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Research Article

Which factors influence spatio–temporal changes in the distribution of invasive and native species of genus *Carassius*?

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Abstract

Within the genus *Carassius* Jarocki, 1822 , the crucian carp (*C. carassius* L., 1758) occurs naturally in the northern part of Middle Danube Basin (Austria, Morava, Slovakia). This species has the least concern status in this region, but observations in the last decades suggest that it is very close to extinction here. The distribution of crucian carp is limited to a small number of vanishing lentic habitats (oxbow lakes, marshlands). These biotopes are in the last stage of succession due to the drying up of the landscape and a reduction in the creation of new natural alluvial habitats. The non-native cyprinid, *C. gibelio* (Bloch, 1782), known as gibel carp and Prussian carp, has gradually become eudominant in a wide spectrum of habitats/biotopes since the 1960s Several biological adaptations of non-native species are generally considered the strong basis for the mass spreading in the invaded area. The other side of the expansion of non-native *C. gibelio* is affected by anthropic activities associated with fish farming, translocation and stocking the fish in open water ecosystems. In this study, we analysed historical scientific data on the distribution of *Carassius* spp. published from the 19th century to the present from the mentioned areas. The results suggest that the number of records of invasive *C. gibelio* has gradually increase in rivers, regulated channels and creeks, which could be considered as natural pathways of spreading. However, the presence of invasive *C. gibelio* in artificial biotopes (fishponds, reservoirs) is continuous from the 1960s. In the area mentioned, the artificial biotopes are managed by national fisheries associations and relate to the historical way of farming in Central and Eastern European countries. To show the current state of the fishing grounds of the Slovak Angling Association, we a created the distribution map based on the *Carassius* spp. catches recorded in last two decades.

Key words: Danube basin, crucian carp, angling, fish farms, habitat lost, climate

Introduction

Fish species of the genus *Carassius* Jarocki, 1822, have acquired a wide range of statuses across the world, including ornamental (Chen et al. 2020), non-native (Morgan and Beatty 2007; Hamilton 2021), and species with high invasive potential (van der Veer and Nentwig 2015). The crucian carp (*C. carassius* L, 1758) was a common species in the Middle Danube area until the 1950s (Holčík 1966; Sedlár and Amena

1989). The species occurred mainly in numerous village ponds and alluvial habitats (Baruš and Oliva 1995). Since the nineteenth century, the number of suitable habitats has significantly decreased (Holčík 1996), due to the gradual liquidation of village ponds, the construction of flood defences and the subsequent loss of alluvial habitats caused by large-scale river channel regulation measures linked to planned agriculture (Jurík et al. 2018). Currently, the crucian carp occurs only sporadic in secondary habitats (e.g., regulated channels, small water reservoirs) and in the isolated river branches, usually with a very low density (authors´ obs.). Currently, the conservation status of this species within the Europe is that of least concern (Freyhof 2010). However, in several European countries, this species has started to be critically endangered. Nonetheless, the survival of *C. carassius* populations now depends on human management (Copp et al. 2008; Sayer et al. 2020), or facilitation of a natural flood regime (Guti 2020). A noticeable change occurred after the 1950s, which is probably linked to the importation of Asian cyprinids through the former Soviet Union (Slynko et al. 2011). Based on published data, non-native *Carassius* species entered the Slovak region of the Danube River in 1962 (Balon 1962). However, the mass spreading of this non-native species in throughout the Middle Danube appears to have begun in the 1950s, primarily underpinned by fish farms operating in Bulgaria and Hungary at the time (Holčík and Žitňan 1978; Holčík 1980). It is also possible that in the Middle Danube, as well as in the other parts of Europe, the spread of common carp *Cyprinus carpio* L., 1758, was supported by Benedictine monks. It is possible that *Carassius* species were at times also accidentally transported as contaminants of purposeful transfers of other species (Rylková et al. 2013). However, the mass occurrence of non-native *Carassius* spp. is not known from the literature to have occurred before the early 21st century. However, records from Europe are convoluted as in some European regions *C. gibelio* (*C. auratus* complex) was considered native, based on the description of this species by Bloch (1872). However, Bloch's museum material has been found to consist of *C. carassius* and hybrid specimen (Paepke 1999), and the taxonomic status was redetermined by Kalous et al. (2012) based on the *C. gibelio* specimen from the Silesian region of Czechia.

In the present study, to identify proportional temporal changes in species distributions for native and non-native *Carassius* species in relation to habitat (biotope), we analysed historical spatio-temporal distribution data from parts of the Middle Danube basin (i.e., presence/absence data for Slovakia and the surrounding river catchments). Further, we considered fisheries *Carassius* catch data recorded by the Slovak Angling Association (Slovak AA) during the last two decades. In doing so, we aimed to comparatively assess historical and recent presence/absence data pertaining to native and non-native *Carassius* spp.

Materials and methods

For the period 1875–2021, a total of 836 sources for presence/absence records for the distribution of *Carassius* species in Slovakia and surrounding watersheds (Middle Danube basin) were assessed (Suppl. material 1). The analysed data contained information concerning faunistic observations, grey literature, and our own unpublished observations from the last 35 years. Literature data included the authors' information about the biotope/habitat recorded or were obtained based on coordinates from historical maps and authors´ database. We excluded from the analyses the less numerous biotope observations, such as those recorded in the mountain and peak lakes (Suppl. material 1, obs. number 26, 47, 49, 89, 190, 242, 262, 308, 367, 384, 412, 797). In our analysis, we considered *C. carassius* as native, and based on the latest designation (Papoušek 2008; Rylková et al. 2013;

Pakosta et al. 2016; Knytl et al. 2022). We designated all species/lineages within the *C. auratus* complex (*C. auratus*, *C. gibelio*, *C. langsdorfii*, lineage "M") that have been recorded in the Danube basins as non-native *Carassius*. Three distributional maps were created based on presence data recorded in A: 1875–1961 (observation of *C. carassius* before first record of non-native *Carassius* spp.); B: 1962–1990 (a period of large-scale river regulation work in Slovakia and intensive imports of Asian cyprinids); C: 1991–2021 (a period of global temperature increase; www.eea.europa.eu/ims/global-and-european-temperatures). We created a distribution map of *Carassius* spp. based on 12,060 *Carassius* catch records from 1,064 Slovak AA fishing grounds (river sections in the administration of the Slovak AA) recorded between 2003 and 2021. Data from the fishing association includes the spatial distribution of fish of the genus *Carassius* (without species identification). Distributional maps were created with the use of QGIS.

Statistical analysis

For analysis of the data we used the non-linear Generalized Additive Models (GAMs) with a binomial family (R environment, packages – mgcv(), visreg()). Changes in the presence/absence of *Carassius* spp. were modelled depending on the time factor in interaction with the habitat type (Table 1 – explanatory variables). The number of dimensions (*k*-model rank) in each GAM model was identified automatically based on the gam.check() function. The quality of the models was determined based on a decrease in the Akaike information criterion AIC(). The results and trend lines of the GAM plots (Figure 1, 2) were constructed based on statistical outputs (Table 1, GAM-*b* in Results) in the R environment with the use of the visreg() package.

Table 1. Approximate significance of smooth terms of generalized additive models (GAMs, binomial family) and a comparison of the statistical models (related to Figure 2A and B) (Deviance explained = 42.7%).

Model Fit	GLMM family	Response	Explanatory	edf	$\chi2$	*p*	AIC	df
3	binomial (logit)	presence/absence of *Carassius* spp.	s(year) - spline parameter year, k = 16 - Model rank, by = biotope				649.1	41.5
			+ biotope					
			s(year):biotope channels	8.6	40.5	*< 0.001*		
			s(year):biotope creeks	1	13	*< 0.001*		
			s(year):biotope reservoir	2.8	0.01	*> 0.99*		
			s(year):biotope oxbows	8.3	11.8	*> 0.32*		
			s(year):biotope rivers	9.9	23.6	*< 0.05*		
			s(year):biotope ponds	2.8	0.06	*> 0.99*		
			s(year):biotope pits	1	8.2	*< 0.005*		
2			s(year) - spline parameter year, k = 16 - Model rank				652.3	19.1
			+ biotope					
1			s(year) - spline parameter year				666.2	14
			+ biotope					

Results

Analysis of 836 scientific observation-based data recorded between 1875 and 2021 revealed changes in the proportion of native and the non-native *Carassius* species recorded in literature sources (Figure 1). The analysed data show a significant non-linear trend (GAM-*b*, $\chi2$ 4.91 = 93.8, $p < 0.001$). A significant decrease in the

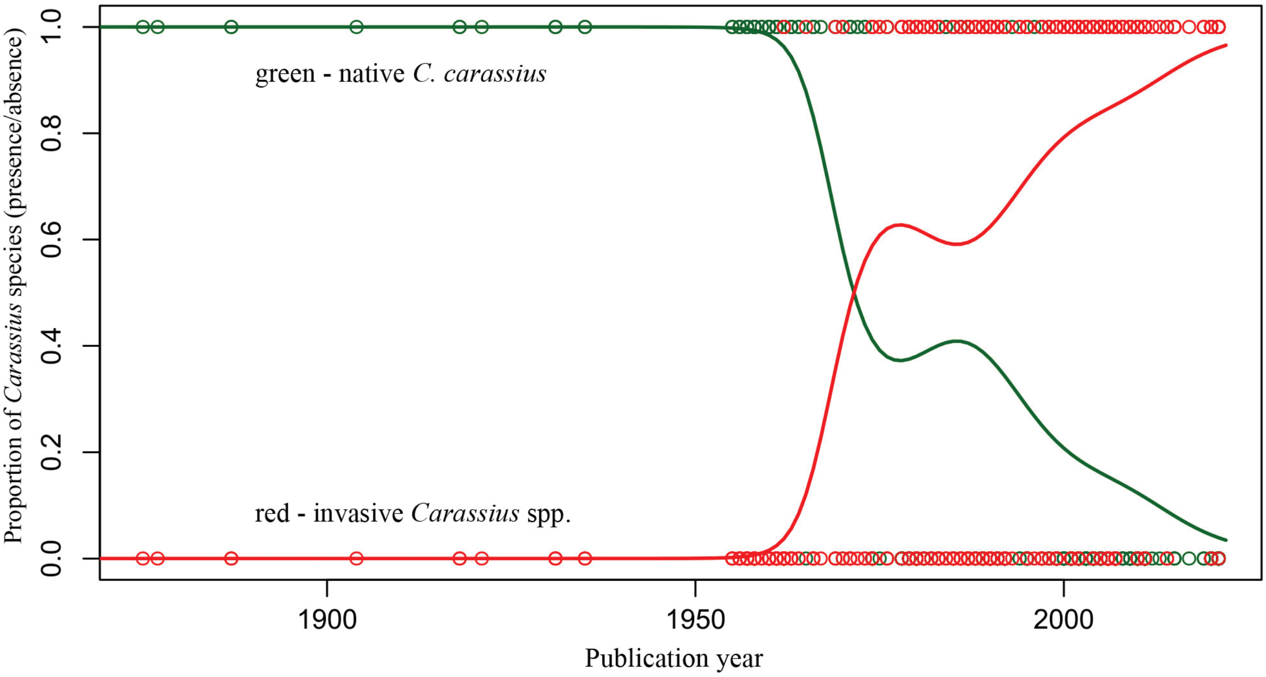

Figure 1. The proportion of presence (1) and absence (0) data (y-axis, one meaning 100% of the information) from the literature that mentions native (*C. carassius*) and non-native *Carassius* species between the years 1875 and 2021 (x-axis) in the river basins of Slovakia and border regions (Middle Danube basin).

literature information (Table 1 – model fit 3; Table 2) for native (*C. carassius*) and an increase for non-native *Carassius* spp. is visible in the interaction with biotope recorded since the 1950s (Figure 2A, B). The amount of information shows a different trend for each biotope, with a significant trend in the rivers, gravel/mining pits, regulated channels and creeks. River oxbows and river side-arms represent the last refuge as well as the biotope of co-occurrence of native and non-native *Carassius* species. Non-significant information trends for fishponds and reservoirs show the permanent presence of non-native *Carassius* spp. and the absence of *C. carassius* in biotopes with high human influence. Spatio-temporal visualisation of the scientific observations of *Carassius* spp. recorded 1875–2021 is shown in the three-distributional maps (Figures 3A, B, C). The extensive predominance of non-native *Carassius* species since the 1990s is visible (Figure 3C). This situation has occurred just 30 years after first official record of non-native *Carassius* species in 1962. A spatial trend map based on the catch data form Slovak AA is shown in Figure 3D.

Table 2. Parametric coefficients of the Generalized Additive Model related to GAM-*b*, Table 1 – Model Fit 3. Presence/absence of scientific literature information (1955 – present) contain data on the native *C. carassius* and non-native *Carassius* species according to year of study in the interaction with the biotope.

Explanatory (Intercept)	Estimate (*C. carassius*/non-native)	Std. Error	z-value (*C. carassius*/non-native)	Pr (> IzI)
intercept	0.06/-0.06	1.91	0.031/-0.031	0.975
s(year):biotope creeks	-1.26/1.26	1.94	-0.651/0.651	0.515
s(year):biotope reservoirs	-121.34/121.34	1683.06	-0.072/0.072	0.943
s(year):biotope oxbows	0.51/-0.51	2.25	0.225/-0.255	0.822
s(year):biotope rivers	-3.65/3.65	3.1	-1.212/1.121	0.225
s(year):biotope ponds	-136.09/136.09	687.43	-0.198/0.198	0.843
s(year):biotope pits	-2.9/2.9	2	-1.045/1.045	0.296

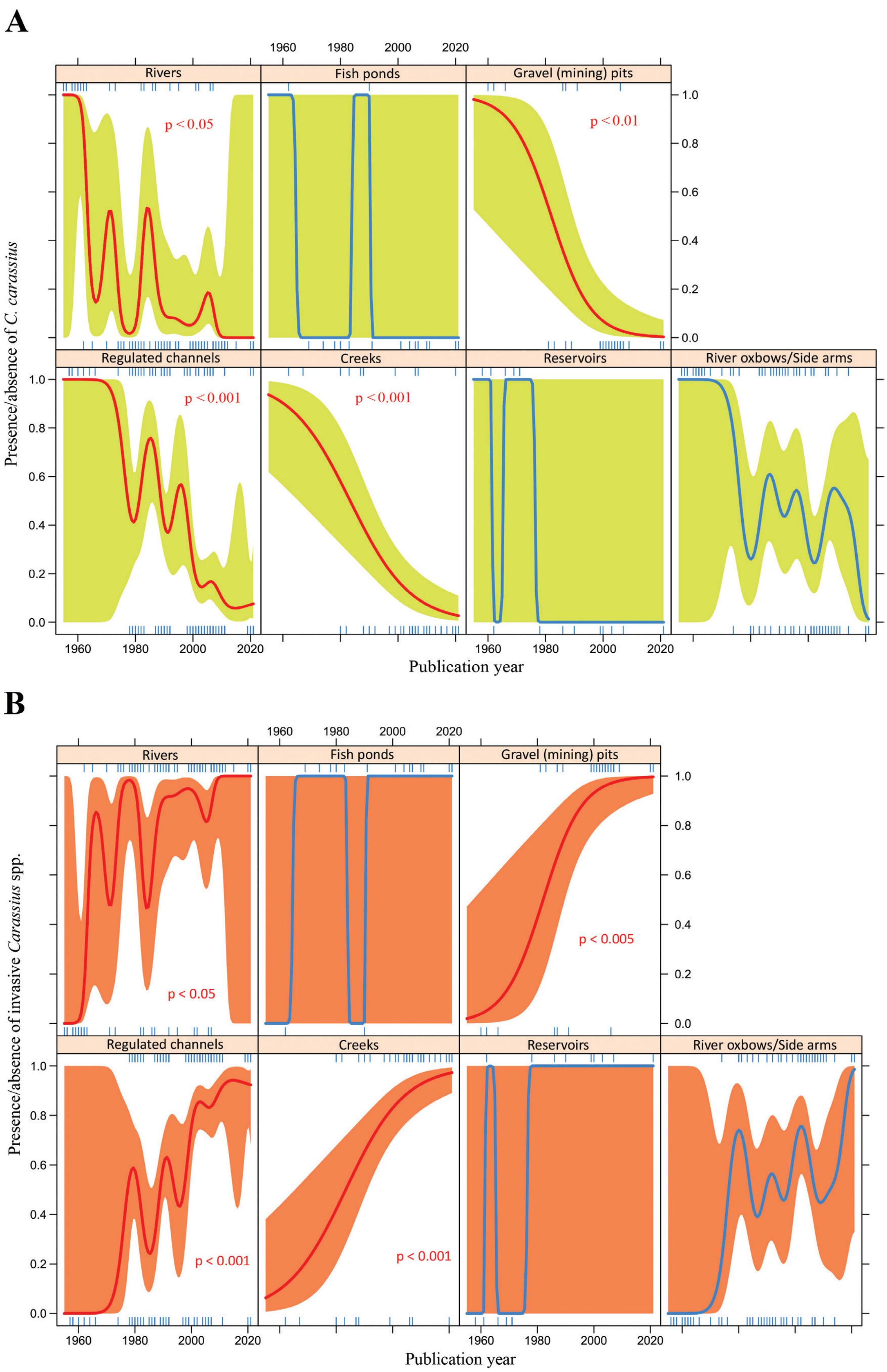

Figure 2. Non-linear GAM-*b* presence/absence (y-axis) plot for the historical information (x-axis; 1955–2021) of the *Carassius* species: **A)** native *C. carassius*; **B)** non-native using the two-way interaction between historical data and type of habitat (biotope) recorded (type of habitat in multi-plots). The red curves describes statistically significant changes in the proportion of information from the specific habitats.

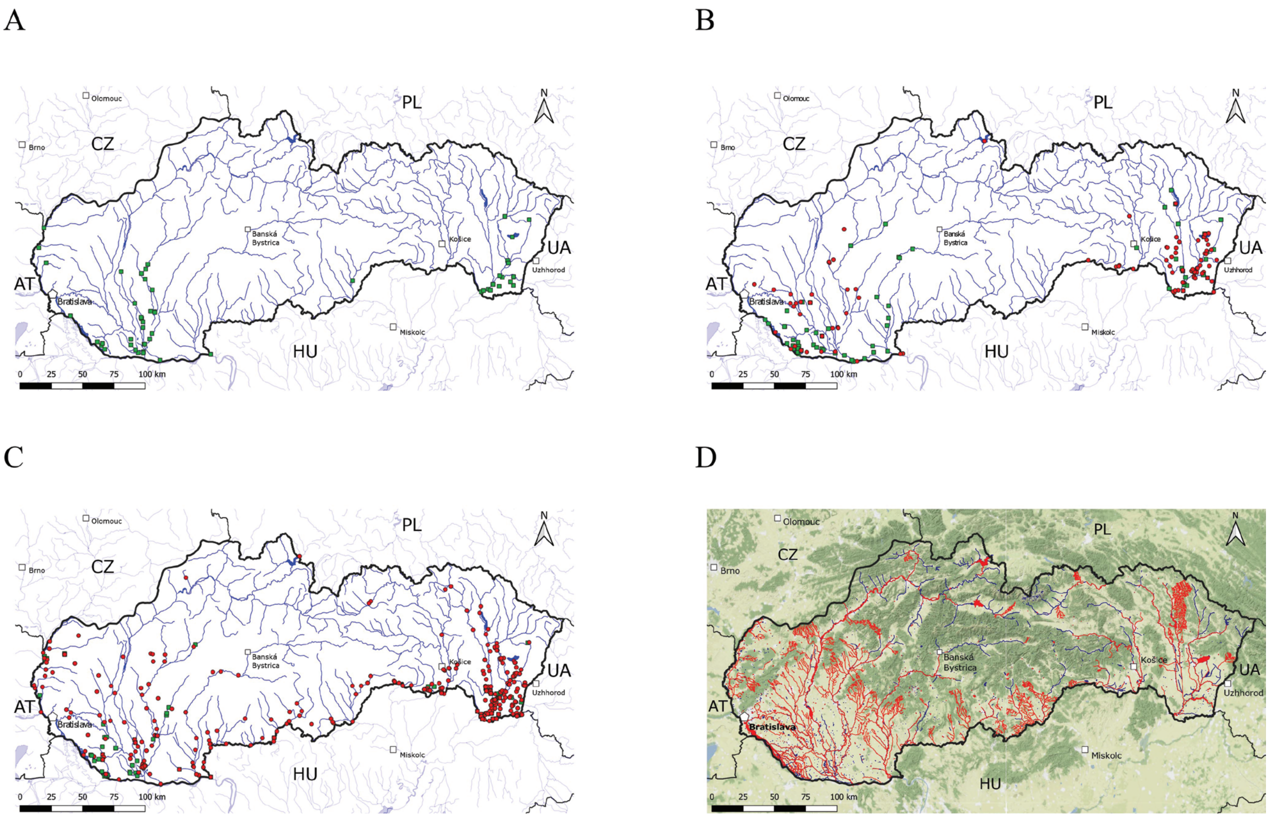

Figure 3. Spatio–temporal patterns of the distribution of the native *C. carassius* (green squares) and non-native *Carassius* spp. (red points) in the river basins of Slovakia (constructed based on scientific literature data – Suppl. material 1) **A)** 1875–1961; **B)** 1962–1990; **C)** 1991–2021; **D)** distributional map of *Carassius* species according to Slovak Angling Association data recorded 2003–2021: blue colour – main catchments of Slovakia (fishing grounds of the Slovak AA), red colour – showing 56.2% of fishing grounds with the catch (presence) of the *Carassius* specimens (constructed based on 12,060 fisheries catches); shades of green color indicate elevation (dark green – mountains, light green – lowlands).

Overall, 1,893 fishing grounds managed by the Slovak AA represents 92% of the total available fishing grounds in Slovakia (data for 2022). The last mentioned figure shows 12,060 catches of *Carassius* spp. recorded by the anglers of the Slovak AA between 2003 and 2021. These specimens were caught in the 1,064 fishing grounds of the Slovak AA, which represents 56.2% of all fishing grounds managed by the Slovak AA. Based on the analysed data, we can confirm the presence of non-native *Carassius* spp. in the Danube basin as well as in a small part of the River Vistula basin in the north of Slovakia (i.e., Dunajec and Poprad River basin).

Discussion

The distribution area of limnophilic fish species (e.g., *C. carassius*, *Misgurnus fossilis* (Linnaeus, 1758), *Umbra krameri* (Walbaum, 1792), etc.) in the Slovak Danube basins is one of the northernmost occurrences within the Middle Danube catchment area (Freyhof and Kottelat 2008). The presence of this species is connected to river side-arm formations associated with the dynamics of natural lowland rivers (Lenhardt et al. 2020). During the last 40 years, a gradual decrease of *C. carassius* has been recorded in the Danube River basin (Holčík 1996; Telcean and Cupşa 2009; Ferincz et al. 2012; Bănăduc et al. 2016, 2020) as well as in the other basins across Europe (Sayer et al. 2010; Mezhzherin et al. 2019). The most probable causes are competition of the native *C. carassius* with other – mainly Asian – cyprinids (*Carassius*, *Cyprinus*, *Ctenopharyngodon*, *Hypophtalmichtys*). The competitive disadvantages of *C. carassius* include limitations in food resources (Busst and Britton 2015), altered hydrology (swirling of sediments, eutrophication) and the behaviour of stocked non-native cyprinids (Richardson et al. 1995). However, factors influencing the process of extinction of the crucian carp are diverse. The most serious factor in the decline of crucian carp in the Middle Danube region has been historical regulation of the river since nineteenth century (Hanušin 1949), and the increase of this regulation associated drainage of the land as part of the agricultural plan of the Communist era, beginning in the 1950s (Jurík et al. 2018). A higher number of literature records of the crucian carp from the 1950s are linked to their presence in regulated channels (Figure 2A). These secondary biotopes represented a refuge for this species after major dewatering of marshlands. The succession and extinction of the last natural habitats have likely influenced the presence of the crucian carp (Figure 2A – river oxbows, side arms). Currently, this trend is being accelerated by climate change (Gómez-Baggethun et al. 2019), which has caused the complete drying of the few remaining lowland habitats in recent years. Historically, the proportion of available information concerning the presence of native *C. carassius* varied across the nineteenth century (Figure 1), with records largely being associated with river regulation. Consequently, the predominance of non-native *Carassius* spp. is continuous from the 1960s, with a short decreasing trend in the 1990s. Here we can assume two waves (peaks) of dispersal that may coincide with the spread of asexual (gynogenetic) females in the 1960s and a second wave of expansions (1990s) connected to the formation of the mixed sexual-asexual *Carassius* populations and the presence of sexual males (Lusková et al. 2004, 2010; Barbuti et al. 2012). In general, localities with the co-occurrence of native and non-native *Carassius* spp. are not numerous (Artaev and Ruchin 2016). Here we hypothesize that the co-occurrence is beneficial for the spreading of clonal non-native *Carassius* females. Polyploid females are reproducing by gyno/hybrid-genesis and during the expansion, they can incorporate part of the genome of other Carassius spp, or use the sperm of native males of *C. carassius* for the production of their clonal offspring (Gui and Zhou 2010; Tapkir et al. 2022). In contrast, F1 crossbreed offspring of native *C. carassius* are probably sterile or they do not reach sexual maturity and their occurrence is rare (Papoušek et al. 2008).

Trends in the literature for creeks and gravel (mining) pits are continuous and increasing, which indicates the spatial and temporal spread from main sources (rivers, ponds, reservoirs). In the case of reservoirs and ponds, temporal changes as recorded within the literature are not significant (Table 1, Figure 2B), indicating that invasive individuals have been continuously present in this habitat type since the 1950s´. Based on this information, we assume different pathways of introduction have occurred for non-native *Carassius* spp.. Firstly, we suspect these include natural dispersal across the river network from the lower Danube basins (Balon 1962; Holčík and Žitňan 1978), with gradual expansion by the non-native *Carassius* spp. from the main river network into smaller streams, as well as into inundation pits (mining, gravel) as a result of flooding events. Secondly, as records for the presence of non-native *Carassius* spp. in reservoirs and fishponds is continuous, from the 1960s onwards (Figure 2B), we infer that their spread in these spread across these environments is underpinned by fish farms and managed fishery biotopes (Mišík and Holčík 1962; Dorko and Terek 1976). The third pathway is the spreading of *Carassius* baitfish by anglers, which was first recorded in the 1960s by Mišík and Holčík (1962) for the Orava Reservoir. Nowadays, according to the applicable law – the Act on Fisheries of the Slovak Republic (No. 216/2018) – the use of live baitfish is still possible, as is the translocation of baitfish between fishing grounds. Consequently, the non-native *Carassius* populations have continued to radiate from their source populations (e.g., fish farms, fishing grounds, pet shops) into the surrounding river basins (Sedlár et al. 1976; Holčík and Žitňan 1978). A temporal increase for records of non-native *Carassius* also reflects the fisheries activities, which are connected to post-communist planning regimes in the Eastern Bloc countries (Britton and Gozlan 2013). Based on our analyses of fisheries data (Figure 3D), the spreading of *Carassius* spp. is likely to be nationwide, with a higher intensity in lowland habitats (lowlands occur in the south part of Slovakia). Moreover, the slow running and stagnant waters, such as reservoirs, small ponds and mining pits in river inundation, are favoured by carp anglers. Fishing grounds with the presence of *Carassius* species represent more than 56% of all fishing grounds managed by the Slovak AA (Figure 3D). Whereas, current scientific data (Figure 3C) indicates that most of the *Carassius* spp. in Slovak River basins are probably non-native specimens of the *C. auratus* complex. Uncontrolled stocking of non-native *Carassius* spp. and their spread from production ponds and subsequent penetration to natural biotopes has also been confirmed in other parts of the Middle Danube basin, such as in Hungary (Takács et al. 2017), Serbia (Lenhardt et al. 2011) and in the Transcarpathian Ukraine (Koščo et al. 2004). Higher haplotype diversity of non-native *Carassius* spp. has been observed, especially within large waterbodies under human pressure, such as tourism, fishing, fish farming (Keszte et al. 2021). The high number of haplotypes is probably a result of introduction from several sources; with subsequent hybridization and occupancy of a wide spectre of ecological niches (Faud et al. 2021). Aside from the human influence, the spread of non-native *Carassius* spp. is accelerated by wide spectrum of the biological adaptations (Tcherfas 1971; Lusková et al. 2010; Fagernes et al. 2017) as well as gynogenetic reproduction of polyploid females (Xiao et al. 2011).

Based on historical data analysis, we can consider the Slovak population of *C. carassius* as critically endangered, with a negative outlook. In conclusion, based on historical data, we call for an urgent re-assessment of the IUCN status for *C. carassius* throughout the Danube River basin. In the case of non-native *Carassius* species, we suggest: i) the prevention of their spread from fish farms into open waters through improved biosecurity protocols; ii) a reduction in population density across biotopes connected to common carp farms (e.g., drainage channels), with management by angling associations for fishing grounds; and iii) acceleration of the adoption of appropriate legislative to prohibit unethical live bait fishing, with strict implementation for compliance.

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Author contribution

JF conceived and designed the study, gathered literature data, conducted statistical analysis and wrote the paper. PK gathered data of the Slovak Angling Association and created the distributional maps. JK provided his own databases and literature and supervised the study concept.

Ethics and permits

Own data provided in this study were authorised through a permit from the Ministry of Environment of the Slovak republic, special yearly permits for electrofishing and in the accordance with all ethical principles.

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References

Artaev ON, Ruchin AB (2016) Prussian and crucian carp: confindness to various types of waters and co-inhabiting species in water bodies within the Mid-Volga Region. Ecology, Environment and Conservation 22(3): 505–510.

Balon EK (1962) Ökologische Bemerkungen über die Standorte der Donaufische mit einer Beschreibung des Fundes des *Carassius auratus* gibelio Bloch, 1783 und *Alburnoides bipunctatus* Bloch, 1782. Věstník Československé společnosti zoologické 26(4): 331–351.

Bănăduc D, Rey S, Trichkova T, Lenhardt M, Curtean-Bănăduc A (2016) The Lower Danube River–Danube Delta–North West Black Sea: A pivotal area of major interest for the past, present and future of its fish fauna—A short review. Science of the Total Environment 545–546: 137–151. https://doi.org/10.1016/j.scitotenv.2015.12.058

Bănăduc D, Joy M, Olosutean H, Afanasyev S, Curtean-Bănăduc A (2020) Natural and anthropogenic driving forces as key elements in the Lower Danube Basin–South-Eastern Carpathians–North-Western Black Sea coast area lakes: a broken stepping stones for fish in a climatic change scenario?. Environmental Sciences Europe 32: 73. [1–14] https://doi.org/10.26686/wgtn.13717981

Barbuti R, Mautner S, Carnevale G, Milazzo P, Rama A, Sturmbauer C (2012) Population dynamics with a mixed type of sexual and asexual reproduction in a fluctuating environment. BMC Evolutionary Biology 12(1): 1–13. https://doi.org/10.1186/1471-2148-12-49

Baruš V, Oliva O [Eds] (1995) Mihulovci a ryby (Vol. 1). Nakladatelství Akademie Věd České Republiky, 624 pp.

Britton JR, Gozlan RE (2013) Geo-politics and freshwater fish introductions: How the Cold War shaped Europe's fish allodiversity. Global Environmental Change 23(6): 1566–1574. https://doi.org/10.1016/j.gloenvcha.2013.09.017

Busst GM, Britton JR (2015) Quantifying the growth consequences for crucian carp *Carassius carassius* of competition from non-native fishes. Ecology of Freshwater Fish 24(3): 489–492. https://doi.org/10.1111/eff.12155

Chen D, Zhang Q, Tang W, Huang Z, Wang G, Wang Y, Li Z (2020) The evolutionary origin and domestication history of goldfish (*Carassius auratus*). Proceedings of the National Academy of Sciences 117(47): 29775–29785. https://doi.org/10.1073/pnas.2005545117

Copp GH, Warrington S, Wesley KJ (2008) Management of an ornamental pond as a conservation site for a threatened native fish species, crucian carp *Carassius carassius*. Hydrobiologia 597(1): 149–155. https://doi.org/10.1007/s10750-007-9220-0

Dorko J, Terek J (1976) K výskytu karasa striebristého *Carassius auratus* (Linnaeus, 1758) na Východnom Slovensku [On the occurrence of silver carp *Carassius auratus* (Linnaeus, 1758) in Eastern Slovakia]. Zborník Pedagogickej fakulty v Prešove Univerzity P. J. Šafárika v Košiciach. Prírodné vedy 14(1): 161–166. [in Slovak with English summary]

Fagernes CE, Stensløkken KO, Røhr ÅK, Berenbrink M, Ellefsen S, Nilsson GE (2017) Extreme anoxia tolerance in crucian carp and goldfish through neofunctionalization of duplicated genes creating a new ethanol-producing pyruvate decarboxylase pathway. Scientific Reports 7(1): 1–11. https://doi.org/10.1038/s41598-017-07385-4

Ferincz Á, Staszny Á, Ács A, Weiperth A, Tátrai I, Pantovits G (2012) Long–term development offish assemblage in Lake Feneki (Kis-Balaton Water Protection System, Hungary): succession, invasion and stabilization. Acta Zoologica Academiae Scientiarum Hungaricae 58(1): 3–18.

Freyhof J (2010) *Carassius carassius*. The IUCN Red List of Threatened Species 2010: e. T3849A10116997. https://www.iucnredlist.org/species/3849/10116997 [Accessed on 19 September 2022]

Freyhof J, Kottelat M (2008) *Carassius carassius*. The IUCN Red List of Threatened Species. www.iucnredlist.org [Accessed 9 June 2022]

Fuad MMH, Vetešník L, Šimková A (2021) Is gynogenetic reproduction in gibel carp (*Carassius gibelio*) a major trait responsible for invasiveness? Journal of Vertebrate Biology 70(4): 21049.1–13. https://doi.org/10.25225/jvb.21049

Gómez-Baggethun E, Tudor M, Doroftei M, Covaliov S, Năstase A, Onără DF, Mierlă M, Marinov M, Doroșencu A-C, Lupu G, Teodorof L, Tudor I-M, Köhler B, Museth J, Aronsen E, Johnsen SI, Ibram O, Marin E, Crăciun A, Cioacă E (2019) Changes in ecosystem services from wetland loss and restoration: An ecosystem assessment of the Danube Delta (1960–2010). Ecosystem Services 39: 100965. https://doi.org/10.1016/j.ecoser.2019.100965

Gui J, Zhou L (2010) Genetic basis and breeding application of clonal diversity and dual reproduction modes in polyploid *Carassius auratus gibelio*. Science China Life Sciences 53(4): 409–415. https://doi.org/10.1007/s11427-010-0092-6

Guti G (2020) Assessment of long-term changes in the Szigetköz Floodplain of the Danube River. In: Bănăduc D, Curtean-Banaduc A, Pedrotti F, Cianfaglione K, Akeroyd JR (Eds) Human Impact on Danube Watershed Biodiversity in the XXI Century, Springer, Cham, 215–240. https://doi.org/10.1007/978-3-030-37242-2_11

Hamilton SN (2021) Expansion of invasive Prussian carp (*Carassius gibelio*) into Saskatchewan, Canada: current distribution and food-web reconstruction using stable isotopes. Doctoral dissertation, Faculty of Graduate Studies and Research, University of Regina. Canada, 81 pp.

Hanušin J (1949) Vodné družstvo na Ondave. Storočnica vodohospodárskej činnosti. [Water cooperative on Ondava River. Centenary of water management activity] Jubilejná monografia. Povereníctvo pôdohospodárskej a pozemkovej reformy. Bratislava, 151 pp. [in Slovak with Slovak summary]

Holčík J (1980) *Carassius auratus* (Pisces) in the Danube River. Acta scientiarum naturalium Academiae Scientiarum Bohemicae, Brno, 14(11): 1–43.

Holčík J (1996) Vanishing freshwater fish species of Slovakia. In: Kirchhofer A, Hefti D (Eds) Conservation of Endangered Freshwater Fish in Europe. ALS Advances in Life Sciences. Birkhäuser Basel, 79–88. https://doi.org/10.1007/978-3-0348-9014-4_9

Holčík J, Žitňan R (1978) On the expansion and origin of *Carassius auratus* in Czechoslovakia. Folia Zoologica 27(3): 279–288.

Jurík Ľ, Halászová K, Pokrývková J, Rehák Š (2018) Irrigation of arable land in Slovakia: History and perspective. Water Resources in Slovakia: Part I, Springer, Cham., 81–96. https://doi.org/10.1007/698_2018_284

Kalous L, Bohlen J, Rylková K, Petrtýl M (2012) Hidden diversity within the Prussian carp and designation of a neotype for *Carassius gibelio* (Teleostei: Cyprinidae). Ichthyological Exploration of Freshwaters 23(1): 11–18.

Keszte S, Ferincz A, Tóth-Ihász K, Balogh RE, Staszny Á, Hegyi Á, Takács P, Urbanyi B, Kovács B (2021) Mitochondrial sequence diversity reveals the hybrid origin of invasive gibel carp (*Carassius gibelio*) populations in Hungary. PeerJ 9: e12441. https://doi.org/10.7717/peerj.12441

Knytl M, Forsythe A, Kalous L (2022) A Fish of Multiple Faces, Which Show Us Enigmatic and Incredible Phenomena in Nature: Biology and Cytogenetics of the Genus *Carassius*. International Journal of Molecular Sciences 23(15): 8095. https://doi.org/10.3390/ijms23158095

Koščo J, Balázs P, Ivanec O, Kovalčuk A, Manko P, Terek J (2004) Príspevok k poznaniu rýb tokov Zakarpatskej oblasti Ukrajiny [Contribution on the knowledge of the ichtyofauna of streams of the transcarphatian region in Ukraine]. Acta Facultatis Studiorum Humanitatis et Naturae Universitatis Presoviensis, Prírodné vedy 40: 138–152.

Lenhardt M, Markovic G, Hegedis A, Maletin S, Cirkovic M, Markovic Z (2011) Non-native and translocated fish species in Serbia and their impact on the native ichthyofauna. Reviews in Fish Biology and Fisheries 21(3): 407–421. https://doi.org/10.1007/s11160-010-9180-8

Lenhardt M, Smederevac-Lalić M, Hegediš A, Skorić S, Cvijanović G, Višnjić-Jeftić Ž, Djikanović V, Jovičić K, Jaćimović M, Jarić I (2020) Human impacts on fish fauna in the Danube River in Serbia: Current status and ecological implications. In: Bănăduc D, Curtean-Bănăduc A, Pedrotti F, Cianfaglione K, Akeroyd J (Eds) Human Impact on Danube Watershed Biodiversity in the XXI Century. Springer, Cham., 257–279. https://doi.org/10.1007/978-3-030-37242-2_13

Lusková V, Halačka K, Vetešník L, Lusk S (2004) Changes of ploidy and sexuality status of '*Carassius auratus*' populations in the drainage area of the River Dyje (Czech Republic). International Journal of Ecohydrology and Hydrobiology 4(1): 165–171. https://doi.org/10.1111/j.1095-8649.2007.01783.x

Lusková V, Lusk S, Halačka K, Vetešník L (2010) *Carassius auratus gibelio*—The most successful invasive fish in waters of the Czech Republic. Russian Journal of Biological Invasions 1(3): 176–180. https://doi.org/10.1134/S2075111710030069

Mezhzherin SV, Kulish AV, Kokodiy SV (2019) Structure and Dynamics of Crucians' Settlements (Cypriniformes, *Carassius*) in Water Systems of Eastern Ukraine. Vestnik Zoologii 53(4): 269–284. https://doi.org/10.2478/vzoo-2019-0027

Mišík V, Holčík J (1962) A note on *Carassius auratus* in Czechoslovakian Silesia. Věstník Československé společnosti zooligcké 26(4): 329–332.

Morgan DL, Beatty SJ (2007) Feral Goldfish (*Carassius auratus*) in Western Australia: a case study from the Vasse River. Journal of the Royal Society of Western Australia 90(3): 151–156.

Paepke HJ (1999) Bloch's fish collection in the Museum fur Naturkunde der Humboldt-Universitat zu Berlin: an illustrated catalog and historical account. Thesis Zoologicae 32. ARG Gantner Verlag KG, 216 pp.

Pakosta T, Vetešník L, Šimková A (2016) Evolution and genetic variability of the *Carassius auratus* complex. In: Benovics M, Kobíkova Z, Gelnar M (Eds) Organizer: Department of Botany and Zoology, Faculty of Science, Masaryk University, Kotlářská 2, 611 37 Brno, Czech Republic Workshop venue: Hotel Beatrice, Prušánky Workshop date: 28–30 November 2016, 58 pp.

Papoušek I (2008) Molekulárně–genetické analýzy druhů rodu *Carassius* ve střední Evropě [Molecular–genetic analyzes of species of the genus *Carassius* in Central Europe] [Doctoral dissertation, Masarykova univerzita, Přírodovědecká fakulta], 85 pp.

Papoušek I, Vetešník L, Halačka K, Lusková V, Humpl M, Mendel J (2008) Identification of natural hybrids of gibel carp *Carassius auratus gibelio* (Bloch) and crucian carp *Carassius carassius* (L.) from lower Dyje River floodplain (Czech Republic). Journal of Fish Biology 72(5): 1230–1235. https://doi.org/10.1111/j.1095-8649.2007.01783.x

Richardson MJ, Whoriskey FG, Roy LH (1995) Turbidity generation and biological impacts of an exotic fish *Carassius auratus*, introduced into shallow seasonally anoxic ponds. Journal of Fish Biology 47(4): 576–585. https://doi.org/10.1111/j.1095-8649.1995.tb01924.x

Rylková K, Kalous L, Bohlen J, Lamatsch DK, Petrtýl M (2013) Phylogeny and biogeographic history of the cyprinid fish genus *Carassius* (Teleostei: Cyprinidae) with focus on natural and anthropogenic arrivals in Europe. Aquaculture 380: 13–20. https://doi.org/10.1016/j.aquaculture.2012.11.027

Sayer CD, Copp GH, Emson D, Godard MJ, Zieba G, Wesley KJ (2010) The decline of crucian carp *Carassius carassius* in its native English range: the example of rural ponds in north Norfolk. Journal of Fish Biology 79(6): 1608–1624. https://doi.org/10.1111/j.1095-8649.2011.03059.x

Sayer CD, Emson D, Patmore IR, Greaves HM, West WP, Payne J, Davies GD, Tarkan AS, Wiseman G, Cooper B, Grapes T, Cooper G, Copp GH (2020) Recovery of the crucian carp *Carassius carassius* (L.): Approach and early results of an English conservation project. Aquatic Conservation: Marine and Freshwater Ecosystems 30(12): 2240–2253. https://doi.org/10.1002/aqc.3422

Sedlár J, Amena P [Eds] (1989) *Atlas rýb* [Atlas of fish]. Obzor. Bratislava, 373 pp.

Sedlár J, Stráňai I, Makara A (1976) Karas striebristý (*Carassius auratus* (Linnaeus, 1758)) v povodí rieky Nitry. Biológia, Bratislava 31(4): 345–351.

Slynko YV, Dgebuadze Y, Novitskiy RA, Kchristov OA (2011) Invasions of alien fishes in the basins of the largest rivers of the Ponto-Caspian basin: composition, vectors, invasion routes, and rates. Russian Journal of Biological Invasions 2(1): 49–59. https://doi.org/10.1134/S2075111711010085

Takács P, Czeglédi I, Ferincz Á, Sály P, Specziár A, Vitál Z, Weiperth A, Erős T (2017) Non-native fish species in Hungarian waters: historical overview, potential sources and recent trends in their distribution. Hydrobiologia 795: 1–22. https://doi.org/10.1007/s10750-017-3147-x

Tapkir S, Boukal D, Kalous L, Bartoň D, Souza AT, Kolar V, Soukalová K, Duchet C, Gottwald M, Šmejkal M (2022) Invasive gibel carp (*Carassius gibelio*) outperforms threatened native crucian carp (*Carassius carassius*) in growth rate and effectiveness of resource use: Field and experimental evidence. Aquatic Conservation: Marine and Freshwater Ecosystems 32(12): 1901–1912. https://doi.org/10.1002/aqc.3894

Tcherfas N (1971) Natural and artificial gynogenesis of fish. Pep. FAO/UNDP (TA). Rome, 2926: 274–291.

Telcean IC, Cupşa D (2009) The backwaters and drainage canals as natural refuges for the lowland rivers' fishfauna (Someş, Crişuri, and Mureş Rivers–north-western Romania). Biharean Biologist 3(1): 37–44.

Van Der Veer G, Nentwig W (2015) Environmental and economic impact assessment of alien and invasive fish species in Europe using the generic impact scoring system. Ecology Freshwater Fish 24: 646–656. https://doi.org/10.1111/eff.12181

Xiao J, Zou T, Chen Y, Chen L, Liu S, Tao M, Zhang C, Zhao R, Zhou Y, Long Y, You C, Yan J, Liu Y (2011) Coexistence of diploid, triploid and tetraploid crucian carp (*Carassius auratus*) in natural waters. BMC Genetics 12(1): 1–15. https://doi.org/10.1186/1471-2156-12-20

Supplementary material 1

Distribution of native and invasive *Carassius* spp. (Danube River basin)

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