

1 **Patterns of genetic variation in native and non-native populations of European catfish *Silurus glanis***  
2 **across Europe**

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61 **ABSTRACT**

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63 Biological invasions are a major component of global change worldwide. But paradoxically, an invasive species  
64 might also have threatened populations within its native range. Designing efficient management policies is needed  
65 to prevent and mitigate range expansions of invasive alien species (IAS) in non-native areas, while protecting them  
66 within their native range. Characterizing genetic variation patterns for IAS populations and deciphering the links  
67 between their native and introduced populations is helpful to (i) assess the genetic state of both native and non-  
68 native populations, (ii) reveal potential invasion pathways, (iii) define IAS management strategies in invaded areas,  
69 and (iv) identify native populations requiring conservation measures. The European catfish (*Silurus glanis L.*) is  
70 the largest European predatory fish. Introduced since the seventies from Eastern to Western Europe, it has  
71 colonized many waterbodies. Yet, little is known about the genetic status of non-native populations and the  
72 invasion pathways used by the species. Besides, some native populations are threatened, requiring conservation  
73 actions. Here, we describe current patterns of genetic variability of native and non-native *S. glanis* populations  
74 across Europe. Using microsatellite markers, we first assessed genetic variation within and between native and  
75 non-native populations. Second, we performed genetic clustering analyses to determine the genetic structure of  
76 multiple catfish populations across Europe and highlight their potential links. We revealed that native populations  
77 are more genetically diverse than non-native populations, and highlight complex introduction pathways involving  
78 several independent sources of introduction, which likely explain the invasion success of this large predatory fish  
79 across western Europe.

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81 **KEYWORDS**

82 European catfish / freshwater / genetic diversity / biological invasion / genetic structure

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## 88 INTRODUCTION

89           The number of species introductions is increasing worldwide as a fundamental component of global  
90 change (Vitousek et al. 1997; Seebens et al. 2017, 2018; Essl et al. 2020). Introduced species sometimes become  
91 invasive alien species (IAS) when they successfully establish in a new area, spread to new surrounding  
92 environments and cause ecological and socio-economic damages (Blackburn et al. 2011). The development and  
93 adoption of efficient IAS management strategies are thus needed to (i) prevent introductions of species that can  
94 potentially become invasive in the introduced area, (ii) prevent introduced species from becoming invasive and  
95 (iii) to mitigate the negative impacts of established IAS.

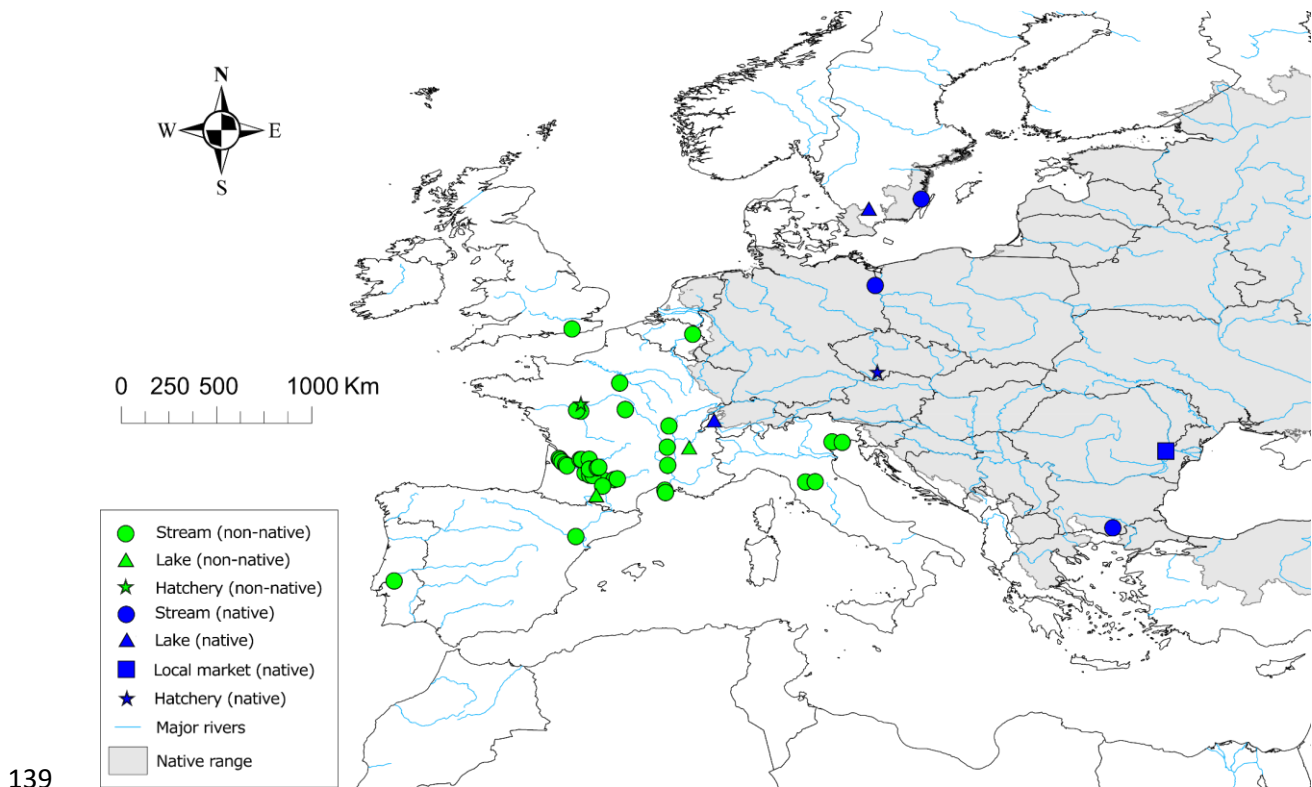
96           The fate of introduced populations is highly dependent on the ecological and socio-economic context they  
97 face in their introduced areas (Blackburn et al. 2011). This context can either foster population expansions in non-  
98 native areas (Uller and Leimu 2011) or population decreases in native areas (Marchetti and Engstrom 2016). This  
99 duality makes comprehensive studies focusing on both the native and non-native distribution ranges of species  
100 particularly valuable to tackle biodiversity conservation issues. These studies can thus be undertaken from two  
101 different standpoints: an *invasion biology* standpoint (e.g., by inferring invasion routes or by assessing genetic  
102 relationships between native/non-native populations), and a *conservation biology* standpoint (e.g., by assessing the  
103 genetic status and/or connectivity of native populations, or by identifying source and target populations for guiding  
104 genetic rescue actions, Ralls et al. 2020).

105           Population genetic tools have proven useful to tackle questions related to both biological invasion  
106 processes and biodiversity conservation (Fitzpatrick et al. 2012; Blanchet 2012). From an invasion biology  
107 standpoint, species introductions generally leave specific footprints on the genetic pool of introduced populations  
108 (Cristescu 2015), and these footprints can be detected through neutral genetic variation assessments and the use of  
109 specific methods (Estoup and Guillemaud 2010). For instance, introduction events can lead to populations with  
110 reduced levels of genetic diversity (compared to source populations) because of the founder effects resulting from  
111 the introduction of individuals harboring only a portion of the whole genetic diversity of the source population(s)  
112 (Edmonds et al. 2004; Dlugosch and Parker 2008; Peischl and Excoffier 2015). Genetic similarities between native  
113 and introduced populations can also help determine potential sources of introductions (e.g., Lombaert et al. 2011;  
114 Perdureau et al. 2013; Krueger-Hadfield et al. 2017). Further, multiple introductions from different genetic sources  
115 can generate specific admixture patterns and/or lead to introduced populations harboring higher genetic diversities  
116 compared to native or source populations (Roman and Darling 2007; Gillis et al. 2009; Pairen et al. 2010). From

117 a biodiversity conservation standpoint, genetic diversity is an overlooked, though key biodiversity facet (Vernesi  
118 et al. 2008; Laikre et al. 2020). Genetic tools facilitate defining conservation units (Funk et al. 2012), understanding  
119 patterns of gene flow among populations (Neigel et al. 2007), identifying hybridization events (Curto et al. 2022)  
120 or assessing population size changes (Beaumont 1999). For instance, demographic collapses occurring in native  
121 populations may produce genetic bottlenecks that can be detected from genotypic data using specific tools (e.g.,  
122 Cornuet and Luikart 1996; Piry et al. 1999). These bottlenecks reduce genetic diversity and effective population  
123 sizes ( $N_e$ ), and might subsequently reinforce demographic declines (Hostetler et al. 2013), ultimately increasing  
124 population extinction risks (Frankham 1995). Indeed, it is generally agreed that populations with  $N_e \leq 50$  are at  
125 high risk of extinction due to genetic erosion, and that at least  $N_e \geq 500$  are needed to avoid any loss of genetic  
126 variation for fitness (Jamieson and Allendorf 2012; Frankham et al. 2014). Identifying populations that have  
127 experienced genetic bottlenecks, disruptions of among-populations gene flow, or displaying low  $N_e$  and/or high  
128 inbreeding rates is thus particularly helpful to define and prioritize conservation actions (Hailer et al. 2006;  
129 Frankham 2015).

130           Here, we conducted a population genetic survey across Europe to get a snapshot of the current spatial  
131 patterns of genetic variation and the genetic relationships between introduced and native populations for a  
132 predatory freshwater fish species. We focused on the European catfish (*Silurus glanis*), a species that has been  
133 widely introduced in Western European freshwaters during the last century. This species is the largest predatory  
134 freshwater fish species in Europe (Cucherousset et al. 2018a). Its native distribution ranges from Eastern Europe  
135 to Western Russia and Turkey (Figure 1: Map representing the location of the European catfish samples. Circles  
136 represent samples from streams and rivers, stars from hatcheries, triangles from lakes and the square from a local  
137 market. Sampling sites in non-native areas are represented in green, while sampling sites located in native areas

138 are represented in blue.).



140 Figure 1: Map representing the location of the European catfish samples. Circles represent samples from streams  
141 and rivers, stars from hatcheries, triangles from lakes and the square from a local market. Sampling sites in non-  
142 native areas are represented in green, while sampling sites located in native areas are represented in blue. The grey  
143 area represents the extant (resident) native area of the European catfish, according to the IUCN (Freyhof 2008).

144 Some populations within the native range have faced sharp demographic declines during the last decades,  
145 although some of them are recovering due to conservation efforts (e.g., populations from Sweden; Palm et al.  
146 2019; Jensen et al. 2021). The European catfish was introduced in Western Europe freshwaters at the end of the  
147 19<sup>th</sup> century, and its spread has accelerated since the early 1990s due to the growing interest of sport anglers for  
148 this species (Cucherousset et al. 2018a). It now occurs in the main French, Belgian, Italian and Spanish river basins  
149 (Cucherousset et al. 2018a) and it is colonizing British and Portuguese rivers (Gkenas et al. 2015). Although  
150 national regulations from many countries in which the species has been introduced and the Union regulation on  
151 invasive species (EU 1143/2014) do not consider this species as invasive or harmful (e.g., in France), an increasing  
152 number of studies suggest that the European catfish might have a significant impact on endangered anadromous  
153 species like the Atlantic salmon (*Salmo salar*), the sea lamprey (*Petromyzon marinus*) or shad (*Alosa alosa*) due  
154 to predation (Boulétreau et al. 2018, 2020, 2021). Conversely, in other European countries such as Portugal, Spain

155 and Italy this species is now considered as a top priority invasive fish, with significant management efforts starting  
156 to be done. The European catfish hence represents an interesting model to simultaneously study both native  
157 conservation-relevant populations and introduced, potentially invasive populations.

158 Here, we specifically used genetic tools to (i) describe the genetic diversity and structure of *Silurus glanis*  
159 populations sampled across Europe, (ii) assess potential genetic relationships between native and non-native  
160 populations, and (iii) evaluate the genetic status of both introduced and native populations. We expected (i) finding  
161 higher levels of genetic diversity in native populations due to founder effects having occurred during the  
162 introduction process of non-native populations, (ii) confirming previously-known or suspected introduction routes  
163 (while revealing potential unreported ones), and (iii) producing useful genetic information (e.g., *Ne* estimates) that  
164 might help inform both conservation actions targeting native populations, and IAS management actions targeting  
165 specific non-native introduced populations.

## 166 MATERIALS AND METHODS

### 167 *Biological and historical overview of European catfish introductions in Western Europe*

168 The European catfish is the largest freshwater fish of Europe, and is considered as one of the twenty  
169 largest fish species in the World (Stone 2007; Copp et al. 2009) with a total length over 2.7 meters and a weight  
170 of 130 kg (Boulêtreau and Santoul 2016). It is also a species with a long lifespan (70 years old maximum;  
171 Bergström et al. 2022). Its physiological temperature optimum ranges between 25 and 27 °C, which makes it better  
172 suited for acclimation in Mediterranean areas rather than Northern Europe territories, although ongoing climate  
173 change may favor its spread in areas at the margin of its thermal range (Copp et al. 2009). It is considered as an  
174 opportunistic predator and its diet includes fish, crustaceans, amphibians, insects and birds (Copp et al. 2009;  
175 Cucherousset et al. 2018b). The species shows a great diet plasticity, with some individuals being able to shift their  
176 diet towards specific prey depending on their individual size, area of residence and period of the year. For instance,  
177 an increasing number of studies suggest that introduced European catfish populations could have a significant  
178 impact on endangered anadromous species like Atlantic salmon (*Salmo salar*), the sea lamprey (*Petromyzon*  
179 *marinus*) or shads (*Alosa alosa*) due to predation (Boulêtreau et al. 2018, 2020, 2021).

180 Several attempts for rearing and introducing European catfish in lakes or ponds for human consumption  
181 have been documented in Western Europe between 1850 and 1960, but most were unsuccessful due to high  
182 mortality, unsuccessful reproduction and or unfavorable climatic events like frosts (e.g., in Italian pools, Gandolfi

183 and Giannini 1979, in Great Britain in 1853, using individuals from current Moldavia, Lever 1977; Davies et al.  
184 2004 or in pools, ponds and some streams in different parts of France; Société nationale de protection de la nature  
185 1865). The first known successful introduction of the European catfish in Western Europe water bodies occurred  
186 in 1956 in the River Adda in Italy (Castaldelli et al. 2013; Supplementary Table 2). Following the 1960s, there  
187 was a higher interest for this species by recreational anglers that might have motivated deliberate introductions in  
188 Western Europe. The species was detected during the 1970s in different countries in Western Europe: the first  
189 successful introduction in France was in 1968 in the Sône Morte River, where it colonized Saône River and the  
190 Rhône river (Valadou 2007); it was introduced in 1974 in the Mequinenza-Ribarroja Reservoir (Ebro River, Elvira  
191 and Almodóvar 2001, Supplementary Table 2), using individuals originating from French populations (Doadrio  
192 2002), and in 1975 in the Netherlands due to an accidental escape from a hatchery of individuals originating from  
193 Hungary (Boeseman 1975). More recently, individuals were detected in the Tagus river in Portugal in 2014. It is  
194 suspected that these individuals probably arrived through natural dispersal from Spain, or were translocated from  
195 Spanish populations by anglers (Gkenas et al. 2015; Gago et al. 2016; Supplementary Table 2).

#### 196 *Field sampling*

197 The fish DNA sampling took place between 2014 and 2018 and was part of a collaborative sampling effort  
198 involving scientists, managers and recreational anglers. No standard sampling protocol was used, as the sampling  
199 was conducted by different groups on different types of water bodies (small/large rivers, lakes), and using different  
200 techniques (e.g., electric fishing, gill net capture, fish-pass). Small fragments of pelvic fins were removed from  
201 each individual, and we aimed to have more than 10 individuals per site for subsequent genetic analyses. A total  
202 of 1,411 individuals were collected from 46 different sampling sites located across 12 different countries in Europe.  
203 Among the 46 sites, 43 were located in wild freshwaters (i.e. rivers and lakes), with five being situated in the native  
204 area and 38 in the non-native area (Figure 1; Supplementary Table 2). We also included samples from two  
205 hatcheries (FRA-HAT in France and CZE-HAT in Czech Republic, Figure 1) and one local market situated in the  
206 native area (Galati market, in Romania, where the individuals presumably originate from Danube River, Figure  
207 1). The higher frequency of non-native populations in the database can be explained by several reasons: (i) a higher  
208 sampling effort in French rivers, as part of a broader project focused on different biological aspects of *S. glanis*  
209 populations (ii) a larger distributional range and abundance of the species in the non-native area (Lyach and Remr  
210 2019; Paz-Vinas and Santoul 2018); and (iii) a lack of capacity, network and infrastructure to obtain samples from  
211 some native areas.



212 *DNA extraction, amplification and genotyping*

213 Nuclear DNA was extracted using a modified salt-extraction method (Aljanabi and Martinez 1997). Ten  
214 microsatellites loci (Supplementary Table 3, Krieg et al. 1999) were co-amplified using standard Polymerase Chain  
215 Reactions (PCR) and two multiplex kits (SilA and SilB; Krieg et al. 2000), following the procedures described in  
216 (Chiarello et al. 2019). Genotyping was performed on an ABI PRISM™ 3730 Automated Capillary Sequencer  
217 (Applied Biosystems, Foster City, CA) at the “Génopole Toulouse Midi-Pyrénées” (France). Allele sizes were  
218 scored using the software GENEMAPPER® v.4.0 (Applied Biosystems).

219 *Quality controls of the genotypic data*

220 To maximize the robustness of subsequent population genetics analyses, we first only kept from the  
221 original dataset individuals for which at least 6 over the 10 loci were successfully amplified. We then only retained  
222 for further analyses sites with a number equal or greater than 8 successfully-genotyped individuals to set a  
223 sufficient minimum sample size threshold across sites. Third, we searched for potential genotyping or  
224 amplification errors (e.g., large allele drop-out and null alleles) using Microchecker V2.2.3 (Van Oosterhout et al.  
225 2004). Then, we assessed whether all markers fit with Hardy-Weinberg equilibrium using the software GENEPOP  
226 V4.7.3 (Rousset 2008). We also tested the presence of significant linkage disequilibria among loci using FSTAT  
227 V2.9.3 (Goudet 1995) using a level of significance for multiple tests of 5%. Levels of significance for Hardy-  
228 Weinberg equilibrium and linkage disequilibrium tests were corrected using False Discovery Rate (FDR)  
229 procedures (Benjamini and Hochberg 1995). Finally, we tested whether our dataset contained loci under selection  
230 using BayeScan V2.0 (Foll and Gaggiotti 2008). Specifically, we performed four independent Markov Chain  
231 Monte Carlo (MCMC) runs by considering 20,000 iterations, a thinning interval of 50, and burning periods of  
232 50,000 iterations. We also made 20 pilot runs (with a length of 5,000 iterations) before starting the calculation and  
233 assumed prior odds of 1,000 to reduce the propensity of detecting false positives. The convergence of the four  
234 chains was checked with a Gelman-Rubin analysis (Gelman and Rubin 1992). Values below 1.1 indicated that  
235 chains reached convergence (Gelman and Hill 2006). An  $\alpha$  value higher to 0.7 was considered as a sign of positive  
236 selection.

237 *Genetic diversity*

238 We first calculated a set of summary statistics that describes genetic diversity at the population level:  
239 expected heterozygosity ( $H_e$ ), calculated using Genetix V4.05 (Belkhir et al. 1996), and two standardized indices

240 of genetic diversity that allow comparisons between samples with unequal numbers of sampled individuals, i.e.  
241 allelic richness (*AR*; Petit et al. 1998) and private allelic richness (*PA*; Kalinowski 2004). *AR* and *PA* measure the  
242 mean number of alleles across loci in a population and the mean proportion of alleles only present in a population  
243 respectively. *AR* and *PA* were calculated using the software ADZE V1.0 (Szpiech et al. 2008), which uses  
244 rarefaction procedures to correct population-specific values to the lowest sample size in the dataset ( $N = 8$ ). We  
245 used non-parametric Wilcoxon test (one *per* genetic index) to test whether genetic diversity differed significantly  
246 between native and non-native populations.

#### 247 *Population genetic structure*

248 We investigated whether the sampled European catfish populations are genetically structured across  
249 Europe and whether individuals from native and non-native populations belong to different genetically-  
250 homogeneous groups of individuals (i.e. clusters). Specifically, we conducted the genetic clustering algorithm  
251 implemented in the package ‘rmaverick’ (Verity and Nichols 2016) of the R statistical software v.3.6.1 (R  
252 Development Core Team 2015). We conducted analyses by considering the two competing admixture models  
253 implemented in the package (i.e. “with” and “without” admixture models), and used the model-choice procedure  
254 implemented in ‘rmaverick’ to determine which of the two models best fits the empirical data. Log-likelihood  
255 plots were obtained using the thermodynamic integration procedure implemented in ‘rmaverick’ to determine the  
256 optimal genetic clusters  $K$  (i.e. the maximum number of sampled sites in our dataset). Runs were performed  
257 considering burning periods of 10,000 MCMC repetitions, 10 runs and 2,000 sampling iterations.

#### 258 *Effective population size estimation and recent population size change detection*

259 We estimated current effective population sizes ( $N_e$ ) using the linkage disequilibrium method  
260 implemented in NeESTIMATOR v.2.1 (Do et al. 2014), assuming critical values equal to 0.1. We considered that  
261  $N_e$  values reflected the overall genetic status of both native and non-native populations, with values of  $N_e < 500$   
262 indicating populations with reduced capacity to adapt to environmental change, and with values of  $N_e < 50$   
263 indicating a high genetic risk of extinction (Jamieson and Allendorf 2012).

264 We further tested for the presence of putative signals of recent demographic changes (e.g., bottleneck  
265 events) by applying the moment-based method implemented in the program BOTTLENECK v.1.2.02 (Cornuet  
266 and Luikart 1996; Piry et al. 1999). This method compares the expected heterozygosity  $H_e$  of a sample (calculated  
267 using the observed allele frequencies from the sample) with the expected heterozygosity calculated using the allele

268 frequencies expected at the mutation-drift equilibrium (i.e. *Heq*, Cornuet and Luikart 1996). Significant  
269 heterozygosity deficiencies are indicative of recent bottleneck signals (Cornuet and Luikart 1996; Piry et al. 1999),  
270 while significant heterozygosity excesses can be viewed as signals of population expansion, or as signals of  
271 introgression of genetically-different alleles in the population through immigration (Luikart and Cornuet 1998).  
272 The significance of mutation/drift equilibrium deviations was tested through Wilcoxon's signed-rank tests, and  
273 significance values were corrected using the FDR correction procedure to account for multiple comparisons  
274 (Benjamini and Hochberg 1995). We performed analyses assuming the multistep mutations model (TPM, Piry et  
275 al. 1999).

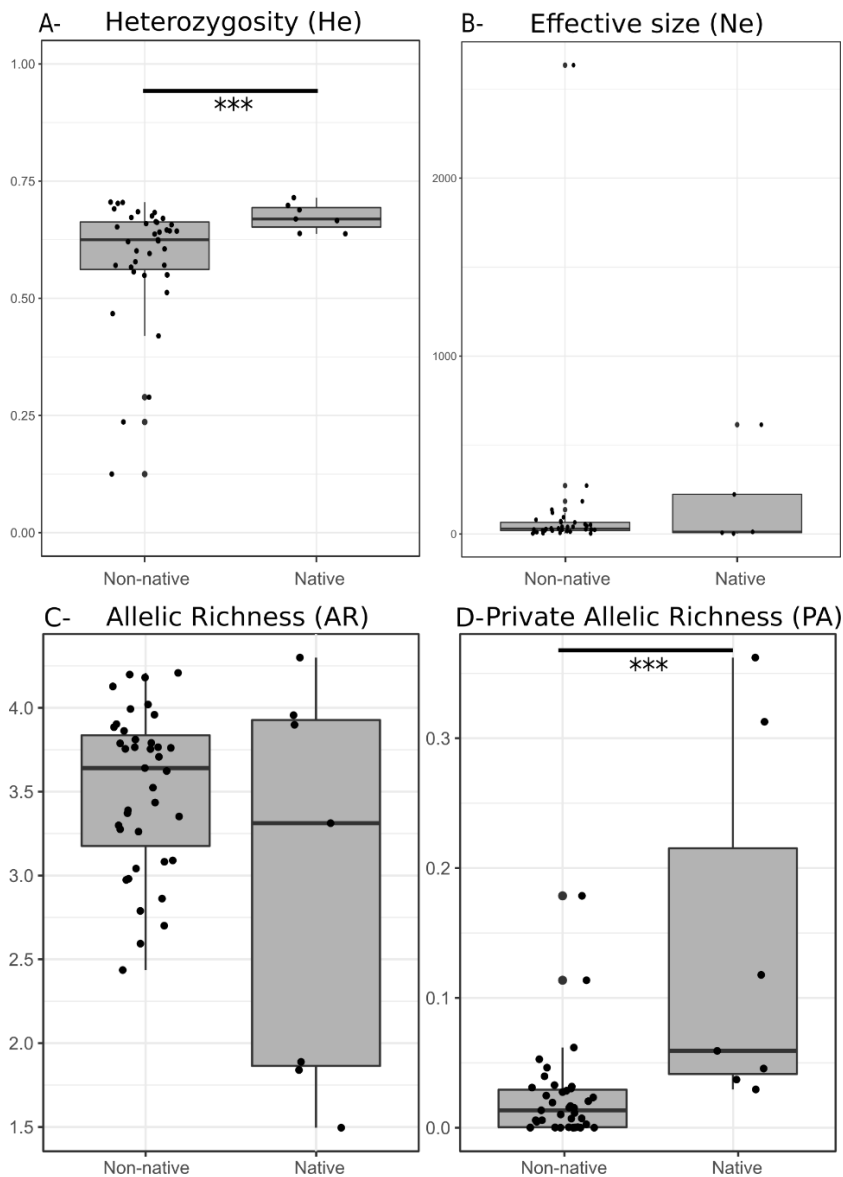
## 276 **RESULTS**

### 277 *Quality control of the genotypic data*

278 We removed 21 individuals (4, 1, 1, 2, 10, 2 and 1 individuals from the Garonne River, the Lot River, the  
279 Tarn River, Fumemortes Channels, Bourget Lake, Danube and Sile Rivers respectively) from the original dataset  
280 because at least 4 loci were not amplified. We found evidence for the presence of null alleles in our dataset for  
281 only 25 locus/population pairs over the 460 possible pairs (see Supplementary Table 4). Moreover, we only found  
282 that 12 locus/population pairs over the 460 possible pairs did not conform to the Hardy-Weinberg equilibrium (see  
283 Supplementary Table 5). Only four pairs of loci in the FRA-DOR-3 population displayed significant linkage  
284 disequilibrium (see Supplementary Table 6). No loci displayed significant evidence of being under selection (see  
285 Supplementary Table 7). Given the lack of general evidence for significant errors or genetic disequilibria, all loci  
286 and all sites were considered for further analyses. Finally, a total of 1,388 genotyped individuals were considered  
287 in the analysis.

### 288 *Genetic diversity*

289 Mean *He* values at the population level ranged between 0.12 (FRA-SAO) and 0.71 (GER-ODE) with a mean value  
290 of  $0.60 \pm 0.12$  among all populations (Supplementary **Error! Reference source not found.**). *He* values were  
291 significantly higher for native populations ( $He = 0.67 \pm 0.03$ ) than for non-native populations ( $He = 0.59 \pm 0.13$ ;  
292 Figure 2-A, p-value = 0.02).



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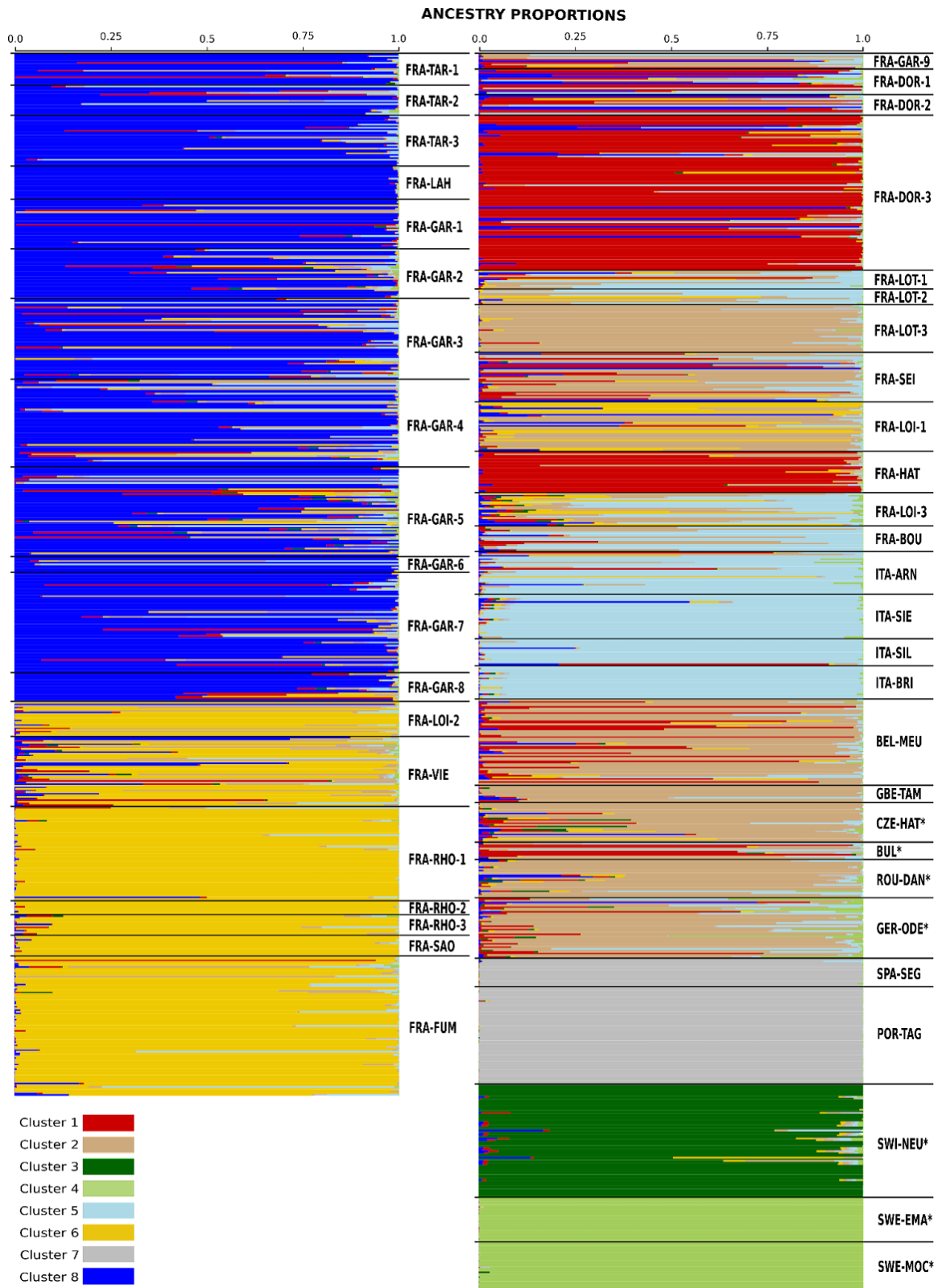
295 Figure 2: Boxplot of genetic indexes. A : panel represents Allelic Richness; B : Private Allelic Richness; C :  
 296 Heterozygosity and D : Ne values. Error bars represent standard deviation.

297 Mean AR values measured at the population level ranged from 1.50 (SWI-NEU) to 4.30 (BUL; Supplementary  
 298 **Error! Reference source not found.**), with a mean AR value among populations of  $3.42 \pm 0.64$ . AR values tended  
 299 to be either higher for non-native populations ( $3.56 \pm 0.42$ ) than for native ones ( $2.99 \pm 1.05$ ), but this tendency  
 300 was not significant (Figure 2-C, p-value = 0.528). Nonetheless, it is worth noting that some native populations  
 301 from Sweden and Switzerland displayed extremely low values of AR (SWE-MOC = 1.84; SWE-EMA = 1.89;  
 302 SWI-NEU = 1.50; Supplementary **Error! Reference source not found.**).

303 At the population level, mean PA values ranged from 0 (FRA-GAR-2, FRA-GAR-9, FRA-TAR-1, FRA-TAR-3,  
304 POR-TAG) to 0.36 (ROU-DAN; Supplementary **Error! Reference source not found.**). Mean PA values were  
305 significantly higher for native populations ( $0.11 \pm 0.12$ ) than for non-native ones ( $0.02 \pm 0.03$ , Figure 2-D, p-value  
306  $<0.001$ )

### 307 *Genetic structure*

308 We detected eight genetic clusters using the ‘rmaverick’ procedure (Supplementary Figure 1 and 2; Figure  
309 3). Overall, admixture levels were low, with a high proportion of individuals displaying a high probability of  
310 assignment to a single cluster (81.6% of individuals displayed a Q-value  $> 0.8$ ), though a few populations displayed  
311 a higher proportion of admixed individuals (e.g., FRA-SEI, FRA-BOU, FRA-LOT-2; Figure 3).



312

313 Figure 3: Ancestry diagram representing the ancestry proportion of each individual to the genetic clusters. Each

314 horizontal bar corresponds to an individual and each colour to a genetic cluster. \* indicates native populations.

315 The spatial distribution of the eight genetic clusters was heterogeneous (Figure 3). Some clusters were  
316 composed only of individuals from non-native populations. For instance, cluster 8 mostly grouped individuals  
317 from several sampling sites located in South-Western France, including most of the sites located in the Garonne  
318 River (all sites encoded as FRA-GAR but FRA-GAR-9; Figure 3 and Supplementary 2), the Tarn River (FRA-  
319 TAR-1,2 and 3) and in the Lahille lake (FRA-LAH). Similarly, cluster 6 grouped individuals from Central and  
320 Eastern France, i.e., sites located in the Loire river basin (FRA-LOI-1, FRA-LOI-2 and FRA-VIE), the Rhône  
321 River (FRA-RHO-1,2 and 3), the Saône River (FRA-SAO) and in the Camargue delta (FRA-FUM). In the same  
322 way, cluster 7 grouped individuals from the Iberian Peninsula, and more specifically from Spain (ESP-SEG) and  
323 Portugal (POR-TAG).

324 We also identified clusters that grouped individuals only from native populations. For instance, cluster 3  
325 grouped all individuals from Switzerland (SWI-NEU), whereas cluster 4 grouped all individuals from the two  
326 Swedish lakes (SWE-EMA and SWE-MOC; Figure 3).

327 Finally, we observed clusters composed of a mix of individuals from hatcheries, native and non-native  
328 populations. Cluster 1 grouped individuals from native areas (Bulgaria, BUL), from a French hatchery (FRA-  
329 HAT) and individuals caught in non-native populations from the Dordogne River in southwestern France (FRA-  
330 DOR-1,2,3, Figure 3). Cluster 2 also grouped individuals from native areas (Bulgaria, BUL; Romania, ROM-DAN  
331 and Germany, GER-ODE), but also from a Czech hatchery (CZE-HAT) and several sites spread across several  
332 rivers in the French and Belgian non-native areas (Loire River, FRA-LOI-1, FRA-LOI-2; Vienne River, FRA-  
333 VIE; Seine River, FRA-SEI; Lot river FRA-LOT-1, FRA-LOT-2; and Meuse river BEL-MEU; Figure 3).

334 We also observed the presence of individuals belonging to different clusters on some rivers. For instance,  
335 for the three sampling sites from the Lot River (FRA-LOT-1-3), all individuals in one site (FRA-LOT-3) were  
336 almost fully assigned to cluster 2, whereas the two other sites (FRA-LOT-1 and FRA-LOT-2) were composed of  
337 a mix of individuals assigned to different clusters (Figure 3). Similarly, individuals from the three sites situated in  
338 the Loire River (FRA-LOI-1-3) were mostly assigned to three different clusters (clusters 2, 5 and 6; Figure 3).

### 339 *Effective population size estimation and recent population size change detection*

340 Estimated  $N_e$  values ranged between 2.2 individuals (SWI-NEU) and 2634.9 (FRA-GAR-2;  
341 Supplementary **Error! Reference source not found.**), with mean and median  $N_e$  values at the population level of  
342  $120.5 \pm 415.2$  and  $28.1 \pm 415.2$  respectively. The difference between native ( $171.6 \pm 228.9$ ) and non-native ( $146.9$

343  $\pm 244.2$ ) mean  $N_e$  values was not significant ( $p$ -value = 0.97). Two populations exhibited very low effective  
344 population sizes within the native range; one population in Romania (ROU-DAN,  $N_e = 7.1$ ) and another one in  
345 Switzerland (SWI-NEU,  $N_e = 2.2$ ). Two populations displayed infinite estimates (BUL, SWE-MOC), and one  
346 population displayed  $N_e$  values higher than 500 individuals (i.e., the second Swedish population, SWE-EMA,  $N_e$   
347 = 614.3). Almost all non-native populations exhibited very low  $N_e$  values (35 out of the 39 non-native populations  
348 had estimated  $N_e < 50$ ; Supplementary **Error! Reference source not found.**). Three populations out of 39 non-  
349 native populations displayed infinite estimates (FRA-GAR-9, SPA-SEG, FRA-RHO-3), an issue that can arise due  
350 to sampling error (Waples and Do 2008).

351           Concerning recent population size changes tests, three populations showed significant  $H_e$  deficiencies,  
352 indicative of a recent genetic bottleneck (two native populations, ROU-DAN and SWI-NEU, and a non-native  
353 population, FRA-LOI-2, Supplementary **Error! Reference source not found.**,  $p$ -values  $< 0.01$ ). We also detected  
354 significant  $H_e$  excesses (which can be interpreted as population expansions) for 13 out of 39 non-native  
355 populations (Supplementary **Error! Reference source not found.**, all  $p$ -values  $< 0.002$ ).

## 356 **DISCUSSION**

### 357 *A complex introduction context involving multiple introductions in Western Europe*

358           The European catfish is the largest freshwater top-predator in Europe. However, little is known about its  
359 invasion dynamics in Western Europe, where the species is non-native and has been widely introduced (in Western  
360 Europe (Copp et al. 2009; Cucherousset et al. 2018b). Our genetic assessment complements other lines of evidence  
361 suggesting that multiple introduction pathways have been involved, leading to a complex historical context of  
362 introductions in Western Europe.

363           Populations of introduced species often display low genetic variation because of founder effects related  
364 to the small number of propagules introduced that survived and founded the new populations (Lawson Handley et  
365 al. 2011). As a result, a genetic diversity pattern whereby non-native populations are less genetically diverse than  
366 native ones is generally expected. Our wide-range assessment of *Silurus glanis* genetic diversity only partially  
367 meets this pattern. Indeed, although we found that  $H_e$  and PA values were significantly higher for native  
368 populations than for non-native populations (a result that was not verified for AR), we identified several non-  
369 native populations (e.g., FRA-BOU, FRA-DOR-1,2 and 3 or FRA-GAR-6) displaying similar or even higher  $H_e$   
370 values than native populations. Further, some native populations (i.e. Swiss and Romanian populations, with  $N_e$



371 respectively equal to 2.2 and 7.1) displayed low  $N_e$  values compared to the  $N_e$  values estimated for many other  
372 non-native populations (e.g. mean value for non-native populations equal to 146.9). This could be explained by a  
373 high propagule pressure due to the occurrence of multiple introductions (Kolbe et al. 2004) of individuals  
374 originating from genetically distinct populations, as supported by our clustering-based analyses (discussed below).  
375 On the contrary, an introduction by a single source of individuals seems to have occurred for some other  
376 populations (Iberian population, POR-TAG, SPA-SEG). This pattern has also been observed for other introduced  
377 non-native freshwater top predators such as the pikeperch (*Sander lucioperca*), a species that also displays higher  
378 genetic diversity in non-native populations because of high propagule pressure due to multiple introductions  
379 (Poulet et al. 2009), suggesting that no single and simple introduction pathway exists for freshwater top predators.  
380 For instance, the Invasive Species Compendium CABI database (<https://www.cabi.org/isc/>) mentions the  
381 occurrence of three over six major invasion pathways for *S. glanis* (i.e. deliberate *release*, *escape* from captivity,  
382 and *stowaway*; Hulme et al. 2008).

383         We identified several patterns that may reflect different histories and pathways of introduction, which  
384 highlights the complexity of the European catfish biological invasion in Western Europe. First, we found a set of  
385 non-native populations that do not belong to clusters represented in native populations. For instance, all  
386 populations from the Garonne River (except FRA-GAR-TOU), the Tarn River or Lake Lahille were assigned to a  
387 single cluster (cluster 8) that was not identified in other areas. This lack of assignment to a native cluster might be  
388 explained by the low coverage by our sampling design of the native range of the species. Although less plausible,  
389 the potential differential effects of genetic drift following introductions in these water bodies might also have  
390 precluded assignment to native source clusters (supposing that we managed to successfully characterize these with  
391 our sampling design). Second, we also observed a set of non-native populations whose individuals were assigned  
392 to clusters also containing individuals from native populations. For instance, individuals from Great Britain (GBR-  
393 TAM) have been assigned to cluster 2, which is also the main cluster represented in the German (GER-ODE),  
394 Czech (CZE-HAT) and Romanian (ROU-DAN) populations. This result is consistent with historical records that  
395 point at an introduction of *S. glanis* individuals from Walachia (an ancient principality corresponding now to  
396 Romania) at the Woburn Abbey in 1880 for breeding purposes (Britton and Davies 2006). We note here that  
397 individuals from Romania were sampled on a local market. We hypothesized that the origin of these individuals  
398 was local (i.e. presumably from the Danube river), although we had no means to confirm their actual origin.  
399 Similarly, Italian populations and populations from Lot River (FRA-LOT-1, FRA-LOT-2) were mainly assigned  
400 to cluster 5, which is also slightly represented in a cluster where Bulgarian individuals are assigned (20 % of the

401 individuals). Based on this genetic similarity, we can hypothesize that these non-native populations could come  
402 from Bulgaria, or that Italian populations might have acted as “bridgehead” population (i.e. by acting as a source  
403 of individuals for introductions in FRA-LOT-1 and 2; Lombaert et al. 2011). Further, populations from the  
404 Dordogne river (FRA-DOR-1,2 and 3) were also assigned to cluster 2, the same cluster that has been inferred for  
405 individuals from both the French hatchery of Chateau Gontier (FRA-HAT) and the Bulgarian sample (BUL). This  
406 suggests that individuals from the hatchery may originate from - or might be genetically close to - individuals from  
407 Bulgaria, and that this hatchery might have produced and/or sold the individuals introduced in the Dordogne river.  
408 Finally, we observed a last set of non-native populations assigned to the same cluster despite inhabiting different  
409 river basins and countries, potentially indicating that one of these non-native populations may have acted as a  
410 “bridgehead” population, favouring the introduction to other non-native areas (Lombaert et al. 2010). Indeed,  
411 populations from the Iberian Peninsula (Spain, SPA-SEG and Portugal, POR-TAG) belong to the same cluster,  
412 although the source population remains unknown. Given the geographical proximity between Portugal and Spain  
413 and the dates of first detection of the species in each country, we confidently suggest that Spanish populations  
414 acted as “bridgehead” populations for individuals introduced in Portugal, supporting hypotheses from the literature  
415 (Gago et al. 2016; Ferreira et al. 2019). We also observed similarities (cluster 6) between Rhône basin populations  
416 (FRA-RHO-1,2 and 3, FRA-SAO, FRA-FUM) and populations from the Loire basin (FRA-LOI-2, FRA-VIE),  
417 which may be explained by the occurrence of a *corridor*-like pathway (according to Hulme’s classification; Hulme  
418 et al. 2008) due to the presence of human-made channels linking the Rhône and Loire basins that might have  
419 favoured European catfish spread (Valadou 2007).

420         The observation that six genetically differentiated clusters were identified within a relatively narrow non-  
421 native area (Loire, Rhône and Garonne rivers in France) provides an indirect support for the occurrence of multiple  
422 introduction events of European catfish. Given the relatively recent introduction events in Europe (around the last  
423 60 years), the propensity for anglers to release individuals alive (Cucherousset et al. 2018b), and the long lifespan  
424 of this species (70 years old maximum; Bergström et al. 2022), a rapid genetic differentiation following  
425 introduction events leading to several genetic clusters remains unlikely. Moreover, individuals assigned to several  
426 genetic clusters are sometimes found in the same river basins, which is strong evidence that multiple introductions  
427 involving different genetic sources occurred in these areas. For example, four clusters have been geographically  
428 defined in the Garonne basin: one cluster covering the Dordogne river (FRA-DOR-1,2 and 3; cluster 1), one  
429 represented by the most upstream population from the Lot river (FRA-LOT-3; cluster 2), another cluster covering  
430 populations from the Lot river (FRA-LOT-1, FRA-LOT-2; cluster 5) and a last cluster covering almost all

431 populations from the Garonne (FRA-GAR-1 to 8) and Tarn rivers (FRA-TAR-1,2 and 3, cluster 8). It is worth  
432 mentioning that the Lot populations are separated by a large dam, which suggests that two different introductions  
433 might have occurred at each side of the dam. These results are supported by records documenting the occurrence  
434 of at least two major introductions through deliberate releases for angling purposes in the Tarn and Dordogne  
435 Rivers, and of at least two other introductions in the Lot River (Paz-Vinas and Santoul 2018). Similarly,  
436 populations from the Loire River are represented by three clusters, i.e. cluster 2 (FRA-Loi-1), cluster 6 (FRA-LOI-  
437 2) and cluster 5 (FRA-LOI-3). Even if individuals in cluster 6 could have dispersed from the Saône River using  
438 the “Canal du Centre” channel as a corridor (Valadou 2007), multiple introductions in this area for angling  
439 purposes have also been mentioned in the literature (Valadou 2007).

440           The European catfish is now widely established in several Western Europe countries (France, Italy,  
441 Belgium) and its expansion is ongoing in many others (Spain, Portugal, Great Britain), hence increasing its  
442 probability of becoming invasive in such areas. The rapid expansion of the European catfish and its establishment  
443 in several Western Europe river basins is probably explained by semi-natural expansion through channels and  
444 human-mediated dispersal involving multiple deliberate and undeliberate introductions. Combined with the life-  
445 history traits exhibited by this species (very large lifespan and body size, behavioural and diet plasticity,  
446 Cucherousset et al. 2018b) and the sport-fishing activity targeting this species, management of this species is  
447 difficult in non-native areas. Possible management measures to avoid expansion in non-native areas could be to  
448 strengthen regulations on importing, selling, breeding, growing and releasing into non-native areas European  
449 catfish, to inform and educate anglers for preventing new releases in the wild, and to remove individuals in areas  
450 where the species causes ecological impacts. Another way to prevent new multiple introductions could be to  
451 regularly monitor for the presence of European catfish in un-invaded rivers using environmental DNA techniques  
452 (Morisette et al. 2021), to quickly detect the presence of the species and prevent future demographic expansion  
453 and environment impacts.

#### 454 *Genetic status of native and non-native populations*

455           Some native populations of European catfish are imperiled due to human pressures or suboptimal thermal  
456 conditions (e.g. cold climate in Sweden; Palm et al. 2019) and have been the focus of conservation actions during  
457 the last decade (Palm et al. 2019; Jensen et al. 2021). We found that some native populations (SWI-NEU, SWE-  
458 EMA, SWE-MOC) present high *He* values and low AR values, a sign of recent bottlenecks (Allendorf 1986) that  
459 is consistent with previous studies in these areas (Triantafyllidis et al. 2002 for Switzerland; Jensen et al. 2018;

460 Palm et al. 2019 for Sweden). These low genetic diversities are probably because geographical barriers (mainly  
461 the Baltic Sea) might have prevented gene flow between the lacustrine ecosystem and other continental populations  
462 and because these populations are peripheral and located at the Northern extremities of the European catfish native  
463 distribution. It is noteworthy that the high  $N_e$  value found for the Swedish population SWE-EMA ( $N_e = 614.3$ )  
464 might be an outlier due to sampling bias, given that a recent survey using more individuals from multiple cohorts  
465 and two alternative estimation methods found  $N_e$  values ranging between 1 and 16 for that population, depending  
466 on the estimation method and year of sampling (Palm et al. 2019). The Neuchatel lake population (SWI-NEU),  
467 which was previously identified as one of the most genetically impoverished native population together with  
468 populations from Greece (Triantafyllidis et al. 2002), is also located at the periphery of the distribution range of  
469 this species. These findings agree with the core-periphery hypothesis stating that populations at the margins of its  
470 range should display lower genetic diversity than populations at the core of the range distribution (Brown 1984;  
471 De Kort et al. 2021). These low genetic diversities come along with genetic differentiation from other native areas  
472 since Swedish and Swiss populations belong to specific clusters (cluster 4 for Swedish populations and cluster 3  
473 for Swiss populations; Figure 3). Moreover, Swiss and Romanian populations both display low  $N_e$  values (2.2 and  
474 7.1 respectively) and signs of recent demographic decreases ( $H_e$  deficiencies; Cornuet and Luikart 1996; Piry et  
475 al. 1999). These populations might thus be at high risk of extinction due to genetic effects (Frankham 2005). We  
476 also note that two native populations present high  $PA$  values (BUL,  $PA = 0.31$ ; ROU-DAN, 0.36), indicating that  
477 these populations harbour unique genetic diversity that should be protected from a biodiversity conservation  
478 standpoint.

479 Populations in Scandinavia are genetically and demographically vulnerable (Jensen et al. 2018; Palm et  
480 al. 2019). Supplementing populations with stocked individuals from Scandinavia could avoid genetic erosion due  
481 to genetic drift, but increasing their genetic diversity through the introduction of closely-related individuals from  
482 non-Scandinavian populations might not be possible since we did not identify populations that are genetically  
483 close to Scandinavian populations in our survey. Non-native populations in our dataset seem genetically healthy,  
484 with thirteen over thirty-nine displaying signals evocative of demographic expansion (i.e. heterozygosity  
485 excesses). Seventeen over thirty-nine of these non-native populations display  $N_e$  values above 50, suggesting they  
486 are genetically healthy enough for maintaining sufficient levels of genetic variation for adaptation over time. It is  
487 however noteworthy that some of these expanding non-native populations (9/13) display low  $N_e$  values (below  
488  $<50$ ), a pattern generally expected for introduced populations (Lawson Handley et al. 2011), despite being  
489 expanding populations. The occurrence of “bucket releases” by anglers that move individuals between different

490 water bodies (Britton and Davies 2006; Syväranta et al. 2010; Cucherousset et al. 2018b) might partly explain  
491 expansion with low genetic diversities in some water bodies. This species may also benefit from better  
492 environmental conditions in non-native areas, a factor that could also explain its expansion in such areas  
493 (Schlumberger et al. 2001) despite low levels of genetic diversity. The European catfish is considered a trophy by  
494 recreational anglers, with the largest individuals being the most appreciated and targeted. This activity that involves  
495 ‘No kill’ practices, is attractive for the tourism economy and might foster the maintenance of sustainable  
496 populations of large individuals. Developing such “no kill” practices could help to protect imperiled populations  
497 in native areas. European catfish’s stocking, mainly for angling purposes, is already common in Central Europe  
498 (Lyach 2021) and the highly dense wild populations situated in non-native areas could also be used as genetic  
499 reservoirs for supplementing populations situated in areas where the species is endangered.

## 500 **CONCLUSION:**

501 This study provides a snapshot of current spatial genetic variation patterns of the European catfish at  
502 across Europe, and on some links between native and non-native populations, by taking into account populations  
503 that had never been sampled and analyzed altogether before. We confirmed that non-native populations of  
504 European catfish present lower genetic diversities than native populations, which is a classical pattern observed in  
505 biological invasions. Even if the species is classified as Least Concern in the IUCN Red List (Freyhof and Brooks  
506 2011), we confirmed that some native populations (from Sweden and Switzerland) have limited genetic diversity.  
507 We also determined some potential genetic relationships between some non-native and native populations. We  
508 failed, however, to identify potential genetic sources for some of the sampled non-native populations. A higher  
509 sampling effort is thus needed, especially in native areas, to broaden our snapshot of current genetic variation  
510 patterns of the European catfish populations by including more potential source populations and to characterize  
511 the introduction pathways. We also found that some native populations presented low  $N_e$  values, a sign of genetic  
512 weakness that calls for reinforced and proactive management measures to be taken to protect these remaining  
513 populations and for the setting up of genetic monitoring programs to measure the efficiency of protection measures  
514 on preserving the evolutionary potential of these populations.

515

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#### 527 **COMPETING INTERESTS**

528 The authors have no relevant financial or non-financial interests to disclose.

#### 529 **AUTHOR CONTRIBUTIONS STATEMENT**

530 FS, IPV and PC contributed to the study conception and design. PC and IPV made the analyses. PC and IPV wrote  
531 the first draft of the manuscript. SB and FS made significant reviewing of the drafts. SB, GL, RB, MC, EGB, PH,  
532 DN, AN, ON, MO, FR, OS and CV commented on previous versions of the manuscript. GL, JF and CV conducted  
533 laboratory analyses. RA, MC, EGB, PH, DN, AN, ON, MO, FR, OS, CV provided samples. The final manuscript  
534 was read and approved by all authors.

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