



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

Paul Castagné<sup>1</sup> · Ivan Paz-Vinas<sup>2</sup> · Stéphanie Boulêtreau<sup>3</sup> · Jessica Ferriol<sup>3</sup> · Géraldine Loot<sup>1</sup> · Charlotte Veyssière<sup>1</sup>, et al. [full author details at the end of the article]

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## Abstract

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

**Keywords** European catfish · Freshwater · Genetic diversity · Biological invasion · Genetic structure

## Introduction

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

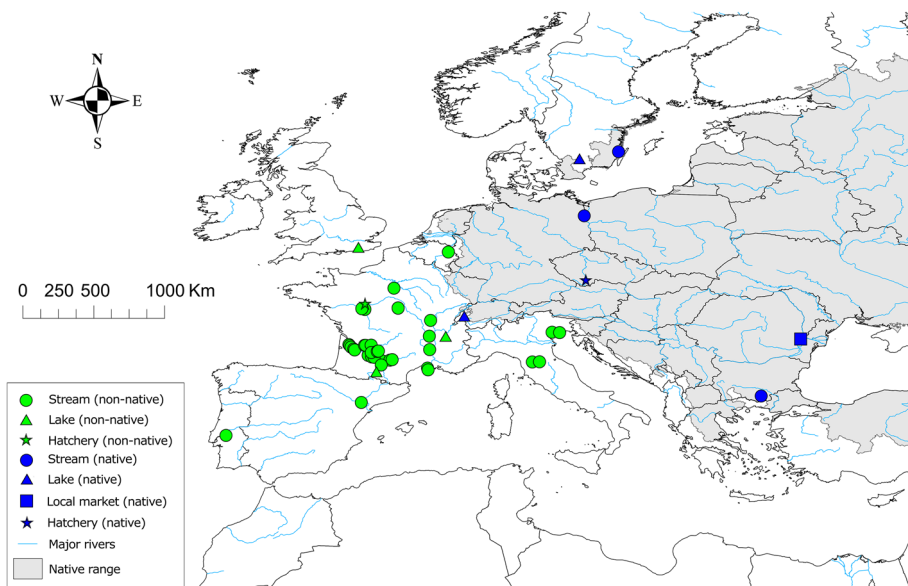
The fate of introduced populations is highly dependent on the ecological and socio-economic context they face in their introduced areas (Blackburn et al. 2011). This context can either foster population expansions in non-native areas (Uller and Leimu 2011) or population decreases in native areas (Marchetti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

Population genetic tools have proven useful to tackle questions related to both biological invasion processes and biodiversity conservation (Fitzpatrick et al. 2012; Blanchet 2012). From an invasion biology standpoint, species introductions generally leave specific footprints on the genetic pool of introduced populations (Cristescu 2015), and these footprints can be detected through neutral genetic variation assessments and the use of specific methods (Estoup and Guillemaud 2010). For instance, introduction events can lead to populations with reduced levels of genetic diversity (compared to source populations) because of the founder effects resulting from the introduction of individuals harboring only a portion of the whole genetic diversity of the source population(s) (Edmonds et al. 2004; Dlugosch and Parker 2008; Peischl and Excoffier 2015). Genetic similarities between native and introduced populations can also help determine potential sources of introductions (e.g., Lombaert et al. 2011; Perdereau et al. 2013; Krueger-Hadfield et al. 2017). Further, multiple introductions from different genetic sources can generate specific admixture patterns and/or lead to introduced populations harboring higher genetic diversities compared to native or source populations (Roman and Darling 2007; Gillis et al. 2009; Pairon et al. 2010). From a biodiversity conservation standpoint, genetic diversity is an overlooked, though key biodiversity facet (Vernesi et al. 2008; Laikre et al. 2020). Genetic tools facilitate defining conservation units (Funk et al. 2012), understanding patterns of gene flow among populations (Neigel et al. 2007), identifying hybridization events (Curto et al. 2022) or assessing population size changes (Beaumont 1999). For instance, demographic collapses occurring in native populations may produce genetic bottlenecks that can be detected from genotypic data using specific tools (e.g., Cornuet and Luikart 1996; Piry et al. 1999). These bottlenecks reduce genetic diversity and effective population sizes ( $N_e$ ), and might subsequently reinforce demographic declines (Hostetler et al. 2013), ultimately increasing population extinction risks (Frankham 1995). Indeed, it is generally agreed that populations with  $N_e \leq 50$  are at high risk of extinction due to genetic erosion, and that at least  $N_e \geq 500$  are needed to avoid any loss of genetic variation for fitness (Jamieson and

Allendorf 2012; Frankham et al. 2014). Identifying populations that have experienced genetic bottlenecks, disruptions of among-populations gene flow, or displaying low  $N_e$  and/or high inbreeding rates is thus particularly helpful to define and prioritize conservation actions (Hailer et al. 2006; Frankham 2015).

Here, we conducted a population genetic survey across Europe to get a snapshot of the current spatial patterns of genetic variation and the genetic relationships between introduced and native populations for a predatory freshwater fish species. We focused on the European catfish (*Silurus glanis*), a species that has been widely introduced in Western European freshwaters during the last century. This species is the largest predatory freshwater fish species in Europe (Cucherousset et al. 2018). Its native distribution ranges from Eastern Europe to Western Russia and Turkey (Fig. 1).

Some populations within the native range have faced sharp demographic declines during the last decades, although some of them are recovering due to conservation efforts (e.g., populations from Sweden; Palm et al. 2019; Jensen et al. 2021). The European catfish was introduced in Western Europe freshwaters at the end of the nineteenth century, and its spread has accelerated since the early 1990s due to the growing interest of sport anglers for this species (Cucherousset et al. 2018). It now occurs in the main French, Belgian, Italian and Spanish river basins (Cucherousset et al. 2018) and it is colonizing British and Portuguese rivers (Gkenas et al. 2015, Supplementary Table 1). Although national regulations from many countries in which the species has been introduced and the Union regulation on invasive species (EU 1143/2014) do not consider this species as invasive or harmful (e.g., in France), an increasing number of studies suggest that the European catfish might



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

have a significant impact on endangered anadromous species like the Atlantic salmon (*Salmo salar*), the sea lamprey (*Petromyzon marinus*) or shad (*Alosa alosa*) due to predation (Boulêtreau et al. 2018, 2020, 2021). Conversely, in other European countries such as Portugal, Spain and Italy this species is now considered as a top priority invasive fish, with significant management efforts starting to be done. The European catfish hence represents an interesting model to simultaneously study both native conservation-relevant populations and introduced, potentially invasive populations.

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

## Materials and methods

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

The European catfish is the largest freshwater fish of Europe, and is considered as one of the twenty largest fish species in the World (Stone 2007; Copp et al. 2009) with a total length over 2.7 m and a weight of 130 kg (Boulêtreau and Santoul 2016). It is also a species with a long lifespan (70 years old maximum; Bergström et al. 2022). Its physiological temperature optimum ranges between 25 and 27 °C, which makes it better suited for acclimation in Mediterranean areas rather than Northern Europe territories, although ongoing climate change may favor its spread in areas at the margin of its thermal range (Copp et al. 2009). It is considered as an opportunistic predator and its diet includes fish, crustaceans, amphibians, insects and birds (Copp et al. 2009; Cucherousset et al. 2018). The species shows a great diet plasticity, with some individuals being able to shift their diet towards specific prey depending on their individual size, area of residence and period of the year. For instance, an increasing number of studies suggest that introduced European catfish populations could have a significant impact on endangered anadromous species like Atlantic salmon (*Salmo salar*), the sea lamprey (*Petromyzon marinus*) or shads (*Alosa alosa*) due to predation (Boulêtreau et al. 2018, 2020, 2021). Several attempts for rearing and introducing European catfish in lakes or ponds for human consumption have been documented in Western Europe between 1850 and 1960, but most were unsuccessful due to high mortality, unsuccessful reproduction and/or unfavorable climatic events like frosts (e.g., in Italian pools, Gandolfi and Giannini 1979, in Great Britain in 1853, using individuals from current Moldavia, Lever 1977; Davies et al. 2004 or in pools, ponds and some streams in different parts of France; Société Impériale Zoologique d'Acclimatation 1865). The first known successful introduction of the European catfish in Western Europe water bodies occurred in 1956 in the River Adda in Italy (Castaldelli et al. 2013; Supplementary Table 2). Following the 1960s, there was a higher interest for this species by recreational anglers that might have motivated deliberate introductions in Western

Europe. The species was detected during the 1970s in different countries in Western Europe: the first successful introduction in France was in 1968 in the Sône Morte River, where it colonized Saône River and the Rhône river (Valadou 2007); it was introduced in 1974 in the Mequinenza-Ribarroja Reservoir (Ebro River, Elvira and Almodóvar 2001, Supplementary Table 2), using individuals originating from French populations (Doadrio 2002), and in 1975 in the Netherlands due to an accidental escape from a hatchery of individuals originating from Hungary (Boeseman 1975). More recently, individuals were detected in the Tagus river in Portugal in 2014. It is suspected that these individuals probably arrived through natural dispersal from Spain, or were translocated from Spanish populations by anglers (Gkenas et al. 2015; Gago et al. 2016; Supplementary Table 2).

## Field sampling

The fish DNA sampling took place between 2014 and 2018 and was part of a collaborative sampling effort involving scientists, managers and recreational anglers. No standard sampling protocol was used, as the sampling was conducted by different groups on different types of water bodies (small/large rivers, lakes), and using different techniques (e.g., electric fishing, gill net capture, fish-pass). Small fragments of pelvic fins were removed from each individual, and we aimed to have more than 10 individuals per site for subsequent genetic analyses. A total of 1411 individuals were collected from 46 different sampling sites located across 12 different countries in Europe. Among the 46 sites, 43 were located in wild freshwaters (i.e. rivers and lakes), with five being situated in the native area and 38 in the non-native area (Fig. 1; Supplementary Table 2). We also included samples from two hatcheries (FRA-HAT in France and CZE-HAT in Czech Republic, Fig. 1) and one local market situated in the native area (Galati market, in Romania, where the individuals presumably originate from Danube River, Fig. 1). The higher frequency of non-native populations in the database can be explained by several reasons: (i) a higher sampling effort in French rivers, as part of a broader project focused on different biological aspects of *S. glanis* populations (ii) a larger distributional range and abundance of the species in the non-native area (Lych and Remr 2019; Paz-Vinas and Santoul 2018); and (iii) a lack of capacity, network and infrastructure to obtain samples from some native areas.

## DNA extraction, amplification and genotyping

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

## Quality controls of the genotypic data

To maximize the robustness of subsequent population genetics analyses, we first only kept from the original dataset individuals for which at least 6 over the 10 loci were successfully amplified. We then only retained for further analyses sites with a number equal or greater

than 8 successfully-genotyped individuals to set a sufficient minimum sample size threshold across sites. Third, we searched for potential genotyping or amplification errors (e.g., large allele drop-out and null alleles) using Microchecker V2.2.3 (Van Oosterhout et al. 2004). Then, we assessed whether all markers fit with Hardy–Weinberg equilibrium using the software GENEPOP V4.7.3 (Rousset 2008). We also tested the presence of significant linkage disequilibria among loci using FSTAT V2.9.3 (Goudet 1995) using a level of significance for multiple tests of 5%. Levels of significance for Hardy–Weinberg equilibrium and linkage disequilibrium tests were corrected using False Discovery Rate (FDR) procedures (Benjamini and Hochberg 1995). Finally, we tested whether our dataset contained loci under selection using BayeScan V2.0 (Foll and Gaggiotti 2008). Specifically, we performed four independent Markov Chain Monte Carlo (MCMC) runs by considering 20,000 iterations, a thinning interval of 50, and burning periods of 50,000 iterations. We also made 20 pilot runs (with a length of 5000 iterations) before starting the calculation and assumed prior odds of 1000 to reduce the propensity of detecting false positives. The convergence of the four chains was checked with a Gelman–Rubin analysis (Gelman and Rubin 1992). Values below 1.1 indicated that chains reached convergence (Gelman and Hill 2006). An  $\alpha$  value higher to 0.7 was considered as a sign of positive selection.

## Genetic diversity

We first calculated a set of summary statistics that describes genetic diversity at the population level: expected heterozygosity ( $H_e$ ), calculated using Genetix V4.05 (Belkhir et al. 1996), and two standardized indices of genetic diversity that allow comparisons between samples with unequal numbers of sampled individuals, i.e. allelic richness ( $AR$ ; Petit et al. 1998) and private allelic richness ( $PA$ ; Kalinowski 2004).  $AR$  and  $PA$  measure the mean number of alleles across loci in a population and the mean proportion of alleles only present in a population respectively.  $AR$  and  $PA$  were calculated using the software ADZE V1.0 (Szpiech et al. 2008), which uses rarefaction procedures to correct population-specific values to the lowest sample size in the dataset ( $N=8$ ). We used non-parametric Wilcoxon test (one *per* genetic index) to test whether genetic diversity differed significantly between native and non-native populations.

## Population genetic structure

We investigated whether the sampled European catfish populations are genetically structured across Europe and whether individuals from native and non-native populations belong to different genetically-homogeneous groups of individuals (i.e. clusters). Specifically, we conducted the genetic clustering algorithm implemented in the package ‘rmaverick’ (Verity and Nichols 2016) of the R statistical software v.3.6.1 (R Development Core Team 2015). We conducted analyses by considering the two competing admixture models implemented in the package (i.e. “with” and “without” admixture models), and used the model-choice procedure implemented in ‘rmaverick’ to determine which of the two models best fits the empirical data. Log-likelihood plots were obtained using the thermodynamic integration procedure implemented in ‘rmaverick’ to determine the optimal genetic clusters  $K$  (i.e. the maximum number of sampled sites in our dataset). Runs were performed considering burning periods of 10,000 MCMC repetitions, 10 runs and 2000 sampling iterations.

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

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

We further tested for the presence of putative signals of recent demographic changes (e.g., bottleneck events) by applying the moment-based method implemented in the program BOTTLENECK v.1.2.02 (Cornuet and Luikart 1996; Piry et al. 1999). This method compares the expected heterozygosity  $H_e$  of a sample (calculated using the observed allele frequencies from the sample) with the expected heterozygosity calculated using the allele frequencies expected at the mutation-drift equilibrium (i.e.  $H_{eq}$ , Cornuet and Luikart 1996). Significant heterozygosity deficiencies are indicative of recent bottleneck signals (Cornuet and Luikart 1996; Piry et al. 1999), while significant heterozygosity excesses can be viewed as signals of population expansion, or as signals of introgression of genetically-different alleles in the population through immigration (Luikart and Cornuet 1998). The significance of mutation-drift equilibrium deviations was tested through Wilcoxon's signed-rank tests, and significance values were corrected using the FDR correction procedure to account for multiple comparisons (Benjamini and Hochberg 1995). We performed analyses assuming the multistep mutations model (TPM, Piry et al. 1999).

## Results

### Quality control of the genotypic data

We removed 21 individuals (4, 1, 1, 2, 10, 2 and 1 individuals from the Garonne River, the Lot River, the Tarn River, Fumemortes Channels, Bourget Lake, Danube and Sile Rivers respectively) from the original dataset because at least 4 loci were not amplified. We found evidence for the presence of null alleles in our dataset for only 25 locus/population pairs over the 460 possible pairs (see Supplementary Table 4). Moreover, we only found that 12 locus/population pairs over the 460 possible pairs did not conform to the Hardy–Weinberg equilibrium (see Supplementary Table 5). Only four pairs of loci in the FRA-DOR-3 population displayed significant linkage disequilibrium (see Supplementary Table 6). No loci displayed significant evidence of being under selection (see Supplementary Table 7). Given the lack of general evidence for significant errors or genetic disequilibria, all loci and all sites were considered for further analyses. Finally, a total of 1388 genotyped individuals were considered in the analysis.

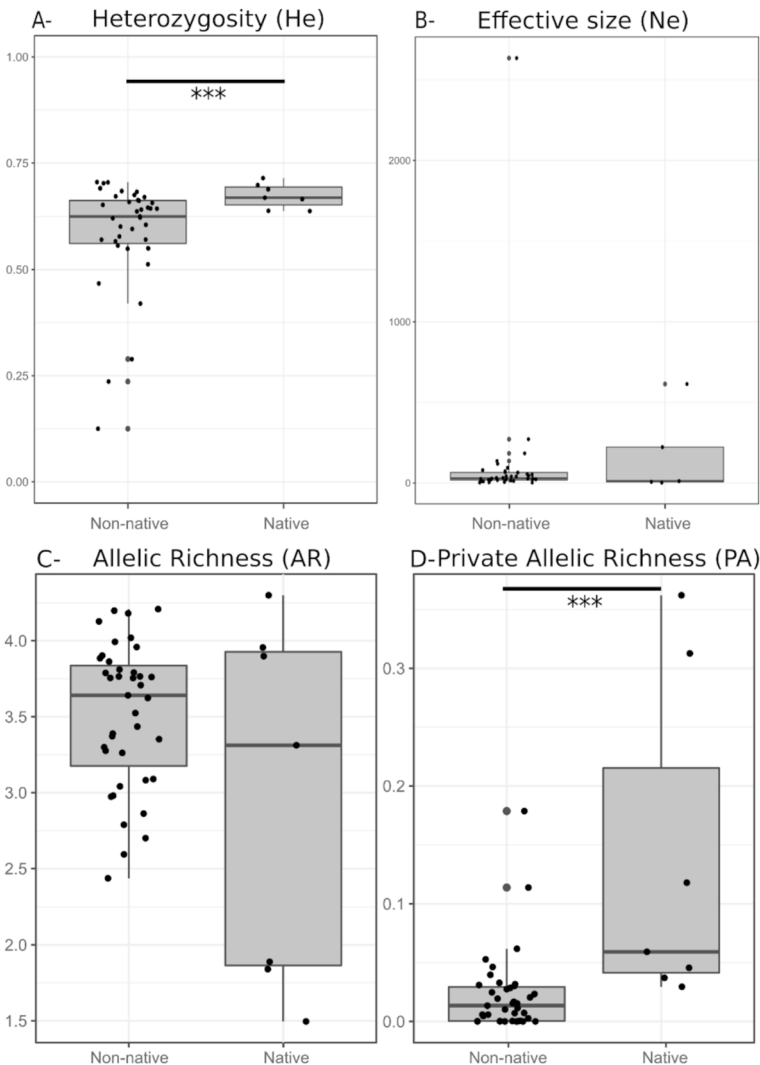
### Genetic diversity

$H_e$  values at the population level were ranged between 0.12 (FRA-SAO) and 0.71 (GER-ODE) with a mean value of  $0.60 \pm 0.12$  among all populations (Supplementary Table 1).



$H_e$  values were significantly higher for native populations ( $H_e = 0.67 \pm 0.03$ ) than for non-native populations ( $H_e = 0.59 \pm 0.13$ ; Fig. 2-A,  $p$ -value = 0.02).

$AR$  values measured at the population level were ranged from 1.50 (SWI-NEU) to 4.30 (BUL; Supplementary Table 1), with a mean  $AR$  value among populations of  $3.42 \pm 0.64$ .  $AR$  values tended 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 was not significant (Fig. 2-C,  $p$ -value = 0.528). Nonetheless, it is worth noting that some native populations from Sweden and Switzerland displayed extremely low values of  $AR$  (SWE-MOC = 1.84; SWE-EMA = 1.89; SWI-NEU = 1.50; Supplementary Table 1).



**Fig. 2** Boxplot of genetic indexes. **A** panel represents Heterozygosity; **B** Effective size; **C** Allelic Richness and **D** Private Allelic Richness. Error bars represent standard deviation. \*\*\* indicates  $p$ -values < 0.001



At the population level, *PA* values were ranged from 0 (FRA-GAR-2, FRA-GAR-9, FRA-TAR-1, FRA-TAR-3, POR-TAG) to 0.36 (ROU-DAN; Supplementary Table 1). Mean *PA* values were significantly higher for native populations ( $0.11 \pm 0.12$ ) than for non-native ones ( $0.02 \pm 0.03$ , Fig. 2-D,  $p$ -value  $< 0.001$ ).

## Genetic structure

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

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

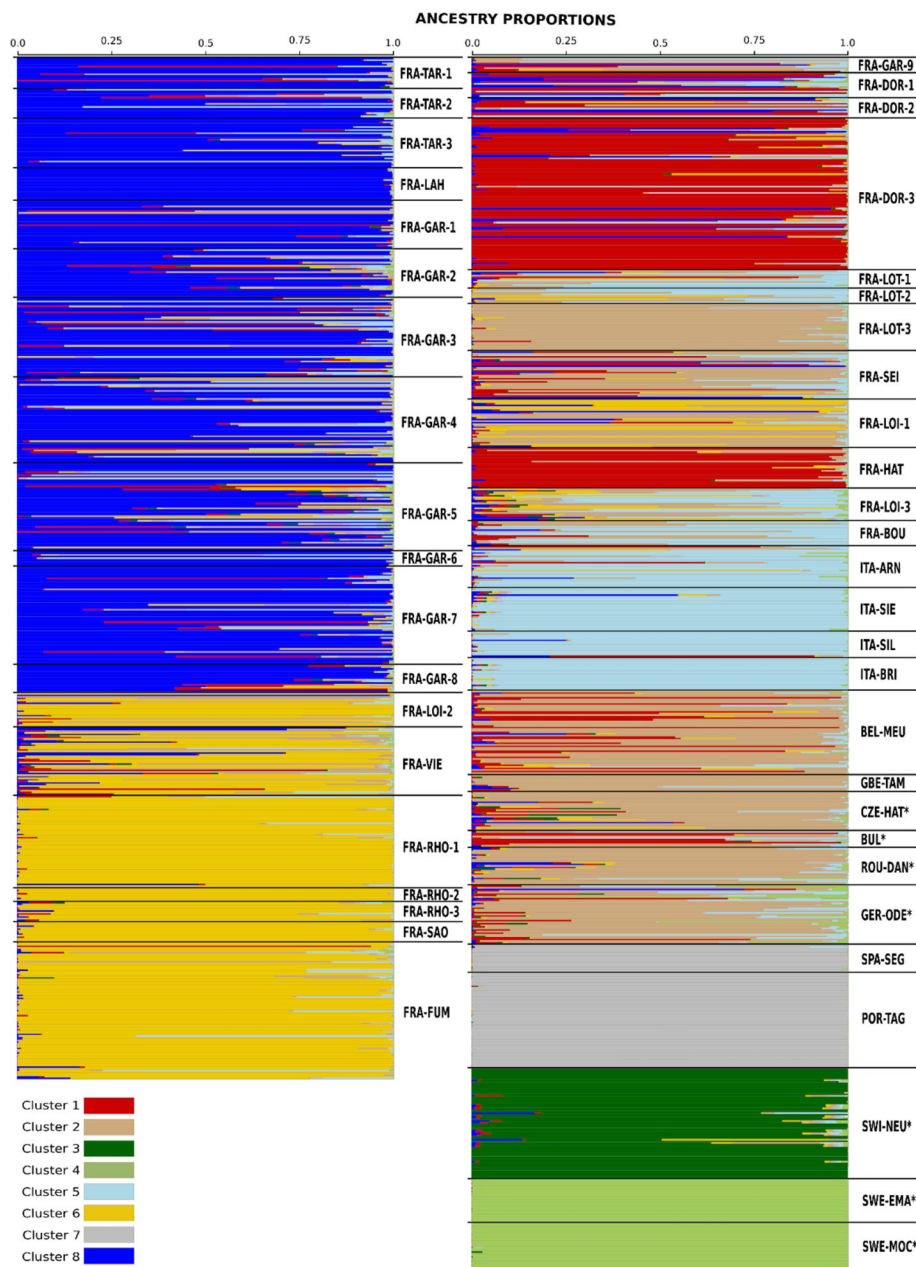
We also identified clusters that grouped individuals only from native populations. For instance, cluster 3 grouped all individuals from Switzerland (SWI-NEU), whereas cluster 4 grouped all individuals from the two Swedish lakes (SWE-EMA and SWE-MOC; Fig. 3).

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

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

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

Estimated  $N_e$  values ranged between 2.2 individuals (SWI-NEU) and 2634.9 (FRA-GAR-2; Supplementary Table 1), with mean and median  $N_e$  values at the population level of  $120.5 \pm 415.2$  and  $28.1 \pm 415.2$  respectively (Fig. 2-B). The difference between native ( $171.6 \pm 228.9$ ) and non-native ( $146.9 \pm 244.2$ ) mean  $N_e$  values was not significant



**Fig. 3** Ancestry diagram representing the ancestry proportion of each individual to the genetic clusters. Each horizontal bar corresponds to an individual and each colour to a genetic cluster. \*Indicates native populations

( $p$ -value=0.97). Two populations exhibited very low effective population sizes within the native range; one population in Romania (ROU-DAN,  $N_e=7.1$ ) and another one in Switzerland (SWI-NEU,  $N_e=2.2$ ). Two populations displayed infinite estimates (BUL,

SWE-MOC), and one population displayed  $N_e$  values higher than 500 individuals (i.e., the second Swedish population, SWE-EMA,  $N_e=614.3$ ). Almost all non-native populations exhibited very low  $N_e$  values (35 out of the 39 non-native populations had estimated  $N_e < 50$ ; Supplementary Table 1). Three populations out of 39 non-native populations displayed infinite estimates (FRA-GAR-9, SPA-SEG, FRA-RHO-3), an issue that can arise due to sampling error (Waples and Do 2008).

Concerning recent population size changes tests, three populations showed significant  $H_e$  deficiencies, indicative of a recent genetic bottleneck (two native populations, ROU-DAN and SWI-NEU, and a non-native population, FRA-LOI-2, Supplementary Table 1,  $p$ -values  $< 0.01$ ). We also detected significant  $H_e$  excesses (which can be interpreted as population expansions) for 13 out of 39 non-native populations (Supplementary Table 1, all  $p$ -values  $< 0.002$ ).

## Discussion

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

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

Populations of introduced species often display low genetic variation because of founder effects related to the small number of propagules introduced that survived and founded the new populations (Lawson Handley et al. 2011). As a result, a genetic diversity pattern whereby non-native populations are less genetically diverse than native ones is generally expected. Our wide-range assessment of *Silurus glanis* genetic diversity only partially meets this pattern. Indeed, although we found that  $H_e$  and PA values were significantly higher for native populations than for non-native populations (a result that was not verified for AR), we identified several non-native populations (e.g., FRA-BOU, FRA-DOR-1, 2 and 3 or FRA-GAR-6) displaying similar or even higher  $H_e$  values than native populations. Further, some native populations (i.e. Swiss and Romanian populations, with  $N_e$  respectively equal to 2.2 and 7.1) displayed low  $N_e$  values compared to the  $N_e$  values estimated for many other non-native populations (e.g. mean value for non-native populations equal to 146.9). This could be explained by a high propagule pressure due to the occurrence of multiple introductions (Kolbe et al. 2004) of individuals originating from genetically distinct populations, as supported by our clustering-based analyses (discussed below). On the contrary, an introduction by a single source of individuals seems to have occurred for some other populations (Iberian population, POR-TAG, SPA-SEG). This pattern has also been observed for other introduced non-native freshwater top predators such as the pikeperch (*Sander lucioperca*), a species that also displays higher genetic diversity in non-native populations because of high propagule pressure due to multiple introductions (Poulet et al. 2009), suggesting that no single and simple introduction pathway exists for freshwater top predators. For instance, the Invasive Species Compendium CABI database (<https://www.cabi.org/isc/>) mentions the occurrence of three over six major invasion pathways for *S. glanis* (i.e. deliberate release, escape from captivity, and stowaway; Hulme et al. 2008).

We identified several patterns that may reflect different histories and pathways of introduction, which highlights the complexity of the European catfish biological invasion in Western Europe. First, we found a set of non-native populations that do not belong to clusters represented in native populations. For instance, all populations from the Garonne River (except FRA-GAR-TOU), the Tarn River or Lake Lahille were assigned to a single cluster (cluster 8) that was not identified in other areas. This lack of assignment to a native cluster might be explained by the low coverage by our sampling design of the native range of the species. Although less plausible, the potential differential effects of genetic drift following introductions in these water bodies might also have precluded assignment to native source clusters (supposing that we managed to successfully characterize these with our sampling design). Second, we also observed a set of non-native populations whose individuals were assigned to clusters also containing individuals from native populations. For instance, individuals from Great Britain (GBR-TAM) have been assigned to cluster 2, which is also the main cluster represented in the German (GER-ODE), Czech (CZE-HAT) and Romanian (ROU-DAN) populations. This result is consistent with historical records that point at an introduction of *S. glanis* individuals from Walachia (an ancient principality corresponding now to Romania) at the Woburn Abbey in 1880 for breeding purposes (Britton and Davies 2006). We note here that individuals from Romania were sampled on a local market. We hypothesized that the origin of these individuals was local (i.e. presumably from the Danube river), although we had no means to confirm their actual origin. Similarly, Italian populations and populations from Lot River (FRA-LOT-1, FRA-LOT-2) were mainly assigned to cluster 5, which is also slightly represented in a cluster where Bulgarian individuals are assigned (20% of the individuals). Based on this genetic similarity, we can hypothesize that these non-native populations could come from Bulgaria, or that Italian populations might have acted as “bridgehead” population (i.e. by acting as a source of individuals for introductions in FRA-LOT-1 and 2; Lombaert et al. 2011). Further, populations from the Dordogne river (FRA-DOR-1,2 and 3) were also assigned to cluster 2, the same cluster that has been inferred for individuals from both the French hatchery of Chateau Gontier (FRA-HAT) and the Bulgarian sample (BUL). This suggests that individuals from the hatchery may originate from—or might be genetically close to—individuals from Bulgaria, and that this hatchery might have produced and/or sold the individuals introduced in the Dordogne river. Finally, we observed a last set of non-native populations assigned to the same cluster despite inhabiting different river basins and countries, potentially indicating that one of these non-native populations may have acted as a “bridgehead” population, favouring the introduction to other non-native areas (Lombaert et al. 2010). Indeed, populations from the Iberian Peninsula (Spain, SPA-SEG and Portugal, POR-TAG) belong to the same cluster, although the source population remains unknown. Given the geographical proximity between Portugal and Spain and the dates of first detection of the species in each country, we confidently suggest that Spanish populations acted as “bridgehead” populations for individuals introduced in Portugal, supporting hypotheses from the literature (Gago et al. 2016; Ferreira et al. 2019). We also observed similarities (cluster 6) between Rhône basin populations (FRA-RHO-1, 2 and 3, FRA-SAO, FRA-FUM) and populations from the Loire basin (FRA-LOI-2, FRA-VIE), which may be explained by the occurrence of a *corridor*-like pathway (according to Hulme’s classification; Hulme et al. 2008) due to the presence of human-made channels linking the Rhône and Loire basins that might have favoured European catfish spread (Valadou 2007).

The observation that six genetically differentiated clusters were identified within a relatively narrow non-native area (Loire, Rhône and Garonne rivers in France) provides an indirect support for the occurrence of multiple introduction events of European catfish.

Given the relatively recent introduction events in Europe (around the last 60 years), the propensity for anglers to release individuals alive (Cucherousset et al. 2018), and the long lifespan of this species (70 years old maximum; Bergström et al. 2022), a rapid genetic differentiation following introduction events leading to several genetic clusters remains unlikely. Moreover, individuals assigned to several genetic clusters are sometimes found in the same river basins, which is strong evidence that multiple introductions involving different genetic sources occurred in these areas. For example, four clusters have been geographically defined in the Garonne basin: one cluster covering the Dordogne river (FRA-DOR-1,2 and 3; cluster 1), one represented by the most upstream population from the Lot river (FRA-LOT-3; cluster 2), another cluster covering populations from the Lot river (FRA-LOT-1, FRA-LOT-2; cluster 5) and a last cluster covering almost all populations from the Garonne (FRA-GAR-1 to 8) and Tarn rivers (FRA-TAR-1,2 and 3, cluster 8). It is worth mentioning that the Lot populations are separated by a large dam, which suggests that two different introductions might have occurred at each side of the dam. These results are supported by records documenting the occurrence of at least two major introductions through deliberate releases for angling purposes in the Tarn and Dordogne Rivers, and of at least two other introductions in the Lot River (Paz-Vinas and Santoul 2018). Similarly, populations from the Loire River are represented by three clusters, i.e. cluster 2 (FRA-Loi-1), cluster 6 (FRA-LOI-2) and cluster 5 (FRA-LOI-3). Even if individuals in cluster 6 could have dispersed from the Saône River using the “Canal du Centre” channel as a corridor (Valadou 2007), multiple introductions in this area for angling purposes have also been mentioned in the literature (Valadou 2007).

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

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

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

et al. 2002 for Switzerland; Jensen et al. 2018; Palm et al. 2019 for Sweden). These low genetic diversities are probably because geographical barriers (mainly the Baltic Sea) might have prevented gene flow between the lacustrine ecosystem and other continental populations and because these populations are peripheral and located at the Northern extremities of the European catfish native distribution. It is noteworthy that the high  $N_e$  value found for the Swedish population SWE-EMA ( $N_e = 614.3$ ) might be an outlier due to sampling bias, given that a recent survey using more individuals from multiple cohorts and two alternative estimation methods found  $N_e$  values ranging between 1 and 16 for that population, depending on the estimation method and year of sampling (Palm et al. 2019). The Neuchatel lake population (SWI-NEU), which was previously identified as one of the most genetically impoverished native population together with populations from Greece (Triantafyllidis et al. 2002), is also located at the periphery of the distribution range of this species. These findings agree with the core-periphery hypothesis stating that populations at the margins of its range should display lower genetic diversity than populations at the core of the range distribution (Brown 1984; De Kort et al. 2021). These low genetic diversities come along with genetic differentiation from other native areas since Swedish and Swiss populations belong to specific clusters (cluster 4 for Swedish populations and cluster 3 for Swiss populations; Fig. 3). Moreover, Swiss and Romanian populations both display low  $N_e$  values (2.2 and 7.1 respectively) and signs of recent demographic decreases ( $H_e$  deficiencies; Cornuet and Luikart 1996; Piry et al. 1999). These populations might thus be at high risk of extinction due to genetic effects (Frankham 2005). We also note that two native populations present high  $PA$  values (BUL,  $PA = 0.31$ ; ROU-DAN, 0.36), indicating that these populations harbour unique genetic diversity that should be protected from a biodiversity conservation standpoint.

Populations in Scandinavia are genetically and demographically vulnerable (Jensen et al. 2018; Palm et al. 2019). Supplementing populations with stocked individuals from Scandinavia could avoid genetic erosion due to genetic drift, but increasing their genetic diversity through the introduction of closely-related individuals from non-Scandinavian populations might not be possible since we did not identify populations that are genetically close to Scandinavian populations in our survey. Non-native populations in our dataset seem genetically healthy, with thirteen over thirty-nine displaying signals evocative of demographic expansion (i.e. heterozygosity excesses). Seventeen over thirty-nine of these non-native populations display  $N_e$  values above 50, suggesting they are genetically healthy enough for maintaining sufficient levels of genetic variation for adaptation over time. It is however noteworthy that some of these expanding non-native populations (9/13) display low  $N_e$  values (below  $< 50$ ), a pattern generally expected for introduced populations (Lawson Handley et al. 2011), despite being expanding populations. The occurrence of “bucket releases” by anglers that move individuals between different water bodies (Britton and Davies 2006; Syväranta et al. 2010; Cucherousset et al. 2018) might partly explain expansion with low genetic diversities in some water bodies. This species may also benefit from better environmental conditions in non-native areas, a factor that could also explain its expansion in such areas (Schlumberger et al. 2001) despite low levels of genetic diversity. The European catfish is considered a trophy by recreational anglers, with the largest individuals being the most appreciated and targeted. This activity that involves ‘No kill’ practices, is attractive for the tourism economy and might foster the maintenance of sustainable populations of large individuals. Developing such “no kill” practices could help to protect imperiled populations in native areas. European catfish’s stocking, mainly for angling purposes, is already common in Central Europe (Lyach 2021) and the highly dense



wild populations situated in non-native areas could also be used as genetic reservoirs for supplementing populations situated in areas where the species is endangered.

## Conclusion

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

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## Declarations

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## Authors and Affiliations

Paul Castagné<sup>1</sup>  · Ivan Paz-Vinas<sup>2</sup>  · Stéphanie Boulêtreau<sup>3</sup>  · Jessica Ferriol<sup>3</sup> ·  
Géraldine Loot<sup>1</sup> · Charlotte Veyssière<sup>1</sup> · Robert Arlinghaus<sup>4,5</sup>  · Robert Britton<sup>6</sup>  ·  
Marlène Chiarello<sup>3</sup>  · Emili García-Berthou<sup>7</sup>  · Pavel Horký<sup>8</sup>  ·  
Delphine Nicolas<sup>9</sup>  · Annamaria Nocita<sup>10</sup> · Oscar Nordahl<sup>11</sup>  · Michaël Ovidio<sup>12</sup>  ·  
Filipe Ribeiro<sup>13</sup>  · Ondřej Slavík<sup>8</sup>  · Chloé Vagnon<sup>14</sup>  · Simon Blanchet<sup>15</sup> ·  
Frédéric Santoul<sup>1</sup> 

✉ Paul Castagné  
paul.castagne@univ-tlse3.fr

Ivan Paz-Vinas  
ivanpaz23@gmail.com

Stéphanie Boulêtreau  
stephanie.bouletreau@univ-tlse3.fr

Géraldine Loot  
geraldine.loot@univ-tlse3.fr

Charlotte Veyssière  
veyssiere.charlotte@gmail.com

Robert Arlinghaus  
arlinghaus@igb-berlin.de

Robert Britton  
rbritton@bournemouth.ac.uk

Marlène Chiarello  
marlene.chiarello@gmail.com

Emili García-Berthou  
emili.garcia@udg.edu

Pavel Horký  
pavel.horky.r@gmail.com

Delphine Nicolas  
nicolas@tourduvalat.org

Annamaria Nocita  
annamaria.nocita@unifi.it

Oscar Nordahl  
oscar.nordahl@lnu.se

Michaël Ovidio  
m.ovidio@uliege.be

Filipe Ribeiro  
fmribeiro@fc.ul.pt

Ondřej Slavík  
oslavik@af.czu.cz

Chloé Vagnon  
chloe.vagnon@gmail.com

Simon Blanchet  
simon.blanchet@lilo.org

Frédéric Santoul  
frederic.santoul@univ-tlse3.fr

- <sup>1</sup> Laboratoire d'Ecologie et Diversité Biologique (EDB), Université Paul Sabatier Toulouse III, Toulouse, France
- <sup>2</sup> Department of Biology, Colorado State University, Fort Collins, CO, USA
- <sup>3</sup> Laboratoire Ecologie Fonctionnelle et Environnement, Université Paul Sabatier Toulouse III, Toulouse, France
- <sup>4</sup> Department of Fish Biology, Fisheries and Aquaculture, Leibniz Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, 12587 Berlin, Germany
- <sup>5</sup> Division of Integrative Fisheries Management, Faculty of Life Sciences, Humboldt-Universität zu Berlin, Phillipstrasse 13, 10115 Berlin, Germany
- <sup>6</sup> Fish Ecology & Conservation Cluster, Department of Life and Environmental Sciences, Bournemouth University, Poole BH12 5BB, UK
- <sup>7</sup> GRECO, Institute of Aquatic Ecology, University of Girona, Girona, Catalonia, Spain
- <sup>8</sup> Faculty of Agrobiology, Food and Natural Resources, Department of Zoology and Fisheries, Czech University of Life Sciences Prague, Kamýcká 129, Suchbát, Prague 620 165 21, Czech Republic
- <sup>9</sup> Tour du Valat - Research Institute for Mediterranean Wetlands Conservation, Le Sambuc, 13200 Arles, France
- <sup>10</sup> Natural History Museum, Florence University, Florence, Italy
- <sup>11</sup> Department of Biology and Environmental Sciences, Faculty of Health and Life Sciences, Centre for Ecology and Evolution in Microbial Model Systems (EEMiS), Linnaeus University, 39231 Kalmar, Sweden
- <sup>12</sup> Laboratory of Fish Demography and Hydroecology, Management of Aquatic Resources and Aquaculture Unit, Freshwater and Oceanic Science Unit of Research-FOCUS, University of Liège, 22 Quai E. Van Beneden, B-4020 Liège, Belgium
- <sup>13</sup> Faculty of Sciences, MARE - Marine and Environmental Sciences Centre/ARNET - Aquatic Research Network, University of Lisbon, 1749-016 Lisbon, Portugal
- <sup>14</sup> UMR CARTEL - Université Savoie Mont Blanc, Chambéry, France
- <sup>15</sup> Station d'Écologie Théorique et Expérimentale du CNRS à Moulis, UAR2029, Centre National de la Recherche Scientifique (CNRS), F-09200 Moulis, France