the main colonization route for these species (Erős 2007; Rabitsch et al., 2013). The recent distribution of gobies seems to correspond with the time of their arrival, their ecophysiological tolerances, and interspecific interactions. Tubenose goby and monkey goby, which species arrived first, are now the most widely distributed, however their abundances are low. In the River Danube, relative abundances of these goby species temporally followed a clear colonization succession, eventuated that actually round goby is the dominant species. Based on the data of consecutive fish assemblage surveys (Erős et al., 2005; Jakovlić et al 2015; Piria et al., 2016), the expansion of gobies is a rapid process and it simultaneously happens with their upstream spread in the Danube and a lateral distribution in its tributary system.

The second trend that we could identify is the decreasing species richness and relative abundance of non-native fish with increasing altitude. Lowland watercourses (i.e. LS, LR and River Danube) are clearly the most infected habitats with non-native species. Larger waterbodies, more diverse and stable habitat structure can be found on lowland areas, and at the same time the relevance of aquaculture and angling activity is higher compared to other areas. On the contrary, highland (i.e. HS, HR) and especially the submontane habitats provide more limited and specified habitat diversity, thus they are appropriate for only a smaller group of fish species (e.g. Schlosser, 1982; Sály et al., 2012).

The third most important trend observed was the effect of fish ponds on the species richness and relative abundance of already established non-native species. This effect is traceable on both local and regional scales. On regional scale, the unintended inter-basin (pond-to-pond) fish transfers facilitate the spread of invaders (not only fish) to distant areas (see: Thomas & Chovet, 2013). The most recent example for this effect is the appearance of amur sleeper in remote areas of Hungary. This species first appeared in North East Hungary (Harka, 1998), and for a long time it was present only in the hydrosystem of the River Tisza (Harka et al., 2003). However, since 2008, the amur sleeper suddenly appeared in distant parts of the country, away from the Tisza region (Erős et al., 2008; Takács & Vitál, 2012; Takács et al., 2015b). Therefore, in accordance with the opinion of other researchers on the mechanisms of Europe-wide expansion of this species (Reshetnikov &Ficetola, 2011; Reshetnikov, 2013; Reshetnikov

& Karyagina, 2015), we suppose a human assisted spread via trans-drainage fish transfers in this case.

On a local level, the fish pond escapes affect both the species pool and the local range abundance distributions of fish species in the recipients (Welcomme, 1988; Bright 1999; Naylor et al., 2001; Gozlan et al., 2010). The escaped fish are both aliens (e.g. gibel carp, topmouth gudgeon, amur sleeper) and natives for the Hungarian Great Plain Ecoregion. (These later ones are usually commercially utilized, foreign-to-streams fishes, such as common carp, or pikeperch - *Stizostedion lucioperca* (Linnaeus, 1758)). Thus local species (i.e. alpha) diversity increases (Takács et al., 2007; Sály et al., 2009, 2012) at the cost of decreasing dissimilarities among the localities (i.e. beta diversity), which process is called biological homogenization (Mckinney & Lockwood, 1999; Olden & Rooney, 2006; Sály et al., 2008). Mostly in the late autumn harvesting period individuals of non-native species are released into the recipient watercourses in high number. These periodic recruitment fluxes may support much higher densities of certain non-native species in many streams than it could be maintained based on internal reproduction only. Therefore, fish farms generally cause periodic overpopulation in the recipient watercourse sections, and thus greatly increase the impact of non-native fishes on the native biota (Erős et al., 2012; Ferincz et al., 2016b). The local effect of fish ponds can be surely mitigated by the compliance of the management proposals and standards of fish farms (e.g. cleaning, disinfection and complete depopulation of ponds after the late autumn harvest); and by the utilization of effective fish escape preventing equipment (e.g. mandatory use of tight fish racks and fish smashing boxes in each pond outflow). However, we believe that the only satisfactory solution to prevent the escape of non-natives from fish ponds would be to prioritise the establishment of totally isolated fish producing systems in the aquaculture policy.

Conclusions

Our results show that simultaneous historic and recent data analyses can give a broader overview about the recent and future trends of invasions. Literature notes show that the flowing waters of Hungary are remarkably invaded by non-native fish species. Analysis of recent countrywide survey data reinforced this statement; moreover, the GIS based data interpretation highlighted some ongoing human facilitated invasions (e.g. amur sleeper) in the study area. Knowing the hydrology of this area, these invasions would mean a considerable threat for all the countries situated to the Danube basin. Our results show that beside the new incomers, the already established non-native species (e.g. gibel carp, topmouth gudgeon) present major risk for their native biota, especially in smaller streams. Stock size of these species seems to be "artificially large" in many cases because they receive continuous supply from fish farms. These findings direct our attention to the fact that the control of the already established non-natives is just as important as the prevention of the new incomers' occurrence. In our opinion, invasions facilitated by climate change (e.g. spread of Gobies) seem to be unavoidable; but the number – and the effect – of human facilitated invasions can be remarkably reduced if the aquarium trade, the angling pond stockings, and the inter watershed fish transports are more rigorously controlled in the future.

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Figure and Table captions

Figure 1 Map of the study area showing the 767 sampling sites distributed among the six habitat types in Hungary and sampled between 2011 and 2015. blue diamond: submontane stream (SS), green dot: highland stream (HS); green diamond: highland river (HR); orange triangle: lowland stream (LS); red dot: lowland river (LR); purple rectangle: River Danube. Dotted line indicates country border.

Figure 2 Temporal trends in the cumulative number of non-native species observed in Hungarian freshwaters. Equation and R^2 values refer to the exponential trend line (a), Temporal changes in the reason of introductions (b) for definitions see text.

Figure 3 Rarefied species numbers by habitat types of countrywide stream fish surveys conducted between 2011 and 2015. a) non-native species only; b) all species. Dotted lines show 95% confidence intervals. For codes see Fig.1.

Figure 4 Interpolated number of non-native fish species in streams and rivers of Hungary. Black dots represent sites with non-native species, whereas open circles represent sites with native species only. Names of the main rivers indicated on the map.

Figure 5 Interpolated relative abundance of non-native fish species in streams and rivers of Hungary (a), and relative abundance of the non-native species as function of altitude (b). Black dots represent sites with non-native species, whereas open circles represent sites with native species only. Names of the main rivers indicated on the map.

Figure 6 Interpolated relative abundances of the eight most frequent non-native fish species in streams of Hungary. Black dots represent sites where the particular species was found and white dots where it was not. Frequency of occurrence values are shown in brackets (see: Table 3).

Table 1 List of non-native fish species and hybrids in the order of their first appearance in Hungary. code: abbreviations of non-native species which occurred during our field surveys. Year: date of first appearance, Order and Family show the taxonomic position. Native range: original distribution area, Reason of occurrence according to Sály (2007): AI: accidentally introduced, II: intentionally introduced, DFS: directly facilitated settler, IFS: indirectly facilitated settler, O: Occasional. Vector: probable reason for introduction. dispersion: active expansion, stocking: intended stocking into natural waters, accidental: unintended stocking, aquaculture: escape from fish ponds, ornamental: release by aquarists. Recent data: if the certain species noted from Hungarian natural waters in the last 5 years. Reference: first, or relevant note of the certain species. [a]: subalpine area; [b]: sporadic recent data from the R. Danube, but intentionally stocked into the Lake Balaton; [c]: false identification; [d]: hybrid? [e]: data with unknown source in the FAO database. For more details see text.

Table 2 Frequency of occurrence, number of species and relative abundance of the non-native fish species in the six stream habitat types. For codes: see Fig. 1. and Table 1. ntot: number of sites examined; nNN: percentage of sites with non-native species; Stot.: total number of species; SNN%: proportion of non-native species in total species number; S: number of species per site (mean±SD); SNN: number of non-native species per site (mean±SD); N: number of individuals captured; RANN%: relative abundance of non-native species; RA%: mean relative abundance; FO%: frequency of occurrence. Bold values written in red and denoted by different letters indicate significant differences between the relevant values of the studied habitat types according to the pairwise Mann-Whitney U test ($p<0.05$)

Table 3 Frequency of occurrence, number of species and relative abundance of the eight most frequent non-native species in the stream habitat types depending on the absence (NP) and presence (PP) of fish pond within a 10 km distance. For habitat and species codes: see Fig. 1. and Table 1. $n_{tot.}$: total number of sites examined; n_{NN}: sites with non-native species; FO_{NN}%: frequency of occurrence of non-native species; S_{NN}: number of non-native species (mean±SD); S_{NN}%: proportion of non-native species from the species occurred in a site; RA_{NN}%: relative abundance of non-native species (mean±SD); FO%: frequency of occurrence of a certain non-native species; RA: relative abundance of the certain non-native species. Red colour, bold labelling and "*" indicate values which were significantly higher ($p<0.05$) in the presence of fish ponds according to the Mann-Whitney U test.

Figure 1

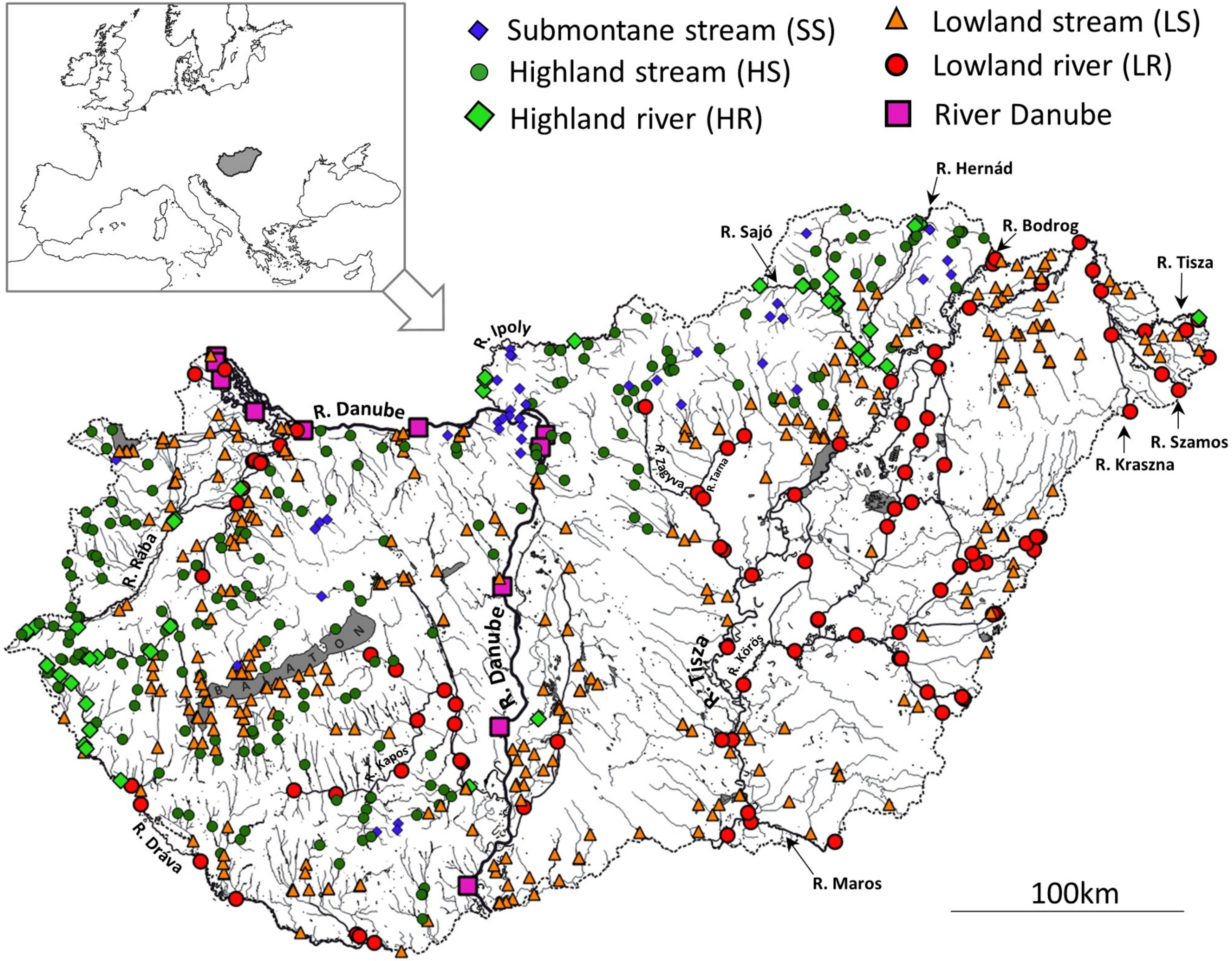
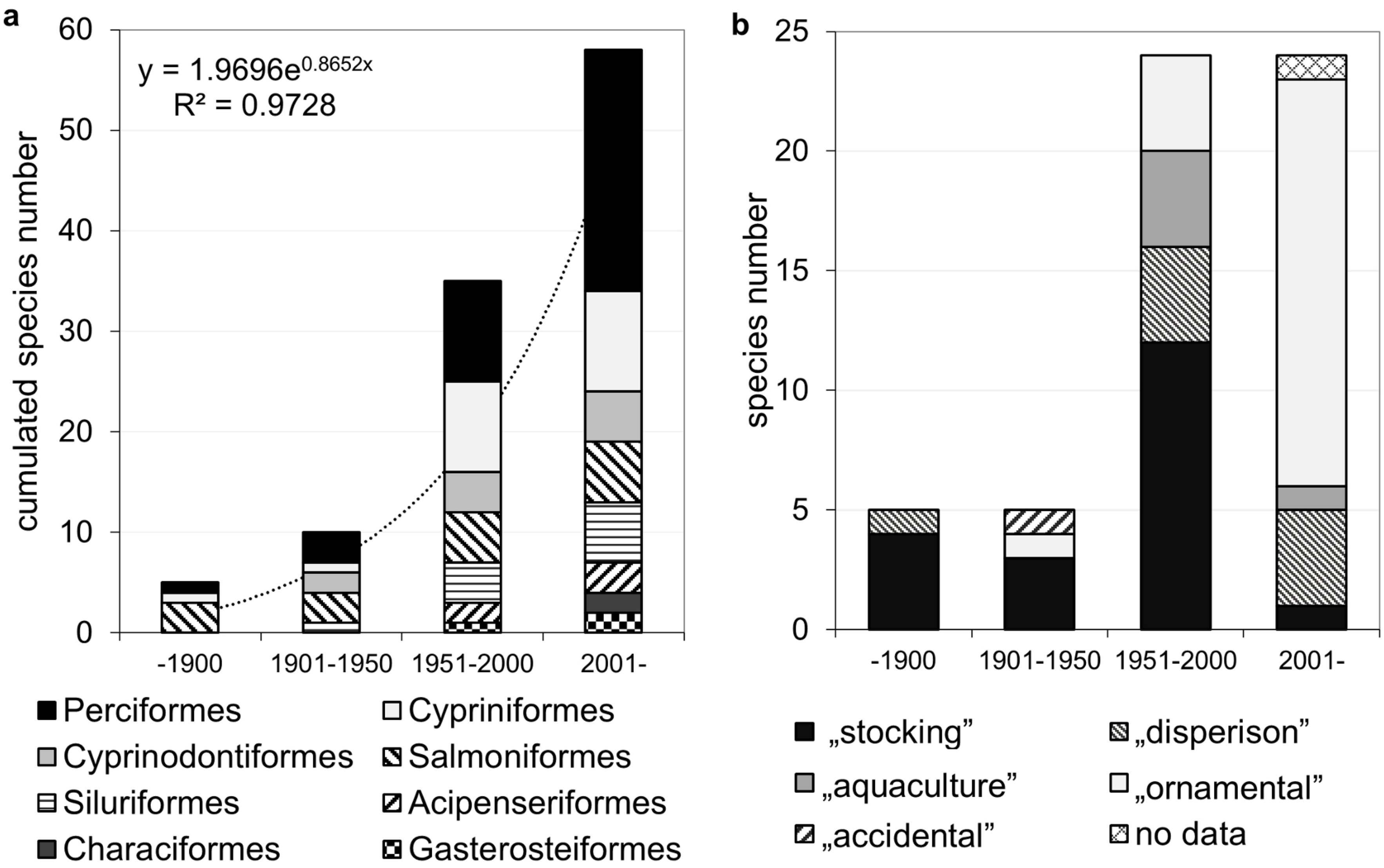
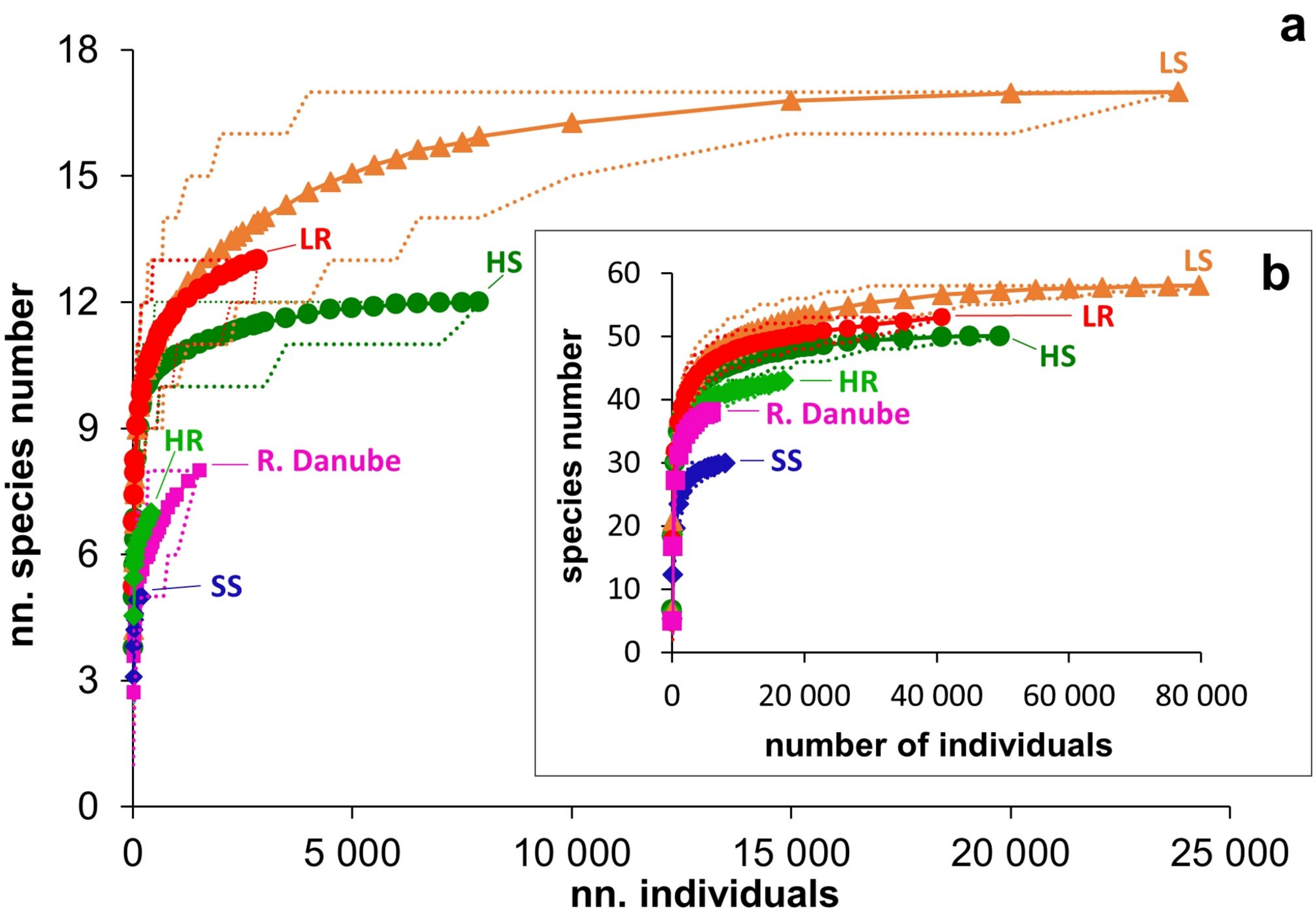

Submontane stream (SS)
Highland stream (HS)
Highland river (HR)
Lowland stream (LS)
Lowland river (LR)
River Danube
R. Hernád
R. Sajó
R. Bodrog
R. Tisza
R. Ipoly
R. Danube
R. Zagyva
R. Tarna
R. Szamos
R. Kraszna
R. Rába
BALATON
R. Danube
R. Tisza
R. Körös
R. Kapos
R. Dráva
R. Maros
100km

Figure 2


a
y = 1.9696e^0.8652x
R² = 0.9728
cumulated species number
0
10
20
30
40
50
60
-1900
1901-1950
1951-2000
2001-
Perciformes
Cypriniformes
Cyprinodontiformes
Salmoniformes
Siluriformes
Acipenseriformes
Characiformes
Gasterosteiformes
b
species number
0
5
10
15
20
25
-1900
1901-1950
1951-2000
2001-
„stocking”
„disperison”
„aquaculture”
„ornamental”
„accidental”
no data

833 **Figure 3**



834

Figure 4

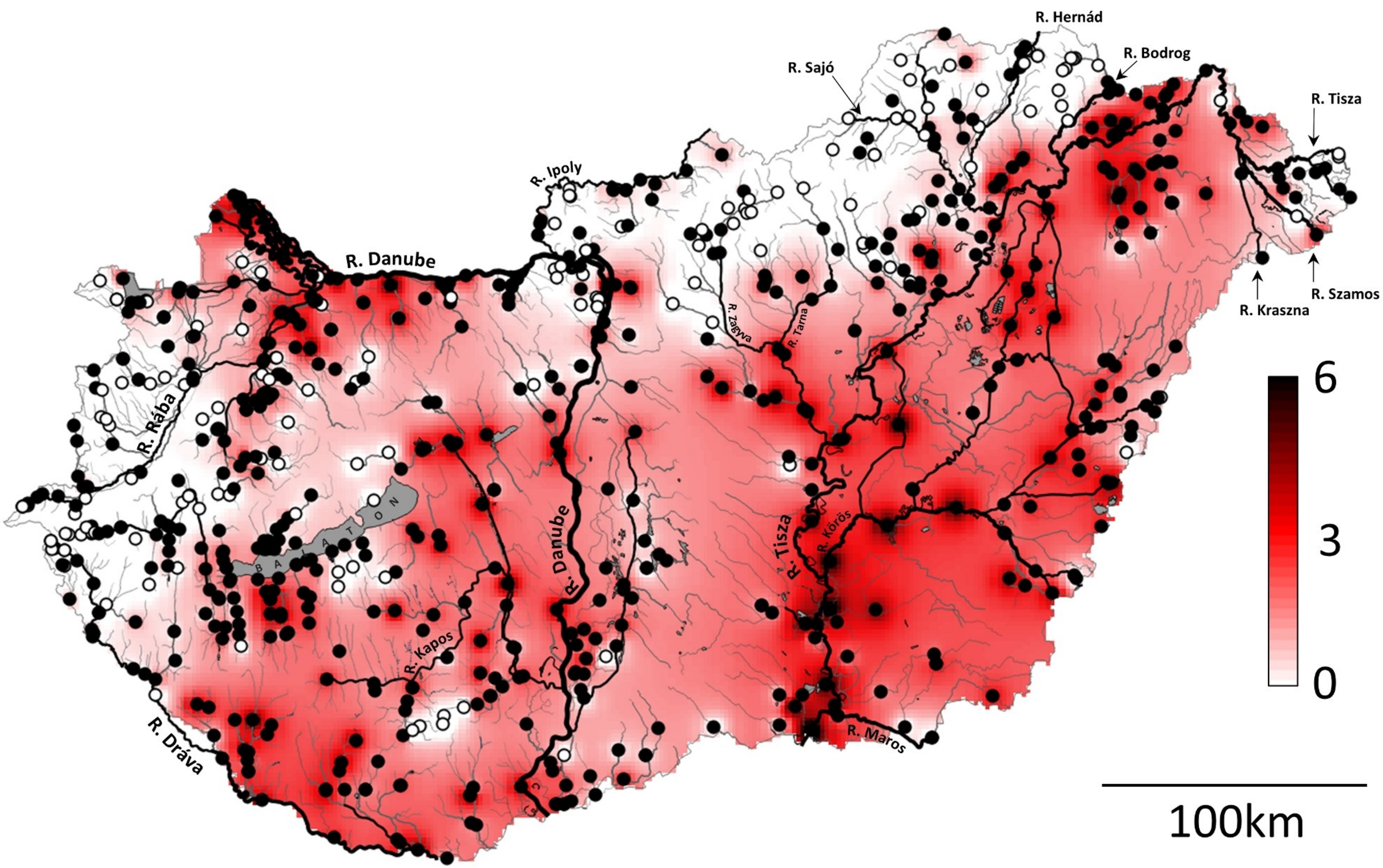

R. Hernád
R. Bodrog
R. Sajó
R. Tisza
R. Ipoly
R. Danube
R. Zagyva
R. Tarna
R. Kraszna
R. Szamos
R. Rába
BALATON
R. Danube
R. Tisza
R. Körös
R. Kapos
R. Dráva
R. Maros
6
3
0
100km

Figure 5

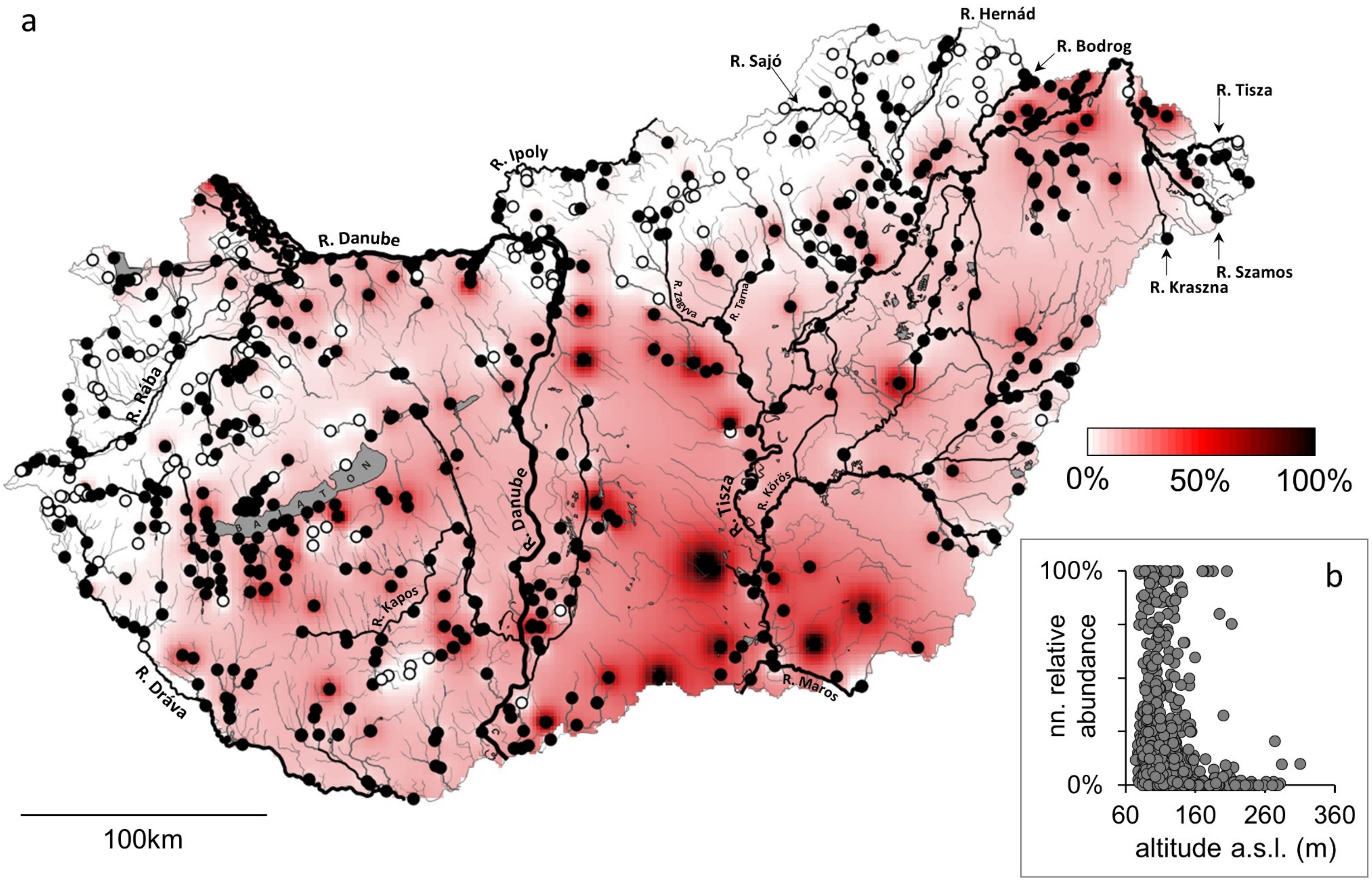
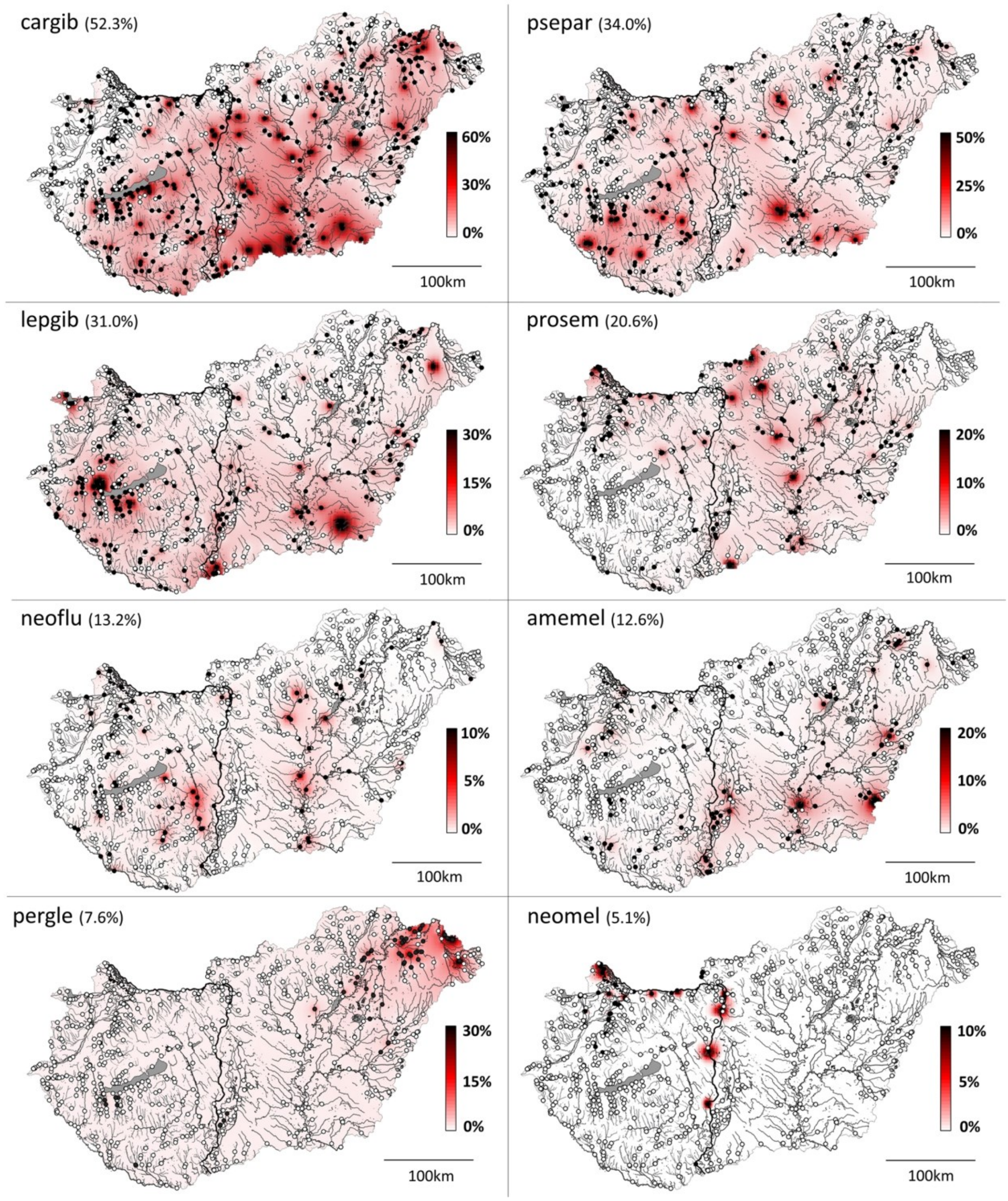

a
R. Hernád
R. Bodrog
R. Sajó
R. Tisza
R. Ipoly
R. Danube
R. Zagyva
R. Tarna
R. Szamos
R. Kraszna
R. Rába
BALATON
R. Danube
R. Tisza
R. Körös
R. Kapos
R. Dráva
R. Maros
0%
50%
100%
100km
b
100%
0%
nn. relative abundance
60
160
260
360
altitude a.s.l. (m)

Figure 6



cargib (52.3%)
60%
30%
0%
100km
psepar (34.0%)
50%
25%
0%
100km
lepgib (31.0%)
30%
15%
0%
100km
prosem (20.6%)
20%
10%
0%
100km
neoflu (13.2%)
10%
5%
0%
100km
amemel (12.6%)
20%
10%
0%
100km
pergle (7.6%)
30%
15%
0%
100km
neomel (5.1%)
10%
5%
0%
100km

Table 1

Nº	Species name	Code	Year	Order	Family	Native range	Reason of occurrence	Vector	Recent data	Reference
1.	*Proterorhinus semilunaris* (Heckel, 1837)	prosem	1872	Perciformes	Gobiidae	Ponto-Caspic	IFS	dispersion	+	Kriesch 1872
2.	*Oncorhynchus tshawytscha* (Walbaum, 1792)		1880	Salmoniformes	Salmonidae	N. America	II	stocking	-	Bíró 1993
3.	*Salvelinus fontinalis* (Mitchill, 1814)		1884	Salmoniformes	Salmonidae	N. America	II	stocking	+	Pintér 1980
4.	*Oncorhynchus mykiss* (Walbaum, 1792)	oncmyk	1885	Salmoniformes	Salmonidae	N. America	II	stocking	+	Bíró 1993
5.	*Carassius auratus* (Linnaeus, 1758)		1891?	Cypriniformes	Cyprinidae	Asia	II	stocking	+	Pintér 1980
6.	*Ameiurus nebulosus* (Lesueur, 1819)	ameneb	1902	Siluriformes	Ictaluridae	N. America	II	stocking	+	Pintér 1980
7.	*Lepomis gibbosus* (Linnaeus, 1758)	lepgib	1905	Perciformes	Centrarchidae	N. America	II	stocking	+	Vutskits 1912
8.	*Micropterus salmoides* (La Cepède, 1802)	micsal	1909	Perciformes	Centrarchidae	N. America	II	stocking	+	Vutskits 1913
9.	*Gambusia holbrooki* (Girard, 1859)	gamhol	1922	Cyprinodontiformes	Poeciliidae	C. America	IFS	accidental	+	Mihályfi 1939
10.	*Poecilia reticulata* Peters, 1859		1932	Cyprinodontiformes	Poeciliidae	C. america	II	ornamental	-	Wieseinger 1975
11.	*Carassius gibelio* (Bloch, 1782)	cargib	1954	Cypriniformes	Cyprinidae	Asia	II	stocking	+	Harka & Sallai 2004
12.	*Coregonus albula* (Linnaeus, 1758)		1955	Salmoniformes	Salmonidae	Europe[a]	O[b]	stocking	+	Pintér 1989
13.	*Coregonus lavaretus* (Linnaeus, 1758)		1955	Salmoniformes	Salmonidae	Europe[a]	O[b]	stocking	+	Pintér 1989
14.	*Gasterosteus aculeatus* (Linnaeus, 1758)	gasacu	1956	Gasterosteiformes	Gasterosteidae	SE. Europe	DFS?	dispersion	+	Sterbetz 1957
15.	*Ctenopharingodon idella* (Valenciennes, 1844)	ctenid	1963	Cypriniformes	Cyprinidae	E. Asia	II	stocking	+	Pintér 1980
16.	*Hypophthalmichtys molitrix* (Valenciennes, 1844)	hypmol	1963	Cypriniformes	Cyprinidae	E. Asia	II	stocking	+	Antalfi & Tölg 1972
17.	*Hypophtalmichthys nobilis* (Richardson, 1845)	hypnob	1963	Cypriniformes	Cyprinidae	E. Asia	II	stocking	+	Antalfi & Tölg 1972
18.	*Mylopharyngodon piceus* (Richardson, 1846)		1963	Cypriniformes	Cyprinidae	E. Asia	II	stocking	-	Pintér 1989
19.	*Pseudorasbora parva* (Temminck and Schlegel, 1846)	psepar	1963	Cypriniformes	Cyprinidae	E. Asia	AI	aquaculture	+	Pintér 1980
20.	*Neogobius fluviatilis* (Pallas, 1814)	neoflu	1970	Perciformes	Gobiidae	Ponto-Caspic	IFS	dispersion	+	Bíró 1971
21.	*Ictiobus bubalus* (Rafinesque, 1818)		1970?	Cypriniformes	Catostomidae	N. America	II	aquaculture	-	Harka & Sallai 2004
22.	*Ameiurus melas* (Rafinesque, 1820)	amemel	1980	Siluriformes	Ictaluridae	N. America	II	stocking	+	Pintér 1989
23.	*Poecilia velifera* (Regan, 1914)		1980	Cyprinodontiformes	Poeciliidae	C. America	II	ornamental	+	Pintér 1980
24.	*Micropterus dolomieu* (Lacepède, 1802)		<1980	Perciformes	Centrarchidae	N. America	II	stocking	-	Pintér 1980
25.	*Xiphophorus helleri* (Heckel, 1848)		<1980	Cyprinodontiformes	Poeciliidae	C. America	II	ornamental	-	Pintér 1980
26.	*Archocentrus multispinosus* (Günther, 1867)		1980?	Perciformes	Cichlidae	C. America	II	ornamental	+	Harka & Sallai 2004
27.	*Hypophtalmichthys molitrix* x *H. nobilis*		1980?	Cypriniformes	Cyprinidae	-	II	stocking	+	Márián et al., 1986
28.	*Ictalurus punctatus* (Rafinesque, 1818)		1981	Siluriformes	Ictaluridae	N. America	II	aquaculture	-	Botta et al., 1984
29.	*Acipenser baerii* (Brandt, 1869)		1981	Acipenseriformes	Acipenseridae	Asia	II	aquaculture	+	Weiperth et al., 2013
30.	*Clarias gariepinus* (Burchell, 1822)		1984	Siluriformes	Clariidae	Africa	II	stocking	-	Harka & Sallai 2004
31.	*Poecilia sphenops* (Valenciennes, 1846)		<1985	Cyprinodontiformes	Poeciliidae	C. America	II	ornamental	+	Botta, 1985
32.	*Polyodon spathula* (Walbaum, 1792)		1992	Acipenseriformes	Polyodontidae	N. America	II	stocking	+	Weiperth et al., 2013
33.	*Ponticola kessleri* (Günther, 1861)	ponkes	1996	Perciformes	Gobiidae	Ponto-Caspic	IFS	dispersion	+	Erős & Guti 1997
34.	*Perccottus glenii* (Dybowski, 1877)	pergle	1997	Perciformes	Odontobutidae	E. Asia	DFS?	dispersion	+	Harka 1998
35.	*Ponticola syrman* (Nordmann, 1840)[c]		1997	Perciformes	Gobiidae	Ponto-Caspic	-	-	-	Guti 1999, Guti 2014
36.	*Pseudotropheus tropheops* (Regan, 1922)		1999	Perciformes	Cichlidae	E. Africa	II	ornamental	-	Koščo & Balázs 2000
37.	*Neogobius melanostomus* (Pallas, 1814)	neomel	2001	Perciformes	Gobiidae	Ponto-Caspic	IFS	dispersion	+	Guti et al., 2003
38.	*Babka gymnotrachelus* (Kessler, 1857)	babgym	2004	Perciformes	Gobiidae	Ponto-Caspic	IFS	dispersion	+	Harka & Sallai 2004
39.	*Orechromis amphimelas* (Hilgendorf, 1905)		2004	Perciformes	Cichlidae	E. Africa	II	ornamental	-	Specziár 2004
40.	*Cichlasoma dimerus* (Heckel, 1840)		2007	Perciformes	Cichlidae	S. America	II	ornamental	+	Takács et al., 2015a
41.	*Gasterosteus gymnurus* (Cuvier, 1829)		2010	Gasterosteiformes	Gasterosteidae	SW. Europe	IFS	dispersion	+	Harka & Szepesi 2010
42.	*Knipowitschia caucasica* (Berg, 1916)	knicau	2009	Perciformes	Gobiidae	Ponto-Caspic	IFS	dispersion	+	Halasi-Kovács et al., 2011
43.	*Morone saxatilis* x *M. chrysops*		2008<	Perciformes	Moronidae	N. America	II	aquaculture	+	Sevcsik A. pers. comm.
44.	*Heterobranchus bidorsalis* (Geoffroy Saint-Hilaire, 1809)		2012	Siluriformes	Clariidae	C. Africa	II	no data	+	Halasi-Kovács & Harka 2012
45.	*Acipenser naccarii* x *A. baerii*		2013	Acipenseriformes	Acipenseridae	-	II	stocking	+	Weiperth et al., 2014
46.	*Labidochromis caeruleus* (Fryer, 1956)		2015	Perciformes	Cichlidae	E. Africa	II	ornamental	+	Weiperth et al., 2015
47.	*Megalechis thoracata* (Valenciennes, 1840)		2013	Siluriformes	Callichthyidae	S. America	II	ornamental	+	Weiperth et al., 2015
48.	*Platydoras armatulus* (Valenciennes, 1840)		2013	Siluriformes	Doradidae	S. America	II	ornamental	+	Weiperth et al., 2015
49.	*Hemichromis guttatus* (Günther, 1862)		2014	Perciformes	Cichlidae	C. Africa	II	ornamental	+	Harka et al., 2014
50.	*Amatitlania nigrofasciata* (Günther, 1874)		2015	Perciformes	Cichlidae	C. Africa	II	ornamental	+	Weiperth et al., 2015
51.	*Amphilophus citrinellum* (Günther, 1864)		2015	Perciformes	Cichlidae	E. Africa	II	ornamental	+	Takács et al., 2015b
52.	*Garra rufa* (Heckel, 1843)		2015	Cypriniformes	Cyprinidae	Asia Minor	AI?	accidental	+	Weiperth et al., 2015
53.	*Parachromis managuensis* (Günther, 1867)[d]		2015	Perciformes	Cichlidae	C. America	II	ornamental	+	Takács et al., 2015b
54.	*Paraneetroplus synspilus* (Hubbs, 1935)		2015	Perciformes	Cichlidae	C. America	II	ornamental	+	Takács et al., 2015b
55.	*Pseudotropheus socolofi* (Johnson, 1974)		2015	Perciformes	Cichlidae	E. Africa	II	ornamental	+	Takács et al., 2015b
56.	*Xiphophorus* sp.		2015	Cyprinodontiformes	Poeciliidae	C. America	II	ornamental	+	Weiperth et al., 2015
57.	*Colossoma macropomum* (Cuvier, 1816)		2015	Characiformes	Serrasalmidae	S. America	II?	ornamental	+	Weiperth et al., 2015
58.	*Pygocentrus* sp.		2015	Characiformes	Serrasalmidae	S. America	II?	ornamental	+	Weiperth et al., 2015
59.	*Coregonus peled* (Gmelin, 1789)[e]		?	Salmoniformes	Salmonidae	Eurasia	no data	no data	-	URL2[e]

Table 2

Habitat type	SS			HS			HR			LS			LR			R. Danube		
n_{tot} (n_{NN}%)	45 (29)			228 (66)			48 (69)			335 (90)			100 (94)			11 (100)		
$S_{tot.}$ (S_{NN}%)	30 (16.7)			50 (24.0)			43 (16.2)			58 (29.3)			53 (24.5)			38 (21.5)		
S	4.49±3.22			7.06±4.05			13.02±4.03			8.08±4.18			14.55±3.61			18.18±3.65		
S_{NN}	0.42±0.75			1.42±1.44			1.06±0.95			2.20±1.35			2.63±1.45			4.36±0.67		
N (RA_{NN}%)	5509 (4.0)			49608 (15.9)			16911 (2.4)			79621 (29.9)			40884 (6.9)			5882 (25.6)		
species code	N	RA%	FO%	N	RA%	FO%	N	RA%	FO%	N	RA%	FO%	N	RA%	FO%	N	RA%	FO%
cargib	143	3.0	17.8	3039	**6.1**[b]	41.2	99	0.6	20.8	13349	**16.8**[a]	70.1	612	**1.5**[b]	60.0	1	0.0	9.1
psepar	15	0.4	11.1	3052	**6.2**[a]	39.9	22	0.1	16.7	2946	**3.7**[a]	42.1	130	0.3	20.0	0	0	0
lepgib	14	0.1	4.4	696	1.4	24.1	27	0.2	18.8	2141	**2.7**[a]	40.3	262	0.6	33.0	2	0.0	9.1
prosem	0	0	0	465	0.9	12.3	87	0.5	20.8	690	0.9	17	768	**1.9**[a]	62.0	30	0.6	36.4
neoflu	45	0.3	6.7	70	0.1	6.6	81	0.5	16.7	290	0.4	9.3	316	**0.8**[a]	38.0	57	**0.9**[a]	72.7
amemel	0	0	0	117	0.2	9.2	1	0.0	2.1	1202	1.5	17.9	462	1.1	16.0	0	0	0
pergle	0	0	0	44	0.1	1.3	0	0	0	921	1.2	14.0	61	0.1	9.0	0	0	0
neomel	0	0	0	84	0.2	2.6	103	0.6	10.4	382	0.5	2.7	192	0.5	9.0	1162	**19.8**[a]	100
babgym	0	0	0	0	0	0	0	0	0	3	0.0	0.3	26	0.1	3.0	108	**1.8**[a]	100
cteide	0	0	0	2	0.0	0.4	0	0	0	10	0.0	1.8	6	0.0	6.0	0	0	0
ponkes	0	0	0	0	0	0	0	0	0	11	0.0	0.3	2	0.0	1.0	148	**2.5**[a]	90.9
gasacu	0	0	0	196	0.4	2.6	0	0	0	47	0.1	0.9	0	0	0	2	0.0	18.2
hypnob	0	0	0	0	0	0	0	0	0	6	0.0	0.3	0	0	0	0	0	0
oncmyk	4	0.2	2.2	5	0.0	1.8	0	0	0	0	0	0	0	0	0	0	0	0
hypmol	0	0	0	0	0	0	0	0	0	58	0.1	1.2	1	0.0	1.0	0	0	0
knicau	0	0	0	0	0	0	0	0	0	0	0	0	8	0.0	5.0	0	0	0
gamhol	0	0	0	125	0.3	0.4	0	0	0	1760	2.2	0.9	0	0	0	0	0	0
micsal	0	0	0	0	0	0	0	0	0	4	0.0	0.6	0	0	0	0	0	0
ameneb	0	0	0	0	0	0	0	0	0	2	0.0	0.3	0	0	0	0	0	0

Table 3

Habitat type	**SS**		**HS**		**HR**		**LS**		**LR**	
pond presence ($n_{tot.}$)	NP (32)	PP (13)	NP (109)	PP (119)	NP (26)	PP (22)	NP (77)	PP (258)	NP (67)	PP (33)
n_{NN} (FO_{NN}%)	5 (15.6)	8 (61.5)	56 (51.3)	94 (78.9)	15 (57.6)	18 (81.8)	51 (66.2)	252 (97.6)	62 (92.5)	33 (100.0)
S_{NN}	0.25±0.67	0.85±0.80	0.87±1.17	**1.93±1.49***	0.88±0.99	1.27±0.88	1.18±1.14	**2.50±1.26***	2.31±1.45	3.31±1.23
S_{NN}%	3.68±9.3	**16.78±17.8***	10.9±12.1	**29.40±24.9***	5.50±6.7	13.19±11.2	17.44±21.5	**34.6±20.8***	14.95±8.4	**24.72±8.6***
RA_{NN}%	0.50±1.8	**12.69±22.1***	4.98±11.4	**27.91±32.9***	1.77±2.6	5.6±7.9	14.3±26.3	33.85±32.1	4.88±6.6	**13.26±11.9***
cargib FO%	9.4	38.5	22.9	58.0	7.7	36.4	35.1	80.6	51.5	75.7
psepar FO%	6.3	23.1	22.0	56.3	7.7	27.3	18.2	49.2	19.4	21.2
lepgib FO%	3.1	7.7	15.6	31.9	3.8	36.4	23.4	45.3	23.9	51.5
prosem FO%	0	0	11.9	12.6	26.9	13.6	11.7	18.6	53.7	78.8
neoflu FO%	6.3	7.7	1.8	10.9	19.2	13.6	5.2	10.5	43.3	27.3
amemel FO%	0	0	5.5	12.6	3.8	0	11.7	19.8	7.5	33.3
pergle FO%	0	0	0	2.5	0	0	5.2	16.7	1.5	24.2
neomel FO%	0	0	3.7	1.7	9.2	0	5.2	1.9	11.9	3.0
cargib RA%	0.11±0.5	10.11±22.5	2.30±9.4	**10.28±19.6***	0.08±0.3	2.2±5.2	7.38±20.2	**20.5±28.0***	0.80±1.4	3.86±6.7
psepar RA%	0.01±0.1	1.28±3.0	0.75±2.9	**10.93±21.8***	0.06±0.2	0.35±0.8	1.44±5.4	**4.57±2.1***	0.18±0.5	0.66±2.1
lepgib RA%	0.05±0.3	0.25±0.9	0.36±1.5	3.26±12.1	0.55±1.6	1.32±3.6	1.21±3.4	**3.42±0.9***	0.18±0.4	1.72±5.1
prosem RA%	0	0	1.35±6.6	0.91±3.5	0.16±0.5	0.72±2.8	1.23±7.0	0.73±3.7	2.28±5.3	1.79±2.3
neoflu RA%	0.32±1.4	0.30±1.1	0.03±0.2	0.26±1.0	0.01±0.0	1.00±2.6	0.23±1.4	0.2±1.0	0.90±1.7	0.47±1.1
amemel RA%	0	0	0.17±1.4	0.55±3.8	0.01±0.0	0	0.73±3.8	1.05±5.1	0.20±0.8	3.22±11.1
pergle RA%	0	0	0	0.12±1.0	0	0	0.82±5.8	1.95±8.0	0.00±0.0	**1.72±2.0***
neomel RA%	0	0	0.08±0.6	0.15±1.3	0.90±2.3	0	0.36±2.0	0.25±3.6	0.19±0.7	0.67±3.9

Supplementary Table 1 List of species recorded during our field investigations of 767 sampling sites between 2011-2015. abbrev: abbreviations of non-native species as it used in tables, figures and in the text; FO%: frequency of occurrence; N: number of individuals captured; RA%: relative abundance in the whole catch, RA_{NN}%: relative abundance within the non-native catch. Blue colour and # sign: species are recorded as non-native, in Hungary. Species are ranked according to their frequency of occurrences. Species names used in accordance with the nomenclature of fishbase.org by date of 03.02.2016.

Rank	Species name	abbrev.	FO%	N	RA%	RA_{NN}%
1.	*Rutilus rutilus* (Linnaeus, 1758)		62.6	23890	11.889%	-
2.	*Rhodeus sericeus* (Pallas, 1776)		57.1	24625	12.255%	-
3.	*Alburnus alburnus* (Linnaeus, 1758)		52.9	46723	23.252%	-
4.	*Carassius gibelio* (Bloch, 1782) #	cargib	52.3	17243	8.581%	46.97%
5.	*Squalius cephalus* (Linnaeus, 1758)		50.5	18574	9.244%	-
6.	*Cobitis elongatoides* Băcescu and Maier, 1969		39.6	4616	2.297%	-
7.	*Esox lucius* (Linnaeus, 1758)		37.4	1307	0.650%	-
8.	*Perca fluviatilis* (Linnaeus, 1758)		34.6	2174	1.082%	-
9.	*Gobio gobio* (Linnaeus, 1758)		34.4	8530	4.245%	-
10.	*Pseudorasbora parva* (Temminck and Schlegel, 1842) #	psepar	34.0	6165	3.068%	16.79%
11.	*Lepomis gibbosus* (Linnaeus, 1758) #	lepgib	30.1	3142	1.564%	8.56%
12.	*Scardinius erythrophthalmus* (Linnaeus, 1758)		29.0	2212	1.101%	-
13.	*Barbatula barbatula* (Linnaeus, 1758)		27.2	6424	3.197%	-
14.	*Blicca bjoerkna* (Linnaeus, 1758)		25.1	2313	1.151%	-
15.	*Proterorhinus semilunaris* (Pallas, 1814) #	prosem	20.6	2040	1.015%	5.56%
16.	*Abramis brama* (Linnaeus, 1758)		17.6	800	0.398%	-
17.	*Misgurnus fossilis* (Linnaeus, 1758)		16.8	894	0.445%	-
18.	*Romanogobio vladykovi* (Fang, 1943)		16.7	1273	0.634%	-
19.	*Sander lucioperca* (Linnaeus, 1758)		16.3	373	0.186%	-
20.	*Alburnoides bipunctatus* (Bloch, 1782)		15.1	5147	2.561%	-
21.	*Leuciscus idus* (Linnaeus, 1758)		15.0	1380	0.687%	-
22.	*Cyprinus carpio* (Linnaeus, 1758)		13.7	586	0.292%	-
23.	*Leuciscus aspius* (Linnaeus, 1758)		13.6	402	0.200%	-
24.	*Neogobius fluviatilis* (Pallas, 1814) #	neoflu	13.2	859	0.427%	2.34%
25.	*Ameiurus melas* (Rafinesque, 1820) #	amemel	12.6	1782	0.887%	4.85%
26.	*Leuciscus leuciscus* (Linnaeus, 1758)		12.3	853	0.425%	-
27.	*Barbus barbus* (Linnaeus, 1758)		11.5	2520	1.254%	-
28.	*Chondrostoma nasus* (Linnaeus, 1758)		10.6	1025	0.510%	-
29.	*Silurus glanis* (Linnaeus, 1758)		8.7	184	0.092%	-
30.	*Perccottus glenii* (Dybowski, 1877) #	pergle	7.6	1026	0.511%	2.79%
31.	*Phoxinus phoxinus* (Linnaeus, 1758)		6.4	3093	1.539%	-
32.	*Barbus carpathicus* (Kotlík, Tsigenopoulos, Ráb and Berrebi, 2002)		6.4	1028	0.512%	-
33.	*Lota lota* (Linnaeus, 1758)		5.4	115	0.057%	-
34.	*Neogobius melanostomus* (Pallas, 1814) #	neomel	5.1	1923	0.957%	5.24%
35.	*Leucaspius delineatus* (Heckel, 1843)		5.1	330	0.164%	-
36.	*Vimba vimba* (Linnaeus, 1758)		4.6	186	0.093%	-
37.	*Tinca tinca* (Linnaeus, 1758)		4.2	70	0.035%	-
38.	*Umbra krameri* Walbaum, 1792		4.0	884	0.440%	-
39.	*Carassius carassius* (Linnaeus, 1758)		3.7	247	0.123%	-
40.	*Sabanejewia aurata* (Filippi, 1865)		3.7	131	0.065%	-
41.	*Zingel zingel* (Linnaeus, 1758)		3.3	161	0.080%	-
42.	*Salmo trutta morpha fario* (Linnaeus, 1758)		3.1	225	0.112%	-
43.	*Ballerus sapa* (Pallas, 1814)		2.9	82	0.041%	-
44.	*Gymnocephalus cernua* (Linnaeus, 1758)		2.9	71	0.035%	-
45.	*Zingel streber* (Siebold, 1863)		2.2	119	0.059%	-
46.	*Gymnocephalus schraetser* (Linnaeus, 1758)		2.1	248	0.123%	-
47.	*Gymnocephalus baloni* Holčík and Hensel, 1974		2.1	64	0.032%	-
48.	*Babka gymnotrachelus* (Kessler, 1857) #	babgym	1.9	137	0.068%	0.37%
49.	*Rutilus pigus virgo* (Heckel, 1852)		1.9	109	0.054%	-
50.	*Romanogobio kesslerii* (Dybowski, 1862)		1.8	148	0.074%	-
51.	*Ballerus ballerus* (Linnaeus, 1758)		1.7	47	0.023%	-
52.	*Ctenopharyngodon idella* (Valenciennes, 1844) #	cteide	1.7	18	0.009%	0.05%
53.	*Ponticola kessleri* (Günther, 1861) #	ponkes	1.5	161	0.080%	0.44%
54.	*Gasterosteus aculeatus* (Linnaeus, 1758) #	gasacu	1.4	245	0.122%	0.67%
55.	*Hypophthalmichthys molitrix* (Valenciennes, 1844) #	hypmol	0.6	59	0.029%	0.16%
56.	*Sander volgensis* (Gmelin, 1788)		0.6	14	0.007%	-
57.	*Oncorhynchus mykiss* (Walbaum, 1792) #	oncmyk	0.6	9	0.004%	0.02%
58.	*Knipowitschia caucasica* (Berg, 1916) #	knicau	0.6	8	0.004%	0.02%
59.	*Gambusia holbrooki* (Girard, 1859) #	gamhol	0.5	1885	0.938%	5.13%
60.	*Micropterus salmoides* (Lacepède, 1802) #	micsal	0.3	4	0.002%	0.01%
61.	*Anguilla anguilla* (Linnaeus, 1758)		0.3	3	0.001%	-
62.	*Eudontomyzon danfordi* (Regan, 1911)		0.3	2	0.001%	-
63.	*Eudontomyzon mariae* (Berg, 1931)		0.1	20	0.010%	-
64.	*Hypophthalmichthys nobilis* (Richardson, 1845) #	hypnob	0.1	6	0.003%	0.02%
65.	*Ameiurus nebulosus* (Lesueur, 1819) #	ameneb	0.1	2	0.001%	0.01%
66.	*Pelecus cultratus* (Linnaeus, 1758)		0.1	2	0.001%	-

Supplemetary Table 2 The effect of the fish pond positions to the non native fish distribution and abundabce data. Values written in red and denoted by letters in the upper case are significantly larger ("a" denotes the highest values) than the relevant values in groups of sites according to the pairwise Mann-Whitney U test (p<0.05). For abreviations see Table 1 and 2.

habitat type	Pond position (no. of sites)		nn spec.	nn spec. prop. (%)	nn rel. ab.	amemel	ameneb	babgym	cargib	cteide	gamhol	gasacu	hypmol	hypnob	knicau	lepgib	micsal	neoflu	neomel	oncmyk	pergle	ponkes	prosem	psepar
SS	downstream (4)	freq of occ.	75%			0%	0%	0%	25%	0%	0%	0%	0%	0%	0%	0%	0%	25%	0%	0%	0%	0%	0%	50%
		mean±sd	1.00±0.82[a]	15.8±13.7[a]	0.09±0.09[a]	0	0	0	0.04±0.08	0	0	0	0	0	0±0.0	0	0	0.01±0.02	0	0	0	0	0	0.04±0.05[a]
	upstream (9)	freq of occ.	56%			0%	0%	0%	44%	0%	0%	0%	0%	0%	0%	11%	0%	0%	0%	11%	0%	0%	0%	11%
		mean±sd	0.78±0.83	17.2±21.4[a]	0.14±0.26[a]	0	0	0	0.13±0.27[a]	0	0	0	0	0	0	0.001±0.01	0	0	0	0.01±0.03	0	0	0	0.01±0.01
	no pond (32)	freq of occ.	16%			0%	0%	0%	9%	0%	0%	0%	0%	0%	0%	3%	0%	6%	0%	0%	0%	0%	0%	6%
		mean±sd	0.25±0.67	3.7±9.3	0.01±002	0	0	0	0.0±0.0	0	0	0	0	0	0	0.0±0.0	0	0.01±0.67	0	0	0	0	0	0.0±0.0
HS	downstream (30)	freq of occ.	67%			10%	0%	0%	33%	0%	0%	0%	0%	0%	0%	20%	0%	3%	0%	3%	3%	0%	3%	40%
		mean±sd	1.17±1.12	19.9±21.7	0.17±0.31	0.0±0.0	0	0	0.10±0.26[a]	0	0	0	0	0	0	0.0±0.0	0	0.0±0.0	0	0.0±0.0	0.0±0.0	0	0.0±0.0	0.07±0.18
	down+upstream (11)	freq of occ.	100%			45%	0%	0%	100%	0%	9%	9%	0%	0%	0%	64%	0%	9%	0%	0%	9%	0%	0%	82%
		mean±sd	3.27±0.9[a]	41.1±15.6[a]	0.42±0.35[a]	0.01±0.02[a]	0	0	0.05±0.06[a]	0	0.03±0.11	0.04±0.14	0	0	0	0.02±0.03	0	0.01±0.02	0	0	0.01±0.03	0	0	0.25±0.32[a]
	upstream (77)	freq of occ.	81%			9%	0%	0%	62%	1%	0%	4%	0%	0%	0%	31%	0%	14%	3%	1%	1%	0%	18%	58%
		mean±sd	2.04±1.53[b]	31.5±26.4[b]	0.30±0.32	0.01±0.05	0	0	0.11±0.18[a]	0.0±0.0	0	0.0±0.0	0	0	0	0.04±0.14	0.0±0.0	0.01±0.01	0.00±0.05	0.01±0.11	0.0±0.0	0	0.01±0.04	0.10±0.21
	no pond (110)	freq of occ.	52%			5%	0%	0%	23%	0%	0%	2%	0%	0%	0%	16%	0%	2%	4%	2%	0%	0%	12%	23%
		mean±sd	0.88±1.17	9.7±12.1	0.06±0.14	0.0±0.01	0	0	0.02±0.09	0	0	0.01±0.05	0	0	0	0.01±0.03	0	0	0.01±0.01	0.0±0.0	0	0	0.01±0.07	0.01±0.03
HR	downstream (4)	freq of occ.	75%			0%	0%	0%	25%	0%	0%	0%	0%	0%	0%	50%	0%	25%	0%	0%	0%	0%	0%	25%
		mean±sd	1.25±0.96	10.4±7.7	0.08±0.13	0	0	0	0.05±0.1	0	0	0	0	0	0	0.01±0.01	0	0.02±0.03	0	0	0	0	0	0
	upstream (18)	freq of occ.	83%			0%	0%	0%	39%	0%	0%	0%	0%	0%	0%	33%	0%	11%	0%	0%	0%	0%	17%	28%
		mean±sd	1.28±0.89	13.8±12.0[a]	0.05±0.07	0	0	0	0.02±0.04	0	0	0	0	0	0	0.01±0.04	0	0.01±0.02	0	0	0	0	0.01±0.03	0.0±0.01
	no pond (26)	freq of occ.	58%			4%	0%	0%	8%	0%	0%	0%	0%	0%	0%	4%	0%	19%	19%	0%	0%	0%	27%	8%
		mean±sd	0.88±0.99	5.5±6.1	0.02±0.03	0.0±0.0	0	0	0	0	0	0	0	0	0	0	0	0	0.01±0.02	0	0	0	0.01±0.02	0
LS	downstream (48)	freq of occ.	100%			21%	0%	0%	77%	2%	2%	2%	2%	0%	0%	31%	0%	4%	2%	0%	19%	0%	23%	46%
		mean±sd	2.31±1.26[a]	35.6±23.5[a]	0.30±0.32[a]	0.02±0.08	0	0	0.18±0.28[a]	0	0.02 0.12	0.0±0.03	0	0	0	0.02±0.04	0	0	0	0	0.01±0.03	0	0.01±0.02	0.04±0.1
	down+upstream (19)	freq of occ.	100%			5%	0%	0%	89%	0%	0%	0%	5%	0%	0%	47%	0%	0%	0%	0%	26%	0%	5%	75%
		mean±sd	2.16±1.21	41.5±25.3[a]	0.52±0.35[a]	0.0±0.01	0	0	0.40±0.41[a]	0	0	0	0	0	0	0.04±0.09	0	0	0	0	0.04±0.1	0	0	0.1±0.02[a]
	upstream (190)	freq of occ.	97%			21%	1%	1%	81%	3%	1%	0%	1%	1%	0%	48%	0.0%	13%	2%	0%	15%	1%	19%	51%
		mean±sd	2.58±1.27[a]	33.7±19.6[a]	0.33±0.31[a]	0.01±0.04	0.0±0.01	0	0.19±0.26[a]	0	0.01±0.07	0	0.0±0.01	0	0	0.04±0.1	0	0.0±0.01	0.0±0.04	0	0.02±0.09	0	0.01±0.04	0.05±0.13
	no pond (78)	freq of occ.	67%			12%	0%	0%	35%	0%	0%	3%	0%	0%	0%	24%	0%	6%	5%	0%	5%	0%	12%	19%
		mean±sd	1.21±1.15	17.5±21.4	0.14±0.26	0.01±0.04	0	0	0.07±0.2	0	0	0.01±0.05	0	0	0	0.01±0.04	0	0.0±0.01	0.0±0.02	0	0.01±0.06	0	0.01±0.07	0.01±0.05
LR	downstream (9)	freq of occ.	100%			22%	0%	0%	89%	0%	0%	0%	0%	0%	0%	33%	0%	44%	0%	0%	11%	11%	89%	33%
		mean±sd	3.33±0.87[a]	24.2±6.6[a]	0.11±0.09	0.02±0.06	0	0	0.04±0.08	0	0	0	0	0	0	0.0±0.01	0	0.01±0.02	0	0	0	0.0±0.01	0.03±0.03	0
	upstream (24)	freq of occ.	100%			38%	0%	0%	71%	13%	0%	0%	0%	0%	4%	58%	0%	21%	4%	0%	29%	0%	75%	21%
		mean±sd	3.33±1.34	24.9±9.4[a]	0.14±0.17[a]	0.04±0.13	0	0	0.04±0.06	0.0±0.0	0	0	0	0	0.0±0.0	0.02±0.06	0	0.0±0.01	0.01 ±0.05	0	0.01±0.02	0	0.01±0.02	0.01±0.02
	no pond (67)	freq of occ.	91%			7%	0%	4%	52%	4%	0%	0%	1%	0%	6%	24%	0%	43%	12%	0%	1%	0%	54%	18%
		mean±sd	2.28±1.44	14.9±8.4	0.05±0.07	0.0±0.01	0	0.0±0.0	0.01±0.01	0.0±0.0	0	0	0.0±0.0	0	0.0±0.0	0.0±0.0	0	0.01±0.02	0.0±0.01	0	0.0±0.0	0	0.02±0.05	0.0±0.01