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1 **Getting off on the right foot: Integration of spatial distribution of genetic**
2 **variability for aquaculture development and regulations, the European**
3 **perch case**

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7 **Short title:** Integration of spatial distribution of genetic variability

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29 **Abstract**

30 Knowledge of spatial genetic variability patterns allows improving conservation actions,
31 translocation regulations, and farming productivity. However, these genetic variability
32 patterns are often considered after issues are observed, long after the beginning of production.
33 By taking into account lessons from other species, we investigate the genetic variability of
34 *Perca fluviatilis*, a species at a nascent stage of production. The genetic variability has been
35 previously studied but, due to discrepancies between conclusions and methodological limits,
36 the spatial distribution of genetic variability in *P. fluviatilis* has not been demonstrated
37 conclusively. Here, we characterise the genetic variability across 84 West-Palaeartic
38 sampling sites using mitochondrial and microsatellite markers. We aim to provide (i) a
39 genetically-based population structure that could act as an impetus for further production
40 improvement and (ii) guidelines for translocation regulations. Our analyses show an uneven
41 distribution of genetic variability. Based on inter-population genetic differentiation, we
42 identify five large geographic scale clusters which are further divided into several subgroups.
43 Local genetic diversity mapping highlights a spatial pattern with several hotspots, which has
44 serious implications in the development of appropriate regulations of translocations.
45 Moreover, we here report an association between genetic differentiations and previously
46 reported zootechnical performances. We ultimately propose guidelines for further
47 investigations of population-specific performances in aquaculture and potentially efficient
48 regulations for policy-makers.

49 **Keywords:** Geographic differentiation - Genetic diversity - *Perca fluviatilis* - Management –
50 Production

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58 **1. Introduction**

59 During the Quaternary, most inland species went through several climatic cycles (Andersen
60 and Borns, 1994). The alternation of Ice Ages and interglacial periods resulted in range shifts
61 which depended on eco-climatic requirements and tolerances of taxa. Temperate-adapted taxa
62 underwent range shrinking during Ice Ages and distribution expansions to at least portions of
63 their initial distribution range during interglacial periods (Avisé, 2000; Hewitt, 2004a; Stewart
64 et al., 2010), while cold-adapted taxa went through the opposite pattern (Fedorov et al., 2008;
65 Magnuson et al., 1979; Martinet et al., 2018; Quinzin et al., 2017). Such movements have
66 shaped the current distribution and genetic variability patterns of species (Hewitt, 2004b;
67 Stewart et al., 2010). First, the distribution of many species was fragmented into different
68 isolated refugia during range shrinking times (Avisé, 2000; Hewitt, 2004b). This led to a
69 decrease of gene flow between populations and, potentially, to geographic genetic
70 differentiations (Hewitt, 2000; Stewart et al., 2010). Second, post-glacial re-colonisations of
71 non-refuge areas led to a loss of genetic diversity through founder events occurring at the
72 expanding front while ancestral genetic diversity was often maintained in refuge regions
73 (Avisé, 2000; Hewitt, 2004b). Finally, the mixing of individuals from different refugia in
74 newly colonised areas created regions of high genetic diversity (i.e. suture zones; Avisé,
75 2000; Hewitt, 2004b). Moreover, species intrinsic features (e.g. limited dispersal, (partial)
76 post-zygotic reproduction isolation) can also contribute to shape local genetic specificities of
77 populations (Behrmann-Godel, 2004; Lecocq et al., 2018, 2017). This has resulted in an
78 uneven distribution of the genetic variability (i.e. genetic diversity and genetic differentiation)
79 across species ranges (Avisé, 2000; Hewitt, 2004b).

80 Meeting human nutritional needs has often required the domestication (*sensu* Lecocq 2019)
81 and trade of wild animal species (Salo et al., 2014; Teletchea and Fontaine, 2014; Velthuis
82 and van Doorn, 2006). However, this development is characterised by challenges which can
83 impede the sustainability of animal production. Successfully domesticating a novel species is
84 a long-term and difficult task since it implies mastering species life cycle in a human-
85 controlled environment (see production development pathways in Teletchea and Fontaine,
86 2014). Furthermore, translocation of individuals within and outside the species native range
87 can occur when the production and subsequent trade begin. This can lead to many
88 conservation concerns (e.g. biological invasion, pathogen spillover, genetic homogenisation;
89 Lecocq et al., 2016a; Mack et al., 2000; Perrings et al., 2010). Knowledge of spatial genetic
90 variability patterns provides key information to enhance animal production development as

91 well as to mitigate its potential negative impacts on wild populations (Danancher and Garcia-
92 Vazquez, 2011).

93 For animal producers, understanding spatial patterns of genetic variability is potentially
94 valuable in order to optimise the exploitation of a particular species in controlled conditions.
95 Indeed, genetically differentiated populations underwent specific evolutionary histories and
96 could have acquired phenotypic specificities (i.e. geographic differentiation; Blanck and
97 Lamouroux, 2007; Forschler and Kalko, 2007; Youngson et al., 2003) through genetic
98 adaptations to local environments (Losos and Ricklefs, 2009). Some of these specificities (i.e.
99 characteristics which are particular to a specific population) can concern biological traits of
100 interest for production, trade, and profit (e.g. improved provision of ecosystem services,
101 higher resilience, higher acceptability by stakeholders; Imsland et al., 2002; Janhunen et al.,
102 2009; Lecocq et al., 2016a, 2016b; Stort, 1974). This leads to different potentials between
103 populations for production. Ultimately, considering these population potentials can foster
104 successful animal production development (e.g. Velthuis and van Doorn, 2006).

105 Globalisation of species production and trade (for agriculture, pets, model organisms for
106 scientific purposes, game, restocking, or biological control agents) leads to translocations that
107 can threaten local species and population(s). While risks related to invasions of non-native
108 species have been widely studied (Mooney and Cleland, 2001; Simberloff et al., 2013),
109 translocations within the distribution range of a particular species have received far less
110 attention (Lecocq et al., 2016a). Yet, they have been shown in some cases to be more
111 detrimental (Buoro et al., 2016). Translocations of genetically differentiated individuals
112 within a species range can lead to outbreeding, genetic homogenisation, or competition issues
113 threatening genetic intraspecific variability (Champagnon et al., 2012; Cross, 2000;
114 Danancher and Garcia-Vazquez, 2011; Rhymer and Simberloff, 1996). This genetic
115 variability (i.e. the combination of local genetic diversity and inter-population genetic
116 differentiation) is seen as one of the key factors to species conservation and survival (Booy et
117 al., 2000; Frankham et al., 2010). Indeed, local genetic diversity and inter-population
118 genetic differentiation contribute to the species ability to adapt to future challenges (Laikre et
119 al., 2005; Sgrò et al., 2011) and to global biodiversity that maximizes species long-term
120 survival chances (Conner and Hartl, 2004; Lecocq et al., 2015; Phillimore and Owens, 2006),
121 respectively. Therefore, preserving genetic variability is an important focus in conservation
122 programs (Laikre et al., 2005; Mankiewicz-Boczek et al., 2013; Sgrò et al., 2011). Given the
123 important advantages of many produced/traded species for human livelihood, health, or

124 economy, a complete interdiction of translocations is not feasible. Therefore, pragmatic
125 translocation regulations are needed. Finding spatial patterns of genetic variability allows
126 developing relevant regulations to preserve population specificities and guidelines for
127 translocations (e.g. Lecocq et al., 2016a, 2015).

128 Despite their potentially valuable integration in incipient species domestication and trade,
129 intraspecific genetic variability patterns often begin to be considered long after the beginning
130 of production (Fleming et al., 2000; Lecocq et al., 2016a; Lemer and Planes, 2012). Indeed,
131 new candidate species often start to be produced without due consideration to issues already
132 encountered with other fish species when spatial patterns of intraspecific variability when not
133 considered early in the domestication process (Fleming et al., 2000; Lemer and Planes, 2012;
134 McGinnity et al., 2003). In this study, we focus our attention on the European perch (*Perca*
135 *fluviatilis* L.), an inland fish species at a nascent stage of its aquaculture production. *Perca*
136 *fluviatilis* is a temperate freshwater and brackish water fish species distributed across the
137 Palaearctic realm (except in most of the Mediterranean Sea coast regions; Stepien and
138 Haponski, 2015). This species, traditionally used in both commercial and recreational
139 fisheries, is the focus of an increasing interest in aquaculture since the 90s in western Europe
140 (Fontaine, 2004; Kestemont et al., 2015; Kestemont and M elard, 2000). Although several
141 major bottlenecks are still observed in aquaculture (Kestemont et al., 2015; Policar et al.,
142 2019), further development of *P. fluviatilis* production can be expected because this species
143 has an increasingly impressive market potential (i.e. current production is largely inferior to
144 European demand; Kestemont et al., 2015). Since the species displays a significant invasive
145 potential (Kestemont et al., 2015) as well as documented intraspecific genetic (e.g. Bergek
146 and Bj orklund, 2009; Nesb o et al., 1999) and phenotypic (Blanck and Lamouroux, 2007;
147 Pimakhin, 2012; Roch et al., 2015) differentiations, it is likely that (i) production potential
148 may vary between populations and (ii) unregulated translocations could lead to dramatic
149 consequences. This suggests that production and translocations of the European perch should
150 be optimised and regulated, respectively, at the nascent stage of its production.

151 The demographic history of the European perch was investigated in previous studies.
152 However, most of these studies focused on limited geographic areas (e.g. Bergek and
153 Bj orklund, 2009; Butkauskas et al., 2012). Only one study investigated the species genetic
154 variability at large geographic scale and identified four genetic groups and three refugia
155 (suggesting a plausible fourth one, not contributing to re-colonisation) during the last glacial
156 maximum (25,000 to 15,000 before present; Nesb o et al., 1999). However, tremendous

157 developments in analytical and statistical approaches occurred since these previous
158 publications. The former large-scale phylogeographic study (Nesbø et al., 1999) was only
159 based on a small part of the mitochondrial genome as well as a few Random Amplification of
160 Polymorphic DNA (RAPD) markers but limitations of such approaches have now been
161 highlighted. First, phylogeographic and population genetic studies based on only a small part
162 of genome, in this case mitochondrial genome, remain controversial because (i) the part of
163 genome analysed is often chosen arbitrarily (Cruaud et al., 2014) and (ii) population
164 differentiations are not always characterised by the accumulation of many genetic differences,
165 making their detection by using small genome part unlikely (Arif and Khan, 2009;
166 Patwardhan et al., 2014). Second, multilocus nuclear markers such as RAPD markers have
167 been replaced by more powerful multi-allelic markers such as microsatellites because RAPD
168 approach presents a low reproducibility and a limited usefulness for meta-analysis (Arif and
169 Khan, 2009; Sunnucks, 2000). Beside potential limitations due to the state of scientific and
170 technical knowledge at the time of previous investigations, an overview of phylogeographic
171 studies investigating specific geographic areas shows discrepancies in conclusions (see for
172 instance Gyllensten et al., 1985 and Olsson et al., 2011). Therefore, due to analytical
173 limitations and discrepancies between conclusions, previous studies have not demonstrated
174 conclusively the spatial distribution of genetic variability in *P. fluviatilis*.

175 In the present study, we establish the spatial genetic variability patterns and the population
176 structure of the European perch through the analysis of four mitochondrial regions and eight
177 nuclear microsatellite markers. By considering these spatial patterns, we aim to provide (i) a
178 genetically-based population structure that could act as an impetus for further improvement of
179 *P. fluviatilis* production and (ii) guidelines for efficient regulations of the species
180 translocations within its natural range to preserve wild intraspecific variability.

181 **2. Material and Methods**

182 *2.1 Sampling*

183 We collected 409 European perch tissue samples from 84 sampling sites (five individuals per
184 sampling site, except for six sites for which less individuals were collected) from different
185 drainage basins (estuaries, rivers, and lakes) across the species native range in western Eurasia
186 and Siberia (Table S1, Fig. 1, and Fig. S1). Sample providers dissected a small piece of caudal
187 or dorsal fins or scales from field captured individuals. Samples were stored in 99% ethanol at
188 – 20 °C. We included samples of *P. schrenkii* Kessler 1874 (seven samples from two sites,

189 Table S1) and *P. flavescens* Mitchill 1814 (sequences from GenBank), the two sister species
190 of *P. fluviatilis*, as outgroups for mitochondrial analyses. All samples were collected
191 respecting both European and national sampling regulations. We isolated genomic DNA using
192 DNeasy® Blood and Tissue kit (QIAGEN France SAS®) (18-h incubation in proteinase K at
193 56 °C). Voucher specimens used in molecular investigations were deposited at the University
194 of Lorraine (Nancy, France).

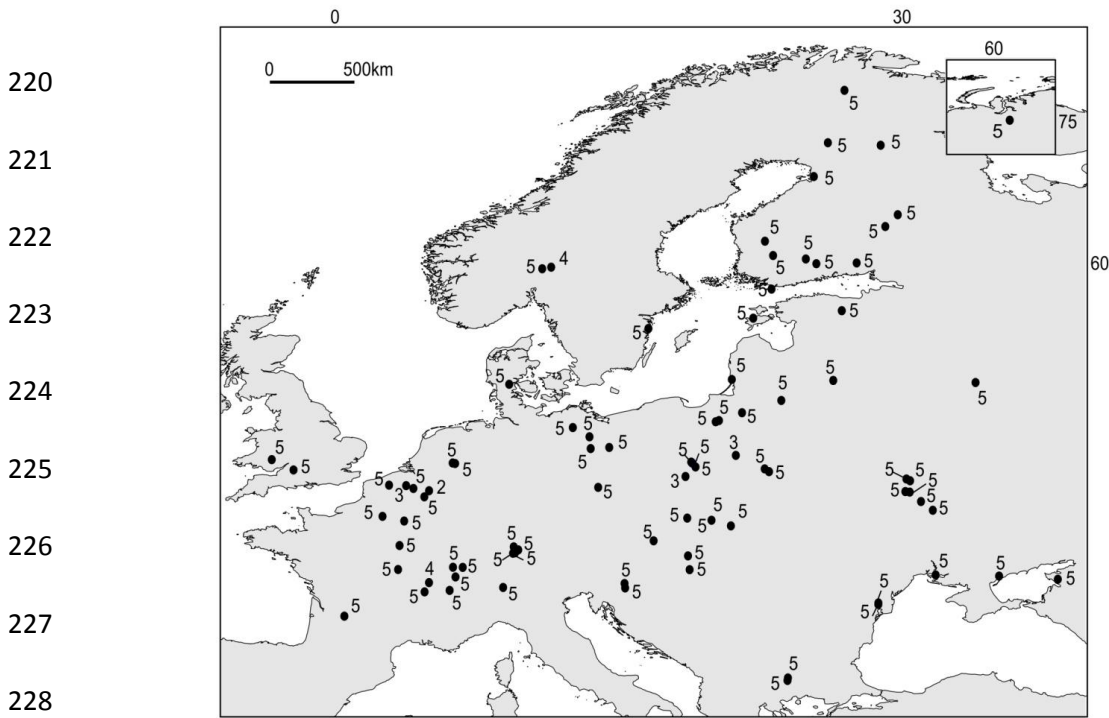
195 *a. Genetic analyses*

196 We selected four mitochondrial regions, commonly used to evaluate phylogeographic patterns
197 of fish species (Costedoat and Gilles, 2009; Makhrov and Bolotov, 2006): cytochrome b
198 (Cytb), D-loop or control region (D-loop), 16S rRNA (16S), and cytochrome oxidase I (COI).
199 Polymerase chain reaction amplifications of Cytb, D-loop, 16S, and COI were carried out
200 using primers L14724F / H15918R (Song et al., 1998), HV2 / CSBD (Nesbø et al., 1998),
201 16Sar / 16Sbr (Palumbi et al., 1991), and jgLCO1490 / jgHCO2198 (Geller et al., 2013),
202 respectively. The reaction components were 10 pmol primers, PPP MasterMix (Top Bio®),
203 DNA (100 - 200 ng/μL), and water. An initial step of five minutes at 95 °C was followed by
204 38 cycles of denaturation at 94 °C for 40 s, 50 s at annealing temperature (55.8 °C for 16S, 49
205 °C for COI, 55 °C for Cytb and D-loop), and one minute extension at 72 °C, and a 10 min
206 final extension at 72 °C. We purified PCR products with E.Z.N.A.® Gel Extraction Kit
207 (Omega Bio-tek®) and single read sequencing was performed by MacroGen Europe
208 (Amsterdam, Netherlands) on a 3730XL (Applied Biosystems) using primers H15918R,
209 CSBD, 16Sbr, and jgLCO1490. We edited sequences of mitochondrial markers using
210 CodonCode Aligner 7.1.2 (CodonCode Corporation, Dedham, Massachusetts, USA). The *P.*
211 *fluviatilis* origin of each sequence was checked in NCBI using BLAST (Zhang et al., 2000).
212 We aligned all sequences using MAFFT (default parameters; Katoh et al., 2017). Translation
213 to proteins for partial COI and Cytb sequences was performed in Mesquite using vertebrate
214 mitochondrial code. We deposited sequences in GenBank (GenBank accession numbers:
215 MG969725 to MG969793; Table S1). Mitochondrial regions were ultimately concatenated
216 into a single

217 alignment for the different analyses using Mesquite 3.20 (Maddison and Maddison, 2001).

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219



229 **Figure 1: Sampling map for *Perca fluviatilis*.** Sampling sites are represented by black circles and
 230 juxtaposed numbers indicate the number of individuals sampled at each site.

231 We selected eight microsatellite markers previously used for *P. fluviatilis* (Ben Khadher et al.,
 232 2015): PflaL1, PflaL2, PflaL4, PflaL6 (developed in *Perca flavescens*; Leclerc et al., 2000),
 233 SviL7 (developed in *Stizostedion vitreum*; Wirth et al., 1999), SVi17 (developed in
 234 *Stizostedion vitreum*; Borer et al., 1999), YP60, and YP111 (developed in *Perca flavescens*;
 235 Li et al., 2007). We performed amplifications through the use of two multiplexes using
 236 fluorescently labelled primers. A first multiplex (A) contained PflaL2 (FAM), PflaL4 (PET),
 237 SviL7 (VIC), Svi17 (FAM), and YP111 (PET). The second multiplex (B) contained YP60
 238 (FAM), PflaL1 (VIC), and PflaL6 (FAM). Polymerase chain reaction was carried out using
 239 Multiplex TEMPase 2X MasterMix (VWR®), 10 pmol fluorescent primer mix, water, and
 240 DNA (100 - 200 ng/μL). PCR conditions for multiplex A were: 95 °C for five minutes, 28
 241 cycles at 95 °C for 30 s, 55 °C for 90 s, and 72 °C for 30 s, and a final extension of 45 s at 60
 242 °C. For multiplex B, PCR conditions were: 95 °C for five minutes, six cycles at 95 °C for 30
 243 s, 48 °C for 90 s, and 72 °C for 30 s, 22 cycles at 95 °C for 30 s, 50 °C for 90 s, and 72 °C for
 244 30 s, and a final extension at 60 °C for 45 s. We diluted PCR products (1:151) with deionised
 245 water and added Hi-Di™ Formamide (Applied Biosystems®) and GeneScan™ 600 LIZ®
 246 Size Standard (Applied Biosystems®). We performed fragment analysis on a 3500 Genetic
 247 Analyser (Applied Biosystems HITACHI®). We scored alleles in Geneious 11.0.2 (Kearse et
 248 al., 2012).

249 2.3 *Spatial distribution of genetic variability*

250 Analyses hereby presented were performed on the concatenated mitochondrial alignment (but
251 see Table S2 and Fig S2 for locus specific results). We calculated haplotype diversities and
252 nucleotide diversities (Nei and Li, 1979) in DnaSP (Librado and Rozas, 2009). We
253 constructed haplotype networks using the median-joining algorithm (Bandelt et al., 1999)
254 implemented in Network 5.0.0.1 (available at [http://www.fluxus-](http://www.fluxus-engineering.com/sharenet.htm)
255 [engineering.com/sharenet.htm](http://www.fluxus-engineering.com/sharenet.htm)), treating insertion-deletion (indel) events as a fifth state.

256 We performed phylogenetic analyses using maximum likelihood (ML) and Bayesian (BA)
257 methods. We partitioned coding genes, COI and Cytb, by base position (1st, 2nd and 3rd) to
258 identify the best-fitting substitution model with jModeltest 2.1.10 (Darriba et al., 2012) with
259 the Akaike information criteria corrected for small sample sizes. Best models are reported in
260 Table S3. We conducted BA in MrBayes 3.1.2 (Ronquist and Huelsenbeck, 2003). Selected
261 models unimplemented in MrBayes were replaced by the closest overparameterised model
262 available (Huelsenbeck and Rannala, 2004). All analyses were performed on concatenated
263 and individual markers. We ran five independent analyses in MrBayes (20 million
264 generations) and the first 380,000 generations were discarded as burn-in. We performed ML
265 analyses in Garli 2.0 (Zwickl, 2006). We carried out five independent runs and evaluated
266 statistical confidence in nodes using 1,000 non-parametric bootstrap replicates.

267 In addition, we generated maps displaying the geographic distribution of local genetic
268 diversity. For this purpose, we first used a sliding window approach to estimate the nucleotide
269 diversity π (Nei and Li, 1979) associated with each cell of a template raster grid covering the
270 study area (spatial resolution: 12.5 arcmin). This method attributes, to each grid cell, a value
271 of nucleotide diversity estimated from sequences sampled within a circle centred on the
272 considered cell. Nucleotide diversity is corrected for unequal sample size and is based on both
273 allelic frequencies and genetic distances between sequences, which are complementary
274 aspects when studying distribution of genetic variability. The sliding window is implemented
275 in a R script available with the toolbox SPADS (Dellicour and Mardulyn, 2014). We tested
276 several values for the radius r (25, 50, 100, and 200 km) used to define the sliding window.
277 Several radius values were tested in order to evaluate the impact of the sliding window extent
278 on the genetic diversity distribution. Starting from the raster files obtained by the sliding
279 window approach, we then performed an inverse distance interpolation with the R function
280 “GDivPAL” also available with the toolbox SPADS (distance weighting parameter $a = 5$). As

281 a third step, we drew a convex hull around fictive circles of 100 km radius centred on
282 sampling locations for each generated interpolation surface in order to define the different
283 “study areas” by cropping the surfaces and thus avoiding excessive extrapolation. Only results
284 with a radius of 50 km are presented and maps with other radius are available in Fig. S3. The
285 use of the sliding window approach allows to avoid the arbitrary “population” delimitation
286 and to minimize the effect of small sampling sizes (Lecocq et al., 2018). Indeed, through this
287 approach, the genetic diversity is estimated within a circle radius. For a particular location, the
288 genetic diversity can thus be estimated from a large number of individuals even though few
289 individuals were sampled per site (except in the case of isolated sampling sites).

290 For the microsatellite dataset, potential errors (allelic dropouts, stuttering, and null
291 alleles) were assessed using the MICRO-CHECKER software (Van Oosterhout et al., 2004).
292 We conducted a factorial correspondence analysis (FCA) as implemented in the program
293 GENETIX 4.02 (Belkhir et al., 2004) in order to get a graphical representation of genetic
294 variation among individuals. We estimated global locus genetic diversity through the
295 computation of two coefficients in HP-RARE 1.1 program (Kalinowski, 2005): number of
296 alleles per locus (A) and allelic richness (Ar). Number of private alleles was assessed in
297 GenAIEx 6.5 (Peakall and Smouse, 2006) and observed (H_o) and expected (H_e)
298 heterozygosities were calculated in GENETIX. As for the analysis of mitochondrial
299 sequences, we generated a map representing the geographic distribution of genetic variability.
300 For this purpose, we estimated and averaged the Bray-Curtis dissimilarity (Bray and Curtis,
301 1957) within a sliding window using the same interpolation protocol detailed above for
302 mitochondrial sequences.

303 *2.4 Population structure*

304 For mitochondrial sequences, we first assessed population structure by estimating Φ_{ST} statistic
305 on sampling sites through an Analysis of MOlecular VAriance (AMOVA; i.e. when
306 considering only one group of sampling sites; Excoffier et al., 1992) performed in Arlequin
307 3.5 (Excoffier and Lischer, 2010) with 10,000 permutations. We then used SPADS to estimate
308 the phylogeographic structure as measured by $N_{ST} - G_{ST}$ (Pons and Petit, 1996), and its
309 statistical significance was tested by recalculating them with 10,000 random permutations of
310 haplotypes in the original data sets. As the global Φ_{ST} estimate was significant, patterns of
311 genetic variation were assessed by Spatial Analysis of MOlecular VAriance (SAMOVA; K=2
312 to K=10; 10,000 iterations, ten repetitions; Dupanloup et al., 2002) as implemented in

313 SPADS. The SAMOVA algorithm assigns sampling sites to groups (or “clusters”) based on
314 geographic vicinity and sequence similarity. The number of clusters reflecting the most-likely
315 genetic structure was chosen based on the maximized among-group variation (Φ_{CT}). Among
316 the ten repetitions performed for a given K (number of clusters) to identify, we systematically
317 kept the run associated with the highest value of Φ_{CT} .

318 For microsatellites data, we first assessed global differentiation by estimating F_{ST} statistic on
319 sampling sites (i.e. when considering only one group of sampling sites) through an AMOVA
320 performed in Arlequin 3.5 (Excoffier and Lischer, 2010) with 10,000 permutations. Genetic
321 population structure was assessed with the Bayesian clustering method implemented in
322 STRUCTURE 2.3.4 (Pritchard et al., 2000) that aims to identify population clusters
323 respecting Hardy-Weinberg and linkage equilibriums. We performed ten independent
324 STRUCTURE runs for each tested value of K ranging from one to 50. Each run was made of
325 10 million Markov chain Monte Carlo iterations, discarding the first one million iterations as
326 burn-in. We used the model with correlated allele frequencies and assuming admixture. The
327 most probable K was identified based on the consensus of the ΔK method (Evanno et al.,
328 2005) and of log-likelihood values associated with each K (“log(P(K)) method”) using
329 STRUCTURE HARVESTER 0.9.94 (Earl and VonHoldt, 2012). We conducted another
330 analysis with the most probable K using the software CLUMPP 1.1.2 (Jakobsson and
331 Rosenberg, 2007) to calculate individual ancestry values (one Q-value per cluster) averaged
332 over ten runs using the “Greedy” algorithm.

333 **3. Results**

334 *3.1 Sequence and microsatellite variation*

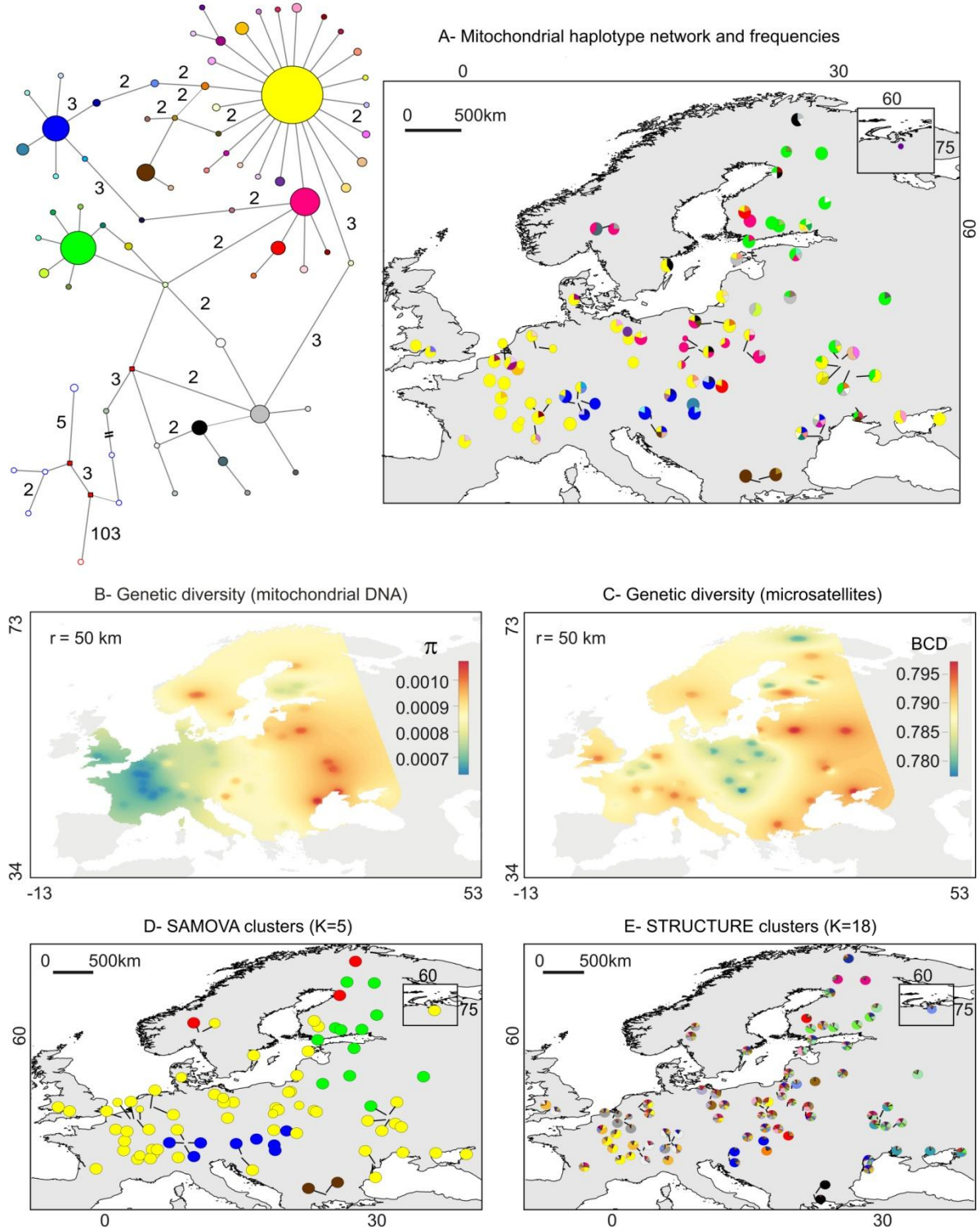
335 The concatenated mitochondrial alignment resulted in 1,893 aligned nucleotides: 541 base
336 pairs (bp) from 16S (10 variable sites), 641 bp from COI (23 variable sites), 399 bp from Cytb
337 (18 variable sites), and 312 bp from D-Loop (seven variable sites; see descriptive indicators in
338 Table S2). Our median-joining network results showed a star-like structure with one
339 dominating haplotype surrounded by several haplotypes (distant from the main haplotype by
340 one or two mutations) as well as other less frequent haplotypes (Fig. 2A). For the
341 microsatellite dataset based on eight markers, there was no significant evidence for the
342 presence of scoring errors across populations. Number of alleles varied from 14 (Yp111) to 40
343 (Svi17) between loci across samples and descriptive indicators are available in Table S4.

344 *3.2 Geographic distribution of genetic variability*

345 Overall, our median-joining network (64 different haplotypes) based on mitochondrial
346 concatenated alignment supported the geographic genetic differentiation between five major
347 groups of haplotypes (Fig. 2A): (i) the current European Plain (i.e. ranges from the Pyrenees
348 Mountains across northern Europe to the Ural Mountains in Russia), (ii) the Danube drainage
349 system and Alpine Foreland (i.e. from Lake Constance in the west to Linz in the east), (iii) the
350 Balkans, (iv) western and northern Fennoscandia, and (v) eastern Europe (i.e. between 20°E
351 and 40°E and between 45°N and 70°N). ML and BA phylogenetic analyses led to similar tree
352 topologies, thus here we present only results obtained with the concatenated matrix with
353 Bayesian analyses. The overall geographic pattern for each marker is similar to network
354 analyses, except for the delineation between western and northern Fennoscandia and eastern
355 Europe (Fig. S4). However, there was no lineage sorting within *P. fluviatilis* and intraspecific
356 lineages were not well supported (Fig. S4). Nonetheless, with all markers and different
357 analyses, Danube individuals formed a monophyletic group. Regarding microsatellites, the
358 FCA showed that Balkans, Danube and Alpine Foreland tended to be slightly separated from
359 other sampling sites (Fig. S5).

360 Mapping of local genetic diversity based on mitochondrial sequences and microsatellites
361 showed that this genetic diversity was unevenly distributed (Fig. 2B-C). The mitochondrial
362 nucleotide diversity was higher in Fennoscandia, surrounding the Danube and along an
363 eastern diagonal (i.e. from Baltic countries to the north of the Black Sea; Fig. 2B). On the
364 contrary, lower diversity was highlighted in western Europe. Genetic diversity estimated with
365 microsatellites was quite homogeneous across the sampling range with lower genetic diversity
366 spots in western and central Europe as well as in southern and northern Finland (Fig. 2C).

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368

369 **Figure 2: Mitochondrial haplotype network, distribution of genetic diversity and population**
 370 **structure of *Perca fluviatilis*.** (A) Mitochondrial median-joining haplotype network and spatial
 371 distribution of haplotype frequencies based on the concatenated alignment. In the network, each
 372 haplotype is represented by a circle, circle sizes are relative to haplotype frequencies and numbers
 373 correspond to the number of mutations that differentiates haplotypes (absence of number
 374 corresponding to a single mutation). Red squares on lines represent undetected/extinct intermediate

375 haplotype states. Black circles correspond to *P. fluviatilis* sequences, empty red circles to *Perca*
376 *flavescens* sequences, and empty blue circles to *Perca schrenkii* sequences. The adjacent map reports
377 the haplotype frequencies in each sampling site and corresponding pie chart colours refer to the
378 corresponding haplotype colour of the network. Pie chart sizes are relative to the number of
379 individuals analysed for each sampling site. (B) Interpolation of genetic diversity (nucleotide diversity
380 π) estimated with the concatenated alignment of mitochondrial sequences ($r=50$ km). (C) Interpolation
381 of genetic diversity (Bray-Curtis dissimilarity “BCD”) estimated with the eight microsatellite markers
382 ($r = 50$ km). (D) Results of genetic clustering based on the concatenated alignment of mitochondrial
383 sequences (spatial analysis of molecular variance). (E) Results of genetic clustering based on
384 microsatellites (STRUCTURE). For clustering analyses (D-E), we only report the clusters identified
385 for the best-supported partition, i.e. $K = 5$ clusters for SAMOVA (based on the concatenated
386 mitochondrial sequences alignment) and $K = 18$ clusters for STRUCTURE (based on microsatellites).
387 On these maps, pie charts sizes indicate the number of samples collected from a sampling site. (For
388 interpretation of the references to colour in this figure legend, the reader is referred to the web version
389 of this article).

390 3.3 Population structure

391 Geographic structuring was significantly supported by analysis of AMOVA which indicated a
392 differentiation over all sampling sites ($\Phi_{ST} = 0.58$, p -value < 0.05). We also found a
393 significant phylogeographic signal ($N_{ST} - G_{ST} = 0.14$, p -value < 0.05). In SAMOVA, Φ_{CT}
394 decreased until $K = 6$ clusters before increasing with higher number of clusters, levelling out
395 at $K = 8$ ($\Phi_{CT} = 0.64$, $\Phi_{ST} = 0.70$, $\Phi_{SC} = 0.17$; Table S5). Two levels of structure were
396 distinguished to fit our results: $K = 2$ and $K = 5$. At $K = 2$, the clustering split sampling
397 locations belonging to the Danube drainage basin along with one sampling location of the
398 Alpine Foreland *versus* all other sampling locations. With increasing number of clusters, the
399 clustering split sampling locations from the (i) Balkans, (ii) eastern Europe, (iii) western and
400 northern Fennoscandia, and (iv) the European Plain. Above $K = 5$, additional clusters
401 corresponded to single sampling sites which made little biological sense. Therefore, structure
402 at $K = 5$ ($\Phi_{CT} = 0.63$, $\Phi_{ST} = 0.70$, $\Phi_{SC} = 0.19$) was considered (Fig. 2D). The $K = 5$ geographic
403 clusters were congruent with results obtained in haplotype networks.

404 Overall AMOVA based on microsatellites revealed a significant genetic differentiation
405 ($F_{ST}=0.21$, p -value < 0.05). STRUCTURE analyses based on this dataset identified a best
406 supported value for $K = 18$ clusters (Fig. S6). Overall, these 18 clusters were consistent with
407 SAMOVA clusters identified with mitochondrial sequences since they appeared as

408 subdivisions of the five SAMOVA clusters: (i) European Plain cluster is subdivided into
409 eleven subgroups, (ii) western and northern Fennoscandia cluster matches with microsatellite
410 subgroups except for the Norwegian sampling site, (iii) eastern Europe cluster is split into
411 three subgroups, (iv) Danube cluster is divided into two subgroups, and (v) Balkans cluster is
412 identical to the mitochondrial one. There were few mismatches with mitochondrial clusters
413 (i.e. in the border areas in southern Fennoscandia, north of the Danube, and in eastern Europe;
414 Fig. 2E).

415 **4. Discussion**

416 Although similar sampling size is used in several other phylogeographic studies (e.g.
417 Fontanella et al., 2008; Loughheed et al., 2013; for fishes: Cook et al., 2017; Santos et al.,
418 2009), our results for regions associated with lower sampling effort (i.e. Scandinavia, South-
419 East Europe, and Russia) should be considered with caution. Indeed, lower sampling efforts
420 could impact the accuracy of genetic diversity estimates or the relevance of population
421 structure analysis. Therefore, we cannot rule out potential artefactual conclusions in these
422 areas. However, we argue that the observed global phylogeographic patterns are likely since a
423 previous study with higher sampling effort in these areas obtained similar results (Nesbø et
424 al., 1999; i.e. specific haplotypes[s] in Scandinavia and southern Europe corresponding to
425 haplotypes found in this study).

426 *4.1 Spatial distribution of genetic variability in *Perca fluviatilis**

427 Mitochondrial DNA-based analyses show an uneven distribution of the genetic variability
428 (Fig. 2A-B). The observed strong genetic structure between populations (Fig. 2A) shapes five
429 major clusters occurring in different geographic regions of the *P. fluviatilis* range (Fig. 2D):
430 (i) the European Plain, (ii) west-northern Fennoscandia, (iii) eastern Europe, (iv) the Danube
431 and the Alpine Foreland (hereafter called Danube), and (v) the Balkans. Mapping of spatial
432 distribution of genetic diversity shows some hotspots across the species range (Fig. 2B): (i) in
433 the eastern diagonal which reflects the suture zone between the European Plain and eastern
434 Europe clusters, (ii) in northern Finland where west-northern Fennoscandia and eastern
435 Europe clusters co-occur, and (iii) in the Alpine Foreland, north of the Danube basin, and in
436 Slovenia where European Plain and Danube clusters meet. Microsatellites-based analyses
437 highlight a similar uneven distribution of the genetic variability. Although more genetic
438 diversity hotspots occur in western Europe, the population structure is overall a subdivision of
439 mitochondrial clusters (Fig. 2C-D). Microsatellites-based results should be carefully

440 considered since they are based on a limited sampling size but their congruence with
441 mitochondrial DNA-based analyses tends to support their relevance (Fig. 2). The differences
442 between the two types of genetic information are most likely due to nuclear genome
443 specificities in effective population size and mutation rates (Arif and Khan, 2009; Johnson et
444 al., 2003; Selkoe and Toonen, 2006) that increase the variability of microsatellite dataset
445 making short-range differentiation more likely (as observed in other species; e.g. Wirth and
446 Bernatchez, 2001).

447 The geographic pattern of genetic variability identified in the present study slightly differs
448 from previous studies on the European perch (e.g. Christensen et al., 2016; Nesbø et al.,
449 1999). Firstly, we detect genetic difference between populations from Danube region and
450 from south-east Europe, which belong to different clusters, while previous studies regarded
451 them as a single unit (Nesbø et al., 1999). Secondly, we highlight the larger geographic range
452 of the European Plain cluster in south-east Europe and Siberia which were previously
453 assigned to the eastern Europe group (Nesbø et al., 1999). These differences are most likely
454 due to the use of different sampling efforts and genetic information. Indeed, current analyses
455 are based on sampling including more populations from Danube and Black Sea regions along
456 with a larger amount of genetic information (i.e. compared to Nesbø et al., 1999).

457 Observed geographic pattern of genetic variability is similar to other European freshwater
458 species (e.g. Durand et al., 1999; Gum et al., 2005; Østbye et al., 2005). However, *P.*
459 *fluviatilis* displays high genetic variability in eastern Europe, Fennoscandia, and central
460 Europe while most European freshwater fish species have their genetic variability hotspots in
461 southern Europe (e.g. Durand et al., 1999; Gum et al., 2005 but see Kotlík and Berrebi, 2001).

462 *4.2 Potential shaping factors of the geographic patterns of genetic variability*

463 The observed genetic variability pattern of the European perch can be poorly explained by
464 current barriers to gene flow (e.g. drainage basins, seas). Therefore, we argue that this pattern
465 and large scale population structure have been most likely shaped by past biogeographic
466 events as for other species (e.g. Costedoat and Gilles, 2009; Hewitt, 2004b, 2001). We
467 suggest that *P. fluviatilis* survived to the last Ice-Age in at least three main refugia (i.e.
468 regions currently displaying strong genetic specificities and higher genetic variability; Fig.
469 2A-B): (i) in the west of the European Plain (between 5°E and 20°E), (ii) in the north-east of
470 the European Plain (potentially located in a large ice dammed lake east of the north European
471 ice sheet; Mangerud et al., 2004; Maslenikova and Mangerud, 2001), and (iii) in the upper

472 part of the Danube drainage basin (i.e. west of 20°E). Two other areas may also have acted as
473 refugia: the Balkans and the west-northern Fennoscandia since they host endemic haplotypes.
474 However, the low genetic variability and the lack of sufficient amount of samples from the
475 above areas makes difficult to assess if these regions (i) were refugia in which repeated or
476 protracted bottleneck events decreased the local genetic diversity (Avise, 2000; Petit et al.,
477 2003) or (ii) were secondarily colonised from one of the three main refugia and then
478 underwent local genetic differentiation (Kotlík and Berrebi, 2001). Additional sampling from
479 eastern drainages and western Fennoscandia are needed to test these hypotheses.

480 The sub-structuring of mitochondrial DNA-based clusters detected by the microsatellite
481 analyses and previous studies (e.g. Bergek and Björklund, 2009; Butkauskas et al., 2012;
482 Olsson et al., 2011) is most likely due to local differentiation phenomena fostered by species
483 intrinsic features. First, the species natal homing behaviour reduces gene flow between
484 populations leading to local genetic structuring (Järv, 2000). Second, species short migration
485 distances (from one to 20 km; Stepien et al., 2015; Zamora and Moreno-Amich, 2002) can
486 further increase the structuring at local geographic scale by decreasing gene flow between
487 adjacent populations. Third, selective disadvantage of foreign individuals due to local
488 environmental conditions and (partial) post-zygotic reproduction isolation between allopatric
489 populations observed in *P. fluviatilis* (Behrmann-Godel, 2004; Behrmann-Godel et al., 2006,
490 2004; Behrmann-Godel and Gerlach, 2008) can limit gene flow and shape genetic
491 differentiation between neighbouring populations.

492 *4.3 Considering spatial patterns of genetic variability for Perca fluviatilis aquaculture:* 493 *Towards an improved production?*

494 Improving *P. fluviatilis* aquaculture is a major challenge for fish farmers since they are facing
495 several bottlenecks which are limiting *P. fluviatilis* economic development such as low
496 survival and growth rates, high growth heterogeneity, cannibalism, or low egg quality
497 (Kestemont et al., 2015). Moreover, genetic diversity is also a limiting factor in breeding
498 programs since it can lead to inbreeding depression (Mignon-Grasteau et al., 2005). One
499 solution to overcome current issues consists in (i) sampling individuals to create fish farmers
500 stocks in genetic diversity hotspots and (ii) taking into account variation of zootechnical traits
501 between geographically distinct populations of the European perch. Indeed, this latter could
502 be potentially relevant since variations in traits related to growth (e.g. growth rate, growth
503 heterogeneity rate), development (e.g. swim bladder inflation rate, survival rate), organoleptic

504 characteristics (e.g. colour, filet quality), and behaviour (cannibalism rate, group structure)
505 have been highlighted in *P. fluviatilis* (Mairesse et al., 2006; Mandiki et al., 2004; Mélard et
506 al., 2003; Pimakhin et al., 2015; Pimakhin and Zak, 2014, Toomey et al., 2019, Vanina et al.,
507 2019). Moreover, differences in growth and survival rates between several populations (i.e.
508 Belgian, Finnish, French, and Italian; Mandiki et al., 2004) correspond to genetically
509 differentiated groups in our analyses (Fig. 2). In the same way, aggressiveness and group
510 structure differ between two Finnish populations and Geneva Lake which belong to different
511 genetic groups (Toomey et al., 2019). Therefore, we suggest that investigations of populations
512 from different genetic groups could allow highlighting populations with divergent
513 performances for aquaculture.

514 *4.4 Implications and future guidelines for conservation, management, and production of the* 515 *European perch*

516 For the time being, the European perch does not seem to be threatened by potential issues that
517 could modify its geographic genetic variability pattern. Indeed, *P. fluviatilis* (i) is not a
518 threatened species (Freyhof and Kottelat, 2008), (ii) has a quite large ecological niche
519 (Kestemont et al., 2015), (iii) has presumably undergone few within-range translocations
520 (often unintentional; but it can constitute up to 11.6% of unintentionally stocked fishes when
521 stocking material is produced in Polish carp ponds, Kaczkowski, 2006), (iv) is not presumably
522 the subject of restocking programs, and (v) has low dispersion potential (Stepien et al., 2015;
523 Zamora and Moreno-Amich, 2002). However, the ongoing development of its aquaculture
524 could change this situation (Fontaine, 2004; Kestemont et al., 2015; Kestemont and Mélard,
525 2000). Consequently, we argue that production, trade, and translocations of the European
526 perch should be regulated at the nascent stage of the production (see also Allendorf, 1991) in
527 order to avoid detrimental problems observed for other fish species (e.g. Fleming et al., 2000;
528 Lemer and Planes, 2012; McGinnity et al., 2003).

529 In this perspective, prohibition of all importations of wild *P. fluviatilis* to lands inhabited by
530 distinct genetic populations should be promoted to hamper potential genetic homogenisation
531 as well as risks of competition with local populations from the translocation of non-native
532 populations performing better (see for example Michener, 1975; Vehanen et al., 2009).
533 Moreover, characterisations of current *P. fluviatilis* farmed stocks have shown specificities
534 compared to wild populations in the neighbouring areas of production facilities (Ben Khadher
535 et al., 2016). This means that escapees from fish farms could lead to genetic introgression and,

536 potentially, fitness decrease in the wild (i.e. hybrid offspring from wild and domestic parents
537 are often less adapted to local environment; Besnier et al., 2015; Bolstad et al., 2017; Tufto,
538 2017). One could expect that using local populations or at least populations belonging to the
539 same genetic group could avoid further issues (Youngson et al., 2003). However, captive
540 breeding leads rapidly to genetic changes through adaptation to captive environment
541 (Williams and Hoffman, 2009). Therefore, regulations aiming at limiting gene flow from fish
542 farms should be strongly encouraged, even in indoor aquaculture for which risks cannot be
543 excluded (Summerfelt and Vinci, 2009).

544 *4.5 Further prospects*

545 The European perch aquaculture is currently at the beginning of its development and we
546 consider that it is a good opportunity to (i) carefully plan future production and translocation
547 management strategies and (ii) investigate genetic units ‘intraspecific differentiation of
548 zootechnical traits to improve production. In order to promote a better management strategy,
549 it could also be useful to delineate evolutionarily significant units (Moritz, 1994), widely used
550 in conservation and fisheries management, by considering other lines of evidence such as
551 phenotypic traits. Here applied to *P. fluviatilis*, the provision of guidelines through the
552 consideration of spatial patterns of genetic variability could be applied to other
553 socioeconomically interesting species exhibiting intraspecific geographic differentiation.

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942 **Supporting Information**

943 All supplementary tables and figures are available at:

944 <https://www.sciencedirect.com/science/article/abs/pii/S0044848618323640>

945 **Table S1 : *Perca fluviatilis* sampling sites.**

946 **Table S2 : Descriptive indicators for each locus and for the concatenated alignment of *Perca***
947 ***fluviatilis*.** G_{ST} , N_{ST} and Φ_{ST} correspond to genetic differentiation metrics (see the text for further
948 details). (*) refers to p-values < 0.05.

949 **Table S3 : Best-fitting substitution models identified with jModeltest for the different genes and**
950 **the concatenated mitochondrial alignment of *Perca fluviatilis*.** Locus corresponds to the gene or the
951 concatenated matrix according to codon position for coding genes (COI and Cytb). Best fitting model
952 corresponds to the model found using jModeltest with the Akaike information criteria corrected for
953 small sample sizes. MrBayes substitution model corresponds to the closest over-parameterised model
954 available.

955 **Table S4: Properties of the eight microsatellite loci of *Perca fluviatilis* used in this study.** A:
956 number of alleles per locus; Ar: allelic richness, H_o and H_e : observed and expected (H_e)
957 heterozygosities.

958 **Table S5: Spatial analysis of molecular variance (SAMOVA) based on the concatenated**
959 **mitochondrial alignment (16S, COI, D-loop and Cytb) for *Perca fluviatilis*.** Analyses were
960 performed for K values ranging from one to 10 with 10,000 iterations and 10 repetitions. For each K,
961 the best run was selected based on its associated Φ_{CT} (see the text for further details). Colours and
962 numbers indicate the SAMOVA clusters identified for each sampling location for a given value of K.

963 **Figure S1: Sampling map for *Perca fluviatilis*.** Sampling sites are represented by blue circles and
964 juxtaposed population names refer to Table S1.

965 **Figure S2: Mitochondrial haplotype networks for each distinct locus as well as for the**
966 **concatenated alignment of *Perca fluviatilis*.** For each mitochondrial locus as well as for the
967 concatenated alignment, we report the median-joining network and the spatial distribution of
968 haplotypes, i.e. pie charts indicating the haplotypes frequencies identified in each sampling site. In the
969 network, each haplotype is represented by a circle and circle sizes are relative to haplotype
970 frequencies. The number attributed to the line separating two haplotypes represents the number of
971 mutations that differentiates these haplotypes (absence of number corresponding to a single mutation).
972 Red squares on lines represent undetected/extinct intermediate haplotype states. Black circles
973 correspond to *P. fluviatilis* sequences, empty red circles to *P. flavescens* sequences, and empty blue

974 circles to *P. schrenkii* sequences. Each map reports haplotype frequencies in each sampling sites and
975 colours refer to the corresponding haplotype colour of the network. Pie chart sizes are relative to the
976 number of individuals analysed for each sampling site.

977 **Figure S3 Interpolation of genetic diversity of *Perca fluviatilis* estimated with the concatenated**
978 **alignment of mitochondrial sequences (nucleotide diversity π) or with the eight microsatellite**
979 **markers (Bray-Curtis dissimilarity “BCD”)** (see the text for further details on the interpolation
980 procedure) for several radius (25, 100, and 200 km).

981 **Figure S4: Majority-rule consensus of the trees sampled by the Bayesian analysis performed on**
982 **the concatenated molecular data matrix (COI, Cytb, D-loop and 16S) of *Perca fluviatilis*.** Values
983 above branches are Bayesian posterior probabilities/Maximum likelihood bootstrap values (only values
984 $> 0.5/50$ are shown). Posterior probabilities and bootstrap values inferior to 0.95 or 95, respectively,
985 are considered as poorly supported. Colour labels of branches refer to geographic areas: yellow for the
986 European Plain Europe, green for Northern and Eastern Europe, brown for the Balkans, and blue for
987 the Danube. *P. schrenkii* and *P. flavescens* were used as outgroups to root the trees.

988 **Figure S5: Factorial correspondence analysis based on eight microsatellites loci in the European**
989 **perch (*Perca fluviatilis*).** Each square represents a distinct sampling location. Sampling locations from
990 the Balkans, the Danube drainage, and the Alpine Foreland are coloured in red, blue, and green,
991 respectively.

992 **Figure S6: STRUCTURE HARVESTER results using ΔK method of Evanno *et al.* (2005) and of**
993 **log-likelihood values associated with each K (“log(P(K)) method”) for *Perca fluviatilis***

994

995 **Declarations**

996 *8.1 Ethics approval and consent to participate*

997 Sample providers complied with institutional, national, and international guidelines and
998 regulations as well as Nagoya protocol to obtain our fish clip samples. No ethic committee
999 approval was necessary for the collection of fish clips. All fish treatments used for sampling
1000 were in accordance with the guidelines of the European Directive (2010/63/EU) on the
1001 protection of animals used for scientific purposes (and the French Animal Care Guidelines).
1002 In addition, *P. fluviatilis* is neither an endangered species nor a species at risk of Extinction
1003 according to the IUCN (Red List category: Least Concern).

1004 *8.2 Competing interests*

1005 Declarations of interest: none

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1015 8.4 Author Contributions

1016 LT, PF, and TL designed the study. LT, TV, JP, ZK, JK, PF, and TL contributed to the
1017 collection of fin samples. LT, TV, and MB contributed to laboratory analyses. LT, TV, SD,
1018 PF, FT, and TL analysed and interpreted the results. All authors participated to manuscript
1019 writing. All authors read and approved the final manuscript.

1020 8.5 Availability of data and materials

1021 Mitochondrial sequences are available in GenBank (accession numbers: MG969725 to
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