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Desiccation frequency drives local invasions of non-native gibel carp (*Carassius gibelio*) in the catchment of a large, shallow lake (Lake Balaton, Hungary)

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ABSTRACT

Although the problem of non-indigenous species and biological invasions has been widely discussed, knowledge is still limited on their prevention and elimination for the successful management of this problem. In this study, we tested relationships between fish community composition, local environmental parameters and habitat management practice in 11 lentic habitats in the catchment of Lake Balaton (Hungary). The frequency of desiccation events (related to fish pond management) proved to be highly important in increasing the dominance of non-indigenous *Carassius gibelio*. We suggest that high frequency of desiccation events and the robustness of this species (tolerance to low oxygen levels, gynogenetic reproduction) can contribute to local invasion cycles in wetlands and fish ponds resulting in their continuously high abundance. Our study suggests that ensuring more controlled and stable water level in these habitats can be a successful tool to manage *C. gibelio* invasions.

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1. Introduction

Successful biological invasions involve complex interactions between the invading species and the characteristics of the recipient habitats (Hayes and Barry, 2008). It is well-known that certain regions and habitats appear to be particularly vulnerable to invasions (Dudgeon et al., 2006). Certain habitat characteristics are hypothesized to favor successful invasion including (1) environmental similarity between the native and invaded habitats, (2) low to moderate environmental variability, (3) high degree of disturbance, especially of anthropogenic origin, and (4) low richness of native species (Elton, 1958; Lodge, 1993). Recent studies suggest that invasions represent matches and continuous interactions between site characteristics and invaders (Shea and Chesson, 2002). A non-indigenous species is able to displace a native one for two kind of reasons: (1) It has 'a priori' natural pre-adaptations to

exploit particular environments. In such cases, invasion is only limited by migration abilities (Allendorf and Lundquist, 2003). (2) If there are no 'a priori' adaptations, some eco-evolutionary changes are needed (Lee, 2002; Lambrinos, 2004). For example, changes in the life history traits (e.g.: age and length at maturity reduction) are often observed in invasive fish populations (Vila-Gispert et al., 2005; Novomenská and Kovác, 2009). Based on the combinations of these two major mechanisms, a migration-based conceptual framework was described: three possible types of invasion scenario were distinguished, as migration change, environmental change and evolutionary change (Facon et al., 2006).

Many non-indigenous species may establish in a single habitat but fail to invade adjacent areas despite having continuous opportunity to migrate and colonize. By examining invasion patterns on regional scale (e.g. catchment scale when dealing with riverine networks), it is possible to determine the driving factors for their success in given habitats, which is crucial to implement management efforts and make predictions for similar systems (Light, 2003). It has long been proposed that increasing intensity or frequency of disturbance facilitates invasions (Elton, 1958; Moyle and Light, 1996; Hierro et al., 2006; Johnson et al., 2008), while recent

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studies indicate that the modification of the original disturbance regime is more important both in terrestrial and freshwater ecosystems (Leprieur et al., 2006; Moret et al., 2006; Clark and Johnston, 2011). For example, the complex life histories of some fish species (e.g., mixed migratory behaviors) are adaptations to periodic disturbances such as fire and flooding. Thus, introduced species may be able to out-perform native species (Rieman and Clayton, 1997), and the adaptation of natives to a given disturbance frequency, is crucial. In this way, the disruption of natural disturbance regimes will increase the likelihood of successful invasions within a given time frame.

Previous studies investigating the distribution patterns of stream fish communities in the Balaton catchment in Central Europe found the predominant role of local variables in community structure (Sály et al., 2011; Erős et al., 2012). However, Sály et al. (2011) demonstrated that non-indigenous species reduced the descriptive power of local environmental variables. They also suggested that the effect of landscape variables on fish communities depended strongly on the level of disturbance, but the types and level of disturbances were not explicitly addressed.

In our study, we tested whether disturbance frequency (derived from human watershed management) can alter local fish communities in the southern catchment of Lake Balaton, leading to the dominance of non-indigenous fish species. We also aimed at assessing the contribution of human watershed management in comparison to other local environmental parameters on the distribution and abundance of non-indigenous fish species.

2. Materials and methods

2.1. Study area

Lake Balaton is the largest shallow lake in Central Europe (area: 594 km², mean depth: 3.2 m), with a catchment area of 5775 km². In the past, the lake was characterized by extreme water level fluctuations (Korponai et al., 2010). Until the 1860s, large wetlands were connected to the southern part of the lake. Afterwards, water level regulation works started by constructing Sió Canal, which reduced the water level of the lake. As a consequence, the connected wetlands mostly disappeared, became astatic or were converted into fish ponds (Korponai et al., 2010; Zlinszky and Tímár, 2013). The shore zone itself has also been drastically altered, by the destruction of the natural ecotone (reed belts) and construction of artificial shore ramparts (e.g. rip-raps). Such changes could have had profound effects on plant and animal communities (Gilvear, 1999).

Table 1
General data of the sampling sites.

Waterbody	Site name	GPS coordinates	Site code	Type	Management
Töreki pond system	Pond X	N46 52.886 E18 00.144	TOR	Recreational (angling) pond	Intensive stocking
Irmapuszta pond system	Pond VII	N46 46.639 E17 44.695	IRM	Fish pond	Intensive stocking, fish farming
Öszöd marsh		N46 49.120 E17 48.219	OSZ	Wetland	None, water level control
Lake Balaton	Sajkod	N46 54.972 E17 50.289	BAL	Shallow lake	Commercial fishing, angling
Kis-Balaton Water Protection System	Reservoir II inlet	N46 38.601 E17 11.301	ING	Reservoir	None
Kis-Balaton Water Protection System	Reservoir I Inlet	N46 39.589 E17 07.632	POG	Reservoir	Commercial fishing, angling
Kis-Balaton Water Protection System	Reservoir I Turn	N46 36.444 E17 09.519	RAD	Reservoir	Commercial fishing
Kis-Balaton Water Protection System	Reservoir I, outflow	N46 37.722 E17 09.398	KAN	Reservoir	Commercial fishing, angling
Kis-Balaton Water Protection System	Connencting channel	N46 38.178 E17 10.861	4TA	Channel	None
Csombárdi pond		N46 26.890 E17 39.440	CSO	Abandoned fish pond (since 2008)	None
Gyótapuszta Pond System	Pond II	N46 32.229 E17 27.071	GYO	Abandoned fish pond (since 2002)	None

Before the water level of the lake was regulated and lowered, water cover of the southern wetlands had been relatively stable, though with a fluctuating water level (Zlinszky and Tímár, 2013). Therefore, the Balaton catchment represents a freshwater system with drastically altered hydrological conditions, including disturbance regime, which may have had a considerable role in the invasion of some non-native species (Sály et al., 2011).

The fish fauna of the lake and its inflows were described previously by Paulovits et al. (1994), Erős et al. (2009), Specziár et al. (2009), Sály et al. (2011) and Ferincz et al. (2012), while less is known about the fish fauna of other lentic habitat types like wetlands, recreational ponds and fish ponds in its catchment. Sampling sites were selected to represent the most typical lentic habitat types of the catchment including fish ponds, recreational and angling ponds, reservoirs and wetlands and a characteristic littoral habitat of Lake Balaton as well. Eleven habitats were surveyed in 2011 (Table 1, Fig. 1).

2.2. Fish sampling

Electrofishing was carried out seasonally, three times at each site: in spring (April/May), summer (June/July), and autumn (October) of 2011. Sampling was conducted along the same transect in each season near the vegetated shoreline from a small, 12 V electric motor powered rubber boat using a SAMUS 725MP, 12 V battery-powered device (used at Pulse DC 380–580 V; 50–70 Hz). This method provides reliable information regarding the community structure (Erős et al., 2009; Specziár et al., 2012). The duration of each sampling occasion was 60 min, which meant a transect length mean of 1606 ± 210 m. Each captured fish was identified to species level, according to the book of Harka and Sallai (2004) and afterwards released, except a randomly selected subsample (30 individuals/sampling) of the non-native gibel (*Prussian*) carp, which were taken to the laboratory for further study. The 0+ (fry, smaller than app. 15 mm) fish were excluded both from field identification and data analysis.

2.3. Environmental parameters

Thirteen habitat variables and six habitat management variables were recorded (Table 2). For littoral macrovegetation cover (Reed, Rmace, LOther, see abbreviations in Table 2), percentage ratios of coverage were calculated based on visual estimation for every 50 m sections of the electrofished transects. In order to calculate percentage ratios, means of sediment characteristics and water depth,

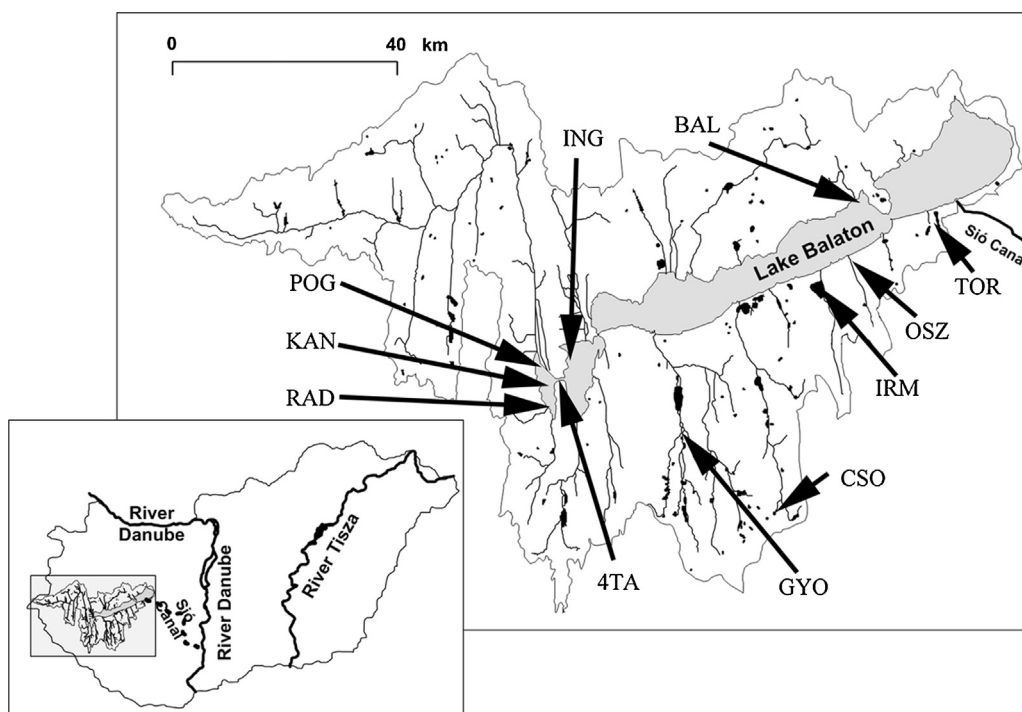


Fig. 1. Map of the Balaton catchment with the sampling sites (See abbreviations in Table 1).

these variables were recorded at 10 randomly selected points close to the transects. These measurements were conducted once, during the summer sampling, when macrovegetation is fully developed. A HORIBA U-10 water quality checker was used to measure turbidity, conductivity and pH at each sampling occasion, mean values were used during the analyses. Surface area and data on habitat management variables were gathered from digitalized topographical maps using GIS software or from literature sources (Dövényi, 2010; VKKI, 2010). The watersheds managers (staff of the national park directorates) were interviewed mainly for the assessment of the occurrence of desiccation events.

2.4. Data analysis

Redundancy analysis (RDA) with an automatic forward selection procedure was applied to explore variables explaining a significant share of the non-indigenous species distribution and abundance. In this process, an unconstrained Principal Component Analysis on the species-habitat datasets was followed by the passive projection of the explanatory variables. The number of permutations in Monte-Carlo simulation were set to 1000. In the first model, we used binary (presence–absence) data of species (without any weighting) occurring at least two sites with all the environmental variables

Table 2

List of the environmental variables used in the RDAs and variance partitioning (all habitat characteristic data were log(x + 1) transformed).

	Name	Abbreviation	Measure	Mean ± SD
Habitat characteristics (Local effects)	Reed (<i>Phragmites communis</i>)	Reed	Shoreline coverage (%)	58.46 ± 27.69
	Reed-mace (<i>Typha</i> sp.)	Rmace	Shoreline coverage (%)	29.76 ± 26.03
	Other macrophytes in the littoral zone (eg.: <i>Carex</i> sp., <i>Juncus</i> sp.)	LOther	Shoreline coverage (%)	9.61 ± 13.65
	Submerse macrophytes (<i>Potamogeton</i> sp., <i>Myriophyllum</i> sp., <i>Ceratophyllum</i> sp.)	Smerse	Coverage (%)	27.07 ± 28.85
	Area	Area	km ²	52.06 ± 156.7
	Silt	Silt	Bottom coverage (%)	62.3 ± 30.92
	Sand	Sand	Bottom coverage (%)	18.46 ± 21.07
	Gravel	Gravel	Bottom coverage (%)	10.38 ± 18.24
	Clay	Clay	Bottom coverage (%)	8.84 ± 11.46
	Turbidity	Turbid	NTU	117 ± 118.7
	Conductivity	Cond	µS/cm	703.38 ± 136.3
	pH	pH		8.41 ± 0.41
	Average depth	Depth	cm	105.38 ± 44.99
	Habitat management characteristics	Activity of commercial fisheries	Fishing	binary data
Water level managed by suction		Suction		9% of answer yes
Water supply from inflow/tributary		Inflow		81.8% of answer yes
Watershed dried out at least once in the last 10 years		Drought		27.3% of answer yes
Human constructed habitat		Constructed		72.7% of answer yes
Protected habitat	Protected		81.8% of answer yes	

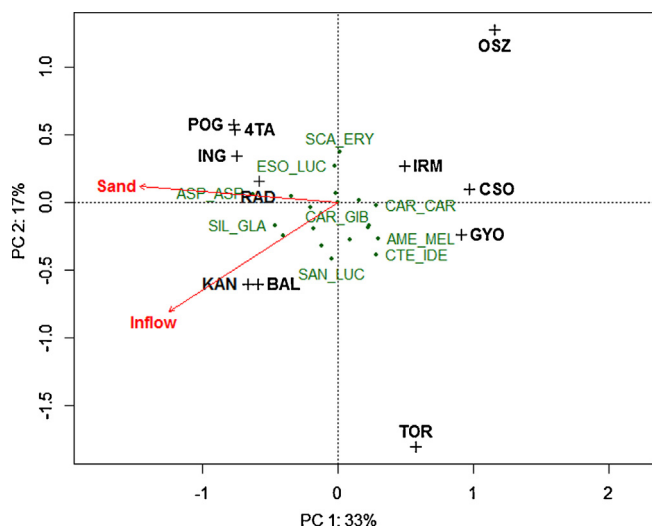


Fig. 2. RDA model for presence-absence data. Red arrows represent the significant environmental variables, species are indicated with green and habitats with black labels. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

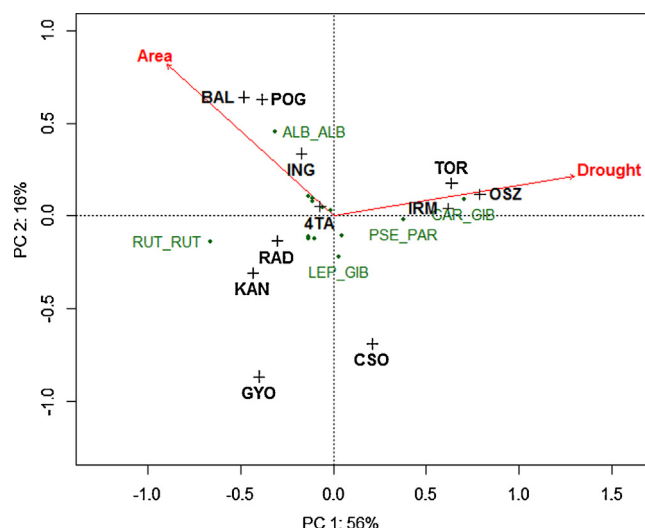


Fig. 3. RDA model for the fish assemblage based on Relative Abundance data. Red arrows represent significant environmental variables, species are indicated with green and habitats with black labels. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

listed in Table 1. As forward selection revealed significant effects both among the ‘habitat characteristics’ and ‘habitat management’ variable groups, variance partitioning was used to assess the relative contribution of the different variable groups (Borcard et al., 1992). A second RDA model was constructed for arcsine-square-root-transformed relative abundance data (i.e.: the ratio between the number of individuals of a given species and the total number of fish caught in each habitat) of dominant species (reaching 5% of relative abundance at least 1 site) using the same procedure. Mean data of the three sampling occasions were used in order to improve the robustness of the results. All analyses were made in R software (R Development Core Team, 2013), with the package “packfor” (Dray et al., 2013) and “vegan” (Oksanen et al., 2013).

3. Results

3.1. Fish communities

The total number of individuals caught was $N = 8899$. Twenty-two fish species were identified at the 11 sampling sites, of which 10 (34.5%) were non-indigenous (Table 3). At least 1 non-native species was recorded at each sampling site, with the lowest number ($n = 1$) in Pogányvári-víz (POG), and with the highest number ($n = 6$) in the Töreki-fishpond (TOR). The non-indigenous gibel carp (*Carassius gibelio* Bloch, 1782) was present at every sampling site. It was the most abundant and, at the same time, the most frequent member of the fish fauna. It constituted 34.21% of all the fish individuals caught (3044 individuals).

3.2. Effects of environmental and habitat management variables on the fish community

The first two axes of the RDA model accounted for 50% of the total variance in the presence-absence data (Fig. 2). Forward selection resulted in two significant explanatory variables: ‘presence of inflow’ from habitat management group, and ‘ratio of sandy bottom’ from the local environmental characteristics group (Table 4).

Two groups of habitats could be separated along the first axis of the RDA triplot, determined by the significant explanatory variables

and species composition: semi-natural habitats with relatively high number of native and low number of non-native species (BAL, POG, KAN, RAD, ING, 4TA). The second group was formed by fish ponds and wetland with relatively low number of native species and high number of non-natives (IRM, TOR, CSO, GYO, OSZ). Significant environmental factors were positively related to the first group and negatively to the second.

The first two axes of the RDA model constructed for the arcsine-square-root-transformed relative abundance data accounted for 72% of the total variance (Fig. 3). The forward selection identified two significant environmental variables: ‘area’ from the ‘local environmental variables’ and ‘occurrence of dry-out’ from the ‘habitat management’ group (Table 5).

Most of the species were associated with the centroid, therefore not labeled on the RDA triplot, while *Rutilus rutilus* (Linnaeus, 1758), *Alburnus alburnus* (Linnaeus 1758), *Pseudorasbora parva* (Temminck and Schlegel 1846) and *C. gibelio* were clearly separated. These species proved to be dominant in different habitat types (Fig. 3). Regarding non-natives, one group of habitats (TOR, IRM, OSZ); two fish ponds and a wetland) was associated strongly with the two dominant non-native species (*P. parva*, *C. gibelio*). The other habitats were mostly characterized by semi-natural fish fauna, differing in the dominant species, which was either *A. alburnus* (BAL, POG, ING) or *R. rutilus* (KAN, RAD, GYO). A group of transitional habitats (4TA, CSO) was also visible.

The factor responsible for the separation of the habitat group dominated by non-native species was the effect of desiccation occurrence. The semi-natural group of habitats differed according to their ‘area’: habitats with the dominance of *A. alburnus* showed a positive relationship with ‘area’.

The significantly explained variance of the RDA model constructed for presence-absence data proved to be 34% in total. Pure environmental [Env: ‘ratio of sandy bottom’] and pure habitat management variables [Use: ‘presence of inflow’] accounted for 12% and 11% of the variability, and 1% of shared effects was detectable. The RDA model for relative abundance data explained 50% variance in total. Pure environmental [Env: ‘area’], shared environmental, habitat use [EnvxUse] and pure habitat use [Use: ‘occurrence of drying-out’] variables accounted for 9%, 12% and 29%.

Table 3
Species composition, relative abundance and diversity of the examined habitats.

Species	Sampling site												Status	
	Scientific name	Common name	Abbreviation	RAD	POG	KAN	4TA	ING	OSZ	BAL	CSO	GYO		IRM
<i>Rutilus rutilus</i>	Roach	RUT.RUT	59.29	35.85	76.86	29.86	28.48	0	21.52	9.20	41.16	0.07	0.08	Native
<i>Carassius gibelio</i>	Gibel carp	CAR.GIB	18.18	8.96	8.42	28.98	21.69	93.14	0.66	26.71	0.47	47.30	64.06	Alien
<i>Lepomis gibbosus</i>	Pumpkinseed	LEP.GIB	0.26	0	1.82	0	2.32	0.29	0.22	29.38	3.95	0.87	0.59	Alien
<i>Cyprinus carpio</i>	Common carp	CYP.CAR	1.32	2.12	2.24	0.71	6.29	0	3.36	0.89	3.26	7.46	5.46	Native
<i>Perca fluviatilis</i>	Perch	PER.FLU	1.84	1.18	3.51	0.18	1.49	0	4.16	10.98	4.88	0	0	Native
<i>Abramis brama</i>	Bream	ABR.BRA	1.58	2.83	0.70	6.54	7.95	0.00	0.95	0	0.47	0	0.17	Native
<i>Leuciscus aspius</i>	Asp	ASP.ASP	3.56	7.55	0.56	1.24	1.66	0.00	0.36	0	0	0	0	Native
<i>Silurus glanis</i>	Wels	SIL.GLA	0.40	0.24	1.40	2.12	5.30	0	0.22	0	0	0.07	0.08	Native
<i>Blicca bjoerkna</i>	White bream	BLL.BJO	7.91	4.72	0.28	11.13	3.81	0	1.60	0	0	0	0	Native
<i>Alburnus alburnus</i>	Bleak	ALB.ALB	1.58	33.73	2.81	2.47	17.38	0	56.60	0	0	0.33	1.60	Native
<i>Scardinius erythrophthalmus</i>	Rudd	SCA.ERY	2.24	2.12	0	13.07	0.99	0.49	3.43	10.39	11.86	0.13	0	Native
<i>Tinca tinca</i>	Tench	TIN.TIN	0.26	0	0	0	0	1.49	0.22	0	1.86	0	0.17	Native
<i>Sander lucioperca</i>	Pikeperch	SAN.LUC	1.32	0	0.70	0	0	0	0.73	2.97	0	0	0.50	Native
<i>Gymnocephalus cernua</i>	Ruffe	GYM.CER	0.13	0	0	0	0	0	0	0	0	0.07	0	Native
<i>Esox lucius</i>	Pike	ESO.LUC	0.13	0	0	1.24	0.50	2.43	0.44	0	2.33	0.67	0	Native
<i>Pseudorasbora parva</i>	Topmouth gudgeon	PSE.PAR	0	0	0.56	2.12	0.99	2.16	0	8.61	0	42.70	23.26	Alien
<i>Rhodeus amarus</i>	Bitterling	RHO.SER	0	0	0.14	0.35	0.66	0	5.32	0	25.58	0.27	0.08	Protected
<i>Neogobius fluviatilis</i>	Monkey goby	NEO.FLU	0	0	0	0	0.50	0	0.07	0	0	0	0	Alien
<i>Ctenopharyngogon idella</i>	Grass carp	CTE.IDE	0	0	0	0	0	0	0.15	0.59	0.70	0	0.76	Alien
<i>Carassius carassius</i>	Crucian carp	CAR.CAR	0	0	0	0	0	0	0	0.30	1.63	0	0	Native
<i>Ameiurus melas</i>	Black bullhead	AME.MEL	0	0	0	0	0	0	0	0	1.86	0.07	0.42	Alien
<i>Hypophthalmichthys molitrix</i>	Silver carp	HYP.MOL	0	0	0	0	0	0	0	0	0	0	2.77	Alien
Number of species	15	10	13	13	15	6	17	10	13	12	14			
Shannon diversity	1.414	1.625	1.000	1.837	2.023	0.297	1.444	1.815	1.741	1.049	1.105			
Number of Individuals	759	421	713	567	601	1009	1370	337	430	1501	1191			

Table 4
Significant environmental variables resulted from the forward selection procedure (presence–absence data).

Variable group	Significant variable	R ²	F value	P value
Habitat characteristics	Sand	0.219	2.518	0.022
Habitat management	Inflow	0.176	2.329	0.027

Table 5
Significant environmental variables resulted from the forward selection procedure (relative abundance data).

Variable group	Significant variable	R ²	F value	P value
Habitat characteristics	Area	0.132	2.638	0.015
Habitat management	Drought	0.469	7.934	0.005

4. Discussion

4.1. Community structure

Two main groups could be differentiated according to their species composition. Fish ponds and wetlands (IRM, TOR, OSZ) were characterized by the highest abundances of non-natives, while reservoirs (POG, KAN, ING, RAD) and the lake itself (BAL) hosted more natural fauna. The latter group was strongly associated with the presence of inflow, which might affect the number of native species and diversity positively by maintaining higher connectivity with other local populations. The spawning migration of native species (e.g. *R.utilus*, *Blicca bjoerkna* (Linnaeus, 1758), *Abramis brama* (Linnaeus, 1758)) to the tributaries could help maintain a stronger population of these fishes (Hladík and Kubečka, 2003).

We found that fish ponds hosted a high number of non-native species which often dominated the communities. The relationship of fish ponds and non-native species has a long history. The most typical reasons for introduction and therefore, pathways for a non-native fish is aquaculture or fish farming and intentional releases of ornamental fish (e.g. Hickley and Chare, 2004; Copp et al., 2005, 2010; Gozlan et al., 2010). *C. gibelio* was originally imported to Hungary in 1954 for fish farming purposes (Szalay, 1954), and numerous similar examples of other species from all over the world could be mentioned (e.g.: Naylor et al., 2005; Casal, 2006). These populations can afterwards act as potential source of invasions. Fish ponds of the Balaton catchment were previously assumed to be the major sources of non-native species as high abundance of non-indigenous species, especially *C. gibelio* and *P. parva*, were found in the neighboring, connected sections of small watercourses (Sály et al., 2011; Erős et al., 2012, 2014). Area covered by fish ponds in the catchment of the investigated stream segments was found to be the most important human disturbance variable, being positively associated with the abundance of non-native species in the surveyed streams. Therefore, the authors formulated the ‘polluting ponds’ hypothesis regarding their role in the spread on invasives (Erős et al., 2012). But this has not been explicitly tested by studying the communities of fish ponds of the Balaton catchment. More evidence on the high persistence of *C. gibelio* and *P. parva* in aquaculture systems and especially in their water-supply canals were provided from South Moravia region of the Czech Republic (Musil et al., 2007). According to our presence–absence data, some non-natives were amongst the most frequent fish species, occurring at every (*C. gibelio*) or almost every (*P. parva*, *Lepomis gibbosus* (Linnaeus, 1758)) site. On the other hand, the analysis of relative abundance data gave some evidence for the ‘polluting pond’ hypothesis (sensu Erős et al., 2012). The high relative abundance of *C. gibelio* in fish ponds (TOR, IRM) definitely supported the theory that high amounts of non-native species might escape from these habitats and contribute to the degradation of natural waters in the catchment.

Reservoirs often suffer from human disturbance, such as extreme water level fluctuations or unnatural water regimes,

therefore their invasion facilitating role has been demonstrated worldwide (e.g. Moyle and Light, 1996; Clavero and Hermoso, 2011; Tarkan et al., 2012a). Our results, however, were contrary to this theory: the surveyed reservoir (sites ING, POG, RAD, KAN) and shallow lake (BAL) habitats were dominated by native fish species. The management history of these sites may provide explanation for this finding. The surveyed reservoirs are parts of the Kis-Balaton Water Protection system and were inundated more than 20 years ago, since when no notable human disturbance (e.g. fish stocking, heavy water level fluctuations) occurred, allowing natural succession processes to operate. After inundation, a rapid invasion of gibel carp was observed. Its colonization was possible naturally, via tributaries of the reservoirs. After 10 years since inundation, its population in the reservoirs declined and stabilized, most likely due to the lower eutrophication tolerance of gynogenetic form. This reproductive characteristic seemed to be effective in the initial, colonization phase of reservoir fish community development. Later on, the stressful hypertrophic environment and the increasing abundance of native competitors are possible drivers towards sexual reproduction and result in lower gibel carp abundance (see details in: Paulovits et al., 2014).

The difference in fish community between intensively (productive; TOR, IRM) and the extensively (non-productive; CSO, GYO) managed fish ponds was also visible. There was no fish harvesting associated drainage in the latter ponds and they were characterized by semi-natural (GYO) or transitional (CSO) fish fauna, in line with the time since they had been abandoned (Table 1). This finding also supports the theory, that the long-term constant water cover might be unfavorable for gibel carp.

4.2. Role of environmental characteristics and habitat management in gibel carp distribution

We found that regular desiccation (or drainage, associated with fish harvesting in fish ponds) can be a major driver of fish community structure. This variable accounted for most of the significant variance in explaining differences in dominance patterns, and no other variable showed a significant relationship with the relative abundance of the species. Management (Use) variables, including desiccation have more powerful effects on relative abundances than on presence–absence. This means that even though the introductions were not inhibited, suitable management may still be able to help suppress the abundance of non-natives in a near-natural state.

We assume that a series of local invasion events occurred in the fish ponds and the wetland which were mediated by periodical (5–10 years) drying-outs. Drainage results in the elimination of the majority of the inhabiting fish. After re-flooding, the fish community structure is species poor and strongly asymmetric, which may be regarded as an early successional phase. It should be noted, however, that the desiccation of a waterbody does not necessarily result in the complete extinction of the local fish fauna. Usually,

some refugia can be found, (e.g. a deeper hole in the lake bed, or the inflow itself), which allows the survival of a small portion of fish. As *C. gibelio* have an effective oxygen deficiency tolerance mechanism (Lutz and Nilsson, 1994), it can successfully cope with such unfavorable periods (Liasko et al., 2011). After the re-flooding of the habitat, the alternative gynogenetic reproduction mechanism of the species (Kalous and Knytl, 2011; Tarkan et al., 2012b) provides an advantage during re-colonization over other species and results in large monodominant communities. At all human-mediated drainage events disrupt natural succession and this maintains pioneer communities over time, dominated by gibel carp.

The dominance of *C. gibelio* at early successional stages was previously found in other habitats of the Balaton catchment (Ferincz et al., 2012; Paulovits et al., 2014). The drastic changes in the hydroperiod length of originally permanent waterbodies (Zlinszky and Timár, 2013), can be interpreted as disturbances and fit well into the 'environmental change' type invasion scenario in the conceptual framework described by Facon et al. (2006). Fish communities of wetland areas of the Balaton catchment are not adapted for such events and therefore, this process is an alteration of the natural disturbance regime, which generally facilitates invasions (Moret et al., 2006; Clark and Johnston, 2011). This scenario is similar in fish ponds, where desiccation occurs in 1–5 year periods associated with fish harvesting. Small-bodied individuals of non-native fish might find refuge in the lake bed or in draining channels until refilling. Moreover, the juveniles of non-natives are stocked accidentally in numerous cases (e.g. Rylková et al., 2013). In the case of wetlands, this process will likely be facilitated by global climate change, since longer dry periods have been predicted for the region (Krüzselyi et al., 2011).

4.3. Role of local invasions on catchment level and management opportunities

Local invasions are probably the main drivers of the source-sink dynamics of non-native species on the catchment level (Erős et al., 2012). Fish ponds, angling ponds and wetlands are source populations of non-natives (mainly *C. gibelio* and *P. parva*), providing continuous pressure for the streams and other semi-natural habitats of the system. Such dynamics were also reported not only in human-modified and non-native-stressed habitats (Woodford and McIntosh, 2010; Glowaczki and Penczak, 2013), but also in case of a beaver-influenced natural landscape (Schlosser, 1998).

The management possibilities on non-native fish invasions are very limited (Britton et al., 2010). The complete eradication (by piscicides or removal) are obviously impossible, as the methods impose substantial collateral damage on native species and need huge effort (Simberloff, 2002; Koehn, 2004). As our study revealed the role of a management related disturbance factor (occurrence of drying-out), this implies the opportunity to control individual invasion events simply by providing continuous water cover in wetlands, and by alternative management (more precise eradication of 'junk' fishes from the draining channels and fish beds) of fish ponds. These implications might result in not only the decline of *C. gibelio* in the studied habitats, but simultaneously in adjoining streams.

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