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1 TITLE

2 Using eco-evolutionary models to improve management of introgression in brown trout.

3

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15 RUNNING TITLE

16 Eco-evolutionary modelling of introgression management in brown trout.

17

18 ABSTRACT

19 The management of intraspecific diversity in many species is usually disconnected from eco-
20 evolutionary processes happening *in natura*. A classic example is embodied in the problem of
21 introgression in hybridised fish populations, wherein management practices are generally unaware of
22 any selective process at work, and therefore generally rely on numbers (adding or removing
23 individuals) to reduce introgression. Such an example can be observed in the French Alps, where
24 native Mediterranean (MED) brown trout have been highly introgressed through decades of stocking
25 with domesticated Atlantic (ATL) brown trout. Recently however, new results shed light on a
26 potential selective mechanism that may affect differentially the fitness of MED and ATL genes
27 depending on the environment (GxE interaction). Using a demogenetic agent-based model able to
28 account for such GxE interaction, we simulate a management scenario implemented in 2005 by some
29 biodiversity managers and scientists, who attempted to restore the Mediterranean gene pool using
30 translocation of near pure MED individuals in Atlantic dominated areas. We show that the model is
31 unable to recreate the observed introgression dynamics if the GxE interaction is not included. This
32 finding implies that i/ eco-evolutionary mechanisms can have large effects on introgression dynamics
33 on very short time scales and ii/, management of intraspecific diversity should increasingly rely on
34 these natural mechanisms, so as to improve management targets and facilitate adaptation to rapid
35 environmental changes.

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37

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39 KEYWORDS

40 Hybridization; *Salmo trutta*; intraspecific diversity; genotype environment interaction;

41

42 INTRODUCTION

43 Management and conservation of intraspecific diversity has the complex task to maximise the
44 protection of standing diversity, a legacy of millions of years of evolution, and to also ensure that this
45 diversity is up to challenge the current environmental change. In the midst of the biodiversity crisis,
46 scientists have become increasingly aware that intraspecific diversity is not only an intrinsic value
47 of species and populations in itself (Piccolo, 2017; Soulé, 1985). It is also, as specified by the tenets of
48 evolutionary biology, the fuel of adaptation, through response to natural selection. In short, the very
49 thing that we seek to protect is also the one thing that might help populations to cope with climate
50 and global change effects (Carroll et al., 2007; Reznick et al., 2019). Paralleling that growing
51 understanding, many recent studies analysed to what extent evolutionary change in populations is
52 caused by human activities and interference (Godineau et al., 2023; Hendry et al., 2017). Their results
53 are generally consistent, and indicate that such evolutionary change is real, massive, and happening
54 on ecological time scales. Hence, selection associated with local anthropogenic pressure can interact
55 with that associated with global change. It is therefore paramount to investigate these interactions
56 so that biological production systems and conservation programs can benefit from and care for
57 evolutionary processes.

58 One such human interference is embodied by anthropogenic hybridization, defined here as the
59 accidental or deliberate admixture of previously isolated genetic pools (Crispo & Chapman, 2010;
60 Rhymer & Simberloff, 1996). One of the most common cause of anthropogenic hybridization (55% of
61 the studies reviewed in (Todesco et al., 2016) is related to the assisted migration of - or 'restocking
62 by' - non-native individuals (either wild or domesticated) or to escapes from livestock (Champagnon
63 et al., 2013). Known negative effects spans from the loss of genetic and phenotypic variation (e.g.
64 through competition, disease transmission, or reduced reproductive success of native individuals), to
65 breakdowns of local adaptations in recipient populations as well as negative demographic effects
66 though lower hybrid fitness (Allendorf et al., 2001; Bohling, 2016; Daupagne et al., 2021; Garant et
67 al., 2007; Verhoeven et al., 2010). In a given restocking situation, it can therefore be difficult to
68 understand or predict the net outcome on population evolutionary dynamics of these various risks.
69 This is all the more problematic that follow-up monitorings after restocking are rare, particularly
70 from a genetic perspective (Kurland et al., 2022; Weeks et al., 2011). Conversely, it is equally
71 challenging to counteract the effects of past anthropogenic hybridization: attempting to bolster the
72 native gene pools by simply restocking with similar gene pools generally leads to disappointing
73 outcomes, notably because each situation might be unique (Allendorf et al., 2001; Bohling, 2016;
74 Genovart, 2009; Gil et al., 2016a). Obviously, knowledge of impacts of restocking on population
75 adaptive potential, their underlying mechanisms, and, whenever possible, a quantitative assessment
76 of these impacts are urgently needed to elaborate exploratory scenarios covering a wide range of
77 plausible outcomes to guide management decisions.

78 Provided some of the above-mentioned elements are available, demo-genetic agent-based models
79 (DG-ABM) are efficient tools to address these challenges (Lamarins et al., 2022). The philosophy of
80 such modelling approaches is to represent explicitly an eco-evolutionary loop, wherein traits involved
81 in fitness variation have a genetic basis that is intergenerationally transmitted. Fitness itself arises

82 from interactions between individuals with regard to their environment. DG–ABM proved to be
83 useful for the exploration of fundamental questions in evolutionary ecology, and also as effective
84 prospective and decision support tools to investigate the interactions between management and
85 natural eco-evolutionary processes (Coulson et al., 2006; Lamarins et al., 2022), notably in the
86 fisheries domain (e.g., Ayllón et al., 2016; Nathan et al., 2019; Piou & Prévost, 2012).

87 The salmonids, as exploited species for both consumption and recreational angling, concentrate a
88 significant part of the historical efforts of restocking and stocking outside their original distribution
89 range (Laikre, 1999; McIntosh, 2011). Among them, *Salmo trutta* L. (Brown trout) is well-
90 appropriated to investigate the impacts of restocking on population adaptive potential. At least five
91 genetically and phenotypically distinct lineages of this widely-distributed species evolved in allopatry
92 during Pleistocene glaciations (Bernatchez, 2001) with possible secondary contacts (Hashemzadeh
93 Segherloo et al., 2021). Since the end of the 19th century, the Atlantic (ATL) lineage has been
94 intensively used for fish farming and intensive river stocking to sustain recreational fishing. In the
95 Mediterranean region, where the eponymic lineage is native (MED), the outcome of these ATL
96 (re)stocking activities varies from total extirpation of native MED populations, to partial or full
97 hybridization and eventually introgression of native MED populations by non-native ATL alleles
98 (Behnke, 1992; Caudron et al., 2009; Gil et al., 2016a). Additionally, these stocking efforts also
99 targeted segments of rivers usually located in upstream high-altitude areas, previously fish-free for
100 reasons related to either biogeography (ice cover of the last glacial maximum, see Splendiani et al.,
101 2016) or to the presence of natural or non-natural barriers. More rarely, native populations managed
102 to remain genetically pure. Across decades, the goals of fish populations managers has however
103 progressively shifted from maximising density and catches, to protecting native diversity (Laikre,
104 1999). Consequently and more recently, managers have tried to mitigate the effect of non-native
105 stocking, through either stopping said stocking, starting native stocking, removing potential non-
106 native and/or hybrid fish, or translocating native fish between rivers (Caudron et al., 2011; Gil et al.,
107 2016a).

108 In the French Alps, located in the Mediterranean basin, biodiversity managers elected in 2005 to
109 translocate native MED fish to an ATL dominated stretch on the River Borne, hoping to significantly
110 reduce the introgression rate (Gil et al., 2016a). Later, in another close river system, a quantitative
111 genetics study shed light on an eco-evolutionary mechanism that may be involved in the dynamics of
112 hybridization in wild populations (D. M. Folio et al., 2021): it was found that eggs sired by MED native
113 females had a higher survival at hatching than eggs sired by ATL females in cold temperatures (2 to
114 4.5°C). This advantage however was fully cancelled when average temperatures were raised (7.5°C).
115 In combination with local heterogeneity in river temperatures, this genotype by environment (GxE)
116 interaction was a potential candidate to explain the observed spatial heterogeneity of the
117 distribution of population introgression rates. The present study takes the opportunity of the well-
118 documented translocation action on the River Borne to investigate the impacts of a translocation
119 management scenario with the higher egg survival of MED females at low temperature on the
120 dynamics of introgression in the MED-ATL trout system. To that aim, we built a DG-ABM coupling (1)
121 a model of resident brown trout population dynamics simulating the effect of competition and
122 temperature on growth and survival, and (2) a simple quantitative genetics model describing the
123 effect of individual introgression rate on survival at hatching in relation to water temperature. Using
124 this model, we simulated the translocation of MED population from the lower part of a watershed to
125 its ATL-dominated upper part, and we tracked the simulated dynamics of introgression and
126 intraspecific diversity changes, accounting (or not) for the GxE interaction relating survival of
127 offspring at hatching, river temperature, and maternal genotype. Thanks to the managers' data and
128 monitoring, we also compare the outcome of our model with the outcome of their management

129 action, so to actually assess whether the inclusion of eco-evolutionary mechanisms allows for better
130 predictions.

131

132 METHODS

133 **Model overview**

134 The MEDITERRANEA model is a demogenetic agent-based model (DG-ABM), implementing the
135 guidelines described in Lamarins et al. ((Lamarins et al., 2022). Its general purpose is to simulate the
136 demographic and evolutionary dynamics of brown trout populations in a spatially explicit
137 environment (a hydrographic dendritic network), with a strong focus on interactions between
138 individuals (e.g., competition driven survival at different life stages and mating systems), and
139 between individuals and environment (e.g., temperature-dependent survival at different life stages).
140 It is particularly suited to simulate these interactions in the context of hybridization between
141 evolutionary lineages (here, MED and ATL) because the individual introgression rate directly
142 determines two key life history traits (egg survival and female preference). The underlying hypothesis
143 is that the same seven quantitative trait loci linearly control the genetic variation in egg survival and
144 female preference, a gross simplification that is yet justified by (1) the absence of detailed knowledge
145 on the genetic architecture of these traits and (2) the opportunity to compare the simulated
146 variation in introgression across time and populations with field observation of introgression rate (Gil
147 et al., 2016a). Additionally, the model integrates tools to simulate the effects of various management
148 actions on the dynamics of the system, such as stocking, fishing, or habitat modification.

149 The model can be downloaded freely at <https://doi.org/10.57745/LIKOGD>. A comprehensive
150 installation guide is available at: https://capsis.cirad.fr/capsis/documentation/installation_guide. A
151 full description of the model is accessible (Folio, 2022), <https://theses.hal.science/tel-04122411>).
152 Additionally, the model provides a user friendly interface with an online help assistance. The model is
153 coded in JAVA language, on the CAPSIS-4 platform (<https://capsis.cirad.fr>). We here provide a brief
154 overview of its structure and characteristics.

155 **Model architecture**

156 The hydrographic dendritic network is composed of reaches of homogenous habitat. Limits between
157 reaches are such that any reach is big enough to host the home range of a typical adult trout
158 (minimum 200m long), but they locate major differences in habitat continuity (slope, confluences,
159 obstacles, etc). The quality of habitat (for growth, reproduction and carrying capacity) can be
160 specified for each reach. Local temperature dynamics in each reach are modelled as functions of
161 season and altitude. Between reaches, weirs can be placed and may influence connectivity in both
162 directions.

163 Fish are modelled in two ways: either a collection (or group) of individuals sharing similar
164 characteristics (a coding trick to improve memory use), or an individual with its own characteristics.
165 Collections of individuals are used from fertilisation up to 8 months old, covering egg stage, hatching,
166 emergence, and early growth. Beyond 8 months old, each fish is modelled individually with its own
167 traits and genetic data (Supplementary File 1). Individuals are diploids and possess a nuclear genome
168 composed of seven bi-allelic unlinked loci for which each allele is related to a specific lineage. Alleles
169 value can either be 0 (MED) or 1 (ATL) at each locus. This simplified genetic architecture is in relation
170 to the data generated by managers that use 7 SNPs to genotype and assign brown trout individuals
171 to their lineage of origin ((D. M. Folio et al., 2021). It allows to compute an introgression score for

172 each individual, which is used at some points in the simulation as an abstract genetic component of
173 traits involved in reproduction and mortality processes (see below).

174 The model updates all information on reaches, weirs, collections of fish or individual fish on a
175 monthly scale, which allows it to depict the within-year changes in environment, biological functions
176 and life stages (growth, movements, mortality, reproduction).

177 **Process overview**

178 The life cycle is modelled as a series of processes at each time step for each individual or groups of
179 individuals (Fig. 1). Ageing and developing allows individuals to change life stages. Eggs hatch at 380
180 degree-days and larvae emerge at 700 degree.days, producing juveniles. At 12 months old, juveniles
181 produce sub-adults, and at 24 months old, sub-adults turn to adult fish.

182 The monthly survival rate S_{stage} is controlled by a stage dependent value (C_{stage}) and is also influenced
183 by the local density of the considered stage ($D_{stage, reach}$):

184

$$185 \quad S_{stag, reach} = D_{stage, reach} \times \frac{e^{(C_{stage})}}{(1+e^{(C_{stage})})} \quad \text{with} \quad D_{stage, reach} = \frac{1}{(1+\frac{Density_{stage, reach}}{K_{max}})}$$

186 Before emergence from the gravel however, $D_{stage, reach} = 1$. C_{stage} is calibrated using empirical data
187 (Folio 2022). Additionally, C_{stage} at hatching is modelled as a quantitative genetic trait, whose inter-
188 individual variation depends on a genetic component (the maternal introgression rate), on an
189 environmental component (temperature) and on their interactions, so as to reflect the available
190 knowledge regarding the GxE interaction in post-zygotic selection:

$$191 \quad C_{stage=hatching} = \alpha + \beta \times T + (Maternal\ introgression - 0.5) \times (\gamma + \delta \times T)$$

192 In the present study, α , β , γ and δ are directly extracted from empirical estimates in the field (Fig. 2,
193 Supplementary file 2), and T is the mean winter temperature in the considered reach over the
194 incubation period. This implies that offspring of MED females have higher survival in cold
195 temperature than offspring from ATL females (data from Folio et al., 2021). Note that the paternal
196 component of offspring genotype does not affect egg survival.

197

198

199 Individual growth is both temperature and density dependent, following a Von Bertalanffy model.
200 Body Size (BS_{t+1}) at time t+1 is a function of previous body size, growth factor k and maximum body
201 size L_{inf} :

$$202 \quad BS_{t+1} = BS_t + BS_t \times k \times (1 - \frac{BS_t}{L_{inf}})$$

$$203 \quad \text{with } k = b \times e^{(-a_{stage} \times density_{stage})} \times ME \times e^{\frac{(optT-T)^2}{2 \times rangeT^2}}$$

204 Where b is the base growth parameter, a is a stage factor for density effect on growth, $ME (=0.7)$ is
205 maturation effect slowing down somatic growth when individuals reach reproductive age, $optT$ is the
206 optimal growth temperature (Elliott et al., 1995; Forseth et al., 2009; Forseth & Jonsson, 1994), T is
207 the monthly mean temperature, and $rangeT$ is an amplitude parameter describing how quickly

208 growth is reduced when T goes farther from $optT$. None of these parameters are genetically
209 controlled in the model.

210 Movement probability between reaches in growth season depends on local density:

$$211 \theta_{stage,reach} = \frac{Density_{stage,reach} * \theta_{max}}{Density_{max} * GQ}$$

212

213 with θ_{max} and $Density_{max}$ are user-determined and GQ is the habitat quality of the reach for somatic
214 growth.

215 Fish then move to the next reach with an equal probability to go upstream or downstream, provided
216 no obstacle is met. If an obstacle is met, the probability to cross said obstacle is ruled by the
217 characteristics of the obstacle. Just before reproduction season, individuals can undertake homing
218 migration, trying to move back to their birth reach. Again, obstacles might prevent them from doing
219 so.

220 Reproduction occurs in December each year. Mature individuals in a reach undergo a process of
221 random encounters. Each female is then associated with a number of males (this number depends on
222 the Operational Sex Ratio defined by user). Females then express a mating preference p based on the
223 dissimilarity D between their own phenotype and the potential partner's phenotype (Gil et al.,
224 2016b) :

$$225 p = \frac{GC * (\frac{e^{(x+y \times D)}}{1 + e^{(x+y \times D)}}) + ((100 - GC) \times q)}{100}$$

226 where x and y are parameters defining the strength of preference (extracted from Gil et al., 2016b),
227 and GC is a scaling factor between the introgression rate and the phenotype (since differences in
228 phenotypes between lineages are only partly related to genetic differences between lineages). In the
229 present case, $GC=35$, and D is computed as the absolute difference between the introgression rate of
230 the target female and of its potential partner. q is a random decimal drawn in a uniform distribution
231 between 0 and 1. $(100-GC)*q$ can be viewed as the environmental component of the variation in
232 mating preference. For each successful mating, a batch of eggs of size $nEggs$ is created such as:

$$233 nEggs = F \times (10 \times BS)^f \times \frac{RQ}{(h * SC)}$$

234 With F and f fecundity parameters, BS the body size of the female, RQ the habitat quality of the reach
235 for reproduction, SC a user defined parameter that describes the number of potential mating within
236 a season per female, and h a parameter describing potential oophagy effects on the redd.

237 All parameters values are provided in Supplementary Information 3.

238 **Simulation scenario(s)**

239 We used the MEDITERRANEA model to simulate a real management action undertaken on brown
240 trout populations in the River Borne, French alps, in the Mediterranean region where the MED
241 lineage is native. This river, as many in the Alps region and in Europe, has been stocked for decades
242 using domestic ATL trout (Caudron et al., 2009; Gil et al., 2016a). In particular, following a major flash
243 flood in 1987 that wiped out populations upstream of an impassable dam, ATL stocking in the
244 upstream part of the river was intensive until 2005, leading to a pure ATL population located

245 upstream. Below the dam however, nearly pure and thriving MED populations remained (mean
246 introgression = 0.2). Then, from 2005 to 2007, managers and scientists elected to translocate weakly
247 introgressed MED trout from the downstream part (altitude ranging from 698 to 784m) to the
248 upstream part (altitude ranging from 838 to 1039m), hoping to restore the MED native lineage in the
249 upstream part of the river. At the time, they hoped that 1/ the translocation would create a MED
250 gene flow in the upstream part and 2/ the translocated population with MED genes could be more
251 adapted to the local environment. Although they had no evidence at this date, behavioural and eco-
252 evolutionary interactions supporting this prediction were discovered later (Folio et al., 2021; Gil et
253 al., 2016a).

254 We modelled this exact scenario, starting from known initial conditions in terms of population
255 structure : near pure MED populations downstream, pure ATL populations upstream. The
256 environment was also recreated: the dendritic structure of the river, the presence of dams that
257 might block movement and, the local habitat quality (see Fig. 3). Of specific importance was the
258 temporal and spatial variation of temperature: we assumed that temperature was negatively
259 correlated with altitude, and could therefore be variable between reaches, reflecting the minimum
260 and maximum temperature provided by the managers (see Supplementary File 3). We then
261 envisioned two alternative scenarios: a neutral scenario, where all individuals survive hatching with
262 the same probability whatever their genotype and therefore introgression, and a selective scenario,
263 based on Folio et al. (2021)'s results, wherein offspring from MED females have higher chance of
264 survival in cold water, and where this advantage cancels at 8°C (see Fig. 2). Our goal was to
265 investigate whether the inclusion of GxE mechanism i/ changes the model's prediction and ii/
266 provides predictions closer to reality than a neutral model would.

267 The model was first run for a decade in order to establish demographic and genetic equilibrium in
268 the downstream and upstream parts of the river (introgression per reach, age, size and maturation
269 variation). Then, during three years, respectively 125, 610 and 370 nearly pure MED individuals were
270 translocated from reach D to reach B, and respectively 135, 282 and 110 from reach D to reach A.
271 Notably, amateur fishing was not allowed in reaches B and B1, but authorised in reaches A and A1.

272 We then monitored population eco-evolutionary dynamics in reaches A and B, as well as in two
273 neighbouring accessible reaches (A1 and B1), during 11 years (2 to 3 generations). More specifically,
274 we looked at the mean introgression per reach, and at the distribution of individual introgression,
275 two measures often used by managers to assess results. The simulations were replicated 20 times.

276

277 RESULTS

278 **Dynamics of mean introgression**

279 Following translocation, the introgression rate decreases slowly from 100% down to 95% when
280 considering a neutral scenario. However, when the GxE interaction is simulated, the introgression
281 rate quickly decreases down to 50% in 10 years (Fig. 4). It is worth noting that this decrease is
282 observed directly in the reaches where the translocations occurred (A and B), but also to some extent
283 in the contiguous reaches (A1 and B1), indicating that the simulated movement rates allow for some
284 spatial homogenization.

285 **Distribution of individual introgression**

286 Looking at the dynamics of individual introgression 4 years and 11 years after translocation (Fig. 5),
287 we notice two very different situations again between the neutral and the GxE scenarios. In the

288 neutral scenario, we observe a production of hybrid genotypes, with individual introgression ranging
289 from 0.5 to 1, 4 years after the translocation. Then, after 11 years, the distribution of individual
290 introgression clearly converges towards mostly pure ATL genotypes. In the GxE scenario however,
291 the initial genotypic diversity is much larger, with even some pure MED genotypes being observed.
292 After 11 years, the distribution is mostly composed of HYB genotypes variously introgressed, and
293 with nearly no pure MED or ATL genotypes in the translocated area.

294 **Comparison with real data**

295 Using data provided by managers on each reach studied (Caudron et al., 2012), we were able to
296 compare the observed mean introgression per reach in 2009 with the mean introgression predicted
297 from the neutral and the GxE scenarios (Fig. 6). First, the neutral scenario was unable to
298 approximate the real results, nor to reproduce spatial heterogeneity in introgression. The GxE
299 scenario provided introgression patterns substantially closer to reality, but it generally overpredicted
300 the mean introgression rate. Additionally, the GxE scenario was able to predict some spatial
301 heterogeneity in introgression between reaches, wherein the mean introgression was higher
302 downstream and lower upstream (in relationship to the altitudinal temperature gradient simulated in
303 the model). To some extent, the same pattern was observed in the real results, but with much more
304 contrast between reaches (lower introgression in translocated reaches than in neighbouring
305 reaches).

306

307 DISCUSSION

308 The present study aimed at using a demogenetic agent-based modelling approach to simulate and
309 predict the results of management practices on introgression dynamics in brown trout. Our findings
310 indicate that neutral and GxE driven scenarios generate very different introgression dynamics on a
311 short time scale. Additionally, GxE scenarios are better at predicting such dynamics than neutral
312 models: a logical conclusion, and yet, it stems from different key points: (1) the existence and the
313 discovery of eco-evolutionary mechanisms involved in the dynamics of introgression; (2) the ability to
314 include these mechanisms in a consistent population model accounting available knowledge in
315 ecology, demography, behaviour, development, and genetics, in interface with human activities, so
316 as to actually quantify the strength of these eco-evolutionary forces in the system dynamics; (3) a
317 detailed description of the management practices, as well as actual data on initial conditions and
318 environmental variation in time and space. This last point is mandatory, because we aimed at
319 reproducing relatively realistic dynamics that generate patterns in limited time and space, often in
320 non-equilibrium situations.

321 **The strength of the GxE interaction**

322 Our results clearly indicate that the neutral scenario and the GxE scenario make two very different
323 predictions. Under the neutral scenario, as intuitively expected, the impact of the translocation is
324 reduced, and depends mostly on the number of translocated individuals with respect to the
325 population size of the upstream reaches. Including the GxE interaction in the model however
326 completely changes the prediction in a handful of years.

327 The parameters used to simulate the GxE interaction were directly extracted from Folio et al. (2021),
328 and they therefore represent actual values estimated in a field experiment, in three natural rivers of
329 the same region presenting contrasted temperatures. In that way, we expect our GxE model to be a
330 possible realisation of what is generally happening in natural populations. It is however only one

331 situation, and it could vary much depending on other factors of environment and on the populations
332 considered throughout the whole Mediterranean area inhabited by the MED lineage. Sensitivity
333 analyses not presented here also indicate that the strength of the GxE interaction has a substantial
334 effect on the evolutionary dynamics (for instance, on mean introgression). It is thus paramount to
335 provide field-based estimates related to the populations and environment of interest to the
336 managers.

337 **Quality of the predictions**

338 Because our case study was based on a management strategy already implemented, it was possible
339 to somewhat compare our predictions to observed results in the field (see Caudron et al., 2012). The
340 neutral scenario performed very poorly, unable to predict the sharp decrease observed in mean
341 introgression following the translocation of MED individuals. The GxE scenario provided a much
342 better fit. This should indicate that the selective mechanism at work in relation to temperature
343 variation is a very likely candidate to explain what actually happened during the translocation. Yet we
344 must temper that fact with several other observations. First, in general, our predictions still tended
345 to underestimate the general speed of change in the observed introgression: this might be due to a
346 stronger GxE interaction, or to lower winter temperatures than those communicated by the
347 managers, but it could also be linked to other non-elucidated selective events along the life cycle, still
348 favouring the MED genes. Second, the fit was not as spatially variable as the observed data. It is
349 noteworthy that the fit was better in translocated reaches than in neighbouring reaches. It is thus
350 very possible that the movement rate in our model was overestimated.

351 **Implications for biodiversity managers**

352 Here, the effect of the GxE interaction indicates that actual conservation efforts must be ecologically
353 allocated: some parts of the rivers where temperature remains colder should be prioritised. In
354 warmer waters, the cost-benefit balance of translocation could be much lower to inexistent. It is
355 equally important to develop models to predict the evolution of these thermal conditions in relation
356 to climate change effects. An important consideration is also the fact that the mating system is
357 generally slightly heterogamous: this implies that even in very cold waters, it might be near
358 impossible to produce pure MED genotypes using translocation without removing the local
359 introgressed populations before, if such a thing is feasible (Rytwinski et al., 2019).

360 It is noteworthy that the present case study is illustrative of other similar case studies performed in
361 the same region (D. Folio, 2022), which generally provide the same results, where translocation is a
362 relatively successful strategy in cold waters. It is also interesting to note that the selective advantage
363 of the MED genes in cold waters included in the MEDITERRANEA model could also be at work in
364 other regions: for instance Vera et al. (2023) have found that the MED genes were more frequent in
365 rivers presenting cold waters in winter (but also in summer) in Spain. In Italy, MED genes were
366 dominating in areas presenting more stable hydrogeological conditions, but the correlation with
367 temperature gradients has not been investigated (Splendiani et al., 2016). In another lineage, the
368 marble trout, it has also been demonstrated that in introgressed areas, the native genes were
369 transmitted by females, as observed in our case, but no eco-evolutionary mechanisms were
370 investigated (Pujolar et al., 2011).

371 The speed of phenotypic and genetic change under selection is very substantial in the present study,
372 and it echoes several other studies on other biological models and under different anthropogenic
373 pressures (Hendry et al., 2017; Kurland et al., 2022; Lamarins et al., 2022). These results point at eco-
374 evolution as a likely efficient force to cope with rapid environmental change, leading to potential
375 rescue effects (Fitzpatrick et al., 2020; Frankham, 2015). As a consequence, we advise that the

376 management of biodiversity should now quickly integrate eco-evolutionary considerations. The
377 MEDITERRANEA model embodies such an approach, resulting from a collaboration between
378 managers and researchers. It provides a comprehensive framework, accessible to expert managers,
379 to simulate management scenarios, and implement management practices based on actual
380 predictions.

381

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564 FIGURE LEGENDS

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566 Figure 1: Representation of the life cycle, with the different processes modelled and their order. In
567 the MEDITERRANEA model, splitted between the individual and the group phase.

568 Figure 2: Offspring survival rate at hatching as a function of maternal introgression and mean daily
569 water temperature over incubation period.

570 Figure 3: Spatial representation of fish translocation carried out in the MEDITERRANEA model based
571 on the structure of the River Borne.

572 Figure 4: Mean introgression as a function of time in the neutral scenario (blue curve) and in the GxE
573 scenario (red curve) in the upstream part of the River Borne.

574 Figure 5: Distribution of individual introgression in the translocated area, at years 14 and 21 after the
575 beginning of the simulation, for the neutral and the GxE scenario.

576 Figure 6: Comparison of mean introgression per reach in the translocated area between observed
577 data (red pentagons) and simulated data (summarised as boxplots to display the 2.5, 25,50,75,97.5%
578 quantiles of the simulated trajectories, with blue boxplots for the neutral scenario and red boxplots
579 for the GxE scenario).

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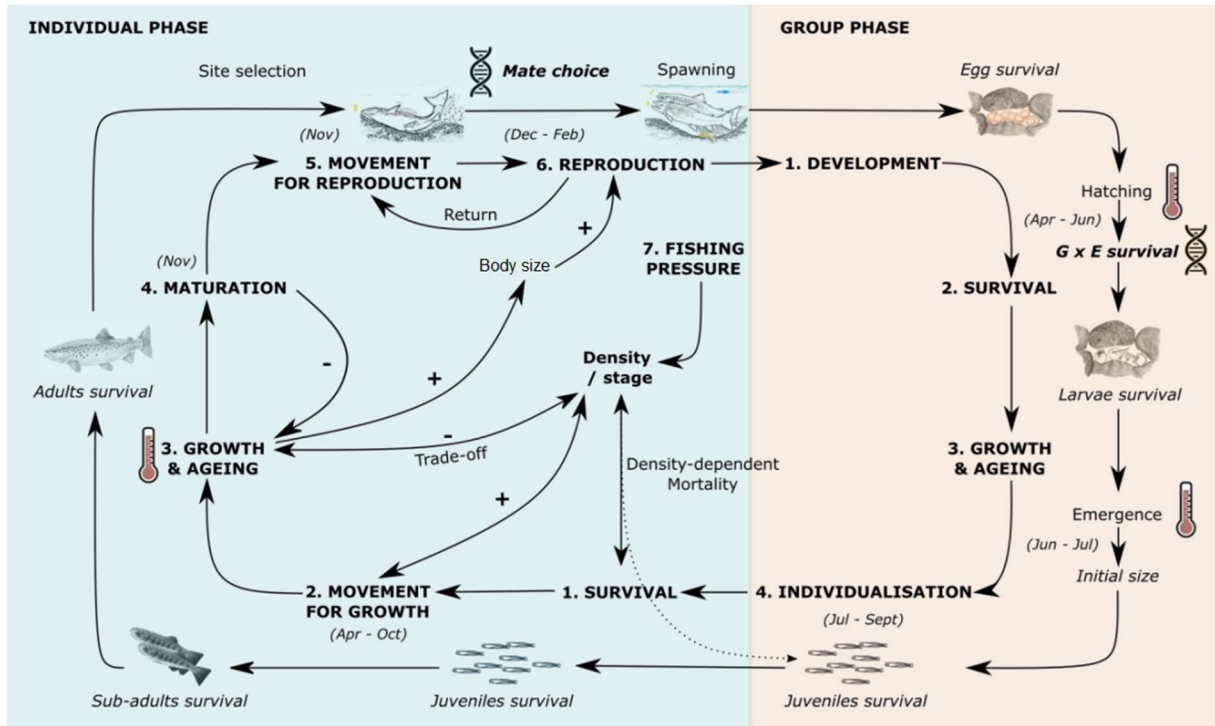
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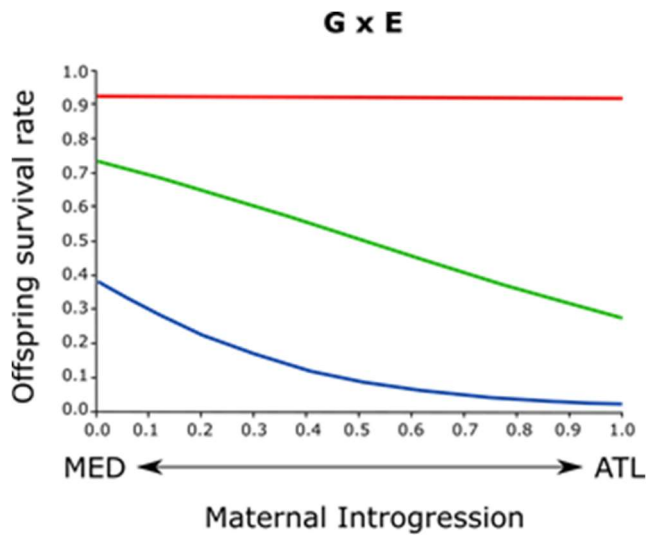
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598 FIGURE 1



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618 FIGURE 2



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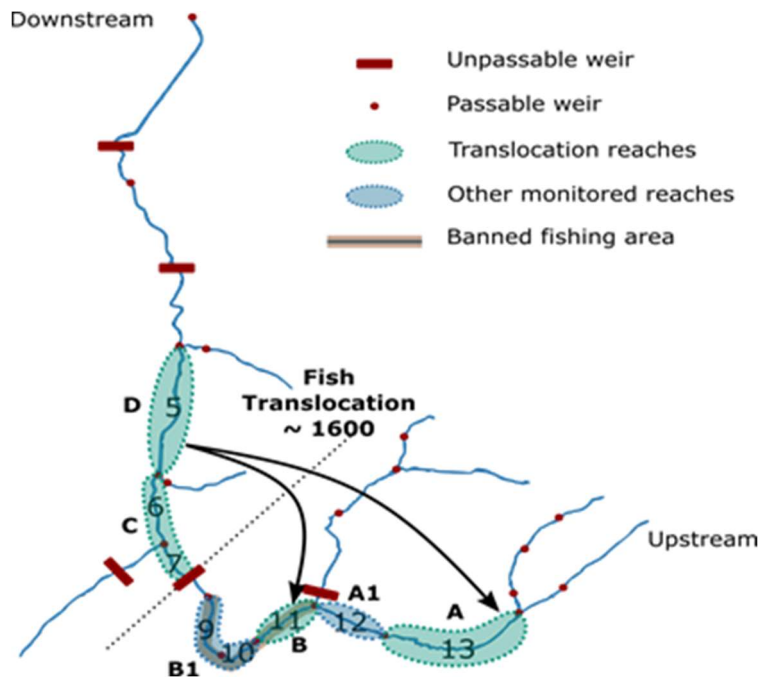
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640 FIGURE 3



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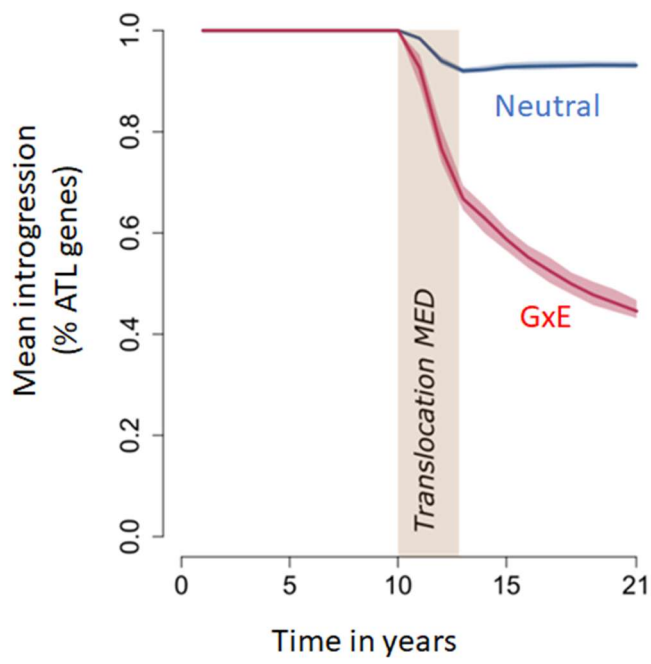
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660 FIGURE 4



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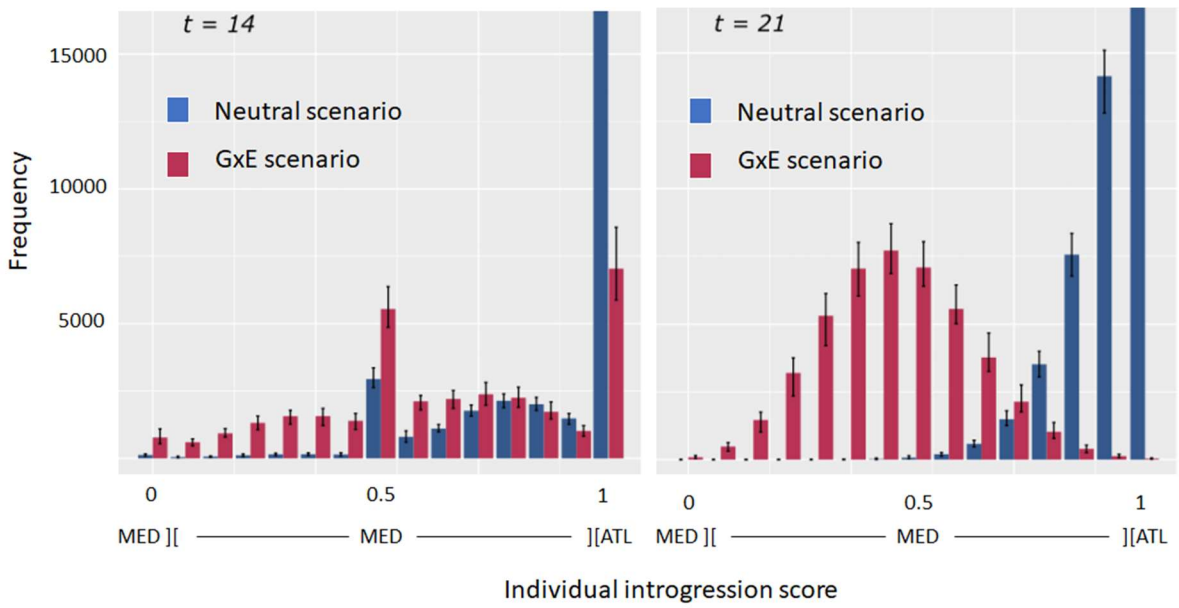
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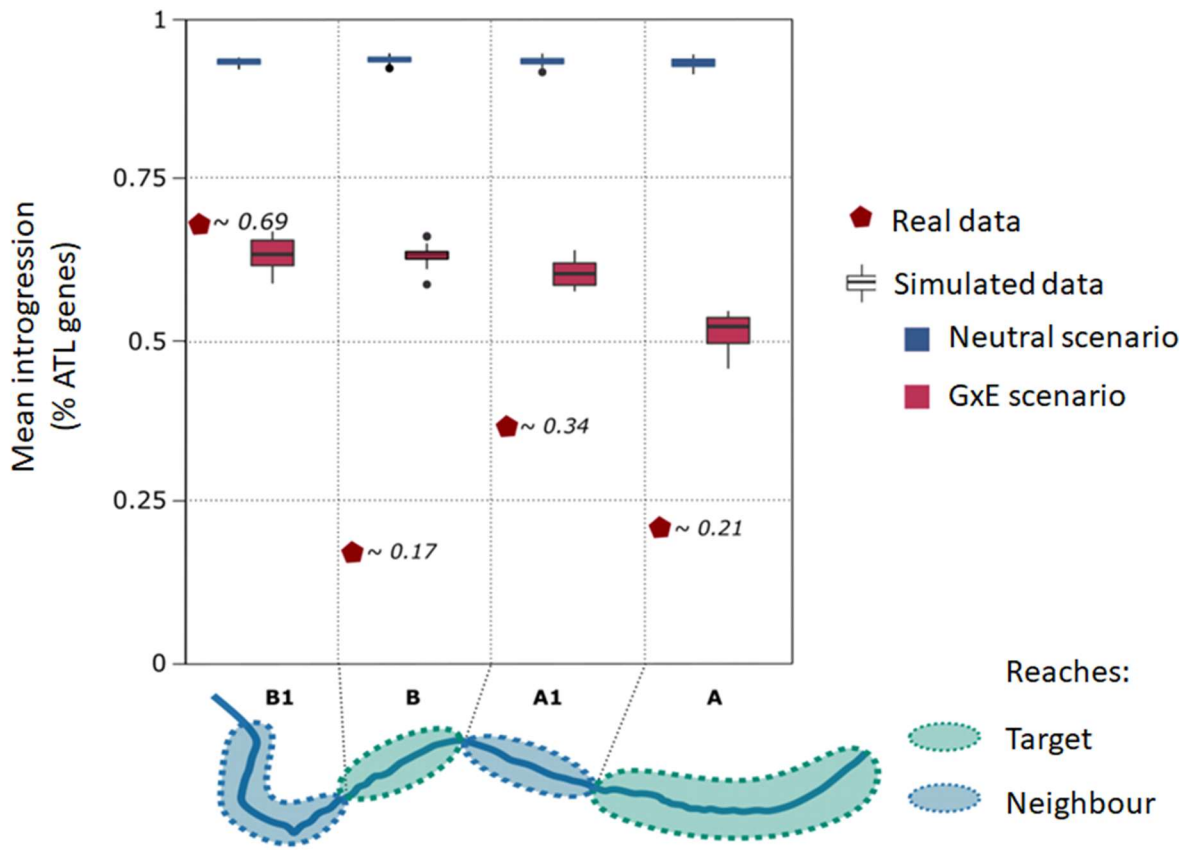
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680 FIGURE 5



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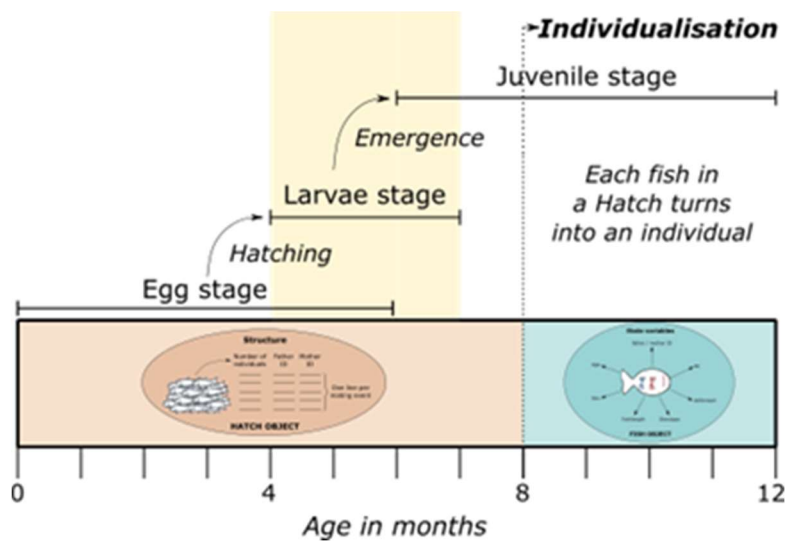
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Supplementary Information 1: Early life stages description in the model.

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Parameter	Value, range of values, variation domain.	Description
C_{stage}	{2.197;1.386;2.197;2.944;2.944}	Monthly survival coefficient per stage.
$Density_{stage, reach}$	[0-10000]	Density per reach and stage.
K_{max}	2	Controls for maximum density in a reach. A value of 2 implies a carrying capacity of 3500 ind.ha ⁻¹
α	{2.197;0.5}	Base survival at hatching (neutral/GxE)
β	{0;-3.2}	Additive temperature effect on survival (neutral/GxE)
γ	{0;-0.03}	Effect of genotype on survival (neutral/GxE)
δ	{0;0.55}	Interaction of temperature and genotype on survival (neutral/GxE)
T	[2-20]	Mean monthly temperature
L_{inf}	50	Theoretical maximum body size (cm) in the considered habitat.
a	{0.45;0.45;0.45}	Density effect on growth.
b	0.23	Base growth parameter.
ME	0.7	Accounts for sexual maturation in the growth model.
$optT$	15	Optimal growth temperature.
$rangeT$	4	Amplitude parameter describing how quickly growth is reduced when T goes farther from $optT$.

ϑ_{max}	0.2	A constant determining maximum movement probability.
$Density_{max}$	[0-10000]	Maximum density per reach
GQ	[0-1]	Reach habitat quality for growth.
GC	[0-1]	Correlation between genotype and phenotype for sexual preference.
x	1.5	Intercept parameter for female preference on male phenotype.
y	-0.2	Slope parameter for female preference on male phenotype.
D	[0-1]	Dissimilarity between the female and the male phenotype
q	[0-1]	Random component of the selection of male phenotype by females.
f	0.0011236	Fecundity coefficient
F	2.36	Fecundity exponent
RQ	[0-1]	Habitat quality of the reach for reproduction
h	2	Oophagy effect on the redd
SC	2	Number of egg batch laid by a female each year

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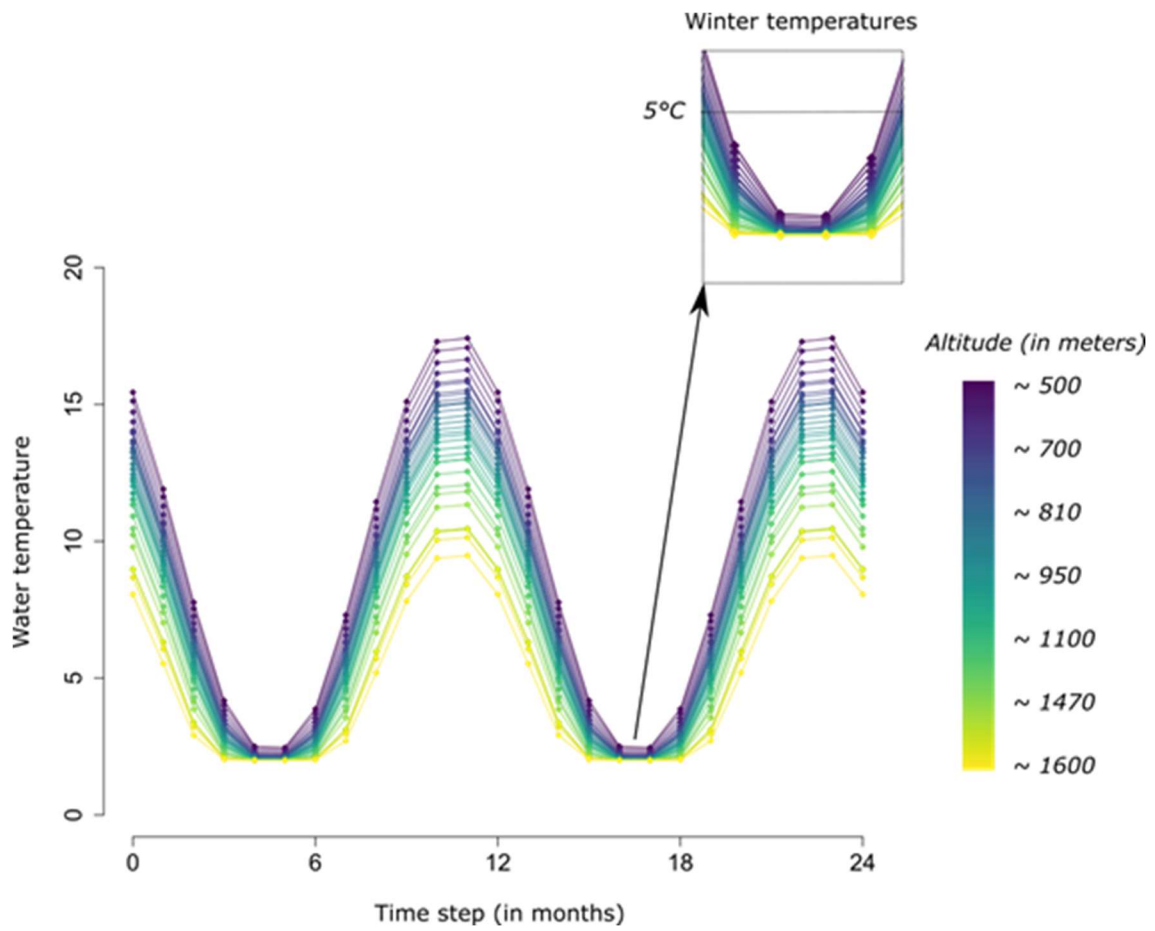
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748 **Supplementary Information 3: Temperature model.**

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751 Temperature model used for simulations carried out on the River Borne. One water temperature is
 752 calculated per reach each month based on altitude. A zoom of winter temperatures shows the
 753 temperature from December to March.

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