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### RESEARCH ARTICLE



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# Captive-bred ancestry affects spatial patterns of genetic diversity and differentiation in brown trout (*Salmo trutta*) populations

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#### Abstract

- 1. Intraspecific genetic diversity is heterogeneously distributed in natural landscapes and often forms repeatable spatial patterns. For instance, in rivers, genetic diversity increases towards downstream areas, whereas genetic differentiation increases in isolated upstream areas. Nonetheless, these patterns can be modified by human-induced perturbations, and documenting the extent to which human activities alter these natural patterns is important for conservation. Among the human pressures that affect freshwater biodiversity, stocking natural populations with captive-bred strains is a common practice worldwide that can strongly alter the genetic integrity of wild populations.
- 2. The main objectives of this study were to document the spatial distribution of captive-bred ancestry in brown trout (*Salmo trutta*) populations from four French basins having been stocked according to different practices, and to quantify for each basin the effect of captive-bred ancestry on the spatial distribution of genetic diversity and differentiation. The four basins were sampled along their upstream-downstream gradient, and a total of 1,686 individuals were genotyped at 192 single nucleotide polymorphism loci.
- 3. For all basins, individuals with a strong assignment to the captive strain were mostly found in upper reaches, although the average proportion of captive-bred ancestry varied strikingly among rivers (from 1.9 to 58.7%). Although spatial patterns of genetic differentiation were not affected by introgression and showed an expected increase with increasing distances from the river mouth in all basins, there was evidence that the classical pattern of downstream increase in genetic diversity was reversed when considering highly introgressed populations.
- 4. These findings demonstrate that the stocking of captive-bred strains can strongly modify natural spatial patterns of diversity, even when stocking occurred many generations ago and has now ended. The study illustrates the major impacts of humans on intraspecific biodiversity patterns, and emphasizes the importance of conservation plans that take into account this artificial distribution of genetic diversity.

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#### KEYWORDS

captive breeding, conservation, fish, genetic admixture, hatchery, intraspecific diversity, introgression, rivers, SNPs, stocking

### 1 | INTRODUCTION

Describing and understanding spatial patterns of biodiversity is a central task in ecology, evolution and conservation sciences (Chave, 2013). Large spatial-scale patterns of interspecific diversity have been widely studied, such as the distribution of species diversity across latitudinal ranges (Gaston, 2000). It has been shown further that intraspecific diversity follows the same global patterns as interspecific diversity, with higher diversity in the tropics and a decrease towards the poles (Miraldo et al., 2016; Manel et al., 2020, but see de Kort et al., 2021). At more local scales (i.e. within landscapes), many studies have assessed patterns of diversity, such as functional diversity (Raffard et al., 2017) and genetic diversity (Charlesworth, Nordborg & Charlesworth, 1997; Manel et al., 2003; Paz-Vinas et al., 2015). Describing and understanding small-scale patterns of intraspecific diversity is of utmost importance for designing effective conservation strategies (Paz-Vinas et al., 2018) as intraspecific diversity is the first biodiversity facet affected by human pressures (Mimura et al., 2017), and constitutes the evolutionary potential of species (Franklin & Frankham, 1998).

In river ecosystems, intraspecific patterns of genetic diversity and differentiation have been widely studied (Labonne et al., 2008; Paz-Vinas et al., 2015). River ecosystems are characterized by their tree-like geometric branching pattern (dendritic network; Benda et al., 2004; Campbell Grant, Lowe & Fagan, 2007), and are strongly structured by elevation, making water flow unidirectional. These characteristics modulate patterns of genetic diversity and differentiation. Indeed, these landscapes strongly constrain habitatcarrying capacities as well as movements of individuals and hence dispersal, with smaller and less connected patches upstream, therefore experiencing more genetic drift (Raeymaekers et al., 2008; Carrara et al., 2014) and asymmetrical gene flow owing to the downstream direction of the water flow (Morrissey & de Kerckhove, 2009). Moreover, colonization history (which usually occurs from downstream towards upstream reaches; Cyr & Angers, 2011) is also crucial in shaping these patterns in river ecosystems (but see Splendiani et al. (2020) for a counter-example with river capture events permitting cross-basin colonization).

Altogether, these mechanisms have been shown to lead to recurrent spatial patterns consisting of a downstream increase in genetic diversity and an upstream increase in differentiation (Paz-Vinas et al., 2015). These mechanisms can be strongly modified by human pressures (Mimura et al., 2017), therefore altering these natural patterns of intraspecific diversity and differentiation (e.g. Prunier et al., 2018). For instance, river fragmentation by weirs or dams generally reduces gene flow (Keller & Largiadèr, 2003; Raeymaekers et al., 2008; Blanchet et al., 2010), which may reinforce downstream increase in genetic diversity and affect the genetic structure of populations (Blanchet et al., 2010; Faulks, Gilligan & Beheregaray, 2011). Similarly, water pollution or habitat destruction can reduce the effective population sizes and thus genetic diversity in lower reaches (Ellstrand & Elam, 1993; Almodóvar et al., 2012), and hence conceal or even invert downstream increase in genetic diversity and increase downstream genetic differentiation.

Some human pressures are more insidious, and may not affect spatial patterns through modifications in population sizes or connectivity directly. Among these pressures, stocking of captivebred individuals is a widespread practice attempting to sustain or enhance populations to improve recreational fishing (Borsuk et al., 2006; Hansen et al., 2009; Burnside et al., 2016). As they are often from different origins (i.e. lineages), and because of unnatural selection pressures and small population sizes in hatcheries, captive-bred individuals often differ genetically from wild ones (Frankham et al., 1986; Blanchet et al., 2008; Christie et al., 2016). The consequences of admixture between wild and captive-bred strains is a concern both for scientists and for river managers (Cagigas et al., 1999; Heggenes et al., 2002; Perrier, Baglinière & Evanno, 2013), as genetic introgression can have substantial genetic and ecological consequences, such as native gene pool replacement, fitness reduction, loss of adaptive potential, changes in morphology and trophic position (Hansen, 2002; McGinnity et al., 2003; De Santis et al., 2021). To our knowledge, however, few studies have investigated the potential effects of stocking on the spatial distribution of neutral genetic diversity in natural riverine fish populations, and in particular on classical patterns such as the downstream increase in genetic diversity and the upstream increase in genetic differentiation (but see Prunier et al., 2018). First, stocking events might directly affect natural patterns of genetic diversity and differentiation by locally introducing non-native alleles (Moran et al., 2005). Moreover, the propagation of these non-native alleles within a river network might depend on the dispersal behaviour of captive-bred or admixed individuals, which may differ from that of wild individuals (Saint-Pé et al., 2018). However, it is not known whether the introduction and the diffusion of non-native alleles can alter in a predictive way the natural spatial patterns of genetic diversity in stocked rivers.

The brown trout (*Salmo trutta*), like most salmonids, naturally exhibits strong patterns of genetic diversity and differentiation at small spatial scales (Aurelle & Berrebi, 2001; Swatdipong et al., 2010; Vøllestad et al., 2012). As it is highly associated with human economic activities (Mills, 1989; Butler et al., 2009), the brown trout has been

domesticated since the nineteenth century (Antunes et al., 2001), and hatchery strains have been largely used worldwide with the aim of satisfying recreational fisheries or sustaining wild endangered populations (Elliott, 1994; Berrebi et al., 2000; Bohling, 2016; Lobón-Cervía & Sanz, 2017). The effects of this practice were rapidly shown to be highly concerning, because of its potential impact on the ecological and evolutionary dynamics of natural populations (Hansen, 2002; Araki & Schmid, 2010; Christie et al., 2012). Therefore, assessing the effect of continuing and historical stocking activities at a multi-basin level, with the aim of describing a general effect of this practice on expected spatial patterns of genetic diversity and differentiation, is highly important for both scientists and managers.

The aim of this study was to assess the effects of stocking and admixture between wild and captive-bred brown trout on spatial patterns of genetic diversity and differentiation in four replicated river systems. By combining river-scale sampling in four independent river basins, the specific objectives were to (i) quantify captive-bred ancestry of supposedly native populations, (ii) test how captive-bred ancestry was spatially distributed within each river catchment and whether this distribution varies among river basins, and (iii) test how captive-bred ancestry affects the relationships between genetic diversity/differentiation and distance to the river mouth (a major geographical factor to describe biodiversity patterns in rivers; Paz-Vinas et al., 2015). Ultimately, this study aimed at providing novel insights to managers for appropriately conserving native alleles from wild populations subjected to the stocking of captive-bred individuals, while taking into account the natural distribution of genetic diversity. The expectations are that captivebred individuals and their descendants might benefit from a higher settlement success in reaches with low native brown trout densities through low intraspecific competition for territories (i.e. for space) and prior effects (Weber & Fausch, 2003; Saint-Pé et al., 2018), thus resulting in a heterogeneous distribution of captive-bred alleles throughout river basins. Low trout densities can occur in highly disturbed sites, including upstream mountain areas in which environmental conditions are generally harsh (stressful winter conditions, low productivity, steeper slopes, high hydrological instability). Upstream reaches of mountain streams can even be naturally fishless (owing to the presence of natural barriers to dispersal for instance), which obviously facilitates the settlement of captive-bred individuals when they are introduced in these areas. All things being equal, captive-bred ancestry is thus expected to occur mostly in upstream areas, although there may be some exceptions (e.g. highly disturbed sites in downstream reaches as a result of human activities). As a consequence, the classical pattern of downstream increase in genetic diversity could be alleviated (or even inverted) because the artificial provision of allochthonous alleles in upper reaches locally increases genetic diversity. In a similar way, the classical pattern of an upstream increase in genetic differentiation could be alleviated because of the shared genetic signature of captive-bred individuals homogenizing gene pools among the upper reaches.

### 2 | METHODS

### 2.1 | Study area

The study focused on four independent French river basins: the Aude, the Ône, the Seuge and the Roya rivers (Figure 1), in which the fish community is dominated by brown trout. All basins are fragmented by weirs and dams mostly located in the main stem, with a mean of 15.5 obstacles per basin (from nine in the Ône River to 18 in the Seuge and the Aude rivers), and they vary considerably in geography, environmental conditions and stocking activity (Table 1). These four river basins, located in southern France, flow from three different mountain ranges: the Ône and the Aude rivers flow from the Pyrenees Mountains, the Seuge River from the Massif Central and the Roya River from the Alps. They naturally harbour two different lineages of brown trout owing to their marine outlet (Bernatchez, 2001): the Atlantic (AT) lineage in the Ône and the Seuge rivers and the Mediterranean (ME) lineage for the Aude and the Rova rivers. The study areas were located in the upper reaches of the catchments: above the most downstream sampling sites, the basins drain on average 205 km<sup>2</sup> (240 km<sup>2</sup> for the Aude basin, 155 km<sup>2</sup> for the Ône basin. 360 km<sup>2</sup> for the Rova basin and 90 km<sup>2</sup> for the Seuge basin).

### 2.2 | Local stocking practices

For more than a century (and especially in the last 50 years), French stocking practices have led to massive introductions of hatcheryreared AT brown trout (the majority of Danish origin) (Antunes et al., 2001), even in rivers naturally inhabited by ME brown trout (Krieg & Guyomard, 1985). However, because this had severe consequences on native populations (Largiadèr & Scholl, 1996; Berrebi et al., 2000; Caudron, Champigneulle & Guyomard, 2006), French managers have changed their stocking practices since the early 2000s. Stocking was either stopped or shifted towards the use of more local strains (e.g. through the use of ME strains for Mediterranean rivers; Caudron, Champigneulle & Guyomard, 2006) in many stocking reaches. Nonetheless, in France (as in many other countries), data on stocking are generally scarce, and only qualitative data about the source of stocking are generally well informed. Table 1 provides the information that was collected from formal discussions with angling departments and local managers about local stocking history, intensity and strategy.

## 2.3 | Sampling hatcheries according to stocking practices

The hatchery strains that have been used in the last 10–30 years in the basins were primarily informed and genotyped to quantify admixture between captive-bred and wild brown trout. For three rivers (the Ône, Seuge and Aude rivers), stocking practices officially


**FIGURE 1** Map of the four river basins studied. The Seuge and Ône rivers are part of the Atlantic lineage, whereas the Aude and the Roya rivers are part of the Mediterranean lineage. The river outlets are indicated by an arrow. Sampling sites with more than 10 individuals are shown by black circles filled with grey. The tone of grey indicates the average proportion of individuals assigned to the captive-bred cluster: the darker the shading, the stronger is the assignment to the captive-bred cluster. The five sites indicated by smaller circles and names in grey were not considered in this study because sample sizes were <10 individuals

ended in the early 2000s (Table 1). In the Ône River, stocking was made from an AT local brown trout hatchery (Soueich) administered by the departmental angling association FDPPMA (Fédération Départementale pour la Pêche et la Protection des Milieux Aquatiques) of Haute-Garonne. The Aude River was stocked with two different Atlantic strains from local hatcheries: Gesse and Fagolle. It was impossible to get samples of the Gesse hatchery as it ceased operating several years ago. The Seuge River was stocked with fish from the hatchery of the angling association of Lozère until 1989; however, as this no longer exists, samples were collected from a small local hatchery derived from it, which was also used to stock this basin. In the Roya River, the story is more complex as it is managed according to two practices. In the downstream sections of the river (below the city of Fontan, ROY-Fon, Figure 1) stocking ended in 2007, whereas in the upstream sections stocking practices are still continuing. The downstream part of the river was stocked with fish

from the Fontan hatchery until 2007 (AT strain, stopped in 2006), then by the Roquebilière hatchery (ME strain, origin unknown) administered by the FDPPMA of Alpes-Maritimes. In contrast, the upper reaches are still stocked with AT strains (unknown origin, most likely from Italian hatcheries), but their tracking is extremely complex. The Roquebilière hatchery was successfully sampled, but Fontan samples were not available. Soueich was therefore used as an AT hatchery to represent stocking in this basin. As a result of the information gathered (Table 1), the Roya River was considered as having been (and being) potentially the most affected by stocking practices, particularly in its upper reaches. According to interviews with local managers, the Ône and the Aude were considered as the second most potentially affected rivers (in number and duration of stocking events). The level of stocking in the Seuge River has been considerably lower than that in the other three rivers (Table 1). For each basin, 30 fish were sampled from each of the available brown

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**TABLE 1** Features for each basin, presenting the outlet (Atlantic or Mediterranean), the mountain range, the elevation range, the basin surface, the discharge source, the number of obstacles (weirs and dams) within studied areas, the known hatcheries used for stocking, the sampled hatcheries, the stocking period and the intensity of stocking

	SEUGE	AUDE	ÔNE	ROYA
Outlet	Atlantic	Mediterranean	Atlantic	Mediterranean
Mountain range	Massif Central	Pyrenees	Pyrenees	Alps
Elevation range (m)	960-1,250	380-1,420	630-1,400	300-1,550
Surface drained by the basin above lowest sampling point (km <sup>2</sup> )	180	155	240	360
Discharge source	Snow-rain	Snow-rain	Snow-rain	Snow-glacier-rain
Number of obstacles	18	18	9	17
Hatcheries used in the basins	Vourzac, Federation of Lozere	Gesse, Fagolle	Soueich	Roquebillère, Italian Atlantic hatcheries
Hatcheries successfully sampled	Vourzac	Fagolle	Soueich	Roquebillère + Soueich
Stocking period	1970s-1995	1970s-2000	1972-1999	1970s-present
Stocking intensity	-	+	++	+++

trout hatcheries used in order to characterize the genetics of the captive-bred strains, and thereby to quantify the genetic admixture between native and captive-bred brown trout.

### 2.4 | Field sampling

Brown trout were sampled using single-pass electric-fishing at 70 sites, with the aim of catching 30 individuals per site. The number of sites per river basin varied from 16 (Seuge River) to 21 (Roya River) so as to cover the whole river network (all the main tributaries and the upstream-downstream gradient of the main stem) for each river (Figure 1). Only small-bodied individuals were collected in order to focus on individuals from one age class (1 year old). In total, 1,724 individuals were captured, with sample sizes ranging from six to 30 individuals per site. Each individual was anaesthetized and measured (total length in millimetres), and a pelvic fin clip was taken for genetic analyses. All individuals were released alive to their original sampling site. Only sites with a minimum of 10 individuals were considered in subsequent genetic analyses, resulting in a total sample size of 1,686 individuals across 65 sites (Appendix S1). Sampling was performed according to permits DDT/SEEF(43) no. 2016-221, DDT/SEE(31) no. 2016-20/05, DDT/SEEF(11) no. 2016-25/05, DDT/SEEF(09) no. 2016-23/05 and DDT/SEEF(06) no. 2016-26/05.

### 2.5 | Genotyping

Individual multilocus genotypes were obtained for 192 polymorphic single nucleotide polymorphism markers (SNPs, Saint-Pé et al., 2019), using the KASP technology performed by LGC Genomics<sup>®</sup> (Smith & Maughan, 2015). These markers were developed from a high-density linkage map (Leitwein et al., 2017) and filtered to be highly polymorphic, evenly spread and spaced on the linkage map, and present in both AT and ME brown trout lineages (see Saint-Pé

et al., 2019 for details). Five ancestry informative SNPs used in previous studies to distinguish individuals (and infer admixture) from the AT and ME lineages (OMM1164, OMM1105, OMM1154, Str541INRA and Str591INRA; Estoup et al., 2000; Caudron, Champigneulle & Guyomard, 2006; Caudron et al., 2012) were included in the array.

## 2.6 | Quantification of captive-bred ancestry and genetic diversity and differentiation

For each river independently, genetic clustering was performed using STRUCTURE 2.3.1 (Pritchard, Stephens & Donnelly, 2000) with the admixture model and the correlated allele frequency model, without prior population information. Runs were performed with a burn-in period of 200,000 and 200,000 subsequent Markov chain Monte Carlo repetitions. The number K of clusters ranged from 1 to 10 and five runs were performed for each value. Markov chain Monte Carlo convergence was checked, making sure the alpha plots showed no substantial fluctuation before the end of the burn-in. Log-likelihood plots and  $\Delta K$  statistics (Evanno, Regnaut & Goudet, 2005) were obtained using STRUCTURE HARVESTER (Earl & vonHoldt, 2012), and were used to infer the optimal K-value. Twenty runs were then performed with this optimal K-value and the 10 best runs (the ones with highest LnP(D) values) were compiled using the Greedy algorithm from CLUMPP (Jakobsson & Rosenberg, 2007) to get final averaged individual Q-values. Graphical displays of STRUCTURE plots were generated using DISTRUCT software (Rosenberg, 2003) with the membership of each individual representing the mean membership over the replicate runs. The probability of assignment (individual Qvalue) to the cluster containing all individuals from the brown trout hatcheries used to stock each basin was directly used as an estimate of individual captive-bred ancestry (Hansen et al., 2001; Vähä & Primmer, 2005; Valiquette et al., 2014). This probability thus varies from 0 to 1: individuals with a score close to 1 are likely to be captivebred fish released or pure descendants of captive-bred fish. For the Roya basin, two steps were used to identify the ancestry origin of captive-bred fish as there were two distinct hatchery strains used to stock (ME and AT). First, the percentage of AT ancestry was assessed; then, for individuals considered as 'Mediterranean', the probability of assignment to the ME hatchery of Roquebillière was determined.

The genetic diversity at each sampling site was estimated over all loci by computing unbiased expected heterozygosity (*He*), while genetic differentiation was assessed by computing the global *Fst* for each site in a given basin using the *adegenet* R package (Jombart, 2008). This measure of differentiation indicates the extent to which a site is genetically differentiated compared with all other sites from the same river.

### 2.7 | Spatial patterns of captive-bred ancestry

In order to confirm putative differences among river basins in terms of introgression levels, the distributions of the captive-bred ancestry proportion cap (averaged at the site level over all sampled individuals) was first compared across basins using the beta regression model  $cap \sim basin$  (using the betareg function from the betareg R-package; Cribari-Neto & Zeileis, 2010). Beta regressions were considered as cap is a proportion theoretically ranging from 0 to 1. To describe the spatial structuring of strains within river basins, the relationship between the captive-bred ancestry proportion *cap* and the riverine distances of each site to the river mouth dtm (calculated with the STARS ArcGis package, Peterson & Hoef, 2014) was then tested using the beta regression model  $cap \sim dtm \times basin$ . Nested Type III ANOVA was used to assess the significance of the interaction term  $dtm \times basin$ and, in the situation where the interaction was not significant, nested Type II ANOVA was used to assess the significance of additive terms dtm and basin. A significant interaction term indicates that spatial patterns of introgression differ among basins.

### 2.8 | Global spatial patterns of genetic diversity and differentiation in response to introgression

The distribution of expected heterozygosity He and genetic differentiation Fst were compared across basins using the linear models  $He \sim basin$  and  $Fst \sim basin$  (Im function in R), and Type II ANOVA was used to assess the significance of the basin effect. As basins showed significant differences in average He and Fst values, the relationships between introgression levels and global spatial patterns of genetic diversity and differentiation were investigated, while taking inter-basin differences into account. To do so, the linear random-intercept models  $He \sim dtm \times cap + (1|basin)$ and  $Fst \sim dtm \times cap + (1|basin)$  were run with a maximum likelihood (ML) estimation (Imer function from the Ime4 R-package; Bates et al., 2015). For each model, nested Type III ANOVA (with Satterthwaite's method for degrees of freedom estimation) was used to assess the significance of the interaction term  $dtm \times cap$ , and when

the interaction was not significant, nested Type II ANOVA was used to assess the significance of additive terms *dtm* and *basin*. Significant interaction terms indicate that spatial patterns of intraspecific diversity (either the downstream increase in genetic diversity or the upstream increase in genetic differentiation) are affected by introgression by stocked individuals.

### 3 | RESULTS

### 3.1 | Spatial patterns of captive-bred ancestry

The proportions of captive-bred ancestry ranged from 0.08 to 94.4% (mean =  $26.3 \pm 30.6\%$ ; Table 2). The proportion of captive-bred ancestry was the lowest in the Seuge River (Figure 1), with all sites exhibiting proportions lower than 4.8% (mean =  $1.9 \pm 1.1\%$ ; Table 2; Figure 2). The Aude River displayed slightly higher proportions, ranging from 1.5 to 25.4% (mean = 8.6  $\pm$  7.3%). In the Ône River, the distribution of captive-bred ancestry proportion was highly heterogeneous (ranging from 1.6 to 94.4%, mean =  $22.6 \pm 30.9\%$ ) with four highly introgressed sites in the upstream part of the basin: NOU-Boo, NGA-Jur, NGA-Mar and NGA-Vga (the last three of these sites belong to one of the main tributaries called Neste de Garin, Figure 1). The Roya basin displayed very high proportions of captivebred ancestry (ranging from 25.5 to 90.7%, mean  $= 58.7 \pm 23.4\%$ ), especially upstream from Fontan ('ROY-Fon', Figure 1), where all sites exhibited introgression levels higher than 70%. No native ancestry was found in the upper reaches, with most individuals being AT or ME brown trout, or hybrids between AT and ME strains (Appendix S2). Captive-bred ancestry from the ME hatchery was also ubiquitous in the downstream reaches, in the form of hybrids between the ME and the native strains (Appendix S2). These differences among basins were highly significant statistically (Type II ANOVA:  $\chi^2_{3,5}$ = 64.4; P < 0.001), with the Aude River showing intermediate levels of introgression when compared with the Seuge and the Ône rivers, and the Roya River showing the highest levels of introgression (Figure 2b).

When investigating the influence of the distance to the mouth *dtm* on the distribution of captive-bred ancestry proportions *cap*, the interaction between *basin* and *dtm* was not significant (Type III ANOVA:  $dtm \times basin \chi^2_{3,9} = 3.5$ ; P = 0.32), indicating that spatial patterns of introgression were similar across basins. Overall, proportions of captive-bred ancestry tended to increase with distance to the mouth (Type II ANOVA:  $dtm \chi^2_{1,6} = 12.2$ ; P < 0.001; Figure 2a).

### 3.2 | Spatial patterns of genetic diversity in response to introgression

Expected heterozygosity (*He*) ranged from 0.061 to 0.398 (mean = 0.182 ± 0.096; Table 2), with significant differences among basins (Type II ANOVA:  $F_{3,61}$ = 56.0; *P* < 0.001). The Aude and the Ône basins showed similar intermediate *He* values whereas the Seuge and the Roya basins showed the lowest and highest values,

**TABLE 2** Summary statistics for the river basins studied (minimum, maximum, mean and standard deviation, SD) of the proportion of captivebred ancestry (*cap*), expected heterozygosity (*He*) and genetic differentiation (*Fst*) estimated across all loci and all sites with a minimum sample size of 10 individuals

		SEUGE	AUDE	ÔNE	ROYA	ALL BASINS
сар	Minimum	0.008	0.015	0.016	0.255	0.008
	maximum	0.048	0.254	0.944	0.907	0.944
	Mean	0.019	0.086	0.226	0.587	0.263
	SD	0.011	0.073	0.309	0.234	0.306
Не	Minimum	0.061	0.066	0.091	0.220	0.061
	maximum	0.110	0.288	0.182	0.398	0.398
	Mean	0.094	0.146	0.139	0.301	0.182
	SD	0.015	0.071	0.022	0.064	0.096
Fst	Minimum	0.044	0.024	0.042	0.055	0.024
	maximum	0.105	0.067	0.135	0.232	0.232
	Mean	0.067	0.04	0.063	0.096	0.069
	SD	0.021	0.013	0.024	0.043	0.035

**FIGURE 2** (a) Proportions of captive-bred ancestry (*cap*) against distance to the river mouth (*dtm*) for each basin. Coloured points, observed data; coloured lines and 95% confidence intervals (based on 1,000 bootstraps) correspond to the fitted values of the beta regression model *cap*  $\sim$  *dtm* + *basin* (as the interaction term *dtm* × *basin* was not significant). (b) Boxplots of captivebred ancestry proportions (*cap*) for each basin. Lower case letters indicate basins that do not differ statistically in their introgression levels



respectively (Table 2, Figure 3b). When investigating the overall influence of the introgression level *cap* on the distribution of *He* along the distance to the mouth gradient *dtm*, while taking differences among basins into account (through the use of a random intercept model), the interaction between *cap* and *dtm* was significant (Type III ANOVA: *cap*×*dtm*  $F_{1,61.7}$ = 6.5; *P* = 0.011), indicating that spatial patterns of heterozygosity differed along the introgression gradient.

To visualize this interaction, fixed-effect predictions of *He* values were computed for a range of introgression levels. When plotted against distance to the mouth *dtm*, predictions indicated a slightly negative relationship between *He* and *dtm* at low introgression levels, in accordance with the classical pattern of downstream increase in genetic diversity. However, this relationship was reversed as introgression increased (Figure 3a).





**FIGURE 3** (a) Expected heterozygosity (*He*) against distance to the river mouth (*dtm*) for each basin. Coloured points, observed data; coloured lines correspond to the fitted values of the random intercept model  $He \sim dtm \times cap + (1|basin)$ , for different theoretical levels of introgression (captive-bred ancestry proportions *cap*). (b) Boxplots of expected heterozygosity (*He*) for each basin. Lower case letters indicate basins that do not differ statistically in their heterozygosity

### 3.3 | Spatial patterns of genetic differentiation in response to introgression

Genetic differentiation at the site level (Fst) ranged from 0.024 to 0.232 (mean = 0.069  $\pm$  0.035; Table 2), with significant differences among rivers (Type II ANOVA:  $F_{3.61}$  = 10.9; P < 0.001). The Seuge and the Ône rivers showed similar intermediate Fst values, whereas the Aude and the Roya rivers showed the lowest and the highest values, respectively (Table 2, Figure 4b). When investigating the overall influence of the introgression level *cap* on the distribution of *Fst* along the distance to the mouth gradient *dtm*, while taking differences among basins into account, neither the interaction between cap and dtm (Type III ANOVA:  $cap \times dtm F_{1.63,8} = 2.2$ ; P = 0.14) nor the additive effect of *cap* was significant (Type II ANOVA: *cap*  $F_{1449}$ = 3.3; P = 0.08), contrary to the additive effect of *dtm* (Type II ANOVA: dtm  $F_{1.64,8}$  = 6.8; P = 0.011). These results indicate that, as expected, genetic differentiation at the site level increased with the increase in the distance to the mouth in all rivers, irrespectively of the level of introgression (Figure 4a).

### 4 | DISCUSSION

### 4.1 | Captive-bred ancestry extent

Although for most rivers stocking stopped six to eight brown trout generations ago, captive-bred ancestry is still present, from very low percentages (4% in the Seuge River, 26 years without stocking), to very high percentages (59% in the Roya River, still heavily stocked in its upstream part). This high variability illustrates the complexity of predicting the genetic consequences of stocking. Nevertheless, this finding is congruent with other studies showing that admixture rates between captive-bred and wild brown trout populations are highly variable, ranging from undetectable contributions to total replacement of native gene pools (Cagigas et al., 1999; Poteaux, 1999; Perrier, Guyomard, et al., 2013; Kazyak et al., 2018). Captive-bred ancestry and introgression outcomes depending on stocking strategies and durations have been widely studied (Barbat-Leterrier, Guyomard & Krieg, 1989; Largiadèr, Scholl & Guyomard, 1996), and shown to be highly variable depending on the context. For instance, Almodóvar et al. (2006) found alarmingly high rates in some Mediterranean rivers, whereas North Atlantic populations showed little or no introgression, which is congruent with the results of this study.

Although not quantified statistically, there was a tendency for the presence of captive-bred ancestry and introgression to be positively associated with stocking intensity, and to how recent the last stocking events were (Martinez et al., 1993; Marie, Bernatchez & Garant, 2010; Gossieaux et al., 2019). Indeed, the Seuge River (where stocking ended long ago) is the least affected, whereas the Roya River (still partially heavily stocked) is the most affected by the stocking of captive-bred fish. Although further data are needed to consolidate these findings, it seems that populations could thus recover from stocking (Post, 2013; Valiquette et al., 2014; Létourneau et al., 2018). This can occur through several mechanisms: lower fitness and survival of captive-bred

**FIGURE 4** (a) Genetic differentiation (*Fst*) against distance to the river mouth (*dtm*) for each basin. Coloured points, observed data; the black line and its 95% confidence interval (based on 1,000 bootstraps) corresponds to the fitted values of the random intercept model *Fst* ~ *dtm* +(1|*basin*) (as captive-bred ancestry proportions *cap* showed no significant contribution to the model). (b) Boxplots of genetic differentiation (*Fst*) for each basin. Lower case letters indicate basins that do not differ statistically in their differentiation



individuals (Aarestrup et al., 2005; Pedersen, Koed & Malte, 2008), genetic drift purging exogenous alleles, competitive exclusion (Blanchet et al., 2008; Saint-Pé et al., 2018), or difference in spawning time (Hansen et al., 2006). Angling pressure after stocking can also determine the survival of stocked fish, as it was shown that stocked fish (and their descendants) were more likely to be caught, hence suffering a higher mortality rate. However, although the cessation of stocking has in some cases enabled a return to a 'natural state' (Hansen et al., 1995; Almodóvar et al., 2001), post-stocking recovery rates in extreme cases such as the Roya River might be low, as was observed in populations in France and Spain (Poteaux, 1999; Araguas et al., 2004).

A major limitation in studies on the genetic impact of stocking, at least in southern Europe, is the lack of reliable information on stocking practices, intensity and duration (de Sostoa & Lobon-Cervia, 1989). Moreover, from our experience, historical archives are often scarce, and because of numerous illegal and hidden stocking events (not consented by angling departments), conclusions on the persistence of captive-bred strains are often difficult to reach. Other salmonids (e.g. brook trout; Marie, Bernatchez & Garant, 2010; Gossieaux et al., 2019) have been much better surveyed in terms of stocking, and therefore, provided the impacts of stocking are consistent across salmonids, they potentially represent more reliable models.

### 4.2 | Spatial patterns of captive-bred ancestry

Interestingly, for all four basins the spatial distribution of captive-bred ancestry was not homogeneous (consistent with Saint-Pé

et al., 2018). In all basins, captive-breeding ancestry was mainly present in upstream reaches, with some upper sites exclusively populated with fish strongly assigned to the captive-bred cluster, whereas in lower reaches, fish strongly assigned to the captive-bred cluster were rare. For instance, in the Ône River, captive-bred ancestry was present in the upper reaches of the Neste d'Oueil ('NOU-Bou' site) and the Neste de Garin ('NGA' sites, Figure 3). This pattern was also observed in the Roya River (Figure 3), as all the upper reaches were exclusively populated with captive-bred strains, although in this basin stocking practices are different between upstream and downstream reaches and are thus probably the main cause of this pattern. These visual patterns were confirmed statistically as a significant relationship between distance to the river mouth of each site and the proportion of captive-bred ancestry was observed. Except for the Roya River for which stocking intensity was probably stronger in upstream reaches than in downstream reaches, it is unlikely that the upstream clustering of captive-bred ancestry in the upper areas only arose from the fact that these areas are generally more intensively stocked. Indeed, there was no evidence from the survey that stocking occurred mainly in upstream areas, but rather it seems homogeneously distributed at the river scale. Conditions in these upper reaches may differ significantly from those downstream in productivity, habitat availability and flow stability (Vannote et al., 1980; Grant et al., 2012), and hence in native brown trout density. Fish assigned to captive-bred clusters may be indirectly favoured by harsher and unstable environmental conditions, leading to extremely low densities of native brown trout and sometimes even fishless stretches (Marie, Bernatchez & Garant, 2012; Splendiani

et al., 2013; Harbicht et al., 2014; Létourneau et al., 2018; White et al., 2018). Various mechanisms may be responsible for this pattern. First, movement patterns between wild and captive-bred strains may differ (Vasemägi et al., 2005; Finnegan & Stevens, 2008; Saint-Pé et al., 2018). Second, competition with the native strain may be low or non-existent in these harsher and less dense stretches, thus facilitating the settlement of non-native strains and improving their reproductive success (Saint-Pé et al., 2018). Third, in some circumstances, the absence of native fish populations in the most upstream areas (fishless stretches) may explain the obvious success of captive-bred fish and their descendants. In the latter case, no signs of native alleles in the population are expected, which may be the case, for example, for the two sites in the Neste de Garin (NGA sites, Figure 1). Further data and studies, including fish density estimates, abiotic parameter measurements and human pressure evaluations, are needed to better identify the factors driving this non-homogeneous distribution of captive-bred ancestry and to allow the applications of this finding to other regions of the world.

### 4.3 | Spatial patterns of genetic diversity in response to introgression

When considering populations composed of individuals mostly assigned to the native cluster (i.e. the supposedly native individuals), there was an overall downstream increase in genetic diversity, meeting theoretical expectations (Ritland, 1989; Morrissey & de Kerckhove, 2009; Paz-Vinas & Blanchet, 2015). Conversely, in populations composed of individuals mostly assigned to the captivebred cluster, genetic diversity significantly increased upstream. Almodóvar et al. (2006), Marie, Bernatchez & Garant (2010) and Marie, Bernatchez & Garant (2012) showed that this may result from differences in origins and genetic drift between captive-bred and wild populations, thus introducing new alleles into wild populations. With captive-breeding ancestry mostly occurring upstream and introgressed populations harbouring allochthonous alleles, the observed upstream increase in genetic diversity could simply be the result of the spatial distribution of strains. This is consistent with Prunier et al. (2018), who found that among various human stressors, stocking had a strong and consistent influence on patterns of genetic diversity in two cyprinid fish species. The introduction of new alleles in a population (and the resulting increase in genetic diversity) might be seen as favourable from a conservation perspective, as higher genetic diversity is generally thought to be associated with higher individual and population fitness (Reed & Frankham, 2003). Nevertheless, this latter interpretation should be taken very cautiously because even if it increases genetic diversity locally, stocking could decrease the species' genetic diversity overall (for instance, by homogenizing genetic pools across populations within a landscape; Valiquette et al., 2014), disrupt locally adapted gene associations (Hayes et al., 1996; Allendorf et al., 2001) and decrease the effective population size of local populations (Almodóvar et al., 2006; Gossieaux et al., 2019). Beyond the direct influence of stocking strategy and intensity on the spatial distribution of genetic diversity, the mechanisms by which allochthonous alleles spread throughout the riverscapes should also be considered. Saint-Pé et al. (2018) found that captive-bred individuals tended to exhibit a higher propensity for movement, moved longer distances and moved preferentially from and towards tributaries in which they are mostly present. Therefore, we suggest that captive-bred strains and wild strains cohabit in a parapatric way, with limited genetic exchanges reinforcing the observed spatial patterns of genetic diversity and having a great effect on wild populations. Indeed, in areas such as the Roya River, humans have rapidly reshaped natural eco-geographical patterns of genetic diversity by stocking captive-bred fish.

## 4.4 | Spatial patterns of genetic differentiation in response to introgression

In all basins, genetic differentiation increased with the increase in the distance to the mouth, whatever the introgression level. For native populations, this finding corroborates theoretical expectations, as populations inhabiting these upper sections of the riverscapes are generally isolated geographically and show small effective population sizes (Labonne et al., 2008; Paz-Vinas & Blanchet, 2015). However, for populations with a high prevalence of captive-bred ancestry, this result is surprising because stocking is expected to homogenize genotypes and thus reduce genetic differentiation among highly introgressed populations (Hansen et al., 2006; Eldridge & Naish, 2007; Halbisen & Wilson, 2009; Marie, Bernatchez & Garant, 2010). Interpreting this pattern is challenging, given the lack of available data on the historical stocking practices in some basins. This unexpected result could, for example, stem from the random loss of captive-bred alleles after a few generations without stocking (all rivers except the Roya) or from the stocking of distinct strains in different parts of the basins such as in the Aude and the Roya rivers, thus reinforcing the genetic differentiation of upstream introgressed populations.

# 5 | CONCLUSIONS AND CONSERVATION IMPLICATIONS

This study focused on a limited number of rivers, which limits the generalization of our findings. The four river basins investigated varied according to factors other than stocking, including levels of fragmentation, human density surrounding the river basins or water flow stability. These factors (and others) may explain the spatial distribution of captive-bred alleles both within and between river basins, but were beyond the scope of this study. Further research is needed to investigate the environmental, historical and anthropogenic factors driving the spatial distribution of captive-bred alleles in wild populations. In this regard we believe that meta-analytic approaches based on previously published papers would be valuable. Nevertheless, these results, together with others before it, yield important insights into the potentially substantial effects of stocking on spatial population patterns

and provide important pieces of information to assist in making future conservation and management decisions.

In most European rivers, stocking has been greatly underestimated, in terms of both timescale and quantities (Horreo & Garcia-Vazquez, 2011; Miró & Ventura, 2013). Its effects are thus still to be assessed, as it can be a major threat to the genetic integrity of individual species, but also to ecosystems (Cucherousset et al., 2012; Cucherousset & Olden, 2020). Indeed, despite its potential direct effects on fitness (Hansen et al., 2009; Lamaze et al., 2012; Morissette et al., 2018), stocking may have significant effects on spatial patterns of genetic diversity and differentiation, even when it ceased many generations ago (Hansen et al., 2009; Marie, Bernatchez & Garant, 2010; De Santis et al., 2021). For example, modifying the spatial or temporal structure of populations can profoundly influence local food webs, with subsequent ecological consequences through community structure of invertebrate prey and primary productivity (Harmon et al., 2009; Cucherousset & Olden, 2020; Raffard et al., 2021) or through non-trophic effects (Whitham et al., 2003; Matthews et al., 2011). In addition, the potential disappearance of conservation units of high interest for the representation and persistence of diversity is another conundrum posed by stocking (Antunes et al., 2001; Moritz, 2002; Ferguson, 2004). In river systems, for instance, it is usually suggested that the upper reaches are where conservation efforts should be focused as they host unique conservation units (populations) of interest (Finn et al., 2011). However, for the brown trout populations studied here, this would imply that conservation efforts would be concentrated in reaches in which most captive-bred genotypes are present, which may be counter-productive in protecting the genetic diversity of wild populations.

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### CONFLICT OF INTEREST

We have no competing interests and we declare no conflict of interests.

### DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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