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Dorinda Folio

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Dorinda FOLIO

Evolutionary management of brown trout intraspecific diversity

Prepared at UMR ECOBIOP, INRAE
And SCIMABIO Interface

President:	François LEFEVRE	(Research Director)	<i>INRAE URFM, Avignon</i>
Reviewer:	Nicolas POULET	(Project manager)	<i>CDR EEE, Toulouse</i>
Examiners:	Annabel PORTE	(Research Director)	<i>INRAE Biogeco, Bordeaux</i>
	Lisa JACQUIN	(Associate Professor)	<i>EDB, Toulouse</i>
Thesis director:	Jacques LABONNE	(Research Director)	<i>INRAE ECOBIOP</i>
Thesis co-director:	Arnaud CAUDRON	(Doctor)	<i>Scimabio Interface</i>

« Voici mon secret. Il est très simple: on ne voit bien qu'avec le cœur. L'essentiel est invisible pour les yeux. C'est le temps que tu as perdu pour ta rose qui fait ta rose si importante. Les hommes ont oublié cette vérité. Mais tu ne dois pas l'oublier. Tu deviens responsable pour toujours de ce que tu as apprivoisé. Tu es responsable de ta rose... »

Le petit prince, Antoine de Saint-Exupéry

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ABSTRACT

Contemporary patterns of diversity are often the result of allopatric evolution driven by either adaptive or non-adaptive processes. The admixture of previously isolated gene pools, through human intervention, often leads to gene flow and hybridization. Intraspecific diversity management is therefore a major issue as diversity represents a resilience mechanism for populations, but also because it holds economic and patrimonial values. A typical example is the admixture of the Atlantic (ATL) and the Mediterranean (MED) lineages of brown trout (*Salmo trutta*). In the French Mediterranean area, a century of intensive stocking from ATL origins led to various outcomes of hybridization with the MED lineage, going from MED resilience to total extirpation *via* full hybridization. Historical management practices aimed at restoring MED populations but failed to reach conservation targets as eco-evolutionary mechanisms (EEMs) driving hybridization were not accounted for. For instance, empirical studies evidenced two potential drivers of hybridization: female heterogamous preference and genotype-by-environment (GxE) interactions on embryonic survival – involving maternal genotype and water temperature.

My thesis aims at investigating how these EEMs interact with other ecological, genetic and demographic drivers to influence the evolution of intraspecific diversity, in a realistic spatiotemporal framework. To do so, I assembled all the knowledge available, both ecological and evolutionary, to create an agent-based demo-genetic modelling framework (DG-ABM): MEDITERRANEA. This DG-ABM allowed me to consider (i) the EEMs driving hybridization, (ii) their genetic bases, (iii) variations in ecological parameters, as well as (iv) management practices. *In fine*, my goal was to answer one question: do eco-evolutionary mechanisms matter for the management of intraspecific diversity? The short answer, in the present case, is yes.

In multiple case studies (real and fictive), I compared various scenarios, including or not EEMs, and considering several alternative management strategies. Heterogamous preference barely influenced the evolution of diversity. On the contrary, GxE interactions played a central role in the evolution of diversity. In cold environments, the implementation of this EEM led to selection against maternally inherited ATL alleles. The strength of that selection mainly changed with temperature variations, highlighting the importance of local conditions. In addition, simulated results were closer to empirical data when GxE interactions were considered. Finally, the implementation of GxE interactions modified the outcome of management strategies, and their efficiency when combined with temperature variations. Consequently, diversity management should always be context-specific and account for such mechanisms, as well as, their underlying ecological factors. Indeed, knowledge about EEMs could help in building more efficient and evolutionary-inspired management strategies. The MEDITERRANEA model, hence, represents an innovative decision-making tool for managers. For instance, it will allow to simultaneously address several objectives, such as conserving native diversity in some areas and maximizing evolutionary potential as a whole in others, in order to cope with future environmental variations.

RESUME

Les patrons de diversité actuels résultent souvent d'une évolution allopatrique, menée par des processus adaptatifs ou non adaptatifs. Le mélange de pools génétiques précédemment isolés, dû à des actions anthropogéniques, mène souvent à des flux de gènes et à de l'hybridation. La gestion de la diversité intraspécifique est donc un enjeu majeur, dans la mesure où la diversité représente un mécanisme de résilience pour les populations, mais aussi car elle recèle des valeurs économiques et patrimoniales. Un exemple typique est le mélange des lignées atlantique (ATL) et méditerranéenne (MED) de la truite commune (*Salmo trutta*). En zone Méditerranéenne, un siècle de repeuplement intensif à partir de la lignée ATL a entraîné une introgression variable des populations MED par des gènes ATL, allant de la résilience des allèles MED à leur disparition, en passant par une hybridation complète. Les pratiques de gestion historiques visant à restaurer les populations MED n'ont pas atteint leurs objectifs de conservation car les mécanismes éco-évolutifs (MEEs) à l'origine de l'hybridation n'ont pas été pris en compte. En effet, des études empiriques ont mis en évidence deux moteurs potentiels de l'hybridation : une préférence hétérogame des femelles et une survie embryon-larvaire différentielle basée sur des interactions génotype x environnement (GxE) – impliquant le génotype maternel et la température de l'eau.

Ma thèse a pour but d'étudier comment ces MEEs interagissent avec d'autres facteurs écologiques, génétiques et démographiques pour influencer l'évolution de la diversité intraspécifique, dans un cadre spatio-temporel réaliste. Pour ce faire, j'ai rassemblé toutes les connaissances disponibles, tant écologiques qu'évolutives, pour créer un modèle démo-génétique individu-centré (DG-ABM) : MEDITERRANEA. Ce DG-ABM m'a permis de considérer (i) les MEEs de l'hybridation, (ii) leurs bases génétiques, (iii) des variations de paramètres écologiques, ainsi que (iv) des pratiques de gestion. *In fine*, mon objectif était de répondre à une question : les mécanismes éco-évolutifs sont-ils vraiment importants pour la gestion de la diversité intraspécifique ? Pour faire simple, dans le cas présent, oui.

En me basant sur de multiples cas d'étude (réels et fictifs), j'ai comparé différents scénarios, incluant ou non les MEEs, et considérant des stratégies de gestion alternatives. La préférence hétérogame influence à peine l'évolution de la diversité. A l'inverse, les interactions GxE jouent un rôle structurant dans l'évolution de la diversité. Dans les environnements froids, la mise en œuvre de ce MEE a conduit à une sélection contre les allèles ATL hérités maternellement. La force de cette sélection change principalement avec des variations de température, ce qui souligne l'importance des conditions locales. En outre, les résultats simulés sont plus proches des données empiriques lorsque les interactions GxE sont prises en compte. Enfin, la mise en œuvre des interactions GxE modifie le résultat des stratégies de gestion, ainsi que leur efficacité lorsqu'elles sont combinées à des variations de température. Par conséquent, la gestion de la diversité devrait toujours être spécifique à chaque contexte et tenir compte de ces mécanismes, ainsi que leurs facteurs écologiques sous-jacents. En effet, des connaissances sur les MEEs structurant la diversité pourraient permettre la construction de stratégies de gestion plus efficaces et inspirées par l'évolution. Le modèle MEDITERRANEA représente donc un outil innovant de soutien à la prise de décision pour les gestionnaires. Par exemple, il sera possible de répondre simultanément à plusieurs objectifs de gestion, tels que la conservation de la diversité native dans certaines zones, mais aussi la maximisation du potentiel évolutif dans son ensemble dans d'autres zones, afin de faire face aux variations environnementales futures.

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1 INTRODUCTION

1.1 BIOLOGICAL DIVERSITY AND ITS IMPORTANCE

Since ancient times, human populations have been aware of the natural diversity surrounding them (Aristotle, 350 BC. J.-C.). Over time, they have been using, interacting with and benefiting from this diversity in many ways. Nowadays, the values of natural diversity to human society are enormous in terms of commercial (consumption and production) and ecological (ecosystem services) values, but also in terms of aesthetic, social, cultural, ethical and scientific values. The concept of biodiversity – for biological diversity – was only introduced towards the end of the 20th century, when the realisation was made that a part of this diversity was endangered (Maris, 2016). The term has now achieved widespread use and encompasses a large spectrum of concepts, including various scales of biological diversity.

Biodiversity represents the diversity of life on earth including genetic diversity, species diversity and ecosystems diversity (*Convention on biological diversity*, 1992; Swingland, 2001). Ecological diversity is the diversity arising from different ecosystems (ex: forest vs ocean). It is also termed ecosystem diversity and it includes all the species, their interactions as well as the physical environment of a given ecosystem. Species diversity also referred to as interspecific diversity, represents the different species found in a given area. It is the most common type of diversity associated with the term “biodiversity”. Finally, genetic diversity refers to the genetic variations – alleles or genes – arising within or among populations of a particular species. It can lead to apparent morphological or functional diversity, making individuals of the same species different. The term intraspecific diversity describes all forms of diversity arising within a single species.

In the context of the biodiversity crisis, although a lot of attention has been devoted to interspecific diversity – *i.e.* variations between species – and its importance for ecological functioning – community

and ecosystems (Downing & Leibold, 2002; Hillebrand & Matthiessen, 2009), intraspecific diversity has been somewhat overlooked (Hoban et al., 2013; Laikre et al., 2010, 2020) despite its ecological and evolutionary importance (A. Caballero & García-Dorado, 2013; Hughes et al., 2008). Recently, the loss of intraspecific diversity has been referred to as a “hidden biodiversity crisis” (Des Roches et al., 2021) as its rate is superior to that of species loss (Mimura et al., 2017). However, it is now receiving more and more attention.

1.1.1 Intraspecific diversity

Intraspecific diversity is a key facet of biodiversity, accounting for a large part of the diversity measured in plants and animals (de Bello et al., 2011; Fridley & Grime, 2010; Siefert et al., 2015). Intraspecific diversity represents all the variations observed within and among populations from the same species, including genetic, phenotypic (Schluter, 2000), and epigenetic variations (Rey et al., 2020). Genetic variations can involve both neutral and functional *loci* (Mimura et al., 2017; Violle et al., 2007) and are central to evolutionary processes, as it is both the material for and the product of evolutionary processes, such as natural selection. Combined with environmental and epigenetic effects, functional genetic variations will result in various types of phenotypic variations, such as morphological, physiological, behavioural or functional variations – in the sense of an individual function in a population or ecosystem (*Figure 1 – 1*). Functional genetic variations will affect the performance of individuals and may influence population dynamics, species interactions as well as ecosystem functioning (Violle et al., 2007). Phenotypic variations can therefore drive ecological dynamics, which in turn can change the available genetic variations, by influencing the transmission to the next generation (*Figure 1 – 1*). Conversely, neutral genetic variations will not have any direct consequences on ecological dynamics. It is often used as a proxy to differentiate individuals belonging to different lineages for example, or to inform on some

important population parameters, such as effective population size (N_e) or gene flow (Mimura et al., 2017).

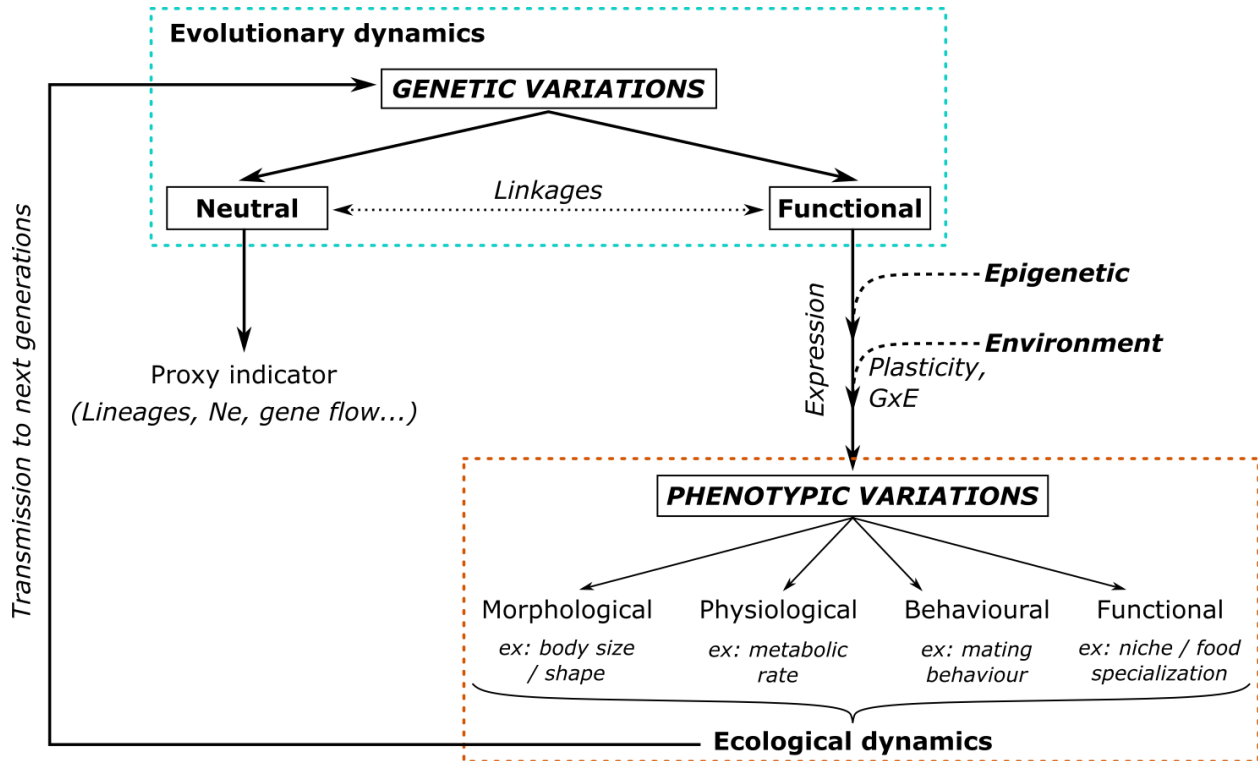


Figure 1—1: The different types of intraspecific diversity - including genetic and phenotypic variations - and their links through ecological and evolutionary dynamics.

It is therefore through changes in intraspecific diversity that an ecological process can lead to an evolutionary outcome and *vice-versa*. This puts intraspecific diversity at the core of the fields of ecology – which aims at understanding interactions between individuals and their environments – and evolution – which studies the changes in genetic variations, *i.e.* the distribution of alleles over time (Figure 1 – 2).

1.1.2 Ecological and evolutionary importance of intraspecific diversity

The realisation that ecological and evolutionary responses of populations can occur on similar temporal scales suggests that intraspecific diversity can have potential consequences on dynamics from genes to ecosystems (Carroll et al., 2007). When environmental changes occur, it is the first level of diversity to be altered (Spielman et al., 2004). Many studies now recognise the crucial role of intraspecific variations in species survival and adaptation and in communities and ecosystems resilience, notably under increasing threats imposed by human activities (Mimura et al., 2017). Indeed, genetic diversity within and among populations increases effective population size and thereby decreases the risks of inbreeding depression (Hoffman et al., 2014) and genetic drift (Charlesworth, 2009; J. Wang et al., 2016). When facing environmental changes, it increases the evolutionary and adaptive potential of populations (Merilä & Hendry, 2014) and hence temporal persistence and demographic stability through Portfolio effects (J. W. Moore et al., 2014; Schindler et al., 2010, 2015). Moreover, intraspecific diversity may influence ecological dynamics at higher levels than the population level, affecting the dynamics of communities and ecosystem functioning (Blanchet et al., 2020; Hughes et al., 2008; Raffard et al., 2021; Violle et al., 2012). For example, Crutsinger, (2016) reviewed how increasing genetic variations help in increasing ecosystem productivity and species diversity, as well as community interactions; resulting in overall ecological stability (Genung et al., 2010).



Figure 1—2: Intraspecific diversity is essential to the fields of ecology and evolution.

1.2 ECO-EVOLUTIONARY MECHANISMS SHAPING BIODIVERSITY

From 1831 to 1836, during his voyage aboard the *Beagle*, Darwin observed distinct patterns of biological diversity that could arise among closely related species but also within species. From his observations, variations in biological diversity could arise in space (“species vary globally” and “species vary locally”) and in time (“species vary over time”). For example, on the Galapagos Islands, he observed several types of finches with beaks of different sizes related to food availability, which resembled a South American finch species. He began to wonder whether these different yet similar finch species could have evolved from the same South American finch species and concluded that natural processes influenced by ecological variations could lead to changes within, and ultimately between species (Darwin, 1859).

Biodiversity stems from the interplay and feedback between ecological and evolutionary mechanisms. On the one hand, evolutionary processes create intraspecific diversity within and among populations through four main eco-evolutionary mechanisms (EEMs): mutation, selection, genetic drift and gene flow. On the other hand, ecological processes determine the role, strength and direction of such evolutionary processes, thereby also influencing intraspecific diversity (*Figure 1 – 3*). Recently, it has been more and more acknowledged that ecological and evolutionary changes may be commensurate in time and interact in a feedback loop (Carroll et al., 2007; N. G. J. Hairston et al., 2005; Pelletier et al., 2009; Reznick, Losos, et al., 2019; Reznick, Bassar, et al., 2019). For example, inter-individual interactions, such as mating or competition, within populations are one of the key drivers of selection, as they directly affect individual fitness at the core of any evolutionary dynamics (Maynard Smith, 1974; Webber & Vander Wal, 2018). As a result, they can drive evolution and adaptation, which in turn can influence the composition of the population, which then can feedback to modify interactions and underlying ecological processes (Haloin & Strauss, 2008; Mimura et al., 2017). The term “eco-evolutionary dynamics” (Hendry, 2017) has been widely used to explicitly represent these feedback loops between responses at different levels, from genes

to ecosystem, at contemporary time scales (Govaert et al., 2019; Hendry, 2017; Pelletier et al., 2009). These feedback loops acknowledge that (1) genetic diversity and its architecture determine the demographic structure and population dynamics through phenotypic expression, (2) demographic structure and population dynamics determine EEMs, *i.e.*, genetic drift, selection and gene flow, which in turn (3) determine genetic diversity (Figure 1 – 3).

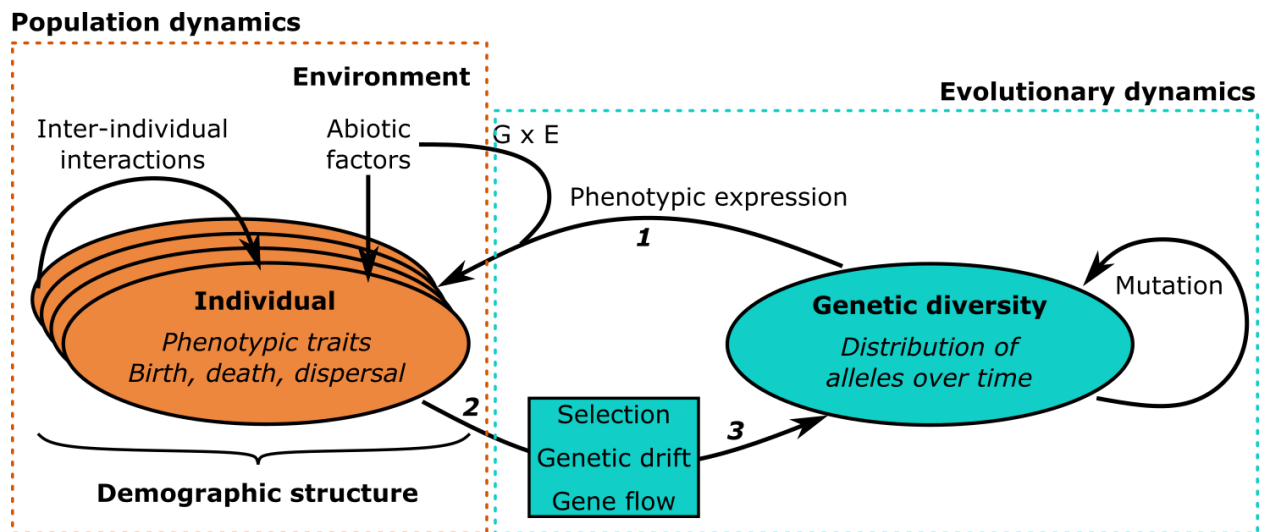


Figure 1–3: Representation of the eco-evolutionary dynamics and the feedback loop between evolutionary and population dynamics.

1.2.1 Description of the eco-evolutionary mechanisms

Mutations. Mutations are changes in the DNA sequence of genes. Although mutation rate for most organisms is low, it is the ultimate source of genetic variations – creation of new alleles in a population (Figure 1 – 4). The effect of mutations on evolution is usually not large, except when other EEMs, such as natural selection, come into play. In regards to selection, mutations can be neutral, deleterious or advantageous – *i.e.* having respectively no effect, a negative or a positive effect on individual fitness. While neutral mutations will not influence evolution directly, deleterious or advantageous mutations will lead

to changes in allele frequencies. Deleterious mutations are usually selected against and purged from the population but can be found in low frequencies – equal to that of mutation rate. Advantageous mutations are selected for and spread through the population, potentially until fixation when selective pressures are high enough or continuous in time.

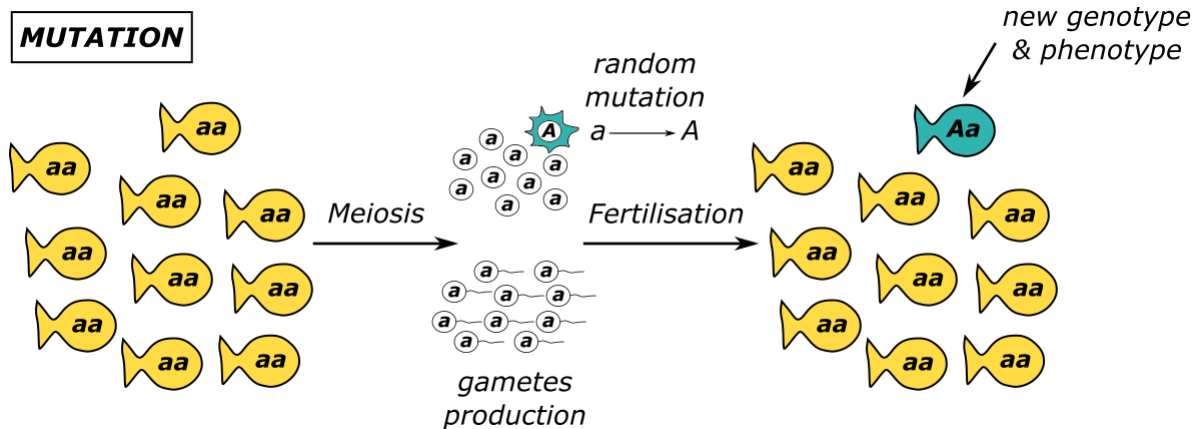


Figure 1—4: Occurrence of a random mutation, which involves the creation of a new allele “A” in a population exclusively made of “a”. When this allele is passed on to the next generation, it will lead to the creation of a new genotype “Aa” in the population and potentially a new phenotype – here “Aa” genotype lead to a blue phenotype whereas the population was only made of yellow phenotypes.

Gene flow. Gene flow represents another important evolutionary force affecting diversity (Seehausen, 2004). The movement of individuals – emigration or immigration – or their gametes – dispersal for plants – between populations can participate in the increase or decrease of diversity through various mechanisms, as it involves the movement of certain alleles into or out of a population (Figure 1 – 5). For example, the immigration of new genetic diversity in a population can help increase diversity *via* genetic rescue (Frankham, 2015; Whiteley et al., 2015). In other cases, gene flow can also lead to the loss of intraspecific diversity through outbreeding depression (Templeton et al., 1986) and maladaptation (Lenormand, 2002).

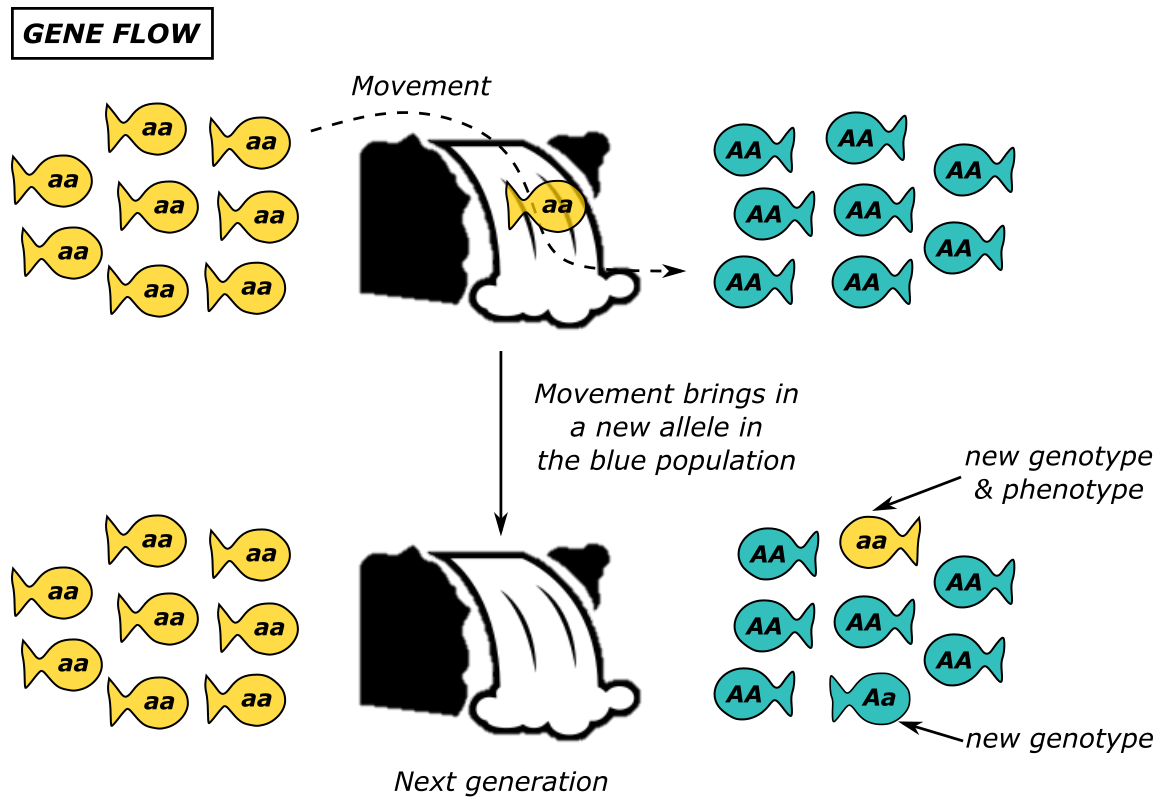


Figure 1–5: Two genetically – “aa” and “AA” genotypes – and phenotypically – yellow and blue phenotypes – distinct fish populations are located respectively upstream and downstream of a waterfall. The movement of some individuals from the upstream to the downstream population brings in a new genotype and phenotype in the downstream population. Successful reproduction of this new phenotype will result in effective gene flow, bringing a new allele and potentially new genotypes, “aa” and “Aa”, into the downstream population.

Genetic drift.

Genetic drift (Boecklen, 1986) is a random process that always happens in non-infinite population size. It involves changes in allele frequency due to chance events – such as random mortality or reproduction that will lead to the random transmission of certain alleles and not others to the next generation (Figure 1 – 6). This mechanism can have a strong impact on small populations, as it can cause the random fixation of alleles, thereby reducing available genetic diversity (Whitlock, 2000).

Populations subject to the effects of genetic drift might be less adaptive and at risk of extinction (Vilas et al., 2006; Whitlock, 2000).

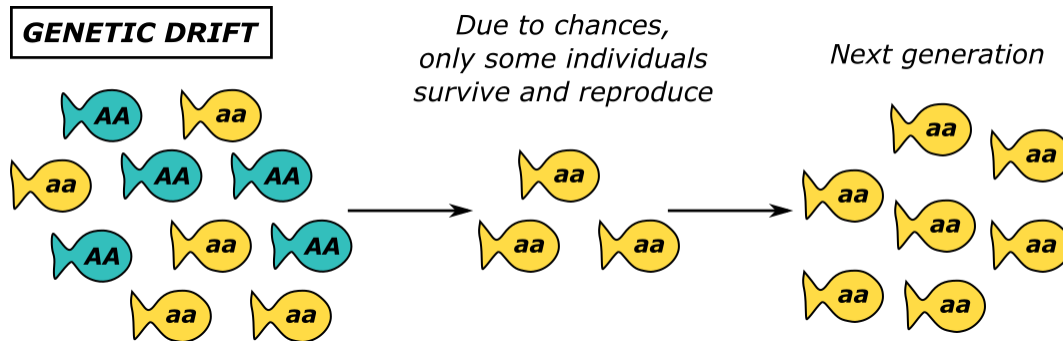


Figure 1—6: Genetic drift is a common process occurring in all non-infinite populations, which leads to the random reproduction and survival of some individuals and can cause changes in the genetic composition of the population. In this example, the initial population is made of an equal proportion of “AA” and “aa” genotypes. Following genetic drift, only a few “aa” individuals managed to survive and reproduce, which caused the loss of the “A” allele, changing the genotypic composition of the next generation – only composed of “aa” genotypes and hence yellow phenotypes.

Natural selection. Natural selection proposed by Charles Darwin is a mechanism for evolution, caused by the inheritance of traits and the competition among different individuals. While intraspecific variations among individuals can give some individuals a fitness advantage – to survive and/or reproduce; due to inheritance, advantageous variations will be more likely to be transmitted to the next generation (Figure 1 – 7). As long as this variation remains advantageous, it will increase in frequency in the population, leading to genetic changes and hence evolution. Natural selection is the process through which adaptation occurs. This process is highly dependent upon ecological variations, as selection can differ among environments. Local adaptation (G. C. Williams, 1966) can happen when the forces of natural selection vary in space – divergent selection, resulting in potential genotype-by-environment – later on

referred to as GxE – interactions (Kawecki & Ebert, 2004). Natural selection drives phenotypic response to changing environmental conditions.

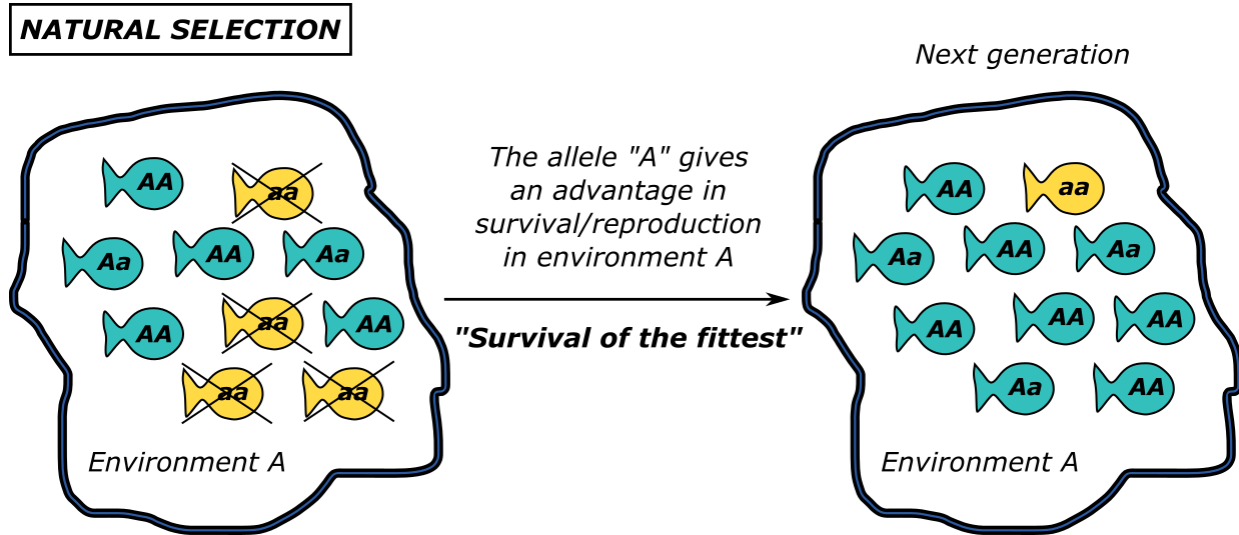


Figure 1—7: In the environment A, the allele “A” confers a fitness advantage to blue individuals. Through natural selection, blue individuals pass on more alleles in that environment. In the next generation, this leads to an increase in the percentage of blue phenotypes and a decrease in that of yellow ones. In this example, as “Aa” genotypes also codes for blue phenotypes through dominance effects, the allele “a” remains segregated in the population and some “aa” individuals may still be found.

Sexual selection. Due to the mechanisms of sexual selection – male competition and female preference – non-random mating may occur based on individual genotypes or phenotypes. For example, preference might be directed toward either similar or dissimilar mates (Figure 1 – 8). While these differences in mating interactions might not always directly change allele frequencies in the population, it often changes phenotypes and genotypes frequencies, and hence the composition of the population, which in turn can further affect mating interactions. Like natural selection, it represents an important EEM, as it directly affects individual fitness, thereby driving evolution.

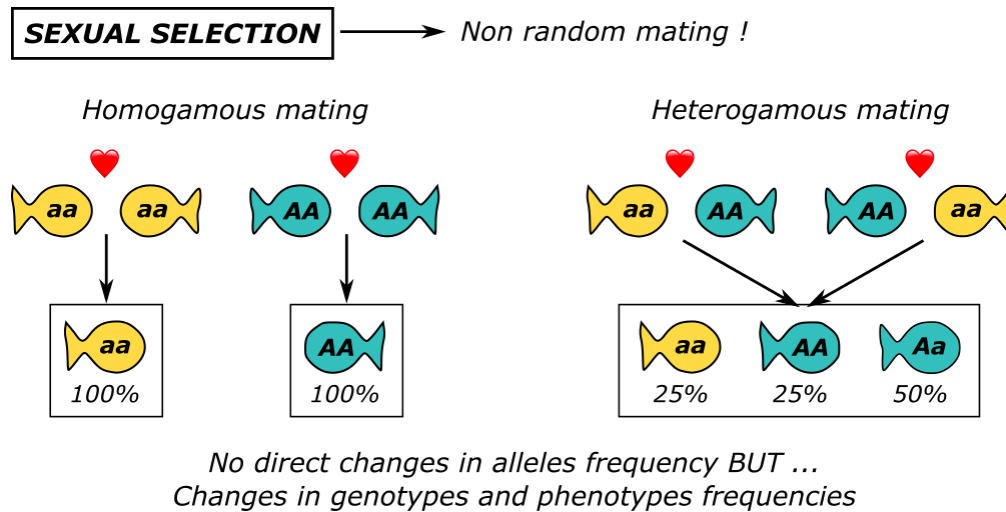


Figure 1—8: In a population composed of different phenotypes, sexual selection mechanisms – male-male competition and female preference – may result in non-random mating. For example, when two phenotypes are available – blue and yellow – the outcome of homogamous versus heterogamous mating will be different. Strictly homogamous mating will lead to the creation of parental genotypes only – “aa” and “AA”, while heterogamous mating will result in the creation of more genotypes – parental one “aa” and “AA” but also a new one “Aa” – similarly to random mating, but in a different frequency.

1.2.2 Creating patterns of diversity: from intra to interspecific diversity

Contemporary patterns of diversity are often the result of divergent evolution (Harrison, 2012), driven by either adaptive or non-adaptive processes (Hendry & Gonzalez, 2008; Mayr, 1970). The interplay between evolutionary mechanisms and ecological processes (EEMs) creates and shapes patterns of diversity through space and time. Understanding these EEMs and how they lead to various patterns of biodiversity is crucial for ecological, evolutionary and conservation sciences (Blanchet et al., 2020; Chave, 2013). At the intraspecific level and for complexes of species, the resulting patterns of diversity at large scales underline the strength and interplay of these EEMs to drive divergent evolution.

Gene pool divergence. Divergence usually follows a separation in the initial gene pool (*Figure 1 – 9*), which can result from the existence of a physical barrier (allopatric evolution), the colonisation of a new niche (peri/parapatric evolution) or the rise of genetic polymorphism (sympatric evolution) within a population. This separation is usually associated with limited gene flow and can lead to two segregated gene pools, which will go through their own eco-evolutionary dynamics independently as described in *Figure 1 – 3*. This may lead to further divergence, as all EEMs will interplay to shape – increasing or decreasing – intraspecific diversity within each gene pool, but also among gene pools – *i.e.* increasing or decreasing divergence. For example, gene flow between differentiated gene pools will generally lead to a decrease in genetic variation among gene pools and an increase within gene pools (Garant et al., 2007). The accumulation of genetic differences among gene pools often results in the evolution of reproductive barriers, causing partial, sometimes even complete, reproductive isolation between gene pools and eventually leading to speciation (Mallet, 2007). By reducing divergence, gene flow generally retards speciation, as it may break the linkage between genes for reproductive isolation and those for adaptation (Coyne & Orr, 2004).

Scales of divergence. The process of divergence between gene pools can happen over relatively short and long time scales (Carroll et al., 2007), and be observed over macro and microgeographic scales (there is recent and mounting evidence for microgeographic adaptation, reviewed in Richardson et al., 2014). It can lead populations down the path to speciation, on a time scale of century to decades when natural selection is involved. Indeed, strong selection can cause substantial differentiation among gene pools on observable time scales, in some instances representing the early stages of speciation (Hendry et al., 2000, 2007; M. K. Schwartz et al., 2004).

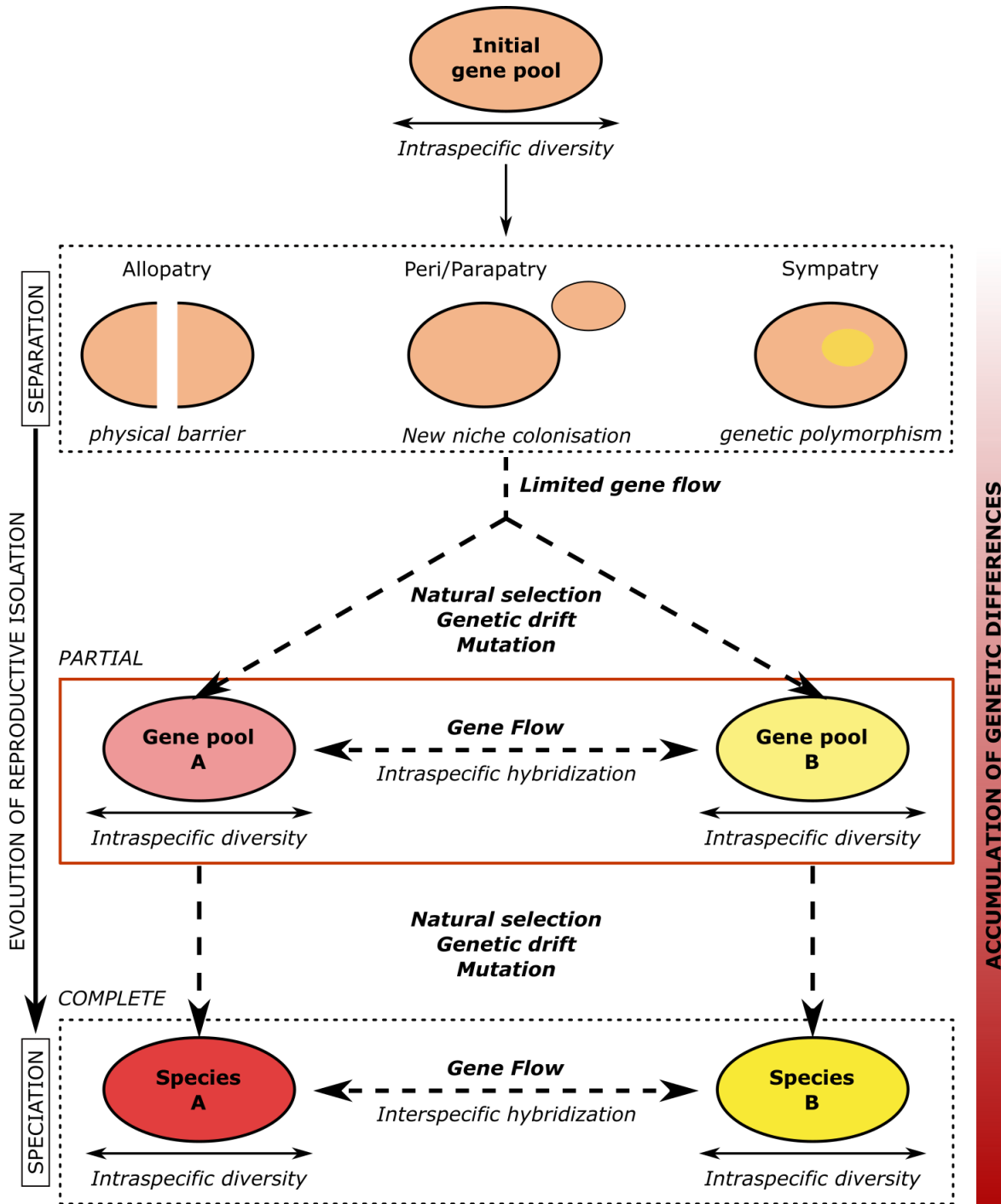


Figure 1—9: Gene pool divergence, driven by adaptive and non-adaptive processes, from intra to interspecific diversity.¹

¹ In the present PhD, I will particularly target a situation where divergence has previously occurred through long period of geographic vicariance, generating incomplete reproductive isolation between gene pools.

Patterns of diversity. Patterns of intraspecific diversity generated by isolation by distance are among the most commonly reported spatial patterns of diversity (Sexton et al., 2014; Wright, 1943), but patterns of isolation by adaptation have also been described (Nosil, 2009; Sexton et al., 2014). Following new niche colonisation, patterns of diversity usually involve a decrease in genetic diversity at boundary ranges and along colonisation routes (Eckert et al., 2008; Kirkpatrick & Barton, 1997; Liggins et al., 2015).

Hybridization. Isolated gene pools may eventually come back into secondary contact naturally and lead to a mixed population. This is known as natural hybridization (Genovart, 2009). Hybridization is defined as the interbreeding of individuals originating from distinct populations or gene pools (Allendorf et al., 2001), may it be intra or interspecific. Natural hybridization mainly happens between otherwise allopatric *taxa*, which have been genetically isolated but not completely reproductively isolated (Genovart, 2009). Natural hybridization is a common evolutionary process in plants and animals (Barton, 2001; Grabenstein & Taylor, 2018; Olden et al., 2004; Twyford & Ennos, 2012), which may play an important role in shaping their evolutionary trajectory (Rieseberg et al., 2003; Seehausen, 2004). Natural interspecific hybridization involves at least, respectively 25% and 10% of recent plant and animal species respectively (Mallet, 2005). Hybridization can have various impacts on diversity (Epifanio & Nielsen, 2001; Genovart, 2009; Todesco et al., 2016) and can potentially lead to a number of different situations (*Figure 1 – 10*):

- ☞ A. The maintenance of both parental gene pools (*Situation A*) without any hybrids. This may happen when natural selection is high and gene flow is low.
- ☞ B. The maintenance of only one parental gene pool and the disappearance of the other one (*Situation B*) that could result from natural selection mechanisms and be environment dependent – one gene pool might be at an advantage in one environment compared to the other.

- ↻ C. The disappearance of both parental gene pools resulting from a high level of genetic exchange between gene pools that will reduce divergence and ultimately lead to a fully hybridized gene pool (*Situation C*). This may occur when gene flow is high, and none or very few natural selection forces are at work. It can result in the appearance of a new species through hybrid speciation (Mallet, 2007).
- ↻ D. The maintenance of all diversity, with the establishment of a stable hybrid zone while the integrity of each parental gene pool is still maintained (*Situation D*). For example, each gene pool might be maintained in their favourable environment with hybrids found in intermediate environments or at boundaries.

In some cases, hybridization can be seen as problematic as it may cause populations to fully homogenise and lead to the extinction of some populations (Rhymer & Simberloff, 1996; Todesco et al., 2016), thereby decreasing diversity and potentially adaptive divergence (Garant et al., 2007). Conversely, hybridization may increase biodiversity by allowing for the creation of new gene complexes or species (E. Anderson & Stebbins, 1954; Grant & Grant, 2002; Seehausen, 2004). With the escalating effects of global warming on biodiversity, it may represent a resilience mechanism against climate change (Chan et al., 2019), as it may increase adaptive potential (Garant et al., 2007).

Hybridization can have a dual impact on gene pools, as it may promote further evolutionary divergence, through reinforcement for example (Hoskin et al., 2005; Servedio, 2004) but also prevent it (Coyne & Orr, 2004; Mayr, 1963). The rate and effectiveness of gene flow in interaction with adaptive processes will control for the integrity of gene pools (Genovart, 2009) and the rate of adaptive divergence (Garant et al., 2007). Hence, the outcome of hybridization will depend on various interacting EEMs, thereby making each situation unique (Genovart, 2009). The concept of reproductive isolation mechanism is used to describe all the mechanisms or reproductive barriers that will regulate gene flow between gene pools (Dobzhansky, 1937).

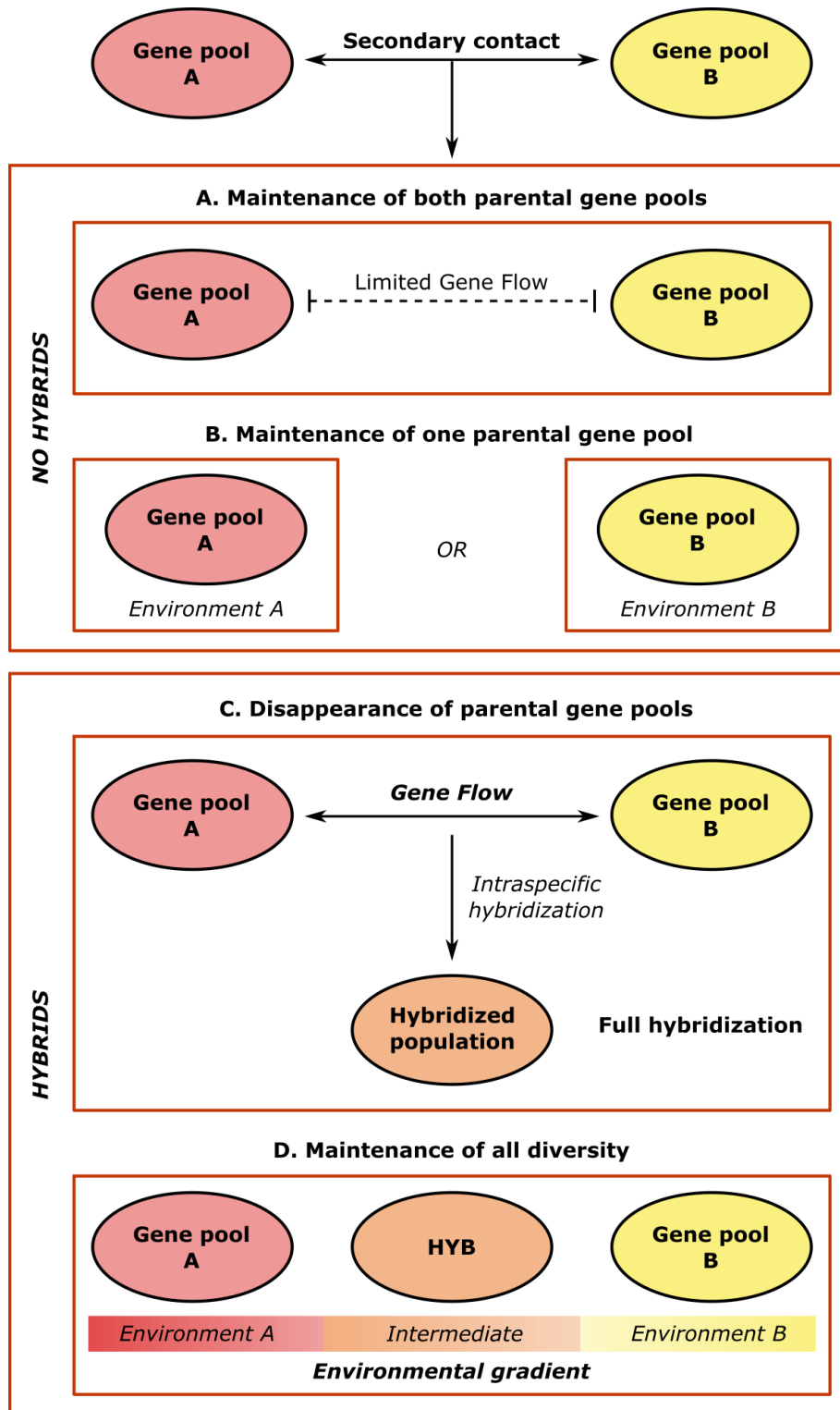


Figure 1—10: During a secondary contact, hybridization may lead to various situations from widespread hybridization to the maintenance of parental populations (“types of hybridization” Allendorf et al. 2001), depending on many ecological factors and related EEMs.

1.2.3 Drivers of hybridization

EEMs play an important and structuring role in the evolution of intraspecific diversity, as they may enhance gene pool divergence or favour hybridization, through various mechanisms. Indeed, on the one hand, these EEMs can lead to the evolution of reproductive isolation barriers between populations (Schluter, 2000). These barriers may limit gene flow, and hence hybridization yet not always fully prevent it (Bettles et al., 2005; Mallet, 2005). Reproductive isolation barriers can act before or after fertilisation, at each step of reproduction and development (Coyne & Orr, 2004). It is generally divided into two types of barriers: pre-zygotic barriers and post-zygotic barriers. On the other hand, the same EEMs can also enhance hybridization by favouring effective gene flow, through enhanced mating between gene pools and/or increased hybrid fitness. Finally, it is also possible that through fitness differences, these mechanisms could favour one gene pool over the other, potentially leading to the extinction of one gene pool.

Pre-zygotic drivers of hybridization. Pre-zygotic drivers may prevent/enhance mating or fertilisation between two populations (Harrison, 2012) by preventing/allowing potential mates from meeting or successfully mating.

☞ ***Ecological isolation.*** Hybridization is impossible when two populations are ecologically segregated (Rundle & Nosil, 2005). Habitat and/or specific biotic interactions – plant-pollinator interactions – can prevent individuals from meeting and hence hybridizing. For example, ecological isolation has been playing an important role in assortative mating observed between two populations of gall wasp that actively select for different species of oak (Egan et al., 2012). It is important to note that habitat isolation is dictated by an active choice of habitat and not geographic vicariance. For example, in some populations, hybridization between native steelhead and coastal cutthroat trout is limited due to the choice of different spawning sites (Buehrens et

al., 2013). However, hybridization occurs to some extent when spawning sites overlap, as hybrid individuals can in some contexts be found.

☞ **Temporal isolation.** The timing of reproduction also controls hybridization, as two populations can only mate if their reproductive timing is synchronous. Temporal isolation has been evidenced in populations of salmonids (Hendry et al., 2004; Limborg et al., 2014; Quinn et al., 2000). For example, in sockeye salmon, individuals reproducing early are genetically differentiated from those reproducing late and display different life-history traits (Hendry et al., 2004). In sympatry, temporal isolation due to shifts in flowering time led to the speciation of two mountain roses species (Osborne et al., 2020). The mechanisms involved in temporal isolation play an important role in preventing hybridization when populations share the same ecological niche. Changes in these mechanisms can promote hybridization. For example, in Australian Banksia, habitat disturbance led to an increase in the flowering season of both species and hence to the disappearance of temporal isolation. This resulted in hybridization (Lamont et al., 2003).

☞ **Behavioural isolation.** Behavioural isolation is an important reproductive barrier in animal species and it often results from sexual selection mechanisms. Every signal involved in sexual selection might play a role in behavioural isolation, especially between species, as they need to recognise conspecific. For example, differences in bird songs might lead to premating isolation between species (Balakrishnan & Sorenson, 2006; Grant & Grant, 1997). Male competition and female preference can both play an important role in hybridization (Lipshutz, 2018) by either driving behavioural reproductive isolation (Southcott & Kronforst, 2018; Tinghitella et al., 2018, 2020) or conversely enhancing hybridization (heterogamous mating: Gil et al., 2015; absence of discrimination and increased random mating: Aubier et al., 2019; Maroja et al., 2009; Wyman et

al., 2011). Assortative and heterogamous mating have been suggested to play an important role in the evolution of hybrid zones (Gil et al., 2015; Schumer et al., 2017). Therefore, different behaviours involved in sexual selection are important to consider while studying hybridization, and even more so since mating systems can drive evolutionary dynamics (Maan & Seehausen, 2011).

Post-zygotic drivers of hybridization. Post-zygotic drivers involve hybrid sterility and viability (Harrison, 2012). It is based on the relative fitness of individuals – hybrids compared to parental gene pools. The consequences of hybridization on individual fitness can be observed directly in the first generation (Araki et al., 2007) or in further generations when backcrosses are involved.

☞ ***Hybrid sterility and non-viability.*** Negative epistasis interactions may lead to the non-viability of F1 hybrids and their sterility. These negative effects will obviously have consequences for hybrids fitness, but also for the fitness of parental populations, which will be investing in wasteful reproduction (Allendorf et al., 2001). In some cases, only one gene pool might be negatively affected, with for example only hybrids resulting from one-way crossing being sterile (Konishi & Takata, 2004); leading to asymmetric hybridization and potentially the extinction of that gene pool.

☞ ***Outbreeding depression.*** Hybrids might be less fit or even non-adapted compared to parental gene pools. The decrease in fitness for hybrid individuals is often due to the exchange of maladaptive genes (Garant et al., 2007) and often happens when gene pools are highly genetically differentiated (Aitken & Whitlock, 2013). For example, the loss of local adaptation has been documented in cases where non-native and/or domesticated individuals have been introduced in wild native populations (Verhoeven et al., 2011). Outbreeding depression might always affect F1

hybrids, but may be detected in F2 or further generations (Goldberg et al., 2005). Genetic incompatibilities, such as negative epistasis interactions may also cause a form of outbreeding depression (Turelli & Orr, 2000).

☞ **Heterosis.** In some cases, hybrid fitness might be superior to that of parental gene pools. This fitness advantage might be associated with an increased growth rate and better survival and/or fertility compared to parental gene pools (Chen, 2010). It is referred to as heterosis (Allendorf & Luikart, 2007) – *i.e.* when heterozygotes have better fitness than homozygotes in a population – and might be explained by the masking of deleterious alleles. Heterosis might represent a very important mechanism for very small and potentially inbred populations (Chen, 2010; Lippman & Zamir, 2007).

☞ **Fitness differences between gene pools.** Fitness differences between gene pools – hybrid included – might vary in different environments due to natural selection processes. For example, a gene pool might be fitter than the other only in a specific environment (Folio et al., 2021). In cases of natural hybridization, each gene pool might show better fitness in its own natural environment, compared to the other (De La Torre et al., 2014), as they may be locally adapted. Such fitness differences are likely to lead to different outcomes of hybridization in space and time based on ecological variations.

Other types of isolation such as gametic incompatibilities (Lobov et al., 2019) or mechanical isolation – incompatibility of sexual organs (Masly, 2011) – could also prevent hybridization between two populations. These mechanisms are mainly involved in interspecific hybridization to maintain the integrity of very divergent *taxa*.

Overall, natural patterns of diversity are shaped in space and time by various EEMs playing in concert to drive the fission – divergence – and the fusion – hybridization of gene pools. However, these patterns are consistently altered by human-induced evolutionary changes (Hendry et al., 2017; Pelletier & Coltman, 2018; Smith & Bernatchez, 2008), which often lead to diversity loss (Ceballos et al., 2017; Mimura et al., 2017; Tilman et al., 2017).

1.3 ANTHROPOGENIC IMPACTS ON BIODIVERSITY

Anthropogenic actions are one of the major drivers of environmental changes (Steffen et al., 2011), imposing strong selective pressures on natural populations. Human-induced selective pressures have been shown to cause rapid phenotypic changes in populations (Darimont et al., 2009; Hendry et al., 2008; Sullivan et al., 2017) that would often translate into genetic changes (Allendorf et al., 2008; Coltman et al., 2003; Uusi-Heikkilä et al., 2015), thereby triggering rapid – contemporary – evolution (Carroll et al., 2007; Schoener, 2011). One of the most famous examples of rapid evolutionary changes that occurred at the very beginning of industrialisation is the case of the peppered moths (*Biston betularia*). In England, before industrialisation, moth populations were mainly composed of a light-coloured morph, better adapted to the environment, as they would blend in lichen-covered trees. Following industrialisation, environmental changes caused by coal pollution caused trees to turn dark and led to a rapid change in moths phenotypes frequency (Tutt, 1896) – the dark morph went from about 0% before 1948 to 98% in 1895 (Kettlewell, 1973). The dark morph that would now camouflage better was favoured compared to the light morph. This shift resulted from strong selection from predators (L. M. Cook et al., 2012). It happened around manufacturing areas where pollution was high, creating patterns of local adaptation across short distances – microgeographic adaptation (Richardson et al., 2014). This example is one among

many (Carroll et al., 2007; Pelletier et al., 2009; Reznick, Losos, et al., 2019) indicating that rapid evolution is particularly common following changes in selection and population structure following anthropogenic disturbances.

1.3.1 Main human threats to biodiversity

Nowadays, the main anthropogenic disturbances faced by natural populations are habitat fragmentation and modification, over-exploitation, pollution, invasive species and climate change (Pelletier & Coltman, 2018). Different *taxa* are influenced at different rates by each of these disturbances but often, several of these threats may affect them simultaneously (Pelletier & Coltman, 2018), amplifying their negative impact on biodiversity (Brook et al., 2008) and thereby affecting natural ecological but also evolutionary dynamics. For example, not only does overexploitation affect population dynamics, it often also acts as a selective agent on populations life history traits – such as smaller body size in fish (Heino et al., 2015; Swain et al., 2007; Uusi-Heikkilä et al., 2015). This is often detrimental to the value of resources (Reznick, Losos, et al., 2019), thereby imposing a feedback on exploitation itself – for example, optimal fishing patterns. It is therefore important to understand and evaluate the effect of human-induced changes on intraspecific diversity (Mimura et al., 2017), for both the persistence of species but also for natural resources exploitation, management and conservation (Pelletier & Coltman, 2018).

1.3.2 Anthropogenic hybridization

Anthropogenic hybridization is considered a major threat to biodiversity (Crispo et al., 2011; Rhymer & Simberloff, 1996), and results from the admixture of naturally isolated gene pools through human intervention. It is caused by a deliberate or accidental introduction of individuals from other *taxa* –

species, lineages or non-autochthonous populations – that may have been domesticated. A recent review (Todesco et al., 2016) reported that the most common causes of anthropogenic hybridization were agriculture (55% of studies), invasive species (54%) and habitat disturbance (36%). Indeed, many ecological interactions can be observed between wild and domesticated individuals – originating from agriculture and aquaculture (Ryman et al., 1995; Utter, 2004) – that escaped or were willingly introduced in natural populations (Drinan et al., 2015; Huvet et al., 2004; Kiang et al., 1979; McGinnity et al., 2003; Reed, Prodöhl, et al., 2015). In salmonids, for example, repeated introductions of domesticated species, such as brown trout and rainbow trout (Gozlan et al., 2010) led to extensive hybridization with wild individuals, at both intra and interspecific levels (Bolstad et al., 2021; Drinan et al., 2015; Hitt et al., 2003; McGinnity et al., 2003), sometimes threatening natural populations of extinction (McGinnity et al., 2003). Hybridization between wild and domesticated rice almost led to the extinction of wild rice (Kiang et al., 1979). Overall, hybridization can have various impacts on genetic diversity and population demography (Epifanio & Nielsen, 2001; Genovart, 2009; Todesco et al., 2016).

1.3.3 *The consequences of hybridization on wild populations*

Hybridization can result in both positive and negative effects on genetic diversity of wild populations. In some cases, hybridization may increase genetic diversity *via* evolutionary rescue (Stelkens et al., 2014; Todesco et al., 2016) and allow individuals to adapt to (Rieseberg et al., 2003) and colonise new environments *via* adaptive introgression (De La Torre et al., 2014; Whitney et al., 2015). Indeed, recombination can sometimes combine the most selectively advantageous genes of the parents or create new advantageous recombinant genotypes (Latta et al., 2007; Lippman & Zamir, 2007; Sain et al., 2002). However, in most cases, hybridization has negative impacts on native populations demography and diversity (Rhymer & Simberloff, 1996; Todesco et al., 2016). Indeed, demographic, pathogenic, and

1.3 Anthropogenic impacts on biodiversity

genetic consequences reducing the fitness of native populations are often observed following admixture (Budy et al., 2013; McGinnity et al., 2003; Závorka et al., 2018 but see Stephens et al., 2020). Hybridization can cause the loss of unique genotypes or advantageous combinations of genes, potentially leading to the loss of local adaptation (Verhoeven et al., 2011) and decreasing population adaptive potential (Allendorf et al., 2001; Bohling, 2016; Garant et al., 2007). For example, hybrid individuals can be more sensitive to pathogens (Goldberg et al., 2005). In the worst case, extinction by hybridization and introgression can occur (Rhymer & Simberloff, 1996; Seehausen, 2006), through two main mechanisms related to hybrids fitness (Allendorf et al., 2001). On the one hand, lower fitness of hybrids individuals can cause demographic swamping, where the wasteful production of hybrids leads to a decrease in population size, and ultimately the disappearance of one or both parental populations (Allendorf et al., 2001; Konishi & Takata, 2004; Wolf et al., 2001). On the other hand, higher fitness of hybrid individuals could lead to genetic swamping, where the population becomes fully hybridized (“Hybrid swarms” Allendorf et al., 2001; Rhymer et al., 1994; Rhymer & Simberloff, 1996). Nevertheless, in other instances, the genetic integrity of wild populations might be maintained despite recurrent hybridization, as it is the case in the context of wolves x dogs hybridization (Pacheco et al., 2017; Pilot et al., 2018).

Anthropogenic hybridization is a conservation issue for managers, it is therefore important to understand if it poses an actual threat to the viability and genetic integrity of wild populations before engaging in any actions (Bohling, 2016). To do so, evaluating the type of hybridization occurring (*Figure 1 – 10*) and its extent – prevalence of hybrid individuals – in a specific context is fundamental (Allendorf et al., 2001; Bohling, 2016), as each case of hybridization is unique (Genovart, 2009). The latter also requires an accurate identification of hybrid individuals, without which estimates might be highly biased.

1.4 MANAGING HYBRIDIZATION

When hybridization poses a threat to native diversity (Crispo et al., 2011; Rhymer & Simberloff, 1996; Seehausen et al., 2008; Todesco et al., 2016), identifying effective management strategies to avoid or reduce introgression is of paramount importance (Allendorf et al., 2001). Various traditional management practices are often implemented to avoid introgression and conserve native populations. These include hybrids and/or non-native individuals' removal and/or sterilisation, the creation of genetic refuge or the transfer of native individuals, as well as the management of human disturbance that may affect hybridization (Allendorf et al., 2001; Bohling, 2016; Gil et al., 2016).

1.4.1 Traditional assumptions underlying management practices

Commonly applied management practices, such as the implementation of genetic refuge, native individual translocation or restocking (Caudron et al., 2006, 2011; Caudron & Champigneulle, 2011; Grobler et al., 2011), or any practices involving admixture, often rely on one assumption: some mechanisms, such as local adaptation or outbreeding depression, will act as a purifying force that could favour the conservation of native—supposedly adaptive—genetic variation (Broadhurst et al., 2008; Hansen et al., 2009; Kronenberger et al., 2018; Ruzzante et al., 2004). However, outbreeding depression can also lead to demographic swamping (Allendorf et al., 2001; Wolf et al., 2001) and be associated with the genetic swamping of adapted genes (Allendorf et al., 2001; Rutherford et al., 2019), which could counter-effect these management practices. An alternative conservation measure is to remove “non-native individuals” (Bohling, 2016; Caudron & Champigneulle, 2011; Guay et al., 2014; Muñoz-Fuentes et al., 2007), but this can only be viable when hybridization is restricted in space or not frequent (Genovart, 2009). Finally, when hybridization leads to widespread introgression and, potentially the genetic rescue of populations (Fitzpatrick et al., 2019), management options to conserve native variation might be limited

(Genovart, 2009). When pure native populations still exist, one solution might be to isolate them to prevent any further gene flow (Bohling, 2016; Guay et al., 2014).

1.4.2 *The importance of considering EEMs driving hybridization*

Mounting evidence indicates that these management practices generally fail at conserving native diversity after admixture had already occurred (Gil et al., 2016; Muñoz-Fuentes et al., 2007; Vincenzi et al., 2012). This is possibly due to the lack of knowledge and consideration regarding reproductive isolation mechanisms (Bajec et al., 2015; Berrebi, Poteaux, et al., 2000; Iacolina et al., 2019; Taillebois et al., 2020), which could help to build more efficient and evolutionary-inspired management strategies. Indeed, effective management of anthropogenic hybridization requires a better understanding of all the EEMs influencing the outcomes of hybridization (Allendorf et al., 2001; Hoffmann & Sgrò, 2011; Seehausen et al., 2008), such as adaptive processes at play and effective gene flow between populations. As Genovart (2009) stated, “if any management strategies are to be useful, then the original cause of the hybridization should first be resolved” and “the more we know about the hybridization process and the ecological factors involved, the more able we will be to analyze each situation” in order to understand the potential consequences of any management practices on diversity dynamics. Indeed, EEMs, demographic characteristics, environmental conditions and management practices will collectively influence hybridization and diversity dynamics. It is therefore important to consider the interactive effects of these factors on the initiation, persistence, and outcomes of hybridization.

Therefore, the identification and consideration of all EEMs involved in reproductive isolation should be a prerequisite to any management decisions in order to avoid counter-productive results. Indeed, considering differential social interactions (e.g. mating preference) and genetic performances (e.g. fitness

differences) between gene pools (Castellani et al., 2015; Nathan et al., 2019) is essential to predict the evolution of intraspecific diversity. For example, knowledge about the fitness of hybrids individuals compared to parents could inform on the expected rate of adaptive introgression (Barrett & Schluter, 2008; Hedrick, 2013) and the stability of hybrid zones (Buggs, 2007; Taylor et al., 2015). Additional information on the ecological factors contributing to such differences could also help in understanding and predicting the outcomes of hybridization in specific environments. Such knowledge could then be used to implement new management practices (Epifanio & Nielsen, 2001; Genovart, 2009; Todesco et al., 2016) to either avoid admixture (if applied soon enough), lesser the extent of introgression, and favour “native” genes conservation when admixture has already occurred (Caudron, Champigneulle, et al., 2012), or to favour diversity when it enhances the adaptive potential of the population (Chan et al., 2019).

1.5 THE RISE OF ECO-EVOLUTIONARY MANAGEMENT IN CONSERVATION SCIENCE

Since they realised the magnitude of their influence on biodiversity loss, human societies have had the desire to conserve biodiversity (Maris, 2016). The notion of “conservation biology” was introduced in 1985 by Soulé as a scientific field focusing on the biology and ecology of species impacted directly or indirectly by anthropic activity. Since recently, management and conservation practices had been traditionally based on ecological solutions (Reznick, Losos, et al., 2019), as they would happen on what was considered an ecological time scale. Management was only thought to influence ecological dynamics – such as population size – whereas evolutionary dynamics were mainly ignored since evolution was seen as a historical process acting on long-time scales (Carroll et al., 2007).

Mounting evidence has now pushed scientists to acknowledge that evolution is a contemporary process that happens on a similar time scale than ecological dynamics (Reznick, Losos, et al., 2019) and in a wide

1.5 The rise of eco-evolutionary management in conservation science

diversity of ecological contexts (Carroll et al., 2007). Evolutionary changes have been shown to have substantial effects on ecological dynamics – sometimes more than changes in important abiotic factors (N. G. J. Hairston et al., 2005). Ignoring contemporary evolution and its potential feedback loops with ecological processes will likely imperil the success of any management practices, even more so in the context of climate change. Indeed, the realisation was made that populations could adapt rapidly to changing conditions threatening them, especially in response to induced anthropogenic changes (Carroll et al., 2005; Hendry et al., 2006; K. J. Rice & Emery, 2003; Strauss et al., 2006).

Considering the underlying eco-evolutionary dynamics when planning conservation decisions can change the recommendations for management actions. For example, Walsworth et al. (2019) showed that ideal management strategies were different based on the inclusion of adaptive evolution. When adaptive responses of populations were absent, the ideal management strategy was to focus on thermal refugia, in order to conserve the ideal habitat of populations. However, when adaptive responses were considered, the ideal management strategy was the prioritisation of traits and habitat diversity in order to conserve the evolutionary potential of the population and decrease the risks of trait-habitat mismatches. Indeed, maximizing beneficial genetic and phenotypic variation should represent a resilience mechanism against environmental change (C. N. Cook & Sgrò, 2018; Jump et al., 2009; López-Pujol et al., 2012; Violle et al., 2012). Overall, it is important to consider evolutionary processes and the adaptive potential of populations to determine what will be the conditions maximizing the chances of populations adapting to changes, in order to provide adequate prescriptions to managers (Carlson et al., 2014; Whiteley et al., 2015).

The idea of including eco-evolutionary dynamics in the management of intraspecific diversity is part of a nascent field termed “evolutionary conservation management”. It can be achieved through modelling,

using DG-ABMs (Lamarins, Fririon, et al., 2022). Indeed, by allowing for the consideration of complex ecological and evolutionary processes (Nathan et al., 2019), as well as management strategies – and their impact on individuals and their interactions, simulations represent an efficient prospective tool to inform decision-making (Gervasi & Ciucci, 2018; Walsworth et al., 2019).

1.6 DG-ABMs: A SIMULATION FRAMEWORK TO MODEL ECO-EVOLUTIONARY DYNAMICS²

The consequences of complex eco-evolutionary relationships on the evolution of diversity may be best explored through simulations using eco-evolutionary models. Indeed, at the very core of these models is the need of specifying the genetically variable and heritable traits, their impact on the focal organism's life history, and the ecological embedding that determines how life-history traits affect and are affected by environmental conditions and the demographic context (Dieckmann & Ferrière, 2004). This can be achieved by various modelling approaches, often based on either analytical models or Demo-Genetic Agent-Based Models (DG-ABMs), which vary in assumptions (*Figure 1 – 11*). DG-ABMs can be defined as individual-based (meta) population dynamics models with heritable trait variation and explicit phenotype-dependent interactions between individuals.

DG-ABMs employ a specific bottom-up approach to fully integrate individual interactions and their outcome over time and space within a population, the result of which will dictate the strength and direction of evolutionary processes at the population level (DeAngelis & Mooij, 2005; Huston et al., 1988). These models acknowledge that individuals by nature have non-uniform responses to their environment. Accordingly, these approaches explicitly depict the interactions between individuals and their effects on

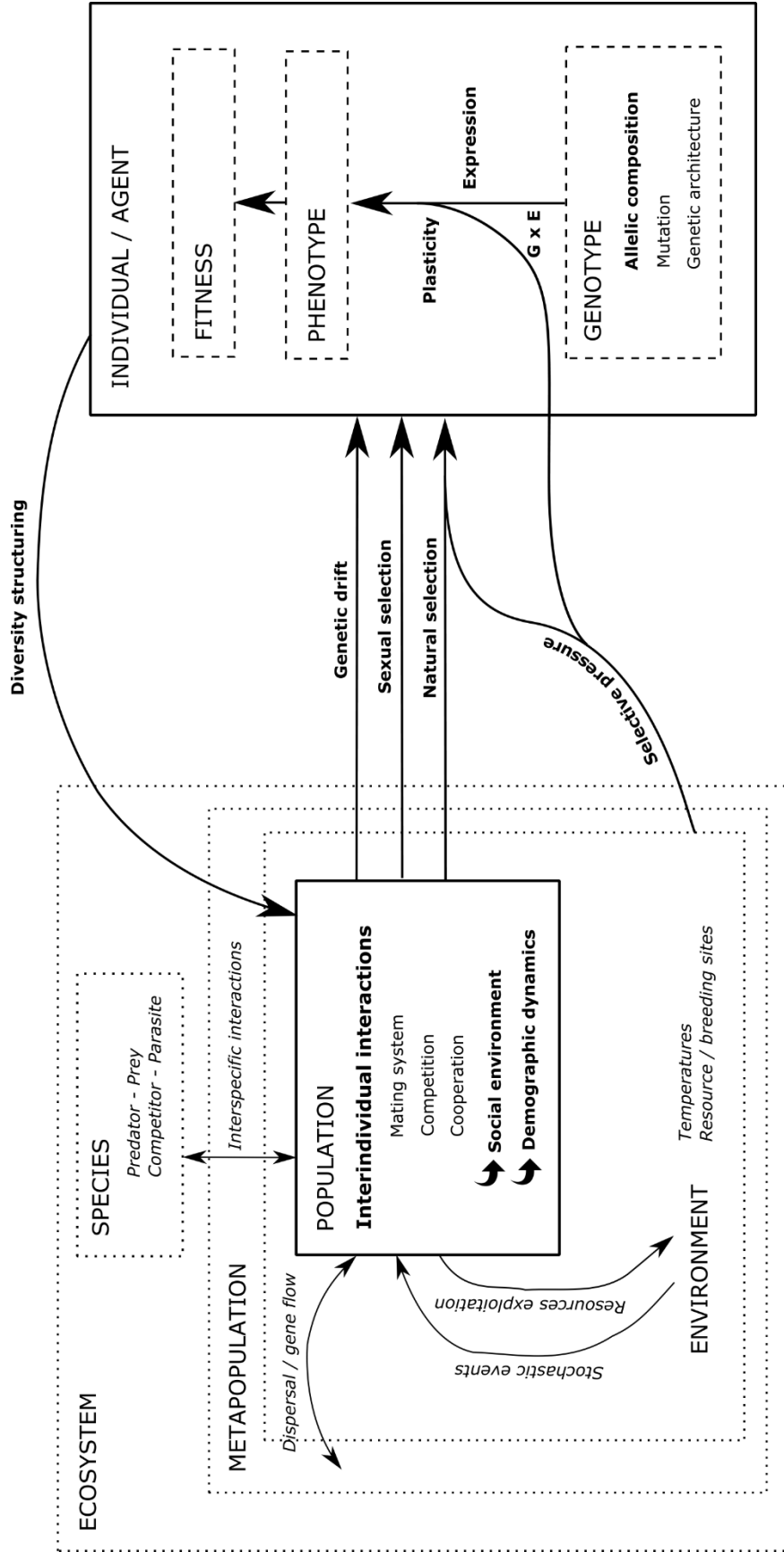
² In this section, I extracted parts of a manuscript written with several co-authors aiming at defining the use and potential of DG-ABMs (Lamarins, Fririon, et al. 2022).

1.6 DG-ABMs: a simulation framework to model eco-evolutionary dynamics

individual fitness, accounting for the social context, and observe the resulting dynamics in terms of distributions of heritable traits and demography (Figure 1 – 12). A key feature of DG-ABMs is that fitness variation emerges mechanically from interactions between individuals (as opposed to assuming an a priori fitness function) and gives rise to the evolution of patterns structuring the population diversity and its dynamics (e.g., genetic architecture, spatial genetic structure). This is radically different from assuming a prescribed relationship between traits and fitness, as done in analytical models and some ABMs (Cotto et al., 2020). This bottom-up construction of fitness in DG-ABMs allows for specific approaches to fundamental and applied questions in ecology and evolution.

	Analytical models	DG-ABMs
Scale	Population	Individual
Population dynamics	Uniform within-populations or within classes	Not uniform, possible structure
Within-population variation	Simplified (2 variants) or Gaussian distribution (QG), no structure	Distribution free, possible structure (e.g. spatial)
Inter-individual interactions	Uniform within-populations or within classes	None ↔ Not uniform, explicitly modelled
Trait-fitness relationship	Hard-coded, eventually with variable parameters	Emerging, flexible
Management practises	Mean impact, not flexible	On individuals and interactions, allows emerging effects

Figure 1—11: Different approaches to model eco-evolutionary feedback loops. This scheme summarises the main differences between two major modelling approaches used to investigate eco-evolutionary dynamics: analytical models on the left and Demo-Genetic Agent-Based Models (DG-ABMs) on the right. Their main difference is that analytical models consider evolutionary and/or ecological processes to be homogeneous within groups of individuals (the population or life-stages), whereas DG-ABMs can account for phenotypic and genotypic variation in groups of individuals, its effects on individual decisions/traits linked to local and instant conditions, and their outcome at the group level (i.e., emerging effects). In particular, some (although not all) DG-ABMs explicitly model inter-individual interactions, and their effects on individual fitness, which emerge in part from these interactions (from Lamarins, Fririon, et al. 2022).



1.6 DG-ABMs: a simulation framework to model eco-evolutionary dynamics

Figure 1—12: A conceptual scheme of demo-genetic agent-based models (DG-ABMs). Individuals (or agents) are characterised by their phenotypic traits, determined by their genotype, the environment, and interactions between them (G, E and GE respectively). The agents together define the population, hence determining its diversity and structure, where inter-individual interactions are explicit and shape the social environment. This social environment influences population dynamics, which ultimately drives evolutionary processes (drift, selection, gene flow). Fitness variations (e.g., survival, fecundity variation) emerge from different outcomes of inter-individual interactions (e.g., mating, competition, cooperation, and information exchange) and give rise to trait evolution via the trans-generational response to selection. This framework, highlighting the feedback loop central to eco-evolutionary approaches, is the core part of DG-ABMs and is identified by solid (units) / dashed (units properties) line boxes and bold arrows. DG-ABMs also offer the opportunity to study eco-evolutionary dynamics at multiple levels of organisations and spatiotemporal scales. At the population scale, habitat structuring and variation in the abiotic environment can be included to account for selection, stochastic events and subdivision of the social environment. These models also allow simulations of several populations' dynamics connected through dispersal with potential gene flow, such as in a meta-population case. At a higher level, community dynamics can be modelled through interspecific interactions between individuals from directly or indirectly interacting species (from Lamarins, Fririon, et al. 2022).

1.6.1 DG-ABMs to better understand eco-evolutionary loops

Explicitly accounting for inter-individual interactions in a bottom-up approach allows DG-ABM to better investigate the building up of fitness resulting from several complex EEMs and the interactions between them. Accounting for the stochastic and context-dependent outcome of, for example, competitive or mating interactions can change the predicted evolution of life-history traits under a prescribed relationship between trait and fitness.

For instance, Fielding (2004) investigated competitive interactions in grasshoppers using an ABM and showed that contrasted optimal values of life history traits can emerge from different types of localised inter-individual interactions, *i.e.* exploitative or size-based competition. In a perch species, the eco-genetic

model of Ivan & Höök (2015) was able to show variable patterns of energy allocation along individual ontogeny, resulting from the interplay between plastic and adaptive responses to selection and density-dependent competition for food. In their DG-ABM of trout population, Ayllón, Railsback, et al. (2018) observed the emergence of different eco-evolutionary outcomes due to explicit competitive interactions for food resources in a changing environment. Finally, with a DG-ABM representing indirect competition among individuals choosing different life-history tactics, Piou & Prévost (2012) showed that climate change may modify salmon population structure through plastic responses.

Reproductive interactions are also known to drive evolutionary dynamics (Maan & Seehausen, 2011). Mate choice strongly depends on the population structure, making the outcome challenging to predict yet rarely random (Klug & Stone, 2021). Explicit representation of sexual interactions is important as sexual selection can sometimes oppose natural selection (Labonne & Hendry, 2010). DG-ABMs, by allowing to observe the outcome of inter-individual interactions, are particularly adapted to explore the evolution of traits considering the dynamic aspects of mating systems such as when sexual preference and competition over mating partners occur, while still accounting for natural selection (Chevalier et al., 2020). In the same line, DG-ABMs also allow to investigate the origin of sexual dimorphism, such as Höök et al. (2021) who stressed the evidence of sex-specific plasticity potentials by looking at perch evolutionary response to the environment. DG-ABMs are also a relevant tool to explore how mating behaviour and population size jointly affect fitness components or population growth rate through Allee effects. For instance, (Berec et al., 2018) considered the rate of mate search as evolvable and found different optimal values of search rates for populations at different densities, resulting in lower Allee thresholds in populations kept at lower densities.

1.6.2 Extending in space, time and levels of organisation

In most examples detailed above, eco-evolutionary dynamics are modelled within a non-spatially explicit population. However, the spatial arrangement of habitats shapes animal movements or gametes propagation and therefore shapes social interactions and sexual networks (He et al., 2019). Since they allow for fine-scale explicit representation of habitats as well as individual movements, DG-ABMs are well suited to represent spatial evolutionary dynamics. Using an individual-based model of dispersal in dendritic networks; Fronhofer & Altermatt (2017) showed eco-evolutionary feedbacks with consequences on meta-population and genetic structure. Hrycik et al. (2019) explored the importance of environmental cues in perch vertical movement and illustrated the role of DG-ABMs in determining appropriate movement rules in spatially explicit ecological modelling. Travis et al. (2010) used a mechanical DG-ABM approach to model the evolution of seed dispersal in plant populations, accounting for likely trade-offs between traits in a patchy landscape. Additionally, sexual selection can determine the reproductive success of immigrants in populations and thus the strength and direction of demo-genetic consequences of dispersal (e.g., demographic rescue, evolutionary rescue *versus* gene swamping...). For instance, Soularue & Kremer (2014) highlighted the major importance of gene flow and assortative mating in shaping the genetic differentiation between populations in a heterogeneous environment.

At the higher level of organisation (e.g., community level), inter-individual interactions between species may also ultimately change the evolutionary outcomes expected from single species systems (terHorst et al., 2018; Weber et al., 2017). DG-ABMs can include multiple species once the interspecific interactions are established; they are thus especially suited to represent both intra and interspecific complexity and may help investigate macro-evolutionary consequences of interspecific interactions, such as speciation (Gavrilets et al., 2007; Weber et al., 2017).

In any case, it appears that DG-ABMs have a large potential to address fundamental eco-evolutionary questions accounting for multiple drivers of fitness, and are increasingly used in an integrative way, allowing effects to flow up and down between organisation levels.

1.6.3 DG-ABMs to assist management strategies

Another key feature of DG-ABMs is their capacity to model the effects of human-induced changes (e.g. selective exploitation, conservation practices) on individuals and their interactions, and investigate the eco-evolutionary consequences. Hence, by allowing emerging effects, DG-ABMs can also be efficient prospective tools to elaborate and assess management strategies. When management consists of demographic control of populations, in particular through individual phenotype-based choices, it can deeply impact all demographic processes and population genetic composition, and therefore the intensity and direction of the evolutionary processes (Lefèvre et al., 2014). For example, selective fishing (or harvesting) directly affects competition among surviving fishes (or trees), while genetic composition determines optimal fishing (or harvesting) patterns. In particular, different DG-ABMs were used to understand how selective fisheries can affect the demography and evolution of fish populations (fisheries-induced evolution), through cascading and sometimes counterintuitive effects on population demographic structure, growth and maturation thresholds (Ayllón, Railsback, et al., 2018; Piou et al., 2015; H.-Y. Wang et al., 2017; H.-Y. Wang & Höök, 2009). By modelling simultaneously the plastic and genetic responses of individuals, DG-ABMs also allow to disentangle the role of selective fisheries and environment in the observed and predicted declining population and in phenotypic changes (Piou et al., 2015).

1.6 DG-ABMs: a simulation framework to model eco-evolutionary dynamics

When evolutionary dynamics and land use planning decisions are linked, DG-ABMs also represent valuable decision support tools. For example, Papaix et al. (2018) and Rimbaud et al. (2018) used a spatially explicit demo-genetic model to assess the joint effect of crop cultivar deployment strategies in space and time and key pathogen life-history traits on epidemiological dynamics, resistance durability and long-term evolutionary control. Using a DG-ABM, Mims et al. (2019) found strong effects of spatial connectivity on demo-genetic outcomes in reintroduced bull trout populations, and allowed identification of watershed areas with higher persistence probabilities.

In the case of hybridization between native/wild and introduced/domesticated gene pools, DG-ABMs allow to study the impact of management on the dynamics of crossing within and between gene pools, which depends on differential social interactions (e.g., mating preference) and genetic performances (e.g., local adaptation) between gene pools (Castellani et al., 2015; Nathan et al., 2019). In this context, DG-ABMs offer an efficient approach to develop genetic enrichment strategies in a prospective approach (which genetic resources and which deployment modalities for which risks?), and conversely to evaluate strategies to preserve the local gene pool from unwanted introgression. In a similar approach for native *versus* transgenic gene pools, Kuparinen & Schurr (2007) and Difazio et al. (2012) studied transgene dispersal capacity in a forestry landscape by using spatially explicit IBMs with differential demographic rates for transgenic and natural trees.

In these different case studies, DG-ABMs offer a relevant framework to evaluate the short- and long-term evolutionary costs and benefits of management actions and to compromise them. For example, it can be used to deal with questions of exploiting a population or a meta-population (e.g., fishing, wood production) while preserving its genetic value and diversity or to determine how to minimise the risks of

demo-genetic collapses of populations facing climate change. Furthermore, by controlling the social context of populations, management drives the overall ecological processes, and thus acts on biotic and abiotic stressors, as well as on the susceptibility of populations to these stressors, and on selection intensity (Jactel et al., 2009).

1.7 A RELEVANT CASE STUDY IN SALMONIDS

1.7.1 *Background on salmonids*

Salmonids embody the above-mentioned situation of diversity since they mostly evolved in allopatry during the Pleistocene glaciations, where geographical reproductive isolation allowed potential divergent evolution to operate (Bernatchez, 2001). They display a high genetic diversity as well as a large diversity of life-history traits. For instance, some species are semelparous while others are iteroparous (Stearns & Hendry, 2003); some might migrate at sea (anadromous) while others remain in freshwater for their entire life cycle (Alexandrou et al., 2013). This diversification might have resulted from variations in environmental and physiological factors during their evolutionary history, notably during the glaciation periods (Macqueen & Johnston, 2014).

Salmonids are the target of a lot of attention throughout the world and represent one of the most managed fish family (Antunes et al., 1999; Davidson et al., 2010; Fraser, 2008; Laikre et al., 1999). This is due to their important socio-economic status, notably through aquaculture and recreational fishing (Davidson et al., 2010; Hindar et al., 2006; Laikre et al., 1999). Many wild populations of salmonids are threatened by human-induced disturbances, including overharvesting, habitat degradation and destruction, domestication and various stocking practices often using domesticated individuals (Fraser, 2008; Glover et al., 2017; Harbicht et al., 2014; Skaala et al., 2014; Waples, 1991).

For instance, each year thousands of domesticated fish escape from fish farms into the wild (Gausen & Moen, 1991; Morris et al., 2008; Reed, Prodöhl, et al., 2015), and the resulting gene flow often has large consequences on diversity. Similarly, stocking practices – aimed at increasing population size to sustain recreational fishing (Champagnon et al., 2012; Laikre et al., 1999; Waples, 1991) – often lead to similar negative consequences on wild populations (Araki et al., 2007; Araki & Schmid, 2010; Fraser, 2008; Leitwein et al., 2016; Utter, 2004). As a consequence, hybridization between wild/native and domesticated/introduced individuals and subsequent introgression represents a huge issue for fisheries managers (Araki et al., 2007; Araki & Schmid, 2010; Bolstad et al., 2017, 2021; Fraser, 2008; Reed, Prodöhl, et al., 2015). For example, introgression by domesticated alleles in salmon led to changes in age and size at maturity (Bolstad et al., 2017), an important life-history trait influencing population dynamics (Ayllón et al., 2016; Carlson & Seamons, 2008).

Since such gene flow may threaten the genetic integrity of wild/native populations, conservation programs usually aim at reducing the impact of domesticated and/or introduced fish into wild populations (Fraser, 2008; Glover et al., 2017; Harbicht et al., 2014; Perrier et al., 2013; Skaala et al., 2014; Waples, 1991). Therefore, many studies have already focused on the genetic consequences of hybridization and gene flow from domesticated strains on native wild populations (Fernández-Cebrián et al., 2014; Laikre et al., 2010; Lamaze et al., 2012; McGinnity et al., 2003, 2009; Muhlfeld et al., 2009; L. Sundt-Hansen et al., 2015; Waples, 1991).

The conservation of salmonids' inter and intraspecific diversity has now become a challenge for scientists and fisheries managers (Waples & Hendry, 2008). For decades, many management practices, such as the translocation of native individuals or stocking with native fry, have been implemented for that purpose. However, mounting evidence indicates that management practices usually fail at conserving native

diversity following such gene flow (Gil et al., 2016; Vincenzi et al., 2012) and may even result in larger genetic consequences (Fernández-Cebrián et al., 2014; Leitwein et al., 2016). Nevertheless, none of them has so far tried to apply evolutionary enlightened management practices by studying and using the available knowledge on potential drivers of hybridization.

Furthermore, salmonids have also been shown to be particularly good models to study eco-evolutionary dynamics in modelling frameworks. For instance, a growing number of DG-ABMs have been developed for salmonids to study adaptation to climate change, hybridization, but also the impact and efficiency of management practices (Ayllón et al., 2016, 2021; Ayllón, Grimm, et al., 2018; Ayllón, Nicola, et al., 2019; Ayllón, Railsback, et al., 2018, 2019; Frank & Baret, 2013; Lamarins, Hugon, et al., 2022; Nathan et al., 2019; Piou & Prévost, 2012; Theriault et al., 2008; H.-Y. Wang & Höök, 2009).

1.7.2 The MED/ATL hybridization complex

Among Salmonids, the brown trout species (*Salmo trutta L.*) displays a high genetic diversity. The species holds at least five genetically and phenotypically distinct lineages (Bernatchez, 2001) that evolved in allopatry for 0.5 to 2 million years during the glacial era, where separated populations colonised different areas across Europe (J.-L. García-Marín et al., 1999), although hybridization may have occurred at some points (Hashemzadeh Segherloo et al., 2021). In France, two of those lineages: the Atlantic (ATL) and the Mediterranean (MED) lineages are naturally found in allopatry. Due to their divergent evolution, they display an important phenotypic divergence. However, until recently (Gil, 2015), there was no information regarding the adaptive aspect of this divergence.

Since the discovery of artificial reproduction at the end of the 19th century, brown trout became the most introduced fish species in the world (Lowe et al., 2000). As one of the consequences, the distinct lineages have been forced back in sympatry. The ATL lineage, in particular, has been intensively used for fish farming and intensive river stocking – using homogeneous domesticated strains – to sustain recreational fishing for more than a century (Beaudou et al., 1994; Berrebi, Povz, et al., 2000; Caudron & Champigneulle, 2007; Krieg & Guyomard, 1985; Largiadèr et al., 1996; Launey et al., 2003; Presa et al., 1994). In the Mediterranean area, where the MED lineage has evolved, the resulting situation displays a mosaic of outcomes regarding intraspecific diversity, with many cases of introgression of native MED alleles by non-native ATL alleles. The mapping of genetic diversity indicates that introgression is heterogeneous in space: going from the total extirpation of the MED lineage to various degrees of hybridization, with some rare patches of pure MED gene pools remaining (Caudron, Champigneulle, et al., 2012). The reason for this spatial heterogeneity and diverse levels of intraspecific diversity cannot be solely explained by management practices (*i.e.*, intensity of stocking using the ATL lineage, Gil et al., 2016).

To counter the observed loss of native biodiversity, many management practices have been applied during the last 20 years in order to restore MED native diversity: the interruption of ATL stocking, the creation of a genetic refuge for MED populations and the reintroduction or transfer of MED trout (Gil et al., 2016). However, mounting evidence suggested that they failed at conserving native diversity. Indeed, while the proportion of non-native ATL trout did decline, hybrids increased in frequency (Gil et al., 2016) and often represent the majority of populations.

Recent studies have pointed out the importance of EEMs involved in reproductive isolation. Indeed, pre-zygotic mating behaviours – female preference (Gil et al., 2015) – and post-zygotic mechanisms – embryonic survival based on GxE interactions (Folio et al., 2021) – may control for the evolution of

diversity dynamics in space and time. These mechanisms could explain the observed heterogeneous spatial patterns of introgression as well as the failure of management practices to restore the MED lineage in some contexts. So far, such mechanisms have not been integrated into the design of management practices for conserving the diversity of native populations and managing hybridization.

Today, despite the will of fishery managers to restore native intraspecific diversity in the Mediterranean area, they lack scientific knowledge and an appropriate tool to guide their management practices.

The overarching goal of my PhD is to investigate the potential of eco-evolutionary concepts to improve the management of intraspecific diversity. To do so, my first aim was to develop a DG-ABM to understand the evolution of diversity dynamics in brown trout while considering the empirically demonstrated EEMs involved in reproductive isolation. The model aims at simulating the population dynamics of brown trout under management interventions for some EEMs. In doing so I will assess the potential role of these EEMs in the structuration of diversity dynamics. Finally, this thesis should fill an identified gap between management and evolution, by creating a decision-making tool that will allow the testing of new management strategies in an eco-evolutionary, objective scientific framework.

1.7.3 Chapters' specific objectives

My PhD will be composed of five other chapters. The second chapter will provide some basic knowledge on the biology and ecology of Brown trout, and then proceed to detail the available knowledge on the MED/ATL hybridization complex. More specifically, it will detail the EEMs empirically identified and potentially involved in the evolution of diversity dynamics. The end of this first chapter will then describe specifically how these mechanisms could be influencing the introgression dynamics, and therefore why

they should be implemented in a modelling approach to measure the extent of this influence. The third chapter will describe in detail the demo genetic individual-based model developed, as well as its user-friendly interface destined to be used in interaction with managers. This model will allow us to actually simulate the qualitative and quantitative impacts of EEMs in an integrative way, on population genetic, phenotypic and demographic structure. The fourth chapter will make a first use of the model to evaluate the actual role of two EEMs – female heterogamous preference and GxE interactions on survival – in driving the evolution of intraspecific diversity. This will first be done prospectively in a very simple case (*i.e.*, a simplified environment) where the two lineages are brought back in secondary contact. Then, we will also use the model in actual case studies applied to real rivers where documented management practices have interacted with EEMs and specific environmental conditions to influence current diversity patterns. Finally, in chapter 5, the model will be used in a more prospective and generic way, so to hopefully produce more general guidelines. This will be done by building simulations carried out in fictitious hydrographic networks whose characteristics (connectivity, initial spatial location of lineages) represent situations typically encountered by managers in the field. The sixth and last chapter will synthesise all the new knowledge produced, and discuss the relevance of integrating elements of evolutionary ecology into the management of intraspecific biodiversity, in the particular case of the MED/ATL complex, but also in a more general context in relation to the major issues of global change and native biodiversity management.

CHAPTER 2

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2 THE SPECIFIC CASE OF BROWN TROUT: THE MED/ATL HYBRIDIZATION COMPLEX

2.1 BROWN TROUT ECOLOGY AND EVOLUTION

2.1.1 *Brown trout life cycle*

The brown trout species, *Salmo trutta*, are part of the Salmonids family. Brown trout is a facultative anadromous fish. Hence, within the species, individuals can be distinguished based on alternative migratory tactics. Resident trout do not migrate and will mature in freshwater, while migrant trout will migrate to sea (anadromous trout) – or sometimes to lakes (lake trout) – for growth and maturation before returning to freshwater for reproduction (P. Caballero et al., 2013). Here, I will only focus on resident trout that spend their entire life cycle in freshwater. For the ideal development and growth of brown trout, high water quality – a neutral pH and good oxygenation – as well as a moderate to high flow stream are required (Maisse & Baglinière, 1999). For reproduction, the species also requires a specific spawning ground with fine *substratum* – 2 millimetres to 5 centimetres (Champigneulle et al., 2003; Maisse & Baglinière, 1999).

At the beginning of the brown trout life cycle (*Figure 2 – 1*), fertilised eggs develop under gravel during an incubation period up to hatching, which happens around 400 degree-days (Killeen et al., 1999). Following hatching, vesicled-fry continue growing under gravel until the resorption of their vesicle. Emergence then happens – juveniles emerge from the substrate – as individuals need to feed and conquer territories, marking the beginning of inter-individual competition (Lahti et al., 2001). A huge variability can be observed in emergence timing, as there are advantages to early, as well as, late emergence (Lelong, 2006). Juveniles then usually move downstream with the water flow. Brown trout will avoid temperatures above 20°C and optimal temperatures for growth can vary between 13 to 16°C depending on their food regime

(Elliott et al., 1995; Forseth et al., 2009; Forseth & Jonsson, 1994). Sexual maturation can occur as soon as two years old. The reproductive season starts around November and can last for up to three months. Most mature individuals will migrate to their spawning ground performing “homing” to their birth site or simply migrating upstream towards suitable spawning habitat. Females select the spawning habitat and dig the nest. Mate choice proceeds – potentially guided by the “agents” of sexual selection: male competition and female preference – followed by spawning and fertilisation. After mating, females will bury the fertilised eggs in the *substratum* (Haury et al., 1999). Females’ fecundity is positively correlated to female body size (Lobon-Cervia et al., 1997).

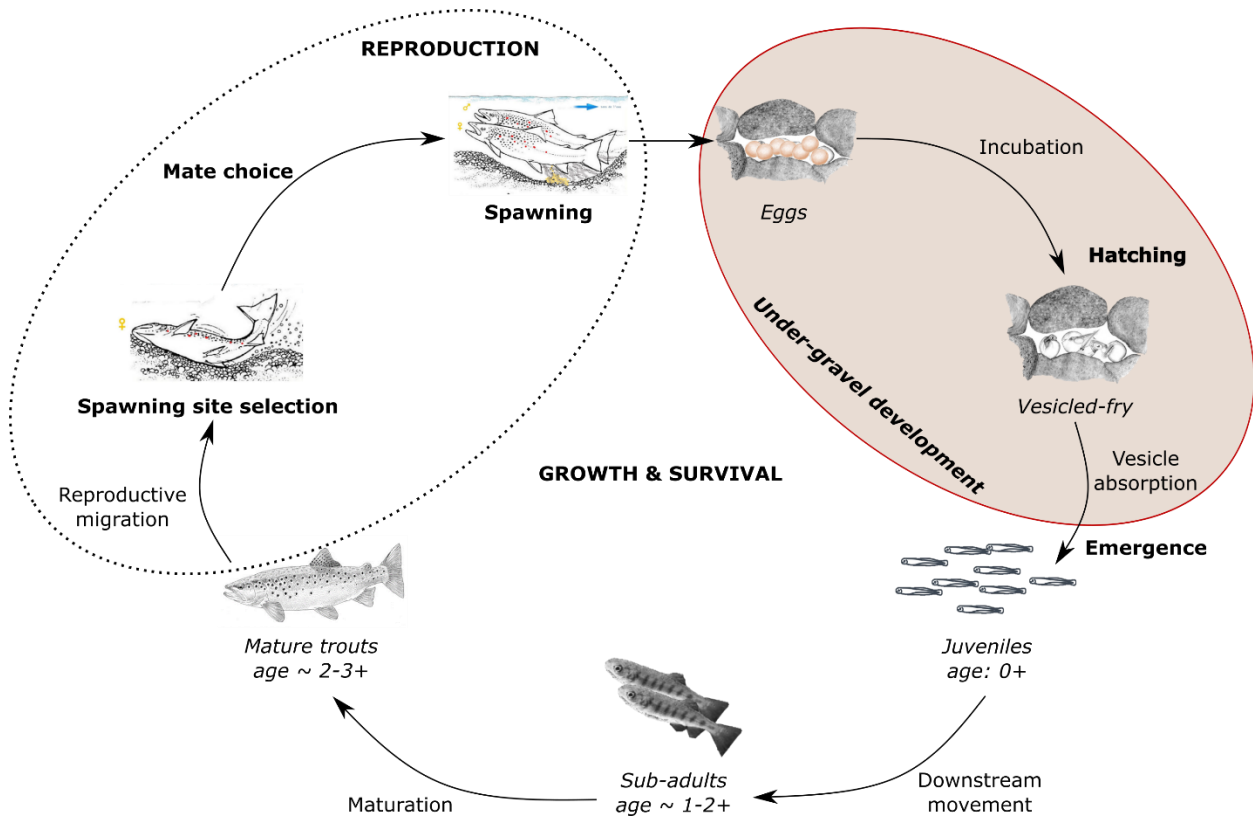


Figure 2—1: Simple representation of the brown trout life cycle. The under-gravel development phase includes hatching and emergence. Growth and survival happen during the entire life cycle. Reproduction happens following maturation and involves migration, spawning habitat selection as well as mate choice performed by females and the spawning act.

2.1.2 The evolution of brown trout diversity in Europe

The brown trout species shows a high level of intraspecific diversity (Bernatchez, 2001), with many genetic and phenotypic variations observed between populations within the species natural expansion range: Europe. These populations evolved in allopatric conditions for 0.5 to 2 million years during the Pleistocene glaciations, where independent genetic evolution arose through vicariance with separated populations colonising different areas across Europe (J.-L. García-Marín et al., 1999). Five distinct genetic lineages (*Figure 2 – 2*) – i.e. groups of individuals sharing the same phenotypic traits and genotypic variations – were then established using mitochondrial DNA (Bernatchez, 2001).

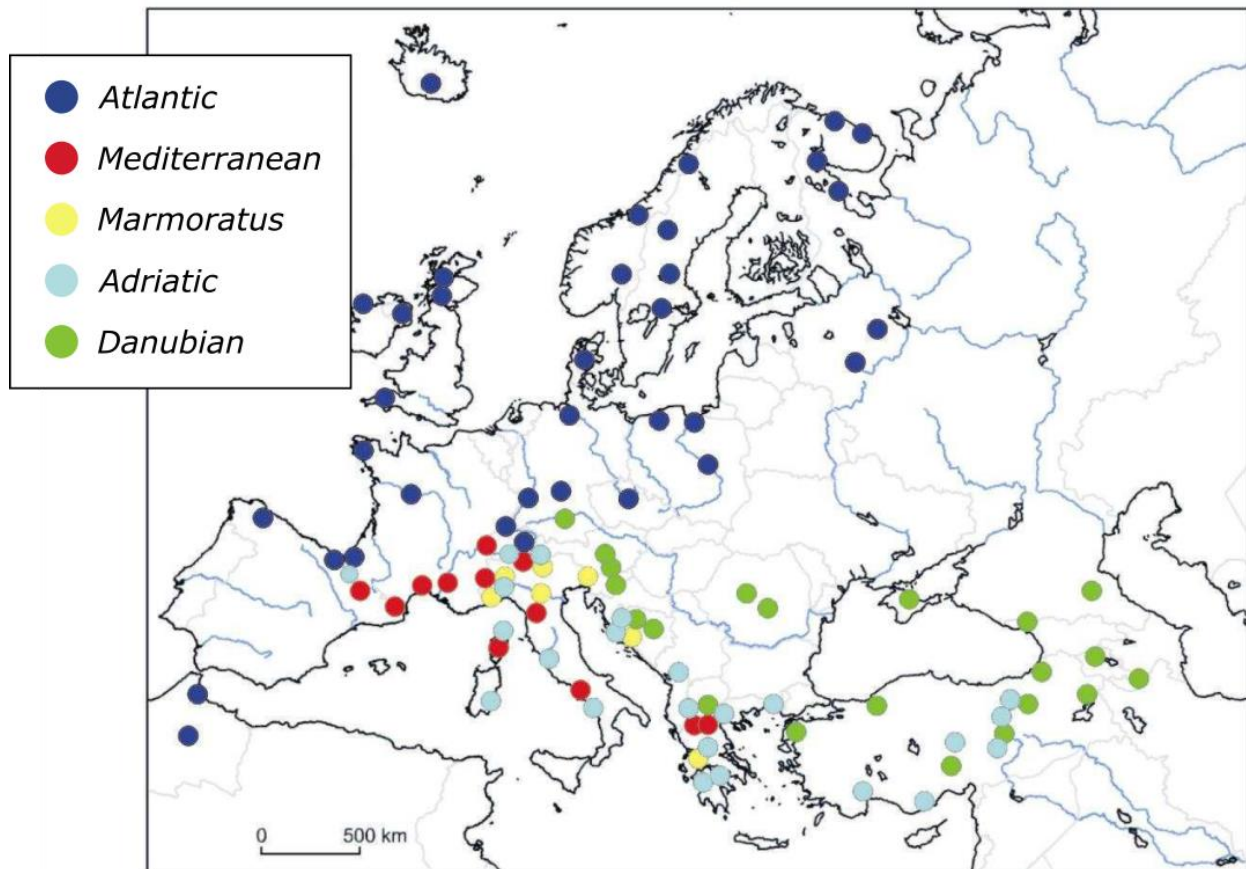


Figure 2—2: Spatial localisation of the five distinct genetic lineages identified by Bernatchez (2001) within brown trout natural expansion range. The figure is extracted from Caudron (2008).

Phylogeography indicates that division happened in two steps. Initially, hydrographic networks of three main brown trout river basins – the Atlantic, the Danubian and the Mediterranean Basin – were segregated due to important climatic events supposed to have happened approximately 700 000 years ago (Webb & Bartlein, 1992). This led to the creation of three main lineages: the Atlantic, the Danubian and the Mediterranean lineages. Then, the MED lineage subdivided into three lineages: The Mediterranean, the Adriatic and the Marmoratus lineages, following divergent evolution that may have occurred by geographical isolation (Keith, 1998). Despite long periods of allopatric evolution, those lineages appeared to have not been fully segregated through space and time, as indicated by some natural secondary contact zone located at the edges of each geographical range (Aurelle et al., 2002; Bouza et al., 2008; Sanz et al., 2006). Recent studies have confirmed that multiple contacts may have happened between lineages (Hashemzadeh Segherloo et al., 2021), possibly due to topological modifications occurring during glacial episodes.

2.1.3 Brown trout diversity in France

In France, there are two lineages of brown trout: the ATL and the MED lineages. They have segregated geographical ranges as mountainous terrains separate the Atlantic and the Mediterranean Basin (*Figure 2 – 3*). MED populations of brown trout are considered to be native to the Mediterranean Basin (Guyomard, 1989; Launey et al., 2003). Many genetic differences have been established between both lineages, at mitochondrial and nuclear genes (Bernatchez, 2001; Guyomard, 1989; Launey et al., 2003). Some microsatellites (str541 and str591) and single nucleotides polymorphism (OMM1144, OMM1105, OMM1154, OMM117) *loci* have been shown to perfectly differentiate the ATL lineage from the MED lineage (Gharbi et al., 2006; Guyomard & Caudron, 2008). Managers and scientists have been using these markers to assign individuals to one of the three following genotypic categories: pure non-native ATL trout

(all alleles are from the ATL lineage), pure native MED trout (all alleles are from the MED lineage) or hybrid (HYB) trout (combination of alleles from both lineages).

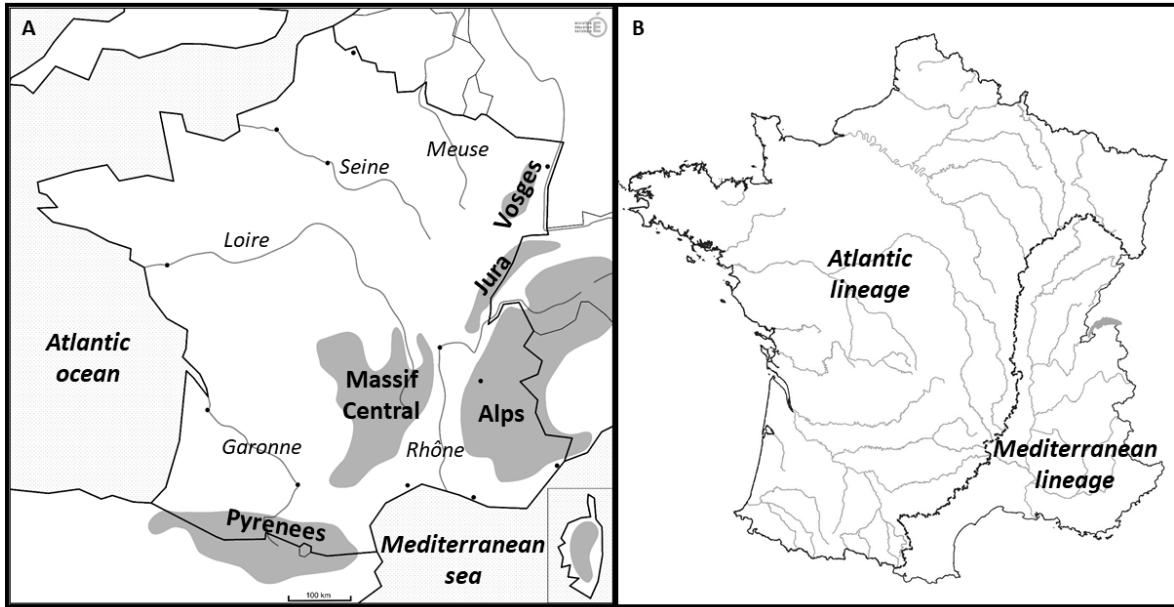


Figure 2—3: (A) Geographical map of France representing the main rivers and mountain ranges. (B) Map of French rivers showing the geographical range of the Atlantic and the Mediterranean lineages with a drawn delimitation line between both watersheds.

These different genotypic categories (*i.e.* genotypes: ATL, HYB, MED) can to some extent be phenotypically differentiated based on robe *criteria*. Indeed, the ATL and the MED lineages present different phenotypes (Figure 2 – 4) and many robe *criteria* (Table 2 – 1), specific to one or the other lineage, have been identified (Aparicio et al., 2005; Largiadèr & Scholl, 1996; Lascaux, 1996). HYB individuals show intermediate phenotypes with a mixture of robe *criteria* from both lineages. For instance, MED trout are characterised by a high number of small spots, mainly black, located on its robe and opercular area while ATL trout has a very low number of those. Instead, they are characterised by larger red spots with a white aureole. The lateral line is absent for MED trout but visible on ATL trout. The presence of black lateral stripes on the flank of MED trout is also a distinctive trait for that lineage. Finally, the opercular macrostigma is a

compulsory, but not an exclusive *criterion* for MED trout, as it is also observed in ATL trout. This trait is often used to validate the attribution of an individual to the MED lineage. For juveniles, some differences in the number and shapes of parr robe marks have also been observed (Mezzera et al., 1997). Saint-Pé et al. (2019) provided an in-depth genomic analysis of the genetic bases of these robe *criteria*, which have already been used as a proxy of lineage characterisation for field observations (Folio et al., 2021; Gil et al., 2015) in Haute-Savoie. However, in other trout populations of the Mediterranean basin, some studies failed to find a consistent correlation between pigmentation patterns and genome-wide admixture (Valette et al., 2020). This suggests that phenotype-genotype correlation might highly depend on the population considered as well as the number and types of markers used.

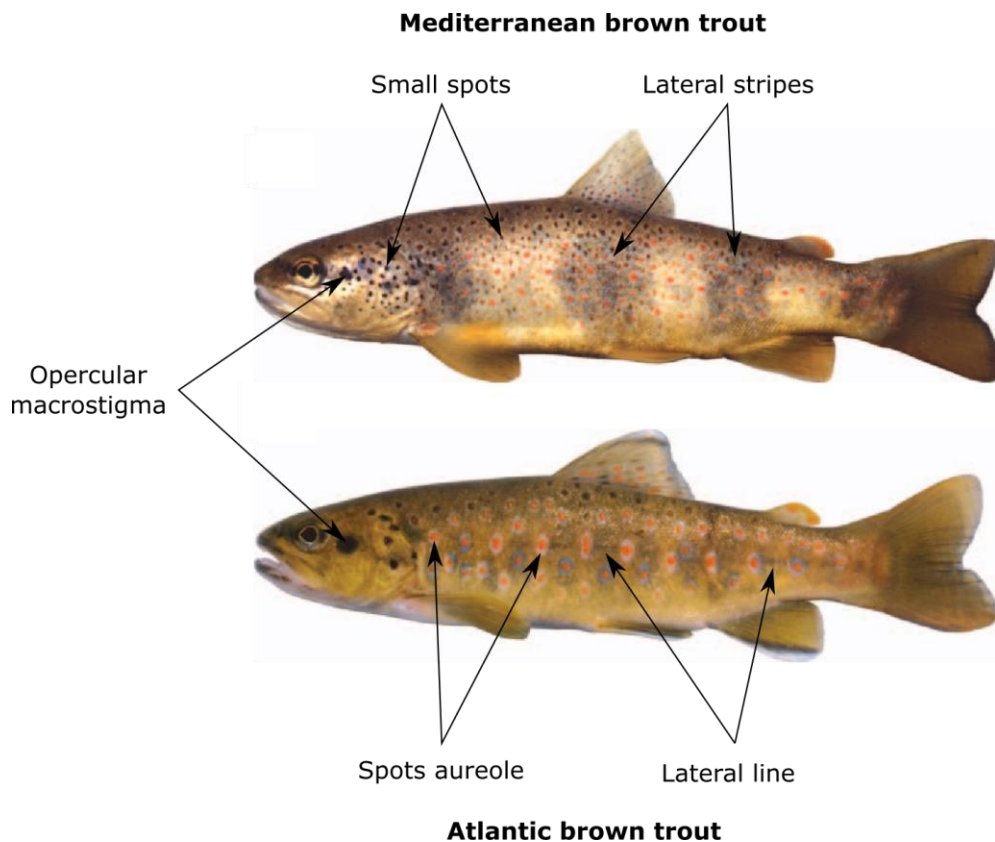


Figure 2—4: Robe criteria characteristic of the MED and the ATL lineages of brown trout. Image modified from Aparicio et al. (2005).

2.2 History on management practices and their consequences on diversity

Table 2-1: Robe criteria used in lineage characterisation. For each possible expected genotype, it is noted whether robe criteria are present, possible, partial, or absent. The number of opercular spots is ranged from high to low. Lateral stripes, spots aureole, lateral line, and the number of opercular spots were used to calculate an expected genotypic score as described in Gil et al. (2015). Opercular macrostigma was used to validate the attribution to the MED lineage, as it is a compulsory criterion in MED individuals. These criteria were used in two main studies for the determination of phenotypic score (Gil et al. 2015) and expected genotypic score (Folio et al. 2021).

Robe criteria	MED	HYB	ATL
Lateral stripes	Present	Possible	Absent
Spots aureole	Absent	Possible	Present
Lateral line	Absent	Partial	Present
Opercular <i>macrostigma</i>	Present	Possible	Possible
Number of small spots	High	Medium	Low

The MED lineage appears to show a higher genetic diversity compared to the other lineages (Suárez et al., 2001). MED populations were less impacted by glaciation events compared to central and northern Europe populations – ATL included – that experienced multiple glacial refuges (J.-L. García-Marín et al., 1999; Hamilton et al., 1989), possibly causing repeated bottleneck events and ultimately leading to a decrease in genetic diversity (Suárez et al., 2001). However, it appears that different MED populations – of the Pyrenees and Haute-Savoie – still present similar distinctive traits.

2.2 HISTORY ON MANAGEMENT PRACTICES AND THEIR CONSEQUENCES ON DIVERSITY

2.2.1 *The rise of stocking*

For more than a century, the main management practice for brown trout populations was river stocking (Baglinière & Maisse, 1991) in order to counter-balance the perceived negative effects exerted by fishing

and anthropic pressures on wild populations. It started at the end of the 19th century when they mastered the artificial reproduction of brown trout (Baglinière & Maisse, 1991). Stocking can be defined here as the introduction of a large number of domesticated trout in rivers. Intensification of this practice followed rapidly and brown trout consequently became the most introduced fish species in the world (Lowe et al., 2000).

Stocking, using domesticated strains belonging to the ATL lineage, (Almodovar et al., 2001) has been reported in several streams of the Mediterranean Basin in France (Barbat-Leterrier et al., 1989; Beaudou et al., 1994; Berrebi, Poteaux, et al., 2000; Guyomard, 1989; Poteaux, Beaudou, et al., 1998), in Spain (Almodovar et al., 2006; Aparicio et al., 2005) and also Italy (Caputo Barucchi et al., 2004; Lucentini et al., 2006). These strains originating from central and northern Europe (Almodovar et al., 2001) were the results of long periods of domestication (Guyomard, 1989); probably up to a century since the beginning of fish farming. Stocking started in this area at the end of the 19th century as recreational fishing had exerted strong pressure on natural populations and; it progressively became an intensive practice during the 20th century in order to sustain fishing (Caudron & Champigneulle, 2007). In Haute-Savoie (*Figure 2 – 5*), 15 to 20 million trouts were poured each year in the rivers. Between 800,000 and 1,000,000 fry were annually stocked in the Dranse system during the 80^s and 90^s (Caudron & Champigneulle, 2007). In the Borne River alone, the number of fry stocked reached the million in 1989 (Caudron et al., 2009).

Stocking practices at that time were quite diverse and hard to quantify as information on precise parts of the river stocked was missing, preventing the calculation of densities introduced (Almodovar et al., 2006). Various information highlighted heterogeneity in stocking practices regarding both the amount of fish stocked and the stages used for stocking (Poteaux, Beaudou, et al., 1998). Eggs, fry, juveniles, sub-adults and adults have been introduced, with densities going from 0.05 to 2.4 kg.ha⁻¹ for sub-adults and adults and from 10 to 103 ind.m⁻² for eggs and fry cumulated.

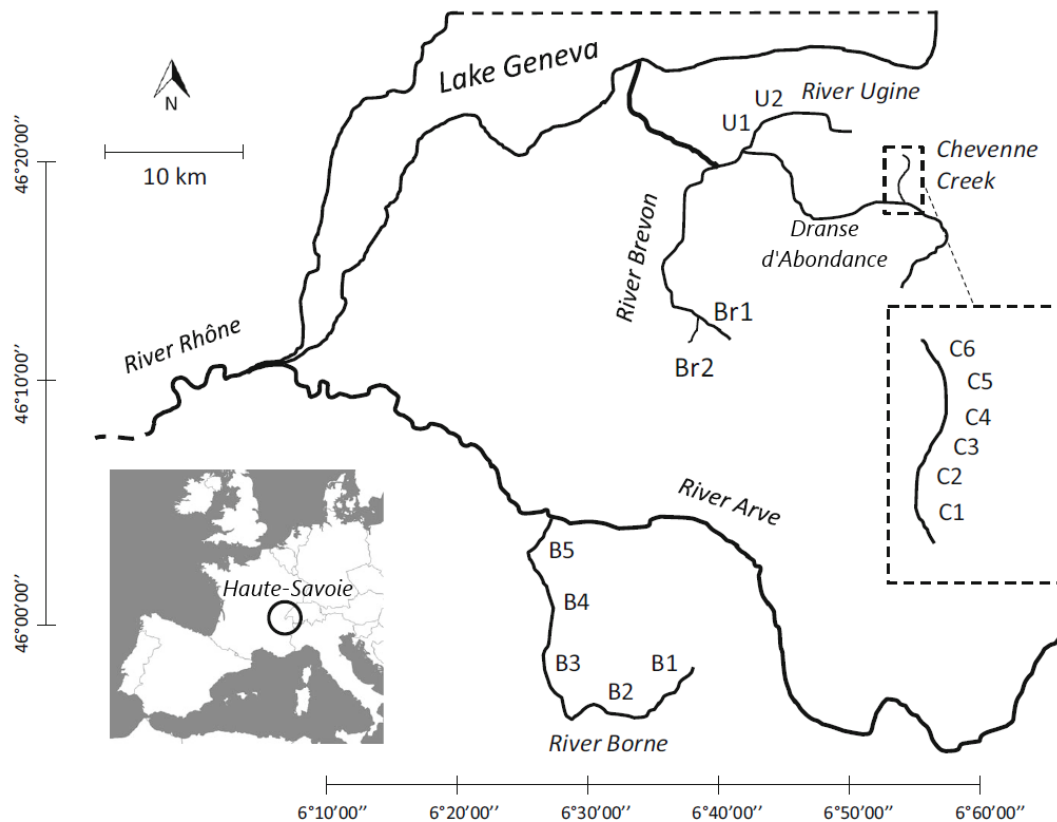


Figure 2—5: Localisation of some study sites on the Haute-Savoie hydro-geographic network among which, the two sites used in this manuscript – the Chevenne Creek and the Borne River. Sampling sites are marked. Figure adapted from Gil et al. 2016.

2.2.2 A shift in management practices

At the end of the 20th century, a shift was observed in management practices, toward the conservation of genetic diversity, as advances in molecular genetics evidenced high levels of intraspecific diversity in salmonids species (Allendorf & Leary, 1988; Ryman et al., 1995; Utter, 1981, 2004; Waples, 1991). Since then fishery managers became progressively more aware of intraspecific genetic diversity and the negative impact that domesticated individuals could have on wild native populations of salmonids when admixture occurs (Ryman et al., 1995; Utter, 2004). In Laikre et al. (1999), geneticists highlighted the

ecological importance of diverse native lineages for the conservation of brown trout intraspecific diversity. Hence, at the beginning of the 21st century in the Mediterranean area, the conservation issues of native trout (Caudron, Vigier, et al., 2012) became the core objective of managers, since the introduction of the ATL lineage in the Mediterranean area caused lineages admixture and resulted in anthropogenic hybridization, threatening native diversity. Stocking practices were, therefore, massively reduced. In Haute-Savoie, for example, stocking densities went down from year 2000 to year 2012 and the total stocked area was reduced – more than twofold. The last decades have seen stocking practices using ATL strains replaced by various practices aiming to conserve and restore native MED populations.

2.2.3 Consequences on diversity

In the Mediterranean area, hybridization led to the introgression of native MED alleles by non-native ATL alleles at the individual and population levels. Introgression is the process where genetic information from one species or lineages is integrated into the genome of another one and partially or fully take over. Introgression can influence intraspecific diversity and affect the conservation of populations at the genetic scale (Laikre et al., 1999). This has many consequences regarding management practices, as managers are currently interested in the conservation of native MED diversity. However, ATL stocking did not lead to homogenous patterns of hybridization in the MED area, despite homogenous implementation. Indeed, genetic studies indicated that the consequences of hybridization were quite diverse with highly heterogeneous introgression rates observed at a micro-geographical scale within a hydrographic network (*Figure 2 – 6*). However, some very frequent situations are found among hydrographic networks. In a majority of cases, hybridization resulted in full admixture (*Figure 2 – 6; 2 – 7: situation A; 2 – 8*) – populations displaying ~ 50% of introgression, *i.e.* an equal proportion of MED and ATL alleles within the population.

2.2 History on management practices and their consequences on diversity

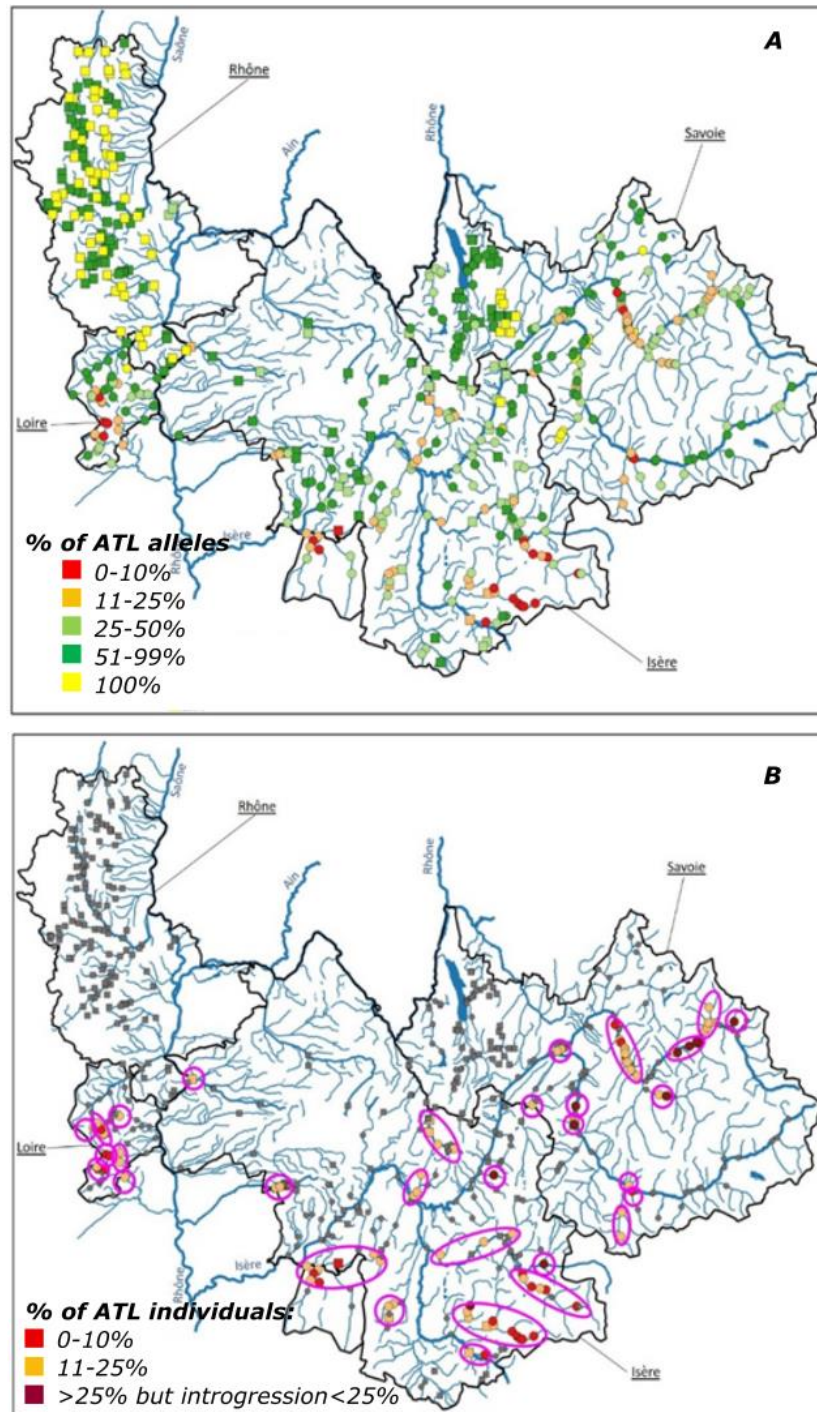


Figure 2—6: Cartographies of (A) the introgression of native MED alleles by non-native ATL alleles (in red: native populations, orange: lowly introgressed populations, light green: hybrid populations, dark green: highly introgressed populations and yellow: non-native populations); (B) lowly introgressed native populations which have been identified as conservation priorities; in some departments of the Mediterranean area: Rhône, Loire, Isère and Savoie. Figures modified from Scimabio Interface.

In some rare cases, both lineages are found in sympatry but without any HYB (*Figure 2 – 7: situation B*). Finally, it is common to find both lineages, with or without HYB individuals along the same river. For example, a gradient of introgression can be observed along the river with ATL individuals upstream, HYB in the intermediate parts of the river and MED individuals downstream in the confluence area (*Figure 2 – 7: situation C*; The Overan Creek: Folio et al., 2021). Both lineages can also be found along the same river segregated by an obstacle, with (*Figure 2 – 7: situation E*; The Chevenne Creek: Caudron & Champigneulle, 2011) or without (*Figure 2 – 7: situation D*; The Borne River: Caudron et al., 2009) the presence of HYB. Pure non-native populations appear to be located where no native population had settled before, often upstream, potentially due to impassable barriers.

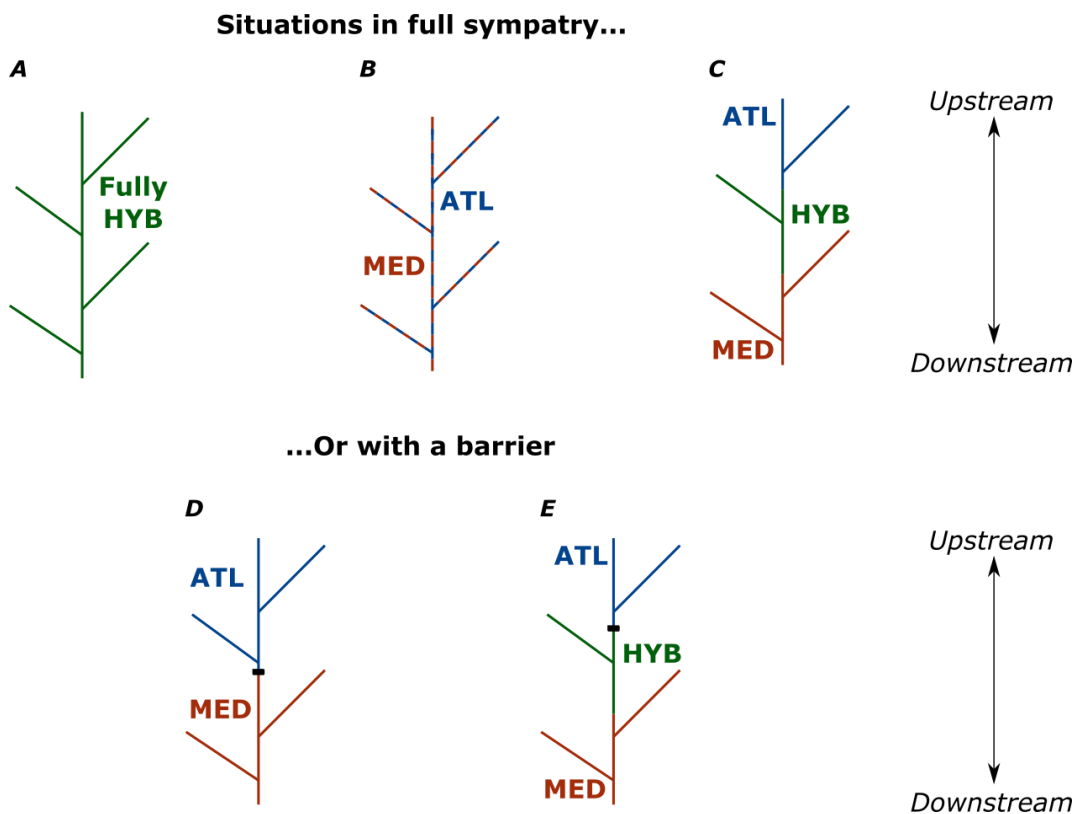


Figure 2—7: Common diversity patterns found within hydrographic networks of the Mediterranean area. ATL non-native populations are often located upstream while MED native populations are found downstream.

2.2 History on management practices and their consequences on diversity

In the Haute-Savoie area (Figure 2 – 8), an INTERREG III program on “autochthonous trout” aimed at identifying and localising persistent MED populations from 2005 to 2008. It indicates that only a few pure native populations and some lowly introgressed populations (<25%) – usually targeted for conservation effort (Laikre et al., 1999) – remain. The intensity of stocking was proposed as an explanation for this spatial heterogeneous introgression. However, historical data on stocking in Haute-Savoie are not enough to explain the observed distribution of introgression (Scimabio Interface, Com. Pers.).

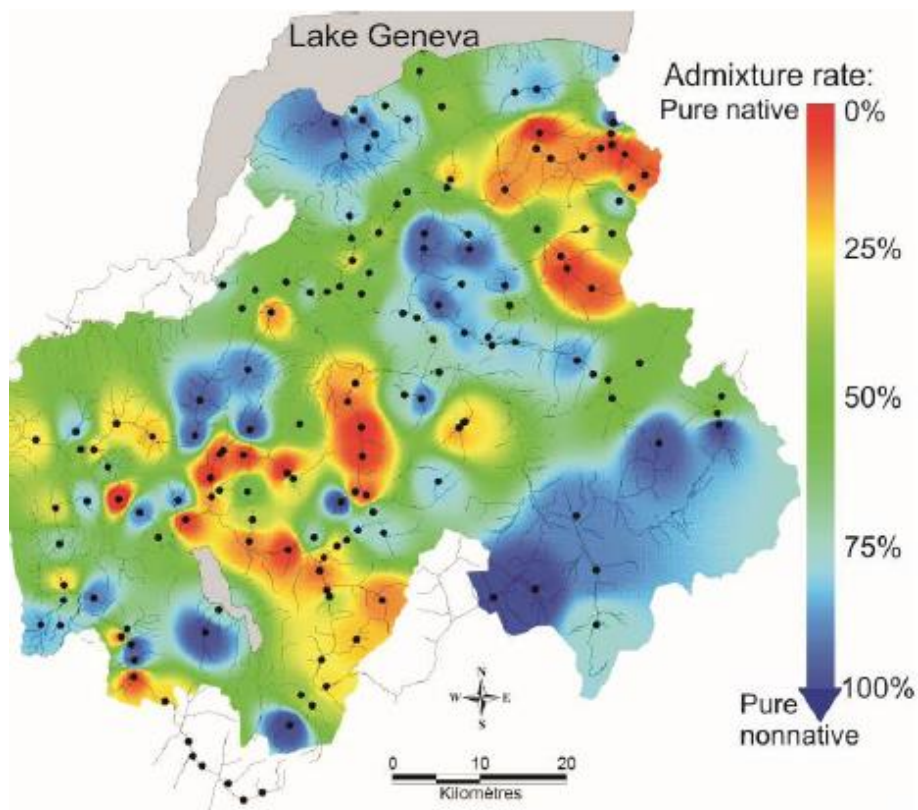


Figure 2—8: Cartography of the admixture rate observed in Haute-Savoie (in red/orange: pure or nearly pure MED populations, in green: fully hybridized populations, in blue: pure non-native populations). Some nearly pure native populations still remain and have been targeted for conservation efforts.

2.3 TOWARD THE CONSERVATION OF THE NATIVE MED LINEAGE

2.3.1 *Native conservation strategies*

Since the last decades, some specific management practices had been implemented to try to conserve and restore native MED populations in the Mediterranean area, notably in the Haute-Savoie. Four management practices were implemented:

- ☞ The **genetic refuge (GR) strategy** is a passive strategy that simply bans ATL stocking. This is usually the first strategy implemented in order to stop further introduction of non-native alleles (Caudron, Champigneulle, et al., 2012; Caudron et al., 2011; Caudron & Champigneulle, 2011). When implemented alone, the assumption is that native populations will be purged from non-native individuals *via* natural selection.

The other strategies are active interventions as they result in the modification of population demography.

- ☞ **ATL removal** is the removal of all non-native individuals – ATL but also HYB – from an area where the introgression rate is high, through electric fishing. This strategy is often conducted before the introduction of MED individuals in order to replace a functional non-native population with a native one (Caudron & Champigneulle, 2011). It is often conducted where both lineages are in allopatry so that all individuals may be removed without having to distinguish between pure native and non-native individuals.
- ☞ **Direct translocation (DT) of MED** individuals is the transfer of individuals from a pure or almost pure MED population to another portion of the river to be colonised (Caudron, Champigneulle, et al., 2012; Caudron et al., 2011). This strategy can be based on the translocation of either adult wild fish only (genitors) or of populations (often from 1+ sub-adults due to catchability).

✎ Finally **stocking with native fry (SNF)** is the introduction of a certain amount of summer-fed fry (2-4 centimetres), around June, produced in hatcheries, but originating from MED wild genitors in a section of the river to be colonised (Caudron et al., 2006, 2011).

DT and SNF, implemented alone, are often used by managers to replace non-native populations, presenting a high introgression and very low densities (< 10 ind.m⁻², often non-functional), by a self-maintaining native population (Caudron, Champigneulle, et al., 2012).

2.3.2 Unsuccessful outcomes

In a previous study, Gil et al. (2016) investigated the impact of some of these management strategies on wild population intraspecific diversity by analysing the evolution of introgression and the genotypic composition of the population. They considered three of the above-described strategies, implemented by scientists and managers in 19 sites for more than 15 years: GR strategy, SNF and DT (see published case studies: Caudron, Champigneulle, et al., 2012; Caudron et al., 2006, 2011). All implemented strategies proved to be unsuccessful regarding the initial management goal of recovering pure or almost pure native MED populations. Indeed, despite a general decrease in the percentage of ATL alleles (introgression rates, *Figure 2 – 9*) and the successful removal of ATL individuals, the number of HYB individuals increased in the populations over a short period (Genotypic composition of the population, *Figure 2 – 10*). However, the magnitude and speed of these changes varied between strategies and among sites. The active strategies showed a higher and faster decrease in ATL alleles and individuals compared to the GR strategy, where the decrease was observed over a long time (*Figure 2 – 9, 2 – 10*). The increase of HYB individuals varied among strategies but more so among sites for a given strategy with some sites where high rates of HYB were observed compared to others. DT appeared to generate less HYB than any other strategies and more MED individuals. For the GR strategy, a few sites even showed counterproductive results, as the

percentage of MED individuals in the population was decreasing (*Figure 2 – 10*), and the introgression rate increasing with the rise of HYB individuals (*Figure 2 – 9*).

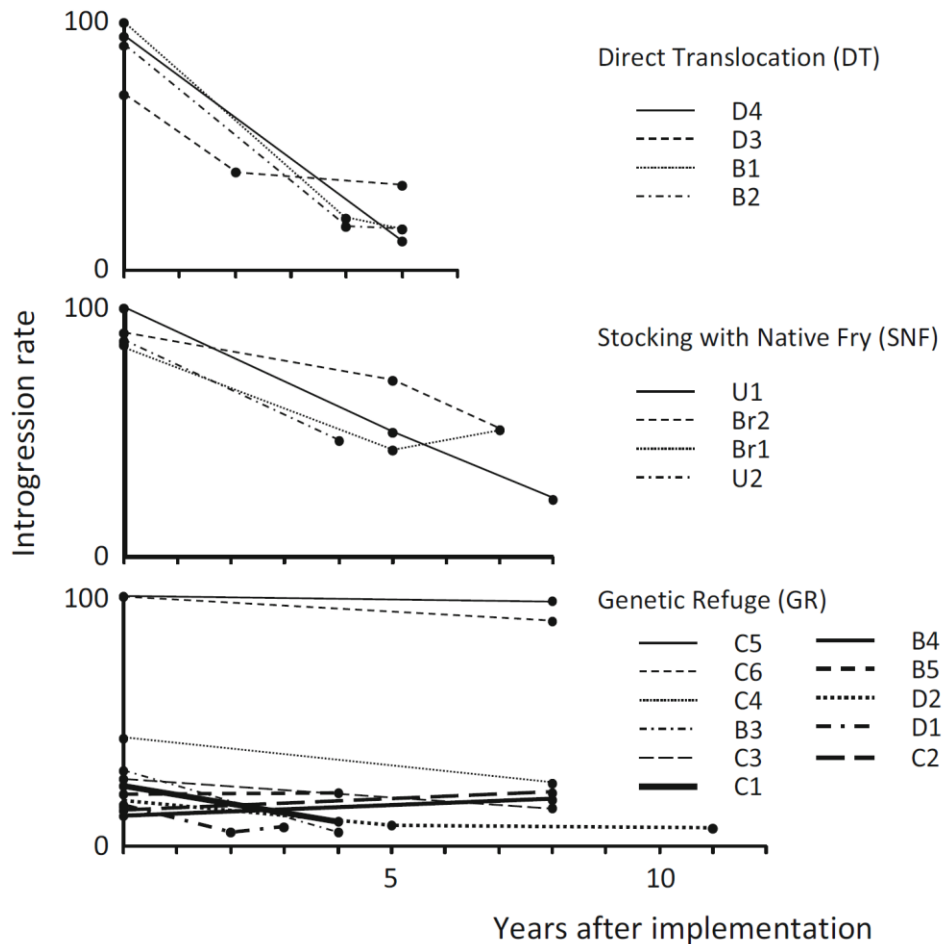


Figure 2—9: “Evolution of the introgression rate (calculated as the percentage of ATL alleles in the population) for each site according to the management strategy implemented.” Figure and legend from Gil et al. 2016.

These results suggest that management practices can quickly influence intraspecific diversity dynamics and that these systematic responses might be driven by a combination of evolutionary processes, likely environment-dependent.

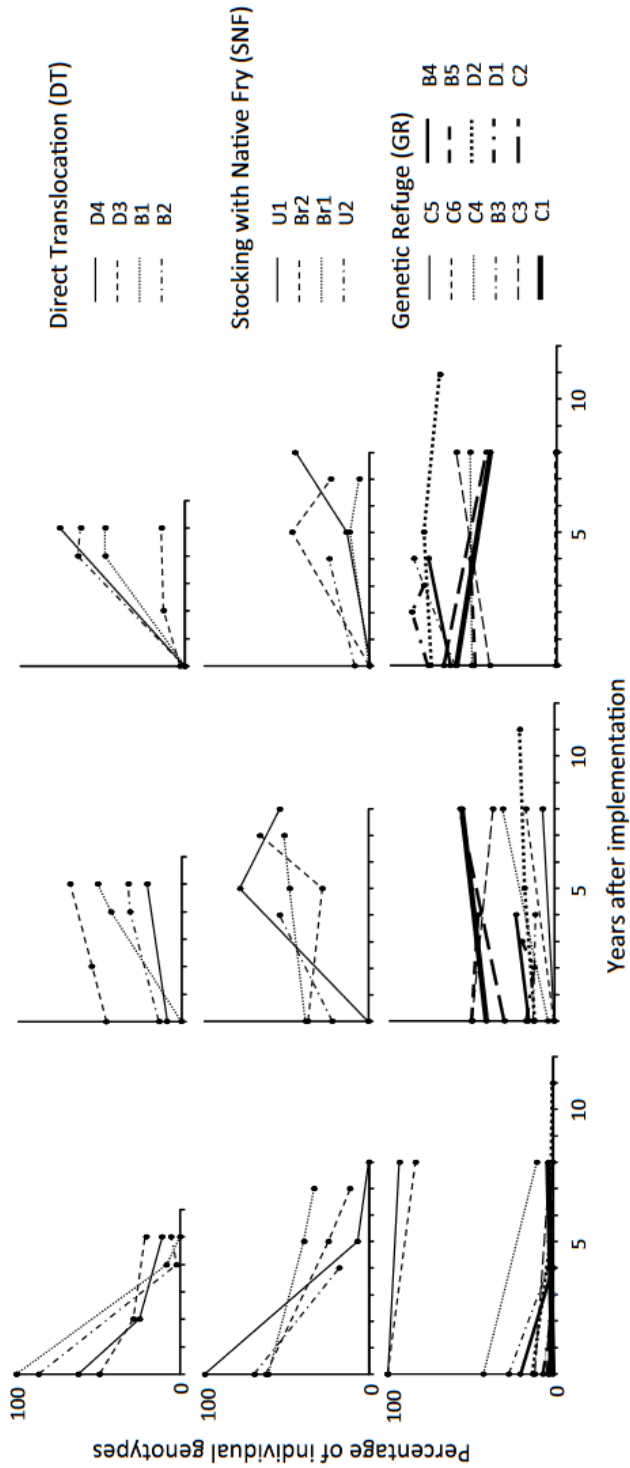


Figure 2—10: “Evolution of the percentage of individual genotypes. Three genotypes possible: ATL (pure Atlantic alien), HYB (hybrids) and MED (pure native Mediterranean), according to all the observed number of hatchery specific alleles at the two diagnostic loci.” Figure and legend from Gil et al. 2016.

Indeed, following the refuge strategy, populations did not purge themselves from ATL alleles, as initially expected. On the one hand, the presence and increase of hybrids indicate a lack of pre-zygotic isolation between the lineages in our study sites, as recently demonstrated in the Dranse system in Haute-Savoie, where patterns of heterogamous mating were observed (Gil et al., 2015, & *Section 2.4.1*). It also suggests that selection against HYB might be low or inexistent. However, in other environments, reproductive isolation barriers, may they be pre- or post-zygotic, may exist as some pure native MED populations are still found in some river stretches. On the other hand, the collapse of pure ATL individuals, but not pure MED individuals following hybridization, suggests that some fitness differences among parental lineages exist. An analysis of post-zygotic survival (Folio et al., 2021, & *Section 2.4.2*), using offspring from all possible crosses between MED, HYB and ATL individuals, indicates a role of maternal genotype-by-temperature interaction on embryonic survival. It appears that the outcome of stocking with ATL individuals has led to a mosaic of situations in terms of observed intraspecific diversity. Environmental, behavioural and possibly selective factors, in addition to the implementation of various management practices, are likely to have generated such diversified outcomes.

2.4 THE ECO-EVOLUTIONARY MECHANISMS DRIVING HYBRIDIZATION

Since observed patterns of diversity are often the result of allopatric evolution (Harrison, 2012), many reproductive isolation mechanisms could have evolved between the previously isolated ATL and MED populations, potentially involving eco-evolutionary mechanisms (Schluter, 2000). In that case, the evolutionary outcome of hybridization and intraspecific diversity dynamics could be driven by a combination of factors differentiating both lineages. For the MED-ATL hybridization complex, many factors have been pointed out, and some experimentally investigated to explain the observed patterns of intraspecific diversity. These studies have focused on two reproductive isolation mechanisms thought to

2.4 The eco-evolutionary mechanisms driving hybridization

be the most influential on diversity dynamics. Gil et al. (2015) focused on pre-zygotic isolation mechanisms and investigated if some behavioural differences existed between both lineages regarding sexual selection – female preference and male competition. Folio et al. (2021) focused on post-zygotic isolation and investigated patterns of offspring survival at egg stage based on parental origins (MED, HYB, ATL) and river temperatures to detect potential genotype-by-environment (GxE) interactions. This section will describe in detail these two reproductive isolation mechanisms, as well as the other factors that have not yet been investigated but may also contribute to diversity dynamics.

2.4.1 Mating preference

Reproductive behaviour, such as female preference, is a potential candidate for pre-zygotic reproductive isolation. Usually, female preference for locally adapted phenotypes (Fisher, 1930; G. C. Williams, 1966) is expected to reinforce reproductive isolation mechanisms, since native individuals might be preferred as mates when they present a fitness advantage compared to non-native individuals “good gene hypothesis (Kirkpatrick, 1996)”. Largiadèr & Scholl (1996) investigated introgression patterns in a northern population of brown trout (Doubs River) and suggested that the mating system was biased toward homogamy in the MED-ATL complex due to some observed linkages disequilibrium and the absence of intermediate phenotypes in this river. However, in other environments, the manifest presence of hybrids suggests that pre-zygotic reproductive isolation is incomplete between the lineages. Using genetic studies, other authors argued that the mating system between both lineages was random since genotypic frequencies observed in some populations matched random pairing (Barbat-Leterrier et al., 1989).

Yet, both these assumptions are based on studies considering the diversity of individuals found in given environments and do not portray the full range of mating behaviour that may occur. Indeed, this diversity is likely to be the result of both pre and post-zygotic selection and the net effect then depends on

environmental conditions (Godineau et al., 2021). Because sexual selection can sometimes oppose natural selection (Labonne & Hendry, 2010), it is compulsory to study mating behaviours in natural environments.

Gil et al. (2015) investigated two potential pre-zygotic isolation barriers potentially involved in sexual selection – female preference and male competition – by directly observing mating behaviours in natural environments. Behavioural patterns were studied based on an individual phenotypic score in order to differentiate lineages. This score is calculated using the presence or absence of several robe *criteria*, which are genetically contrasted between lineages (*Table 2 – 1*; Aparicio et al., 2005). Subaquatic cameras were placed in a few Haute-Savoie Rivers: the Dranse d'Abondance, the Chevenne, the Serve and the Borne during reproductive season. Videos were then analysed and specific behaviours recorded. Detailed experimental settings are available in Gil et al. (2015).

This section describe results produced exclusively by Jordi Gil (Gil, 2015) that will be useful in the understanding of my PhD and its hypothesis.

2.4.1.1 Male-male competition

Intrasexual competition can condition access to females during reproduction and antagonistic behaviours have already been described in salmonids (Esteve, 2005; Greeley, 1932; J. W. Jones & Ball, 1954; Tentelier et al., 2011), where size is usually the factor involved in competition (M. W. Jones & Hutchings, 2001). In the MED-ATL complex, if one lineage happened to be more aggressive compared to the other one, access to females could be variable based on males genotype, and such biased access could tip the scales toward a biased mating and reproductive success, a potential source for partial reproductive isolation. In his PhD, Gil also aimed at evaluating if male aggressiveness was lineage dependent and targeted.

2.4 The eco-evolutionary mechanisms driving hybridization

In this experiment, aggressive behaviours were counted and included lateral threat, chasing and biting. Three models were then tested to evaluate if a male phenotype influenced his probability of (i) attacking, (ii) being attacked or if (iii) aggressiveness was oriented based on both male phenotypes – targeting similarity or dissimilarity. For the three models, results indicated that male competition was not affected by phenotypes – and hence lineages. This experiment only confirmed the importance of body size in male-to-male competition.

2.4.1.2 Female preference

Intersexual female preference is widely recognised in salmonids and many phenotypic traits are under sexual selection (such as fin size (Quinn & Foote, 1994), size (Petersson et al., 1999), male/female size ratio (Labonne et al., 2009). Colour and patterning also play an important role in sexual selection (Auld et al., 2019; Cuthill et al., 2017) and melanin colouration appears to reflect honest signals to conspecifics in salmonids (Jacquin et al., 2017; Marie-Orleach et al., 2014; Wedekind et al., 2008) and could hence potentially be under female preferences. In the MED-ATL complex, potential female preference based on phenotypic differences among lineages (*Table 2 – 1*) could either drive or counter pre-zygotic isolation.

Gil et al. (2015) aimed at uncovering patterns of female preference based on male robe *criteria* defined in Table 1. A behavioural model considering a succession of possible behaviours was used (based on a model developed by Labonne et al., 2009). After a male arrived, the female could either leave or stay, and if the latter, be inactive or active, *i.e.* start digging. Female preference was considered as the probability of staying and being active. Multiple preference models were then tested. A null model only considered the effects of male-female size ratio and operational sex ratio (OSR, Labonne et al., 2009). It was the base of all other models. A dissimilarity model implemented a value of dissimilarity between male and female

phenotypic scores, where 0 accounted for similar partners while 1 corresponded to an encounter between ATL and MED phenotypes. This model aimed at distinguishing between homogamous, heterogamous or non-phenotypic preferences. The last model was lineage dependent and aimed at testing if preference was dependent upon female phenotype, male phenotype and the interaction between both. The aim here was to be able to test if local females or maybe all females (universal preference) tended to prefer local and potentially adapted males (G. C. Williams, 1966), or the opposite. Model selection was performed based on Deviance Information *Criterion* (DIC, Spiegelhalter et al., 2002).

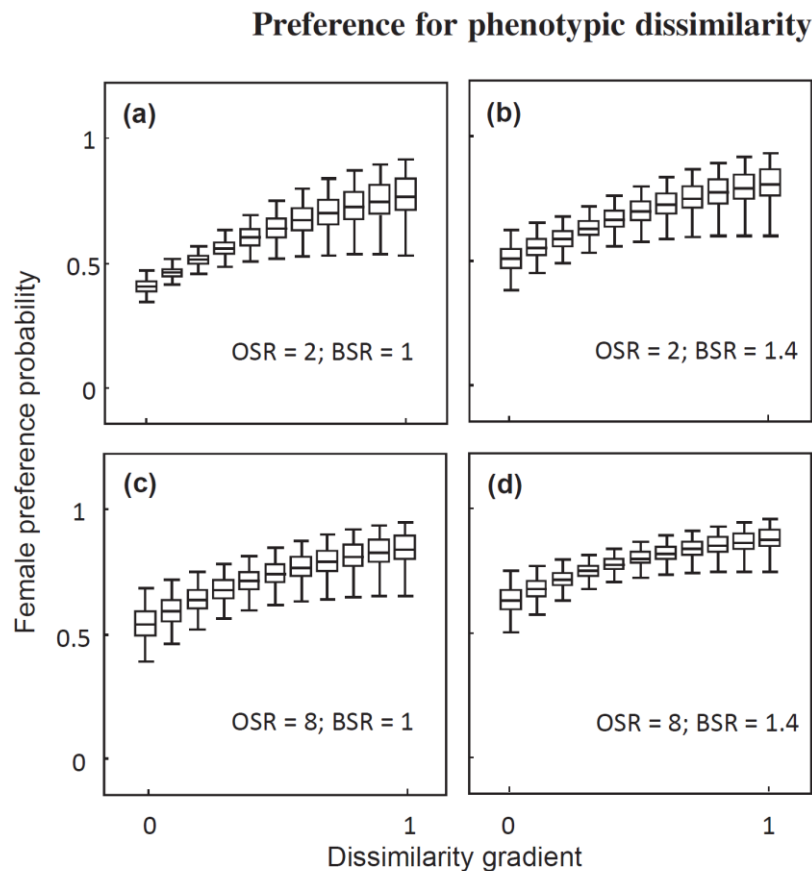


Figure 2—11: Predictions for general female preference ($s \times a$) for an average female, when (a) $OSR = 2$, $BSR = 1$; (b) $OSR = 2$, $BSR = 1.4$; (c) $OSR = 8$, $BSR = 1$; (d) $OSR = 8$, $BSR = 1.4$. Figure extracted from Gil et al 2015.

2.4 The eco-evolutionary mechanisms driving hybridization

The authors found that the model selected for female preference was the dissimilarity model, which indicated that female preference was positively correlated to the dissimilarity score. Therefore, the more dissimilar a male is to a female, the more she will stay on the nest and start digging (*Figure 2 – 11*). On the extreme, this would mean that each lineage will tend to prefer the other one – a MED female will more likely stay and dig for an ATL male rather than for a MED male (more than fold 2) and vice versa. However, within observed data, encounters between individuals of opposite pure lineages were scarce (see Gil et al., 2015) and incertitude increased passed a dissimilarity value of 0.6. In addition, the higher the size ratio was the lower the impact of dissimilarity was on female preference and the more likely female will have stayed and dug, which confirmed the importance of body size in female preference (Labonne et al., 2009; Petersson et al., 1999). Overall, females probability to stay and dig was around 50% no matter males phenotype. Probability for a female to stay and dig increase with the increased in OSR.

These findings indicate that mating is mainly determined based on a size-ratio and on a phenotypic dissimilarity-based female preference as well as a size-based male-to-male competition. In the MED-ATL context, since both lineages appear to have similar growth rates (Data from Scimabio Interface), size – for individuals of the same age – should not be a factor that would advantage one or the other lineage when growth happened in the same environment. However, in cases where growth would have happened in very different environments – for example when individuals are translocated – size could represent an advantaging factor for one lineage since the growth environment would have conditioned access to resources and density-dependent growth (Lobon-Cervia, 2007; Lorenzen & Enberg, 2002). Similarly, if mortality rates are different (Gil, 2015), then body size distribution could vary among lineages and hereby influence mating.

Focusing on lineage differences, female preference indicates that the mating system in those environments is biased toward heterogamy, with females favouring males partially or entirely dissimilar to their own phenotypes. In the MED-ATL complex, heterogamous mating could catalyse hybridization and accelerate the decrease of extreme “pure” ATL and MED phenotypes, potentially affecting the distribution of pure genotypes. These results are in accordance with some patterns of diversity observed in Haute-Savoie where populations are now fully hybridized despite the implementation of various management practices to conserve MED diversity (Gil et al., 2016). These findings oppose some expected assumptions that local males are preferred as mates (Fisher, 1930; G. C. Williams, 1966) and counter the genotypic observations made by Largiadèr & Scholl (1996) and Barbat-Leterrier et al. (1989), which respectively suggested that mating system between MED and ATL trouts could be biased toward homogamy or simply be random. However, even if heterogamous mating is more likely in the populations studied; the actual mate choice will be environment-dependent. Mating systems could therefore be very different in other environments and observations made by Largiadèr & Scholl (1996) and Barbat-Leterrier et al. (1989) be true elsewhere. Nevertheless, mating systems cannot be solely inferred from a posteriori genotypic analyses as usually done (Metcalf et al., 2008; E. Rubidge et al., 2005) since selection could have already wiped out a part of the genetic variation.

2.4.2 GxE interactions

In his thesis manuscript (Gil, 2015), J. Gil investigated patterns of offspring survival at egg stage in *Salmo trutta* with respect to parental genotypes – using markers related to the original MED and ATL lineages – in interaction with river temperature to detect potential GxE interactions. During my own PhD, I used Gil’s data and analyses to write a publication in order to make these results accessible to the scientific

2.4 The eco-evolutionary mechanisms driving hybridization

community (Folio et al., 2021). I here included parts of this publication, because these results are central to model the effects of selection on the product of hybridization.

Selection can act very strongly during early stages of development in salmonid species, notably as a function of temperature (Huuskonen et al., 2003; Ojanguren & Braña, 2003; Régnier et al., 2013), a factor that can show contrast at small scales (Brown & Hannah, 2008; Daigle et al., 2016). Offspring from the ATL lineage were expected to be adapted to relatively warm temperatures (8-10°C) for pre-hatching survival as already demonstrated (Jungwirth & Winkler, 1984; Ojanguren & Braña, 2003; Régnier et al., 2013), a thermal range often encountered in their distribution area. For the MED lineage, which evolved experiencing a wider range of contrasting temperatures (Daigle et al., 2016), we hypothesised that their offspring should at least outperform ATL offspring in cold water rate (6 to 4°C) since ATL offspring display very low survival at such temperatures (Ojanguren & Braña, 2003; Régnier et al., 2013). To assess the real importance of temperature on post-zygotic selection, our experiment was performed directly in natural environments where substantial temperature contrasts are observed during winter (Burt et al., 2011). In that way, other uncontrolled known and unknown factors can interactively affect survival, and any significant effect of temperature variation on offspring survival can therefore be deemed as an important driver of natural evolution (J. T. Anderson et al., 2014; Genovart, 2009).

2.4.2.1 *Materials and methods*

Genitors sampling and study sites. This experiment was performed in the Haute-Savoie region, France, part of the Rhone river basin, originally occupied by the MED lineage of *Salmo trutta*. In this region, a century of ATL *Salmo trutta* introduction has generally led to the presence of ATL individuals located upstream, HYB individuals located in the intermediate parts of the rivers, and MED individuals located

downstream in the confluence areas (Figure 2 – 7). Adult *Salmo trutta* were sampled from the Overan Creek, a four kilometres long tributary of the Borne River (46.55'57.68N'';6°24'07.40E'', Figure 2 – 12 A, B) that harbours sufficient genetic variation required for the present study. Adults were selected on robe criteria, which can be used to some extent as proxies of genetic lineages characterisation (Table 2 – 1). Experimental fertilisation was then conducted (Figure 2 – 13) and eggs were placed in natural environments. For more details on the protocol see (Folio et al., 2021).

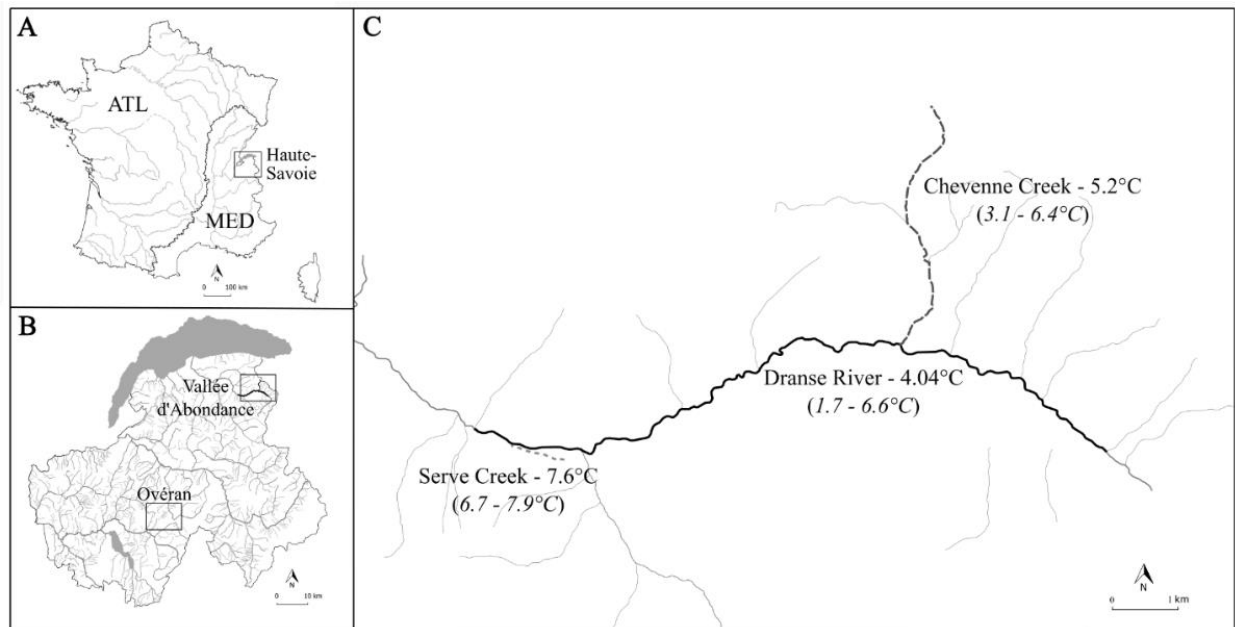


Figure 2—12: Map of France with the delimitation between the Atlantic (ATL) and the Mediterranean (MED) basins as well as a focus on the Haute-Savoie region (A) where river locations for adult *Salmo trutta* sampling and egg incubation are indicated (B) and topography of the Dranse d'Abondance system with our three thermally contrasted rivers(C). Mean water temperatures are indicated and in brackets are minimum and maximum-recorded water temperatures over the study period.

Three neighbouring rivers were selected in Haute-Savoie, to later deposit eggs during their incubation period, in order to represent a thermal contrast to test for GxE interactions (Figure 2 – 12 B, C): the Dranse River (46°16'52.94N'';6°42'39.55E'', slope = 4%, altitude at source = 1500 m) and two of its tributary

2.4 The eco-evolutionary mechanisms driving hybridization

streams, the Chevenne Creek (46.17°54.04N'';6°47'22.09E'', slope = 10%, altitude at source = 1250 m) and the Serve Creek (46.16°49.60N'';6°42'40.83E'', altitude at source = 840 m). They had respectively low (4.04°C), intermediate (5.2°C) and high (7.6°C) mean water temperatures (averaged from the 1st December 2013 to the 30th March 2014).

Fertilisation protocol.

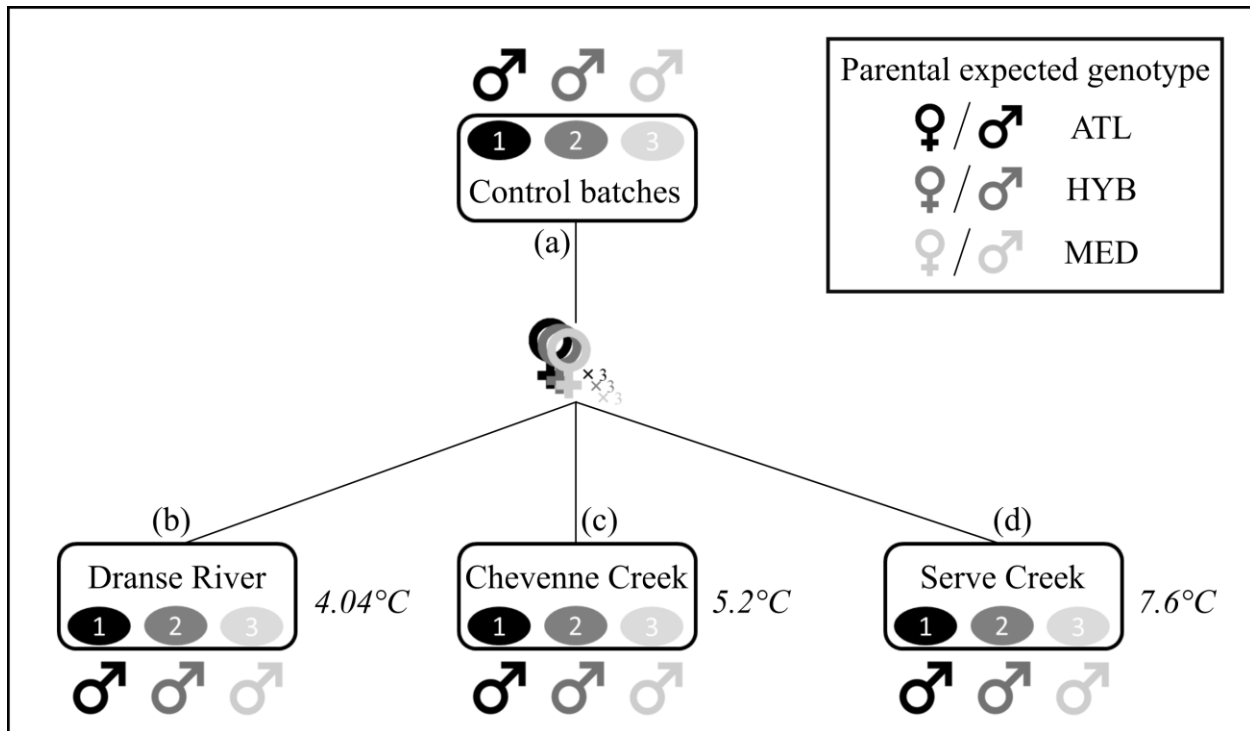


Figure 2—13: Experimental design for the fertilisation protocol using individuals selected based on their expected genotypes. For each of the nine females, three of each expected genotype (MED, HYB, and ATL), clutches were divided into four batches. Three were destined to be placed in the three thermally contrasted rivers (b, c, and d) and the remaining one (a) was kept to control for egg fertilisation in the experimental fish farm (Thonon-les-Bains, INRAE, E74 300-4). Each batch was then divided into three sub-batches (1, 2, 3) in order to be fertilised by semen from either, expected MED, expected HYB, or expected ATL males; making a total of 81 sub-batches for our field experiment. From Supplementary material 3 Folio et al., 2021.

Genotypic studies. To assess parental genotype, genitors pelvic fins were clipped and analyzed at six diagnostic markers (four single nucleotide polymorphism loci: OMM1144, OMM1105, OMM1154 and OMM1117 and two microsatellites: str541 and str591) perfectly differentiating the ATL and the MED lineages in *Salmo trutta* (Gharbi et al., 2006; Guyomard & Caudron, 2008). Offspring genotype was not assessed. A genotypic score was attributed to each parent and determined based on the allele number of each lineage on all loci. An individual presenting 12 MED alleles was given a genotypic score of 1, deemed as a pure MED genotype, whereas an individual with 12 ATL alleles was given a genotypic score of 0, hence deemed as a pure ATL genotype. All other intermediate scores were referred to as HYB genotypes. Although genotypic scores were obtained *posterior* to fertilisation, they were indeed strongly correlated to robe *criteria*, ensuring that our fertilisation protocol allowed us to cross parents of the desired genotypic scores (Folio et al., 2021; Supplementary Material 4).

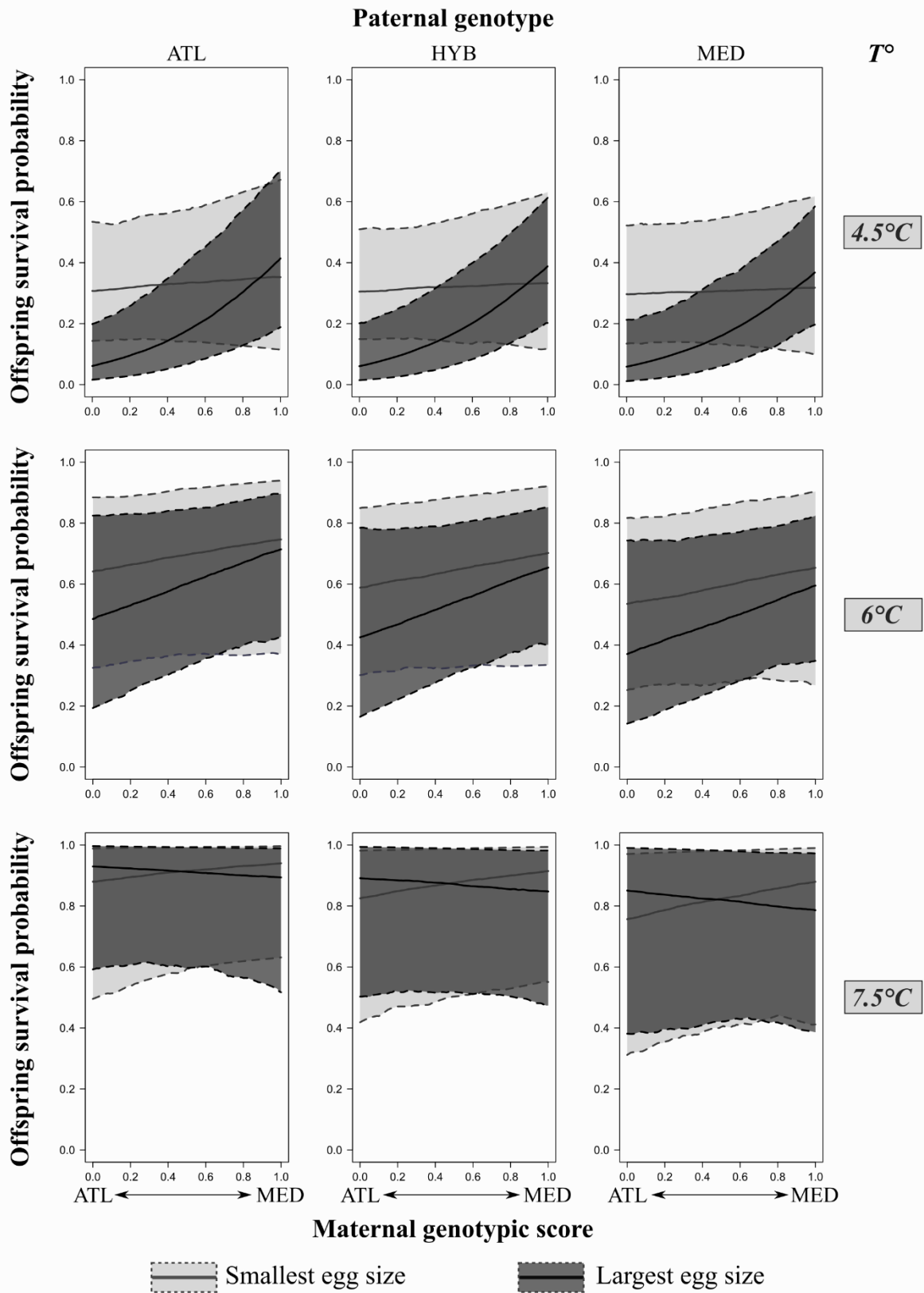
Statistical analyses. We analysed offspring survival probability p (ratio of the surviving fry number conditional on the initial egg number placed in each incubation box) as a function of parental GxE interactions using mixed-effects logistic regression. To do so, we tested for linear effects of maternal (MG) and paternal (PG) genotypes – *i.e.* genotypic score – in interaction with a linear effect of average temperature during the incubation period (T°) for the incubation box l . Since rivers presented contrasted temperatures, the required time to reach 400 degree-days varied significantly among incubation boxes. Therefore, we decided to control for the number of days spent in the incubation box before hatching ($Days$). We also considered egg size (E), as well as the occurrence of *Saprolegnia* (S), to respectively control for maternal investment and disease-related effects on offspring survival. We tested for other targeted interactions of interest between both parental genotypes and temperature, and between egg size, maternal genotype, and temperature. Pseudo replication related to the identity of males (α_i) and females (β_j) was treated using random effects. We also included a random effect for the three rivers (γ_k)

2.4 The eco-evolutionary mechanisms driving hybridization

to effectively disentangle pure temperature effects from other unknown environmental factors. Statistical inference was conducted in the Bayesian framework using Markov Chain Monte Carlo (MCMC) techniques as implemented in JAGS software (Plummer, 2003). For more details, see Folio et al. (2021).

2.4.2.2 Results

Most of the factors of interest and most of their interactions were significantly different from zero, pointing at complex patterns of variation in offspring survival probability. It is noteworthy that the only non-significant interactions were those including both maternal and paternal genotypes. All other interactions including maternal genotype and temperature were significant, indicating that GxE interactions occurred (see Table 1 in Folio et al., 2021). *Figure 2 – 14* describes the predicted distribution of survival probability of offspring, as a function of parental genotypes, temperature, and egg size, allowing us to envision the shape and strength of the GxE interactions. In general, offspring survival was higher at warm temperatures than at cold temperatures. For the largest eggs (5.25 mm), at cold (4.5°C) temperature, the survival probability for offspring of MED females was at least three times higher than that of offspring of ATL females, but this difference nearly disappeared for the smallest eggs (3.75 mm). At intermediate temperature (6°C), offspring from MED females still had a slightly higher survival probability than offspring from ATL females, whatever the egg size. At warm temperatures (7.5°C), the relationship between maternal genotype and survival disappeared, as well as the effect of egg size. The paternal genotype effect, though weak, was mainly expressed at high and intermediate temperatures, favouring offspring sired by ATL males, hinting at another potential GxE interaction. The addition of the female and male GxE interactions implied that offspring survival was often the highest for hybrid descendants sired by ATL males and MED females, whereas other hybrids (different crosses) displayed intermediate survival in most cases.



2.4 The eco-evolutionary mechanisms driving hybridization

Figure 2—14: Predictions of offspring survival probability at low (4.5°C), medium (6°C), and high (7.5°C) temperatures as a function of maternal genotypic score, for ATL (0), HYB (0.5), and MED (1) paternal genotypes. Values for the smallest (3.5 cm) and largest (5.25 cm) eggs found in our sample are represented separately to account for egg size variation. Solid lines are posterior means while dotted lines are 95% credible intervals. Predictions were performed using male ID 23, female ID 9, and the Dranse River as random effects. The effect of *Saprolegnia* was discarded from the predictions.

2.4.2.3 Discussion

Evidence of gene-by-environment (GxE) interactions.

As hypothesised, temperature contrasts

between rivers substantially affected offspring survival in our experiment. Offspring generally had higher survival at the highest temperature studied, which falls within the range of optimal temperatures for the survival of *Salmo trutta* during the pre-hatching stage (Jungwirth & Winkler, 1984; Ojanguren & Braña, 2003). Ojanguren & Braña, (2003) reported an average 70% decrease in ATL offspring survival (at egg stage) for a decrease of temperature from 7.5 to 4.5°C, very much in line with our findings for ATL females. In particular, for the ATL lineage, offspring from larger eggs performed worse than those from smaller eggs at low temperatures, confirming previous experimental results in captivity (Régner et al., 2013). However, for the same egg size, offspring from MED females had a three times higher survival probability than offspring from ATL females at cold temperatures. This constitutes a major selective advantage in cold environments for carriers of MED maternal genes. It is also noteworthy that, generally, egg size is positively correlated to female body size in salmonids, as is fecundity (Lobon-Cervia et al., 1997): large females lay large and numerous eggs, and therefore can massively contribute to population growth. To our knowledge, there are no documented differences between lineages regarding this size-dependent allocation strategy. Thus, the present GxE interaction, mediated by maternal investment, we here uncovered may fundamentally alter the genetic structure of populations through boosted population growth by strongly favouring MED maternal ascendancy in cold environments.

Focusing on the effects of paternal genotype now, we also found a GxE interaction involving temperature contrast. Genes from ATL males tended to slightly improve offspring survival, but more so at warm temperatures. The strength of this effect however was much lesser than the above-mentioned female GxE interaction, a somewhat logical outcome since maternal effects are often stronger than paternal effects during earlier phases of development (R. S. Burton et al., 2006; T. Burton et al., 2020; Huuskonen et al., 2003; Régnier, Bolliet, et al., 2012). The fact that we did not find any significant interactive effect between paternal and maternal genotypes seems to preclude any assumption regarding the possible benefits of increased heterozygosity (Dahl et al., 2006; Edmands, 2007; Fraser et al., 2008; Meldgaard et al., 2007; Weatherhead, 1999; Wells et al., 2019), such as higher diversity at functional *loci* like MHC (Jacob et al., 2010; Landry et al., 2001; Turner et al., 2009 but see Labonne et al., 2016; Tentelier et al., 2017). Therefore, ATL males may carry good genes – for some environments - that MED males do not have. One possible speculation to explain this is to turn to the *SEX locus* in salmonids (Yano et al., 2012, 2013), which is only present in males: some beneficial genes could be segregated with this *locus* only in the ATL lineage.

Potential consequences on diversity and reproductive isolation.

It is noteworthy that even if our experiment was realised on a small spatial scale, we may have found footprints of adaptation to temperature wherein some genotypes performed better in cold environments than others; where other studies (also focusing on the embryonic stage) involving a single lineage failed to do so (Clark et al., 2013; Stelkens et al., 2012). While evidence for adaptation to cold conditions in high altitudes was demonstrated at the species level, for *Salmo trutta* (Jungwirth & Winkler, 1984) or *Salvelinus alpinus* (Arctic char, (Huuskonen et al., 2003)), lineage-related adaptation to temperature is to our knowledge not documented. Low temperatures are often reached in alpine systems, such as the Dranse d'Abondance, where the MED lineage evolved since the post-glacial period (Bernatchez, 2001). This potential lineage-related adaptation to cold conditions indicates in our case that despite several generations in sympatry,

2.4 The eco-evolutionary mechanisms driving hybridization

gene flow has not erased the link between the set of 6 diagnostic markers that were previously designed on the two separate lineages and genes under potential selection (de Lafontaine et al., 2015; Fitzpatrick et al., 2020; Lamaze et al., 2012). Of particular interest is the fact that robe *criteria* were well correlated to our genotypic score, whereas recent results indicate that such an approach may still miss a large part of the recent genetic admixture (Saint-Pé et al., 2019). This indicates that additional investigations of lineage differences regarding adaptation to cold (MED) or warm (ATL) temperatures could produce even more insightful data to further our understanding of intraspecific diversity dynamics in hybrid zones, and to understand how thermal environment could control for post-zygotic reproductive isolation (Leitwein et al., 2016). Given the recent progress in the taxonomic status of Brown trout (Hashemzadeh Segherloo et al., 2021), it is also likely that such hybridization events, through their consequences on fitness variation, are central to the evolution of the whole species (or species complex).

2.4.3 Other potential drivers

Other mechanisms have been hypothesised to contribute to the evolution of diversity dynamics in the MED-ATL complex. Some of these mechanisms have been ruled out while others remain unexplored.

☞ ***Fitness differences.*** More fitness differences between both lineages might exist later on in life. In his PhD work (Gil, 2015), using angler catches, Gil indicates that captured MED individuals are generally older than captured ATL individuals suggesting differential survival at adult stage. MED individuals may live longer and hence have a higher lifetime reproductive success, potentially contributing more to the population than ATL individuals do. Other fitness differences may arise from local adaptation, as it is possible in Salmonids (Fraser et al., 2011). The MED lineage, native to the Mediterranean area, could be locally adapted to specific mountainous

environments. They may have been at an advantage compared to domesticated introduced ATL individuals during stocking. In addition, it has been reported that after their introduction domesticated ATL individuals were less likely to survive compared to MED native individuals (Caudron & Champigneulle, 2002).

☞ ***Sensitivity to fishing.*** Some studies (J. L. García-Marín et al., 1998; Mezzera & Largiadèr, 2001) indicate that domesticated individuals, as well as hybrids, are more represented within an angler catch, suggesting different catchabilities of individuals based on their origin. For example, in cutthroat trout, catchability is positively correlated with the level of domestication (Dwyer, 1990). In the MED/ATL hybridization complex, some studies have pointed toward a higher catchability of ATL individuals compared to MED ones (Caudron, Champigneulle, et al., 2012). This could influence the relative abundance of each lineage and cause variable gene flow between populations. When stocking happened, this could have favoured native MED individuals over introduced ATL ones.

However, after many years in sympatry, these observations might not hold since individuals from both lineages would have undergone many generations of selection in the same environment.

☞ ***Female choice for spawning habitat.*** In some typical fast-flowing and steep streams, such as the Chevenne Creek, it has been observed that MED females use a high diversity of spawning habitats with five main types (Champigneulle et al., 2003). For instance, MED females as often select unusual spawning habitats – such as “side pools” – as classical riffle habitats. In addition, a high percentage of nests (65%) are built in protected areas where water velocity is low. Sheltered spawning substrates were usually preferred compared to unsheltered ones. A flood destroyed a part of the nests indicating that unusual and sheltered habitats were less

2.5 The importance of eco-evolutionary mechanisms in the evolution of diversity

destroyed than other more classical habitats. Genotypic analyses on various nest sites also indicated that ATL females would more generally select classical spawning habitats for reproduction (Scimabio Interface, Com. Pers.), suggesting that habitat could constitute an important post-zygotic reproductive isolation between the two lineages. Indeed, the MED habitat diversification strategy might be advantageous as it might lower the chances of nest scouring and give a higher survival chance to offspring from the MED lineage, which will be recruited in the next generation. This could explain the persistence of native MED populations in some rivers. Almodovar et al. (2006) also evidenced a correlation between introgression and factors related to habitats such as flow, conductivity, bicarbonates concentration and pH, with stable flow and “fertile” water being favourable to ATL individuals.

2.5 THE IMPORTANCE OF ECO-EVOLUTIONARY MECHANISMS IN THE EVOLUTION OF DIVERSITY

In the Mediterranean area, intensive stocking from non-native origins led to various outcomes of hybridization with the native MED lineage, going from MED resilience to full hybridization, and in some cases total extirpation. In addition, the implementation of various native conservation practices also led to many unexpected outcomes regarding intraspecific diversity. Results suggested that many EEMs – behavioural and selective factors – could have interacted with management practices to drive the evolution of intraspecific diversity in the MED-ATL context. Indeed, in natural environments, behavioural and selective factors are some substantial driving forces.

On the one hand, reproductive interactions are known to drive evolutionary dynamics (Maan & Seehausen, 2011). Assuming random, homogamous or heterogamous mating might completely change the outcome of diversity as it may, for example, play a role in shaping genetic differentiation between

populations (Soularue & Kremer, 2014). Moreover, mate choice strongly depends on population structure and hence available intraspecific diversity, making the outcome challenging to predict anyway, yet rarely random (Klug & Stone, 2021). Therefore, knowing the existence of heterogamous female preference (Gil et al., 2015), it is essential to investigate the evolution of diversity dynamics considering the dynamic aspect of mating systems in order to grasp the actual role of mating preference in structuring diversity dynamics.

On the other hand, genotype-by-environment interactions could drive post-zygotic reproductive isolation mechanisms, and result in a mosaic of intraspecific diversity patterns, depending on the local environment (Folio et al., 2021). As natural selection is an important evolutionary mechanism shaping patterns of diversity (G. C. Williams, 1966), understanding GxE interactions is paramount to predict the evolution of diversity dynamics in a specific context. Indeed, information on the relative fitness of each category of individuals (native, hybrids, non-native) under various environmental conditions could help to predict the expected rate and extent of adaptive introgression (Barrett & Schluter, 2008; Hedrick, 2013). It is therefore important to grasp the role of GxE interactions and environmental conditions – *i.e.* selective pressures – in structuring diversity dynamics.

In our case, depending on selective pressure experienced in a given environment – may they be biotic for inter-individual interactions or abiotic for environmental variables – reproductive isolation between the MED and the ATL lineages may fluctuate in space and time. Consequently, it is clear that the underlying EEMs cannot be discarded when implementing management practices, as not accounting for such driving forces could jeopardise management efficiency. In addition, considering such specific knowledge could help build more efficient and evolutionary-inspired management strategies, which could be context-dependent.

2.5 The importance of eco-evolutionary mechanisms in the evolution of diversity

However, acknowledging the existence of such mechanisms is insufficient to actually measure their impact on hybridization and diversity dynamics, with or without considering interventions of fisheries managers. To grasp the actual role of these EEMs, one has to actually project and consider how they will interact with the other ecological, genetic, and demographic drivers, among which management practices. Therefore, the aim of my PhD is to use a DG-ABM approach to integrate all the knowledge available, including these EEMs, so to *in fine* be able to answer one question: **do eco-evolutionary mechanisms really matter for the management of intraspecific diversity?** To answer this question, I will use a DG-ABM model I developed during my PhD to evaluate whether these mechanisms really impact the evolution of diversity on short time scales, as we expect them to, considering the contemporary and rapid interplay between ecology and evolution (Carroll et al., 2007; N. G. J. Hairston et al., 2005; M. T. Kinnison & Hairston Jr, 2007; Pelletier et al., 2009; Reznick, Losos, et al., 2019; Reznick, Bassar, et al., 2019).

The next chapter focuses on the construction of this DG-ABM model: MEDITERRANEA, which allows for the consideration of known EEMs – and their genetic basis – as well as management practices and specific environmental variations. More specifically, this chapter will describe the model's purpose, assumptions and specific processes, as well as how to use it *via* its user-friendly graphical interface.

CHAPTER 3

« Remember, it's better to create something and be criticized than to create nothing and criticize others". »

Ricky Gervais

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3 MEDITERRANEA: A DG-ABM TO SIMULATE THE EVOLUTION OF INTRASPECIFIC DIVERSITY IN BROWN TROUT

My first goal was to develop a demo genetic agent-based model to understand and predict the evolution of intraspecific diversity dynamics between two genetically distinct lineages of *Salmo trutta*: the Mediterranean (MED) and the Atlantic (ATL) lineages. While another modelisation framework has been developed for brown trout in the Mediterranean area (in Spain, Ayllón et al., 2016), their specific objectives do not match managers' nor ours. In addition, the degree of precision of both models varies, and managers may not be able to inform certain parameters owing to Ayllón et al., (2016) model. Furthermore, their model does not implement different lineages, which is the essence of this work. For instance, the core idea of this approach is to include eco-evolutionary concepts in the management of intraspecific diversity in order to account for previously demonstrated lineage-based behavioural and fitness differences since they will interact with management practices and may play an important role in hybridization dynamics. This modelling framework allows to consider inter-individual variability in life-history traits and behaviour, as well as their genetic basis, and to implement different eco-evolutionary scenarios under various environmental conditions and management practices. This second chapter will first give an overview of our modelling approach, and will then focus on a detailed description of our model (based on ODD, Grimm et al., 2006, 2010), with its specific processes and possible management practices simulations. Finally, it will describe the user-friendly interface and model initialisation.

3.1 AN OBJECT-ORIENTED MODELLING FRAMEWORK

MEDITERRANEA uses an object-oriented modelling framework to simulate the evolution of brown trout intraspecific diversity on a discrete time step. Objects, also called classes, are specific modelling entities

characterised by state variables and methods adapted to their internal structure. They are useful for the simulation of ABM as they allow for a simple – realistic or conceptualise – representation of agents with their characteristics, as well as processes. Objects are created using an initial set of state variables but are dynamic in time. They can be accessed using a unique object reference (ID) and modified through specific methods. Their state can be visualised at each time step throughout the simulation.

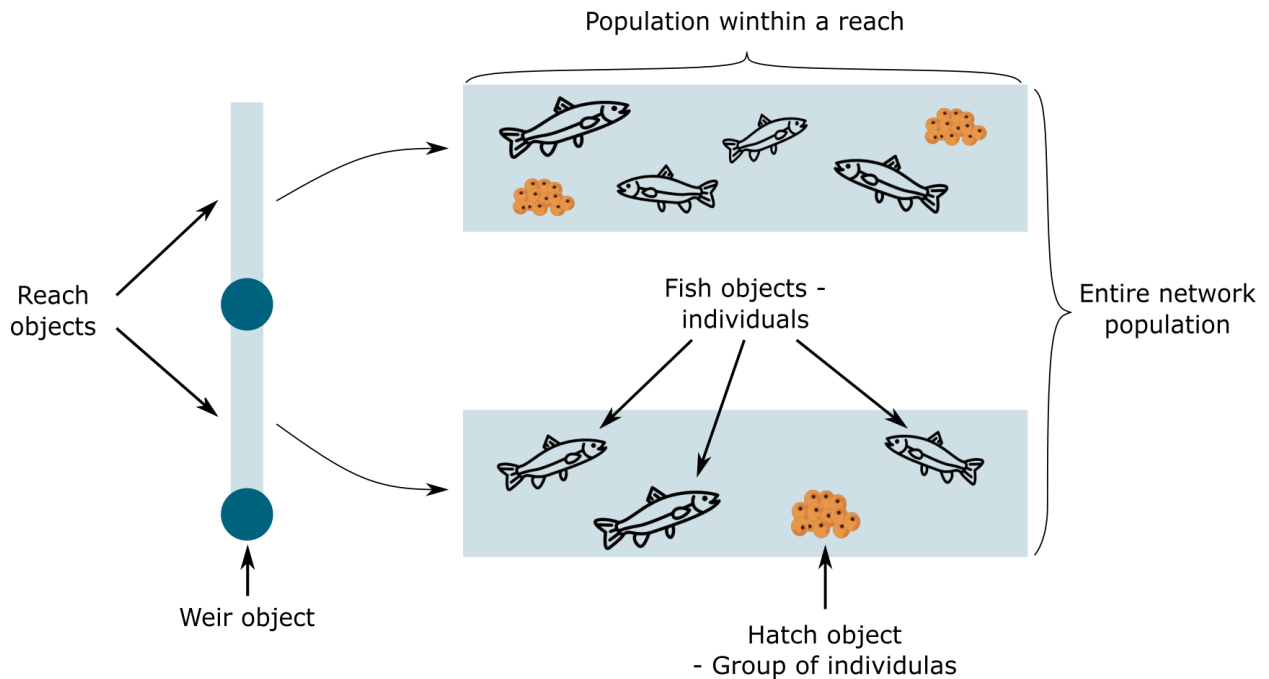


Figure 3—1: Representation of the main objects used in MEDITERRANEA to simulate its virtual environment.

MEDITERRANEA uses a wide collection of objects to describe and manipulate the components of its virtual environment – habitat, individual, genome... (Figure 3 – 1). For example, habitat is described using two types of topological "node" objects – reaches and weirs –, which store information regarding spatial coordinates, and neighbouring node objects. Individuals are modelled as fish objects, which state variables can be a unique ID, life history traits values, or even a genotype. Individual processes, such as survival or movement, are methods of fish objects, called individually for each fish object. Hatch objects

Chapter 3. MEDITERRANEA: A DG-ABM to simulate the evolution of intraspecific diversity in brown trout are used to model groups of individuals sharing similar characteristics (time of creation, habitat...). They are created to simulate cohorts of juveniles in a specific location, as they can be excessively numerous. This represents a way to generate a lower number of objects to accelerate simulation time and save memory. Finally, species objects are used to define the genome structure of a fish object and are characterised by a genetic map, allelic diversity and effect as well as kinship (when multiple species are defined). All individuals belonging to the same species share the same genetic architecture. There is only one species object in MEDITERRANEA as the model only implements one species.

MEDITERRANEA runs under CAPSIS-4, a simulation platform initially used for forestry models that uses a Java language. CAPSIS-4 has been developed by the AMAP laboratory since 1999. It is a user-friendly tool (graphical interface) for scientists and managers. Various types of models can be implemented in CAPSIS-4 and simulations can be run in an interactive (graphical user interface) or script mode. In the graphical user interface, all or a subset of time steps can be visualised, and all objects and variables of interest are observable through different graphical options (*Section 3.6.2*). In the script mode, the user can only record a set of individual or population level variables of his choice over time. Since 2004, CAPSIS-4 has also been used to model fish populations' eco-evolutionary dynamics (Labonne et al., 2008; Labonne & Hendry, 2010), from which the MEDITERRANEA model is derived. A software package for MEDITERRANEA is available under the CAPSIS-4 simulation platform and as an executable file, which only contains the CAPSIS-4 simulation platform and MEDITERRANEA (model, graphical interface and If required original codes), allowing users to install and interact with the model interface. Java and Java Runtime Environment (JRE) have to be installed. CAPSIS-4 offers a detailed installation guide, as well as general documentation on the software (<http://capsis.cirad.fr/capsis/documentation>). Online documentation is also available for the MEDITERRANEA module at the following address (http://capsis.cirad.fr/capsis/help_en/mediterranea).

3.2 MODEL OVERVIEW

MEDITERRANEA is a simulation tool that aims at investigating the evolution of brown trout intraspecific diversity while considering the effect of (i) EEMs, (ii) environmental conditions and (iii) management practices on hybridization dynamics. It represents explicitly the entire life cycle of brown trout (*Figure 2 – 1*) with individual life-history traits from birth to death, reproduction and traits transmission between generations, in a spatially explicit environment. Individual processes, such as survival and growth, are explicitly modelled and calibrated based on general knowledge available for brown trout, as well as specific data originating from MED and HYB populations of the Mediterranean area (Scimabio Interface and the Fishing Federation FDPPMA 74).

3.2.1 Scales of the model

Organisational scales. This model is multi-scale and three levels of complexity are considered: (i) the gene level, (ii) the individual level and (iii) the population level. At the gene level, seven bi-allelic neutral *loci* are implemented, each allele belonging to a specific lineage in order to track the evolution of genetic diversity dynamic. Information at the gene level codes for a trait related to lineages and hence a genotypic category (in our case, we defined: MED, HYB or ATL), which will influence reproductive behaviour and fitness at the individual level. Most processes – survival, growth, reproduction... – happens at the individual level. Therefore, the performance of different individuals – in terms of reproduction and survival – will vary based on the biotic and abiotic environment they experience. This will in turn influence the population level, referred to as a group of individuals at a given time step, as it will dictate changes in the frequency distributions of alleles and genotypes in the population. Changes at the population level will then influence the biotic and abiotic environment experienced by individuals and consequently affect both the individual and the gene level. Over generations, natural and sexual selection will act together to

Chapter 3. MEDITERRANEA: A DG-ABM to simulate the evolution of intraspecific diversity in brown trout select advantageous genetic variations. The population level can represent the entire population of the hydrographic network or that of one reach or a sub-group of reaches.

Time scale. Model dynamics are based on simulating the life cycle of brown trout. Individual processes happen on a discrete temporal scale with continuous processes – survival, growth, ageing and migration – happening on a monthly time step and discrete events – mate choice and reproduction – taking place at given time steps during the reproductive period.

3.2.2 Model architecture

To model its virtual environment, MEDITERRANEA explicitly represents habitat, individuals, groups of individuals and genome structure.

3.2.2.1 Modelling space and habitat

Space is implemented as a spatially explicit hydrographic network composed of two types of habitat elements: reaches and weirs (*Figure 3 – 2*). Reaches are assumed to be units of river habitat, large enough to represent an individual home range. Habitat is homogeneous within each reach but can differ between reaches. Weirs are positioned between reaches and can be virtual connection points or represent real barriers. While water discharge is not modelled, altitude is accounted for and will influence temperature dynamics. The hydrographic network is oriented: it has one single root, which can be considered as the mouth of the river, or simply an outlet if only a part of a watershed is envisioned.

Modelling reaches. Each reach is characterised by several habitat variables informing on its surface, altitude, quality and fishing regulations (*Appendix A: Table 1*). Therefore, spatial environmental variation arises between reaches. Reach surface is calculated using reach length and mean width. Combined with

a habitat quality variable (labelled carrying factor), it determines each reach carrying capacity. Habitat quality for reproduction affects individual decisions for reproductive movement as well as female fecundity. Altitude is used to implement temperatures, with higher altitudes being associated with lower temperatures. Fishing regulations are based on various variables such as regulation in force – standard fishing or reserve mode for example – or catch size limits, which will determine the proportion and category of individuals that may be fished.

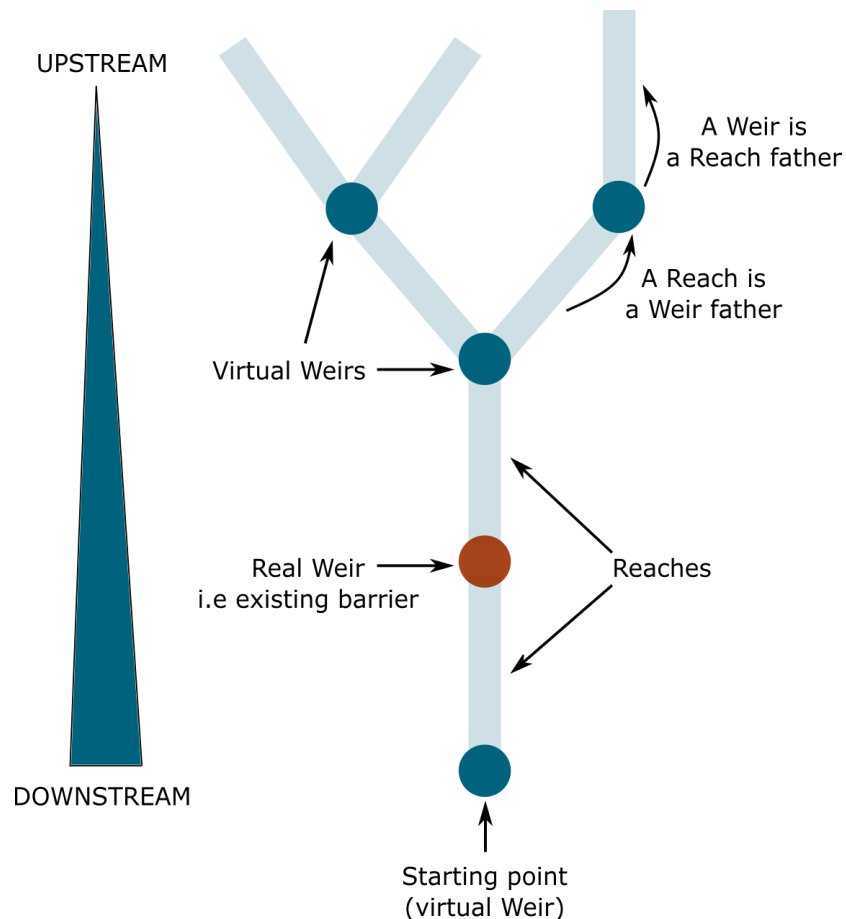


Figure 3—2: Spatial structure of a hydrographic network in MEDITERRANEA, represented by the interconnection of two objects: Reaches and Weirs, respectively representing river sections and real barriers or virtual connection points. Each object has a father object always located downstream, which is a Reach for Weirs and a Weir for Reaches. The characterisation of a network always starts from downstream and the starting point (first object) is always a Weir.

Modelling weirs. A weir is placed between each pair of reach. Each weir is characterised by the presence or absence of a fish pass and by its passability (*Appendix A: Table 2*) – difficulty for an individual to pass upstream or downstream of a weir to join an adjacent reach. When the passability is total in both directions, the weir is “virtual”, in the sense that it does not affect the simulation.

3.2.2.2 Modelling groups of individuals

As explained before, groups of individuals can be created based on a single object, for the sake of memory consumption. This is especially useful just after reproduction, thus avoiding the creation of hundreds of thousands of objects, as hundreds of thousands of eggs and fry can be produced. We named these groups “hatches”, for they represent the progeny of two parents within a nest. Hatches can be used to pool multiple individuals from egg stage to early juvenile stage, up to 8 months. After 8 months, individualised fish are created using hatches information *via* a process called individualisation (*Figure 3 – 3*).

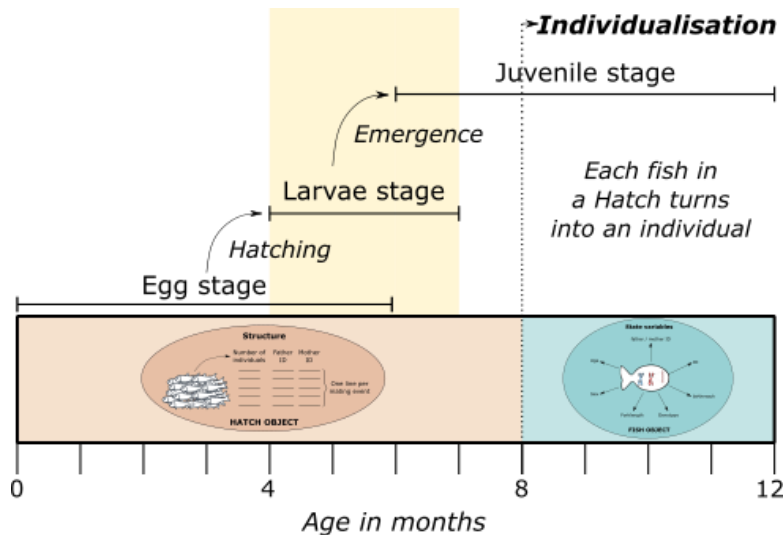


Figure 3—3: Individual life stages from egg stage up to juvenile stage and corresponding objects. Individuals are within a Hatch object for 8 months. Then they are individualised into fish objects. The timing and windows for hatching and emergence are indicated in yellow.

A hatch clusters the number of eggs created in a given reach at a given time step. One line represents one mating event – *i.e.* the mating between one male and one female – and informs on the maternal and paternal ID (Figure 3 – 4). Within hatches, individuals are sharing similar characteristics, such as age and average body size (Appendix A: Table 3). They undergo the following processes: survival, growth, ageing and ultimately individualisation. Maternal gene-by-environment selection applied at hatching is implemented using maternal ID. As long as individuals are in hatches they cannot move between reaches and do not have any genotypic information. At individualisation (Section 3.3.8), the number of juveniles left in the hatch will be turned into individualised fish and parental ID used to create their genome.

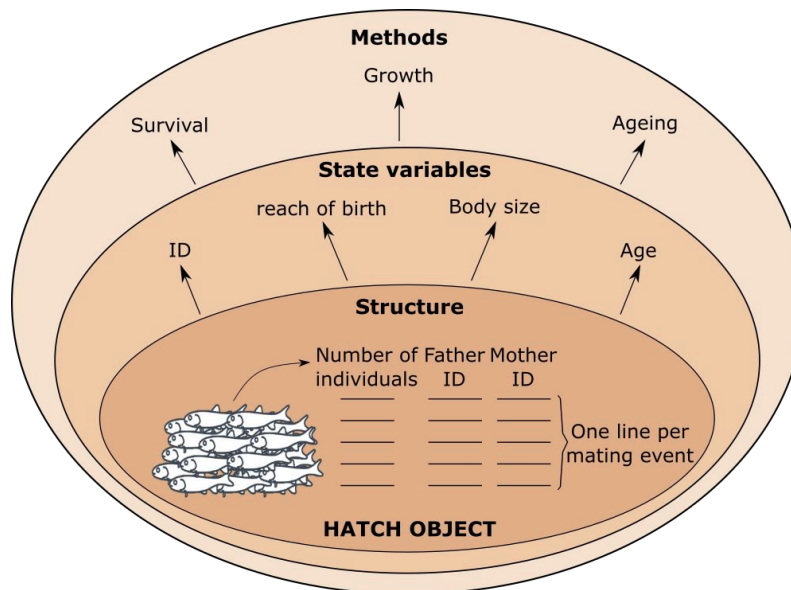


Figure 3–4: Representation of a hatch object in MEDITERRANEA – representing groups of individuals – with its main state variables and methods.

3.2.2.3 Modelling individuals

Individualised fish (Figure 3 – 5) each have their own characteristics (such as size, age and genotype Appendix A: Table 4). They undergo the following individual processes: survival, growth, movement and reproduction. Individuals are located in a specific reach at a given time step but they can move from one

Chapter 3. MEDITERRANEA: A DG-ABM to simulate the evolution of intraspecific diversity in brown trout reach to another when a passable weir connects them (movement process). They can interact with each other directly, *via* reproductive processes – including mate choice and potential male competition – or indirectly *via* a density-dependent mechanism effect on growth and survival mimicking competition. Individuals are meant to perceive environmental and phenotypic clues when making their decisions. Individual interactions and their related processes always happen within a reach.

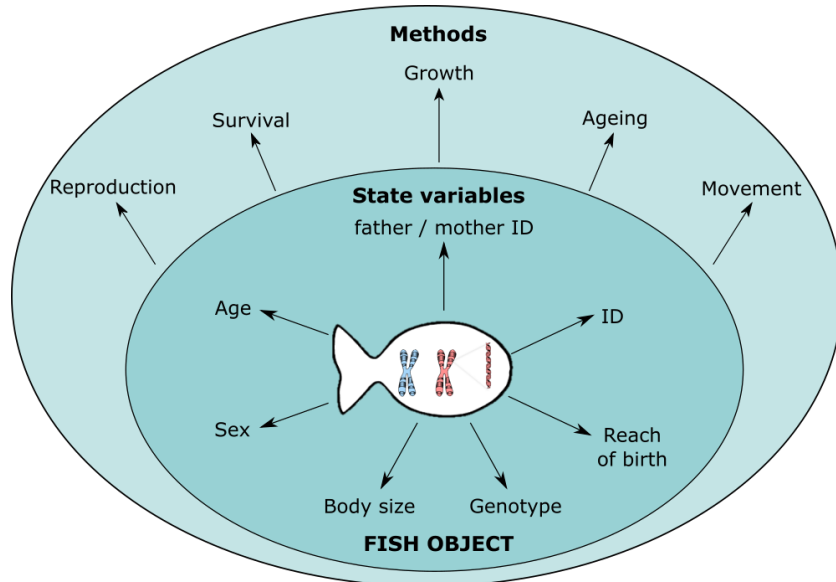


Figure 3—5: Representation of a fish object in MEDITERRANEA – representing an individual – with its main state variables and methods.

3.2.2.4 Modelling the genome structure

In MEDITERRANEA, there is only one species: *Salmo trutta fario*, hence, all individuals have the same genome structure. Individuals are diploids and possess a nuclear genome made of seven bi-allelic unlinked neutral *loci* for which each allele is related to a specific lineage. In the model, the genetic structure to differentiate alleles from each lineage is coded in a binary way with ATL alleles valued at 1 and MED ones valued at 0 (Figure 3–6). This is the lineage information transmitted to offspring, which inherit two alleles

for each *locus*: one maternally and one paternally. In the genetic structure, the first allele in a pair is inherited maternally and the second one paternally.

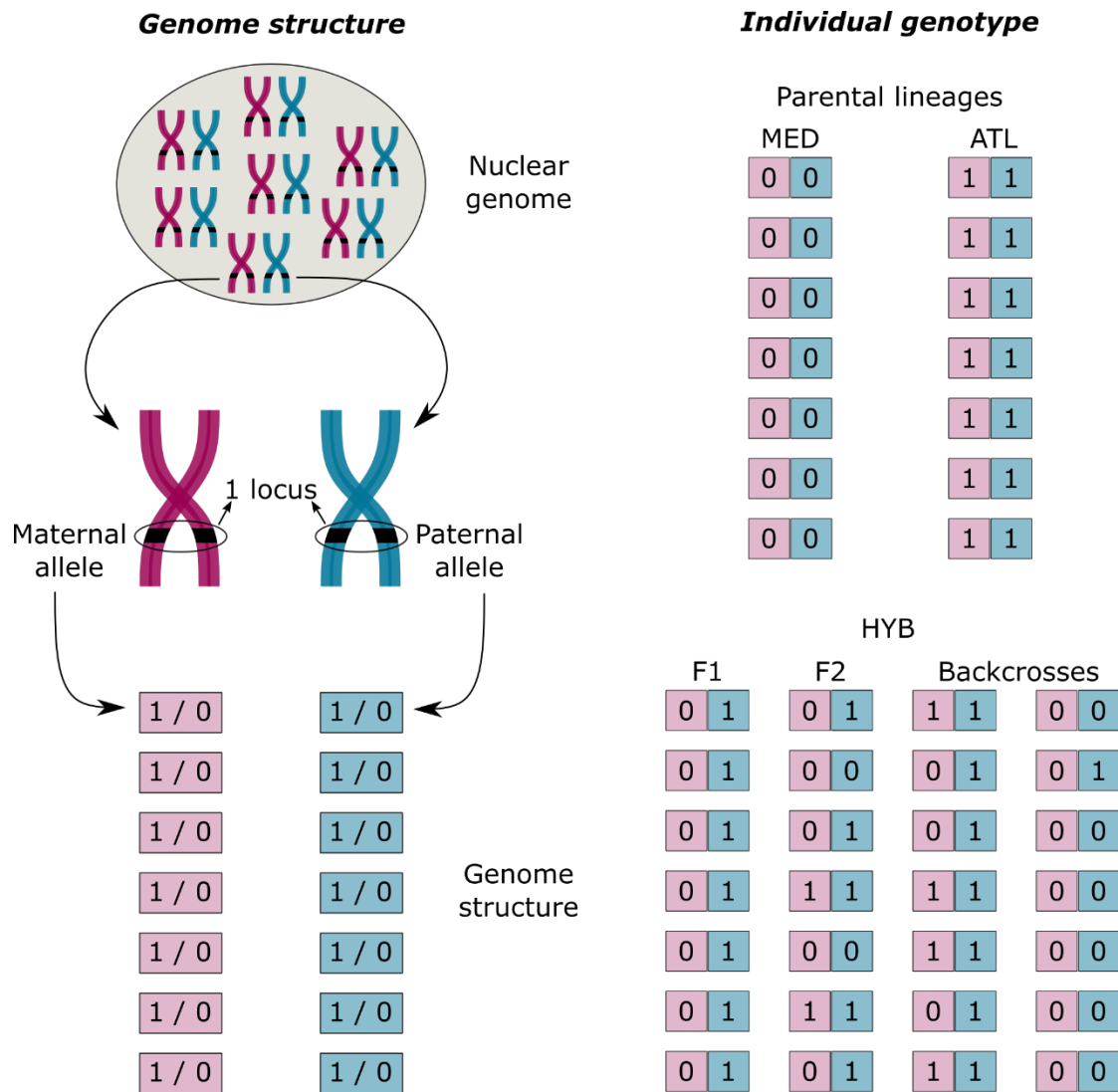


Figure 3—6: Representation of the genome structure of *Salmo trutta* and individual genotype with examples of corresponding allelic combinations. The genome structure is diploid and made of seven unlinked loci, here represented on different chromosomes. For each locus, individuals inherit an allele maternally and one paternally. For all loci, alleles are simply coded in a binary way: 0 to represent the MED lineage and 1 to represent the ATL lineage.

These 14 alleles constitute our genetic map and are used to calculate individual introgression. Individual introgression refers to the introgression – or takeover – of MED alleles by ATL alleles within an individual genome. This choice of genetic structure is based on the use by managers of seven known single nucleotide polymorphism (SNP) and microsatellites *loci* perfectly differentiating the ATL lineage from the MED lineage (Gharbi et al., 2006; Guyomard & Caudron, 2008). Allelic effects are equal and additive within and between *loci*, *i.e.* dominance effects are not considered. Recombination is maximal and *loci* are hypothesised to belong to separate chromosomes. Therefore the value of the resulting trait, here individual introgression, corresponds to the mean of allelic values (1 or 0) at all *loci*. The value of this trait can be used to infer a genotypic category - what I will sometimes refer to as individual genotype: MED when individual introgression is 0, *i.e.* all 14 allelic values are 0 (MED allele); ATL when individual introgression is 1, *i.e.* all 14 allelic values are 1 (ATL allele); HYB for all other intermediate scores of individual introgression, *i.e.* presence of both MED and ATL alleles (*Figure 3 – 6*). This simplification is meant to compare most of our results to results obtained by managers.

3.2.3 Process overview and scheduling (*Figure 3 – 7*)

During population dynamics, processes affecting habitat, individuals and groups of individuals are called. Habitat and time are first updated. The population dynamics then start. Individuals and groups of individuals undergo development, ageing and survival, which rates vary depending on life stages (egg, larvae, juveniles, sub-adults and adults). Development and ageing make individuals go from one life stage to another (*Figure 3 – 8*). During the early phases of life, development is temperature-dependent (Killeen et al., 1999) and involves hatching (eggs to larvae) and emergence (larvae to juveniles). To account for reproductive isolation barriers, a post-zygotic survival rate may be applied at hatching to implement

maternal genotype-by-temperature (referred to as GxE) interactions on embryonic survival (Folio et al., 2021). Processes happening from egg to juvenile stages are affecting hatches.

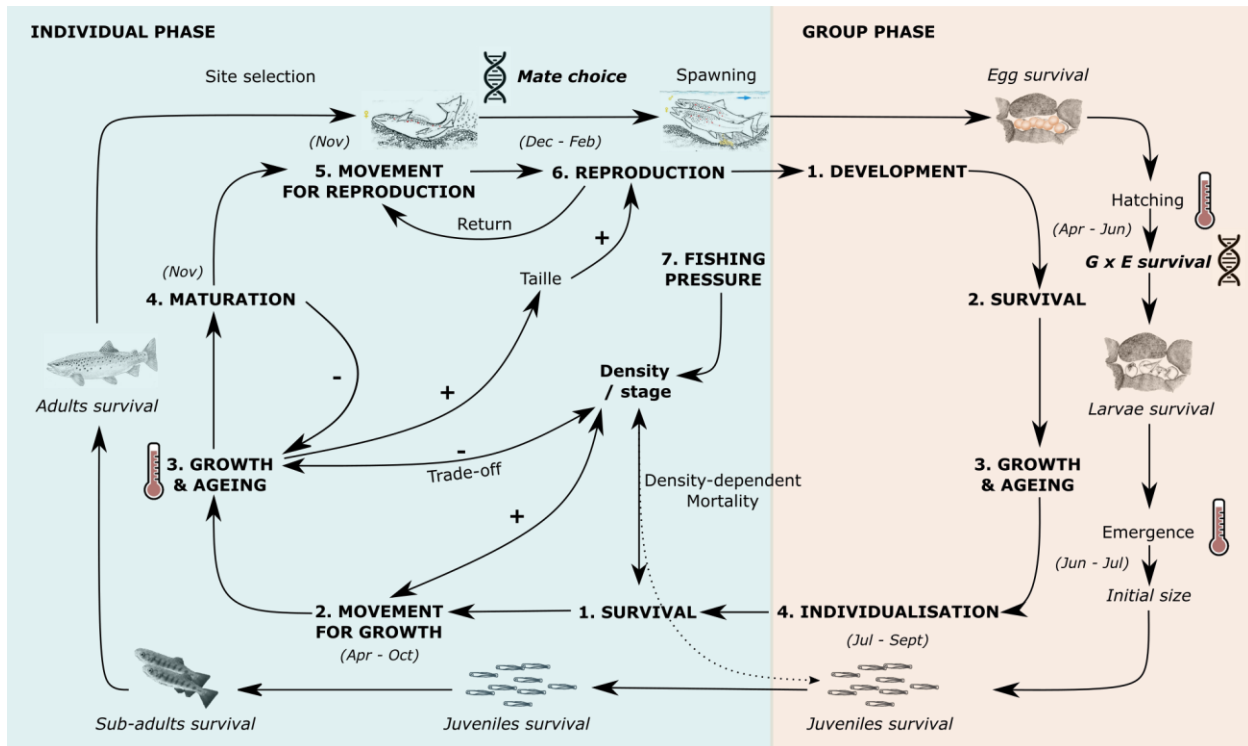


Figure 3—7: Process overview and scheduling. Population dynamics is split into two parts: the individual phase and the group phase. Orders and interactions between processes, as well as potential genetic or phenotypic and temperature effects, are represented.

After 8 months, the individualisation process happens and individuals are created using hatches information. This process happens only once per hatch, and then the hatch disappears. After survival is applied to individualised fish, the movement process happens for the growth period. Individuals decide to move from one reach to another, or not, based on experienced density. Following the movement process, density-dependence growth and ageing happen. Individual body size and age are updated. In

November, the maturation process takes place. Following maturation, individuals engage in the movement process for reproduction, which happens in two main steps. First, individuals decide to move or stay in their current reach for reproduction. Then, those who decided to move choose between upstream movement – a decision that can be made based on habitat quality for reproduction – and “homing”, *i.e.* movement toward their birth reach. From December to February – *i.e.* during mating season – individuals go through reproductive processes, involving individual sampling, sexual selection and fertilisation after a female has accepted to mate with a male. To consider potential pre-zygotic reproductive barriers (Gil et al., 2015), multiple options of mate choice, such as phenotypic-based female preference or male competition can be chosen from during model initialisation. When reproduction is over, individuals who moved try to return to their last known growth reach. Following reproduction, new hatches are created. At the end, individuals will go through a fishing process, but not individually. The fishing method will randomly draw out a given proportion of individuals that fit fishing regulation input.

3.2.4 Model stochasticity

Since it is an agent-based model, most processes in MEDITERRANEA are inherently stochastic. Indeed, processes such as survival or movement for example involve a part of randomness as they depend upon the realisation of a Bernoulli random draw with a given probability. Random inter-individual interactions are also a source of stochasticity that will influence reproduction. Indeed males are randomly sampled to constitute a female available mating pool. Mate choice is then also a probabilistic function based on females acceptance to mate with a given male through her expressed preference. From its stochastic nature, the model will generate variability among simulations.

3.3 SUB-MODELS: DETAILED PROCESSES

3.3.1 Development and ageing

Individuals or groups of individuals will develop and age, going from one life stage to the other based on temperature or age thresholds (*Figure 3–8*). Age is counted in months since the model runs on a monthly time step. Eggs become larvae after hatching and larvae become juveniles following emergence, based on temperature. At 12 months, juveniles become sub-adults, and at 24 months, sub-adults become adults. Survival and growth processes will vary based on individual stages.

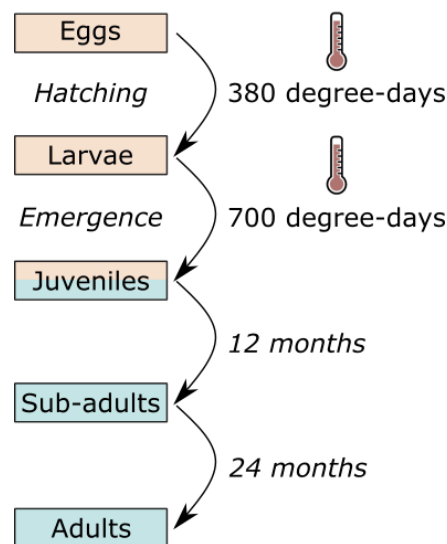


Figure 3–8: Development and ageing threshold to go from one life stage to another. Under-gravel development is based on temperature and post-emergence development on age in months. Hatches are represented in light orange and individuals in light blue.

Embryonic development. Hatches, created after reproduction, are initially at egg stage. They will then undergo hatching and emergence processes, to become larvae and then juveniles, based on an environmental clue: accumulated temperature. Accumulated temperature is calculated at each time step since the creation date (*i.e.* birth) of each hatch and corresponds to the sum of monthly accumulated

Chapter 3. MEDITERRANEA: A DG-ABM to simulate the evolution of intraspecific diversity in brown trout temperature (in degree-days) experienced within a reach over a given number of months, up until the current time step (*Figure 3 – 9*).

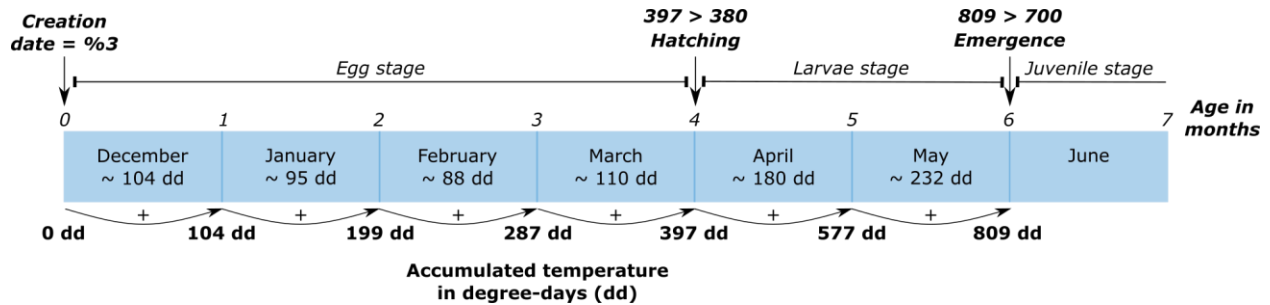


Figure 3—9: Accumulated winter temperature (in degree-day) and resulting hatching and emergence time for a given hatch created in December ($t = \%3$). Monthly cumulated temperatures are indicated and summed up until emergence has happened.

The accumulated temperature required for eggs to hatch is approximately 400 degree days and emergence usually happens after around 720 accumulated degree days (Killeen et al., 1999). As processes happen monthly in the model, hatching and emergence will only happen when monthly and not daily accumulated temperature will be above this threshold. This means that some individuals, meant to hatch midway through a month, will only hatch the following month. Therefore, as we assume that all individuals will be hatching at the beginning of a given month, we set our threshold slightly lower at respectively 380 and 700 degree-days.

3.3.2 Survival

Survival happens monthly and is stage-dependent. The survival rate is calculated as follows for each stage:

$$Survival\ rate_{stage} = \frac{e^{Coef_{Stage}}}{(1 + e^{Coef_{Stage}})} * DE_{stage} \quad (Equation\ 3 - 1)$$

Survival rate is the individual survival applied monthly for each stage. It is based on a stage-dependent survival coefficient (*Coefstage*), which has been parameterised based on survival data on brown trout populations located in the Mediterranean area (Data from Scimabio Interface). The survival rate is counter-balanced by density-dependent (*DE*) mortality (Elliott, 1994) to mimic competition and control for maximum carrying capacity. *DE* is stage-dependent, as we hypothesised that competition mainly happens between individuals of the same stage and not among stages, as they are often found in different types of habitats (Kaspersson et al., 2012).

For under-gravel survival, *i.e.* egg and larvae stage, *DE* values 1 as we hypothesised that survival at those stages is not impacted by competition and resulting density-dependent mortality.

For post-emergence stages, *i.e.* juveniles, sub-adults and adults, *DE* is expressed as follows:

$$DE_{stage,reach} = \frac{1}{(1 + \frac{Density_{stage,reach}}{KmaxE \times carrying\ factor_{reach}})} \quad (Equation\ 3 - 2)$$

For each stage, depending on the density experienced within a reach, *DE* will act as a more or less strong brake on survival. Density is calculated at each time step, per reach and stage, and is expressed in individuals per metre square (ind.m⁻²). *KmaxE* is a survival parameter that allows the user to manage maximum carrying capacity within the hydrographic network. The default parameter is 2, which equals approximately 3500 ind.ha⁻¹. It has to be informed during model initialisation and bespoke to each population, using the user interface. Indeed, exact densities matching this parameter will be highly network-dependent as individual movement – which itself depends on weirs – can influence densities.

The following figure (3 – 10) indicates densities reached at demographic equilibrium as a function of *KMaxE* in a simple hydrographic network made of only one reach.

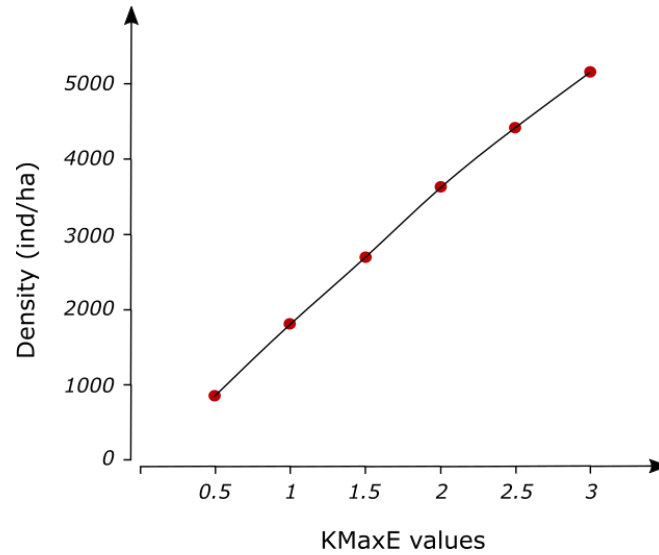


Figure 3—10: Observed densities at demographic equilibrium in a simple hydrographic network (a single reach of a hectare) for various values of K_{maxE} .

Note that this density-dependent effect can be different between reaches. Indeed, *carrying factor* is a reach variable that indicates habitat quality for resources. By multiplying K_{maxE} , it allows to set a specific maximum carrying capacity for each reach. *Carrying factor* can be modulated using a scale parameter, wherein 0 implies, a bad habitat hence null carrying capacity, and 1 implies a very good habitat hence maximum carrying capacity. A value of 0.5 means that density is that reach will only reach half of the maximum carrying capacity allowed in the hydrographic network.

Post-zygotic isolation. In addition to the above-described mortality process, extra mortality can be simulated to recreate known post-zygotic isolation mechanisms, as I described in the previous chapter (Section 2.4.2) and a published manuscript (Folio et al., 2021). This recreates the interactive effect of maternal genotype x temperature on embryonic survival, *i.e.* egg stage survival from birth to hatching. It is applied once to hatches at hatching time – when its accumulated temperature is above 380 degree-days. It is expressed as follows:

$$Post - zygotic\ survival\ rate = \frac{e^{PostZygotic\ Coef}}{(1 + (e^{PostZygotic\ Coef}))} \quad (Equation\ 3 - 3)$$

$$PostZygotic\ Coef = \beta + \alpha * winterT^{\circ} + (maternal\ Introgression - 0.5) * (\delta + \gamma * winterT^{\circ}) \quad (Equation\ 3 - 4)$$

Where β , α , δ and γ are the equation parameters informed in a logit scale. In the user interface, a pre-set button exists to directly set the values found in Folio et al., 2021 for post-zygotic isolation. The following figures show the effect that each parameter has on offspring survival rate.

β is the slope intercept. Its default value is that of egg stage survival coefficient.

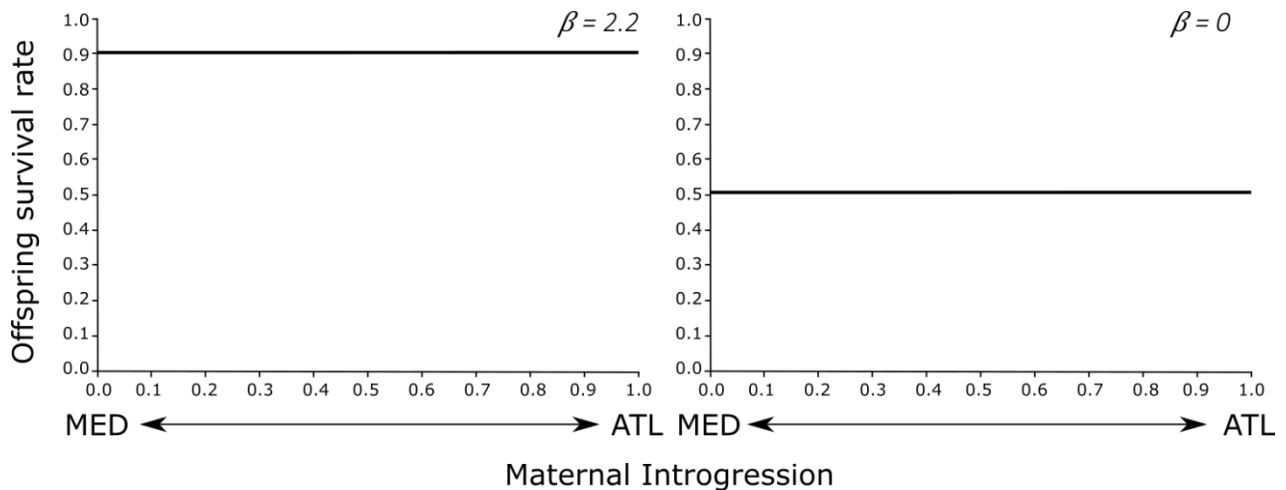


Figure 3—11: Effect of slope on post-zygotic embryonic survival.

α is the parameter used to adjust the effect of mean winter temperature ($winterT^{\circ}$) on survival. Positive values will make this survival coefficient increase with temperature.

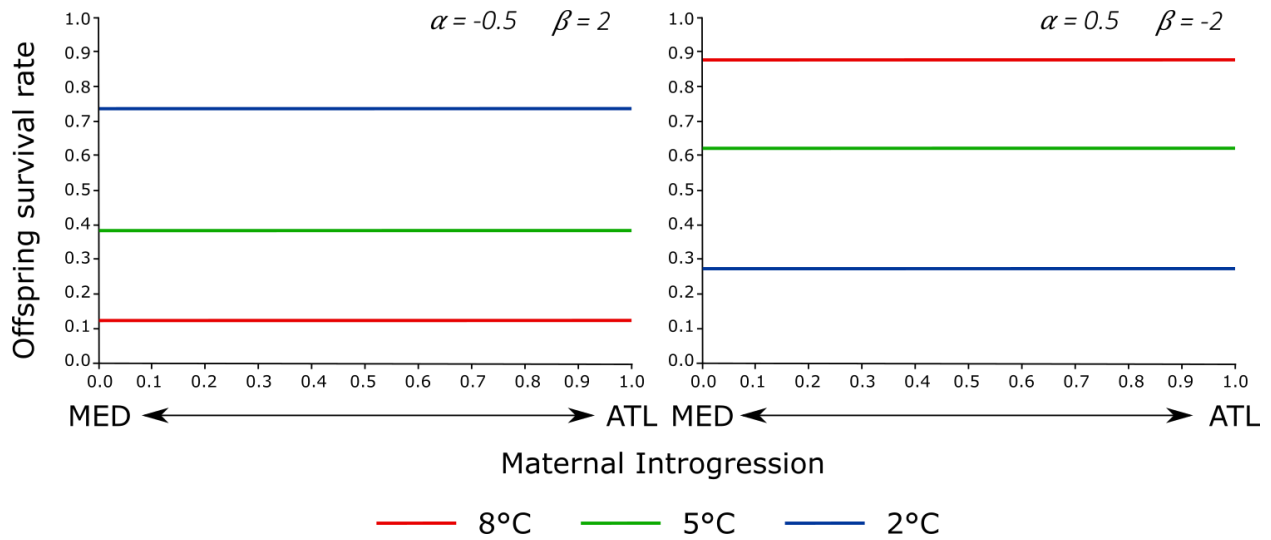


Figure 3—12: Mean winter temperature effect on post-zygotic embryonic survival. Positive or negative values of α and β can be used to determine the relationship (positive or negative) between temperature and embryonic survival.

δ is the parameter used to set the effect of maternal genotype, in order to favour offspring survival of one or the other maternal lineage.

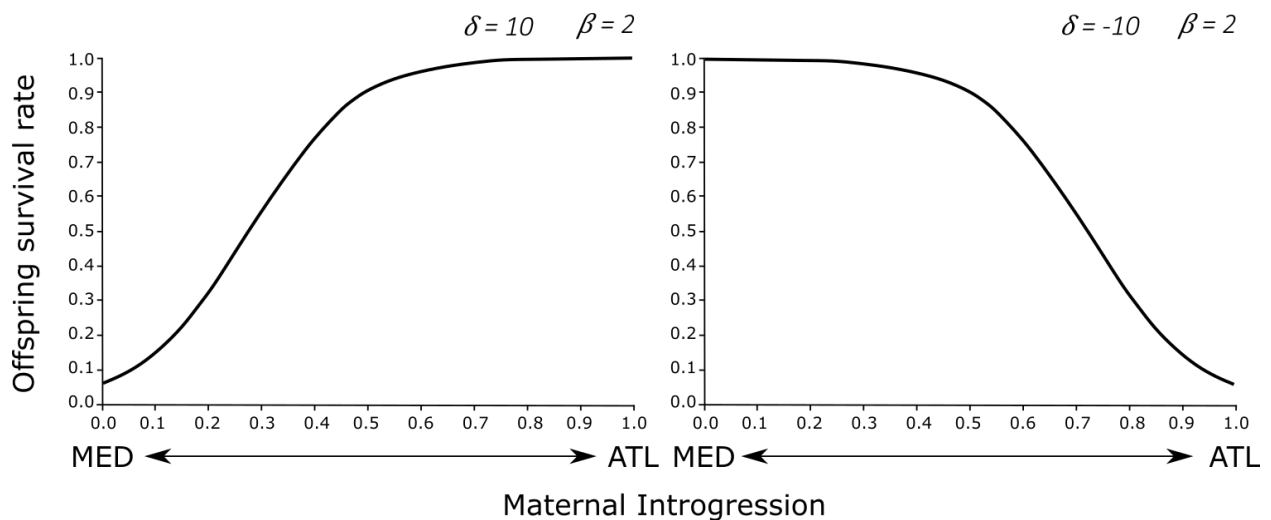


Figure 3—13: Maternal introgression (genotype) effect on post-zygotic embryonic survival. Negative values give an advantage to the MED lineage while positive values favour the ATL lineage.

γ is the interaction parameter between maternal genotype and mean winter temperature. It can be adjusted to favour one lineage in some given temperature conditions and the other in different ones.

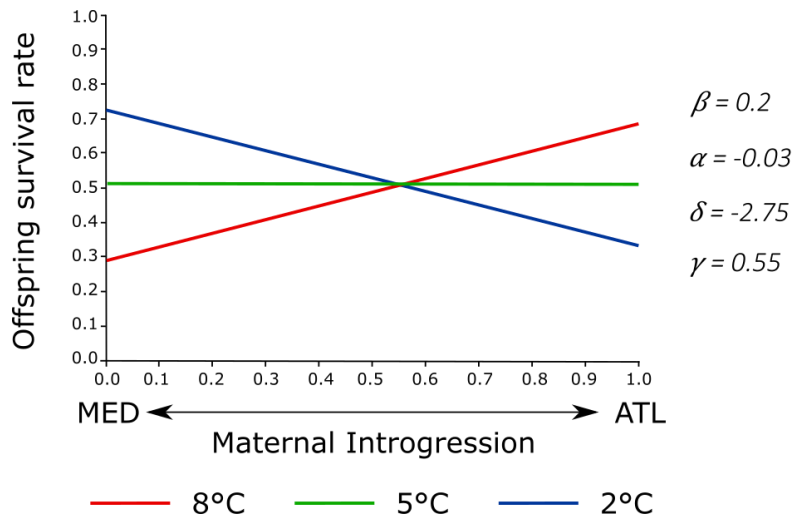


Figure 3—14: Effect of a maternal gene by temperature interaction on embryonic survival. This combination of values allows the user to give an advantage to the MED lineage in colder winter temperatures and to the ATL lineage in warmer winter temperatures.

3.3.3 Growth

From emergence, individuals go through the growth process to update their body size, *i.e.* defined as the fork length of a fish. Individual growth is based on a modified von Bertalanffy function (von Bertalanffy, 1938). In the model, the growth parameter k dictates the size-at-age relationship based on various factors. Indeed, this parameter depends on experienced temperature, density and maturation since temperature influences individual growth (Elliott et al., 1995; Forseth et al., 2009; Forseth & Jonsson, 1994; Richard et al., 2015) and in order to account for the trade-off between density-dependence and growth (Lobon-Cervia, 2007; Lorenzen & Enberg, 2002; Richard et al., 2015), as well as that between reproduction and growth (Berg & Fleming, 2017). Each month, individuals' body size is updated as follows:

$$Body\ size = body\ size + body\ size * k * \left(1 - \frac{body\ size}{maximum\ body\ size}\right) \quad (Equation\ 3 - 5)$$

Maximum body size is set by the user and represents the size towards which individual body size will tend.

The growth parameter k is expressed as follows:

$$k = base * growthDE * ME * e^{-\frac{(optimalTemp-temp)^2}{2*tempAmpE^2}} \quad (Equation\ 3 - 6)$$

Where, $base$ is the equation slope, a very sensitive parameter that allows accelerating or slowing down growth. This parameter should be set within [0.22-0.25] to have a classic and realistic growth. The higher the parameter, the faster the growth.

To account for density-dependent growth, $growthDE$ is expressed as a negative exponential function that takes a density effect parameter (a) multiplied by current density. $growthDE$ is stage-dependent.

$$growthDE_{stage} = e^{(-a_{stage} * density_{stage})} \quad (Equation\ 3 - 7)$$

The density effect parameter (a) was calibrated based on observed patterns of body size distribution as a function of density obtained by electric fishing (Data from Scimabio Interface). The higher a is the stronger the effect of density on growth will be. Its variation range is [0-2] with 2 being a high value that may not be biologically realistic. No density-dependent effect is accounted for when $a = 0$, hence growth is maximal. When a increases, growth decreases. For a given density of 1 ind.m⁻², individuals achieve approximately 10% of their maximal growth when $a = 2$ ($growthDE = 0.13$); 50% when $a = 0.7$ ($growthDE = 0.5$) and 64% when $a = 0.45$.

A maturation effect parameter (ME) is used to model the trade-off between growth and reproduction. It is a rate [0-1] that simply decreases the growth of mature individuals as they are now investing in reproduction. For non-mature individuals, this parameter is set at 1. For mature individuals, this

parameter was calibrated so that the growth curve fit the observed difference of size-at-age between 1+ and 2+ individuals (Data Scimabio Interface). Its default value is 0.7, hence I hypothesised that individuals now invest 30% of their resources in reproduction. In the model, I also consider that this energy allocation is similar between individuals – more specifically, it does not vary based on sex or individual genotype since there is no evidence of different allocation strategies.

The temperature effect is calculated based on experienced water temperature (*temp*), a parameter indicating optimal temperature for growth (*optimalTemp*) – estimated around 15°C for brown trout in summer (Elliott et al., 1995; Forseth et al., 2009; Forseth & Jonsson, 1994) and a curve amplitude parameter (*tempAmpE*). Growth will progressively decrease symmetrically around the optimum when temperature increases or decreases based on the curve amplitude.

The evolution of size-at-age (Figure 3 – 15) can be visualised in the user interface when setting growth parameters, as a function of altitude – and hence temperature – and density.

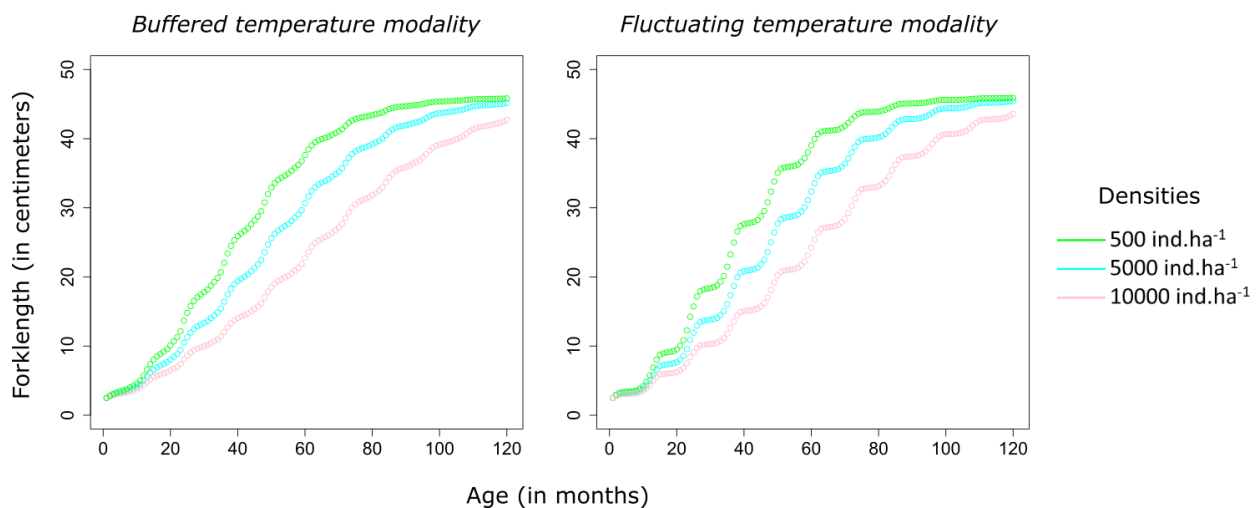


Figure 3—15: Evolution of size-at-age trajectory using MEDITERRANEA default settings for three scenarios of densities (500, 5000, 10000 ind.ha⁻¹) and two different temperature models: a buffered modality with yearly temperatures ranging from 8 to 12°C and a fluctuating modality with yearly temperatures ranging from 5 to 16°C.

3.3.4 Movement

Movement during the growth period. During the growth phase, individuals can move among reaches for growth purposes. Movement decision is based on a movement threshold probability θ , calculated using a given movement probability and two environmental cues: experienced density and reach maximum carrying capacity.

$$\theta_{stage,reach} = \frac{Density_{stage,reach} * Movement\ proba}{Maximum\ density * carrying\ factor_{reach}} \quad (Equation\ 3 - 8)$$

Movement probability is the maximum value θ can take. It is low in our settings (0.2) as reaches are big enough to cover individuals' home range. Since θ is density-dependent, it varies among individuals of different stages (juveniles, sub-adults, adults) and belonging to different reaches. Reach maximum carrying capacity is determined using the *maximum density* allowed in the river – informed by the user – multiplied by the reach *carrying factor*, a variable that informs on habitat quality for resources. *Density, per stage and reach*, is calculated by the model at each time step.

Individuals are more likely to decide on moving if density, and hence competition, is too high in their current reach. Individuals who decided to move then have a choice between upstream or downstream movement. This choice is made based on a given probability to move downstream, informed during initialisation. Individuals then try to move in their given direction. Movement can only be done one reach at a time. Chances of success depend on habitat variables. If no reach is available, movement fails. If a reach is available, then weir passability is assessed. If it is fully passable, movement succeeds and the individual changes reach. If the weir is partially passable, movement success is proportional to weir passability. Therefore, some individuals may pass while others will not. If an unpassable barrier exists, movement fails (*Figure 3 – 16*).

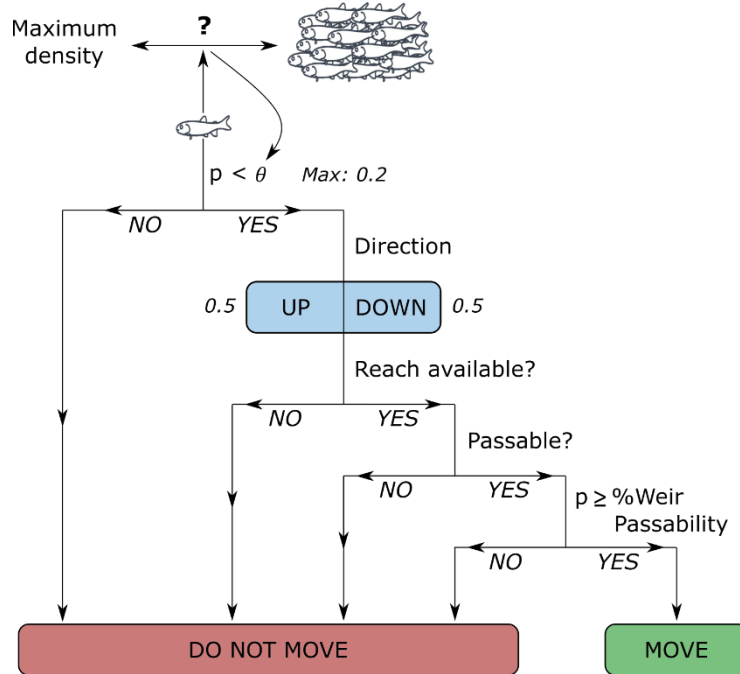


Figure 3—16: Diagram of individuals' movement decisions during the growth period. To determine movement, individuals undergo two sequential choices: moving or not, and movement direction (up or down). Their chances of moving are then determined by habitat variables: availability of a reach and passability of the connecting weir.

Movement during the reproductive period. In November (time step = 2), just before the reproductive season, individuals' movement for reproduction happens for individuals whose age is > 15 months, as 16 months is the minimum age for early maturation. Movement happens in two main steps. First, the decision for movement is made based on a certain movement probability threshold, specific to the spawning season. Individuals who decide to move will choose between "homing" and upward migration based on a given probability of "homing" (Figure 3 – 17).

☞ **"Homing".** Individuals attempting homing try to go back to their reach of birth for reproduction. They first assess the most direct path from their current reach to their reach of birth. Then they try to move toward their birth reach following that path. A method checking if

the individual can pass weirs or not will determine where the individual final destination for reproduction is: his reach of birth in case of success or another reach in case of failure on one weir.

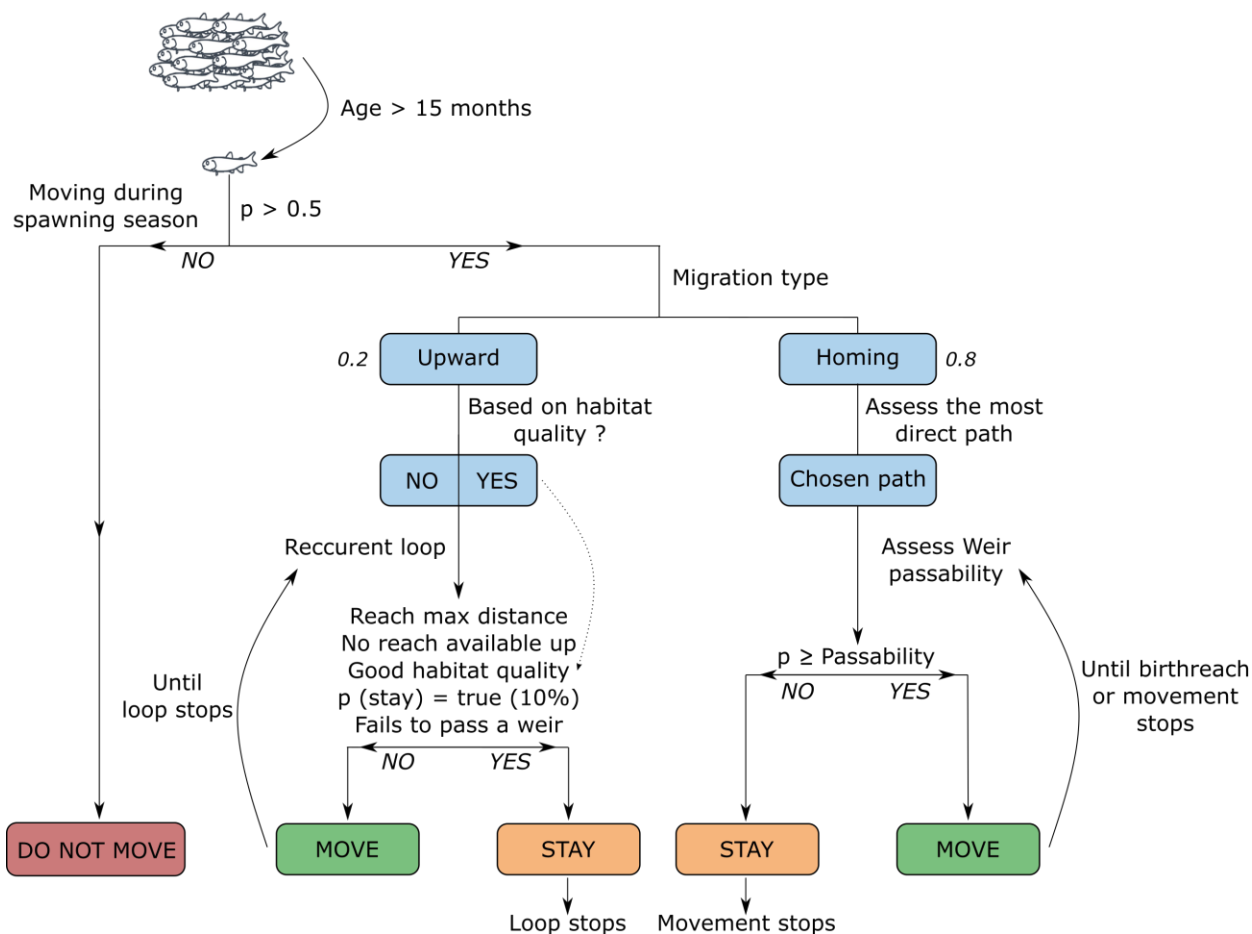


Figure 3—17: Diagram representing movement choices faced by individuals during reproduction. To determine if movement happens, individuals undergo two sequential choices: moving or not and the type of movement (upward or homing). Based on their choice their chances of moving are then subject to other conditions.

☞ **Upward Migration.** Individuals who do not perform homing try to move upstream. The process is a recurrent function assessing movement feasibility sequentially and one reach at a time. Movement stops when individuals have managed to migrate their maximum allowed

distance – set by the user, reached the most upward part of the river (no reach available to go to), drawn a probability to stay (10% chances), or failed to pass a weir. When an individual manages to pass a weir, he will update his maximum distance left (-1) and the loop continues. Upward migration can also depend on habitat quality for reproduction – user setting – as fish may choose their spawning ground, based on substrate type and availability for example (Heggenes, 1988). If so, individuals decide to stay in their current reach for reproduction when habitat quality for reproduction is above a certain threshold. Otherwise, he continues moving.

Returning. Individuals, who migrated, try to return to their last known growth reach after reproduction. For that, they will move one reach at a time and undergo the same movement process described in upward migration. Depending on weirs passability they may or may not reach their target reach.

3.3.5 Maturation

In our model, individuals may undergo sexual maturation, meaning that they will be able to participate in reproduction. More precisely, their probability to mature is age and sex-dependent (*Table 3 – 1*). Older individuals have higher chances to mature. Males have higher chances to mature at an early age compared to females. These rules were established to recreate observed patterns in maturation for Mediterranean populations of brown trout (Scimabio Interface, Com. Pers.). In the model, this process happens in November, just before the beginning of reproduction. Note that once an individual has been deemed eligible for maturation, he will mature every year.

Table 3 – 1: Maturation thresholds probabilities for males and females of various age classes.

Males		Females	
Age (> to in months)	Maturation threshold probability	Age (> to in months)	Maturation threshold probability
51	100%	51	100%
39	98%	39	90%
27	90%	27	40%
15	45%	15	4%

3.3.6 Reproduction

The reproductive season starts in December and is spread over 3 months (Gil et al., 2015; Labonne et al., 2009). Reproduction happens between individuals within the same reach. A mating pool is created within each reach and constituted by available mature males and females – *i.e.* which still have mating opportunities left. In the model, males can mate up to 10 times per season, whereas females can only mate up to twice. Reproductive processes happen as follows: individuals are sampled from the reach mating pool, male competition and female preference will guide mate choice, and ultimately fertilisation happens (*Figure 3 – 18*). This represents one mating event in the model. It will happen each month during the reproductive season up to twice if mature females are still available.

Individuals sampling. All available and mature females undergo mating event processes, but not all males do. Indeed, each female is presented successively with a few males randomly sampled from the reach mating pool. The number of males sampled per female is drawn from a Poisson distribution with a mean rate determined by an OSR value informed by the user. This value is set at four, meaning that a female mating pool is on average formed by four males. Females can only mate with one male during one mating event; hence, multiple mating is not simulated. Therefore, when a female accepts to mate with a

male, she stops assessing potential other males available in her mating pool. This male will father all offspring created during this mating event. If a female refuses to mate with any of the sampled males, she will not reproduce during this mating event.

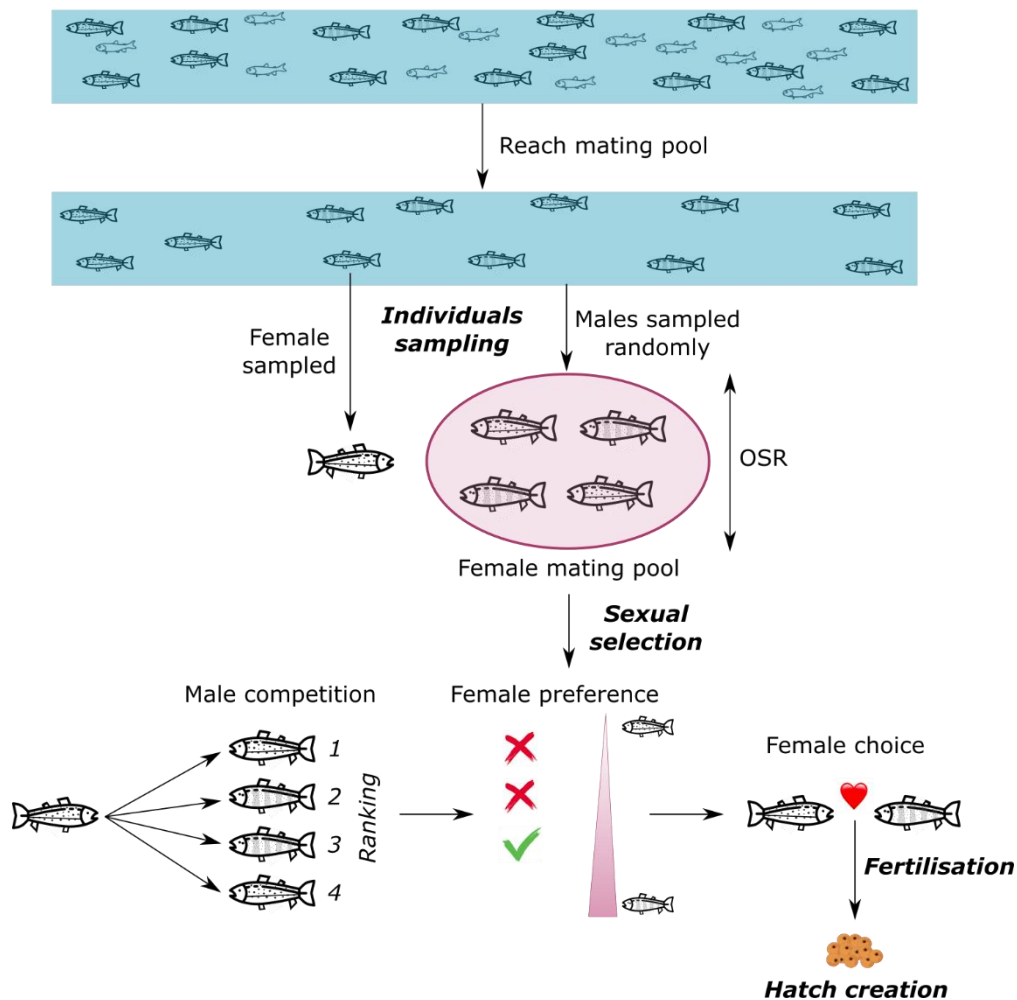


Figure 3—18: Representation of the reproductive processes implemented in MEDITERRANEA, including individual sampling, sexual selection, fertilisation and hatch creation.

Sexual selection. Male competition determines the order in which males are displayed to females. Female preference guides females' decision to mate with a given male.

☞ **Male Competition.** During the male competition process, males within a female mating pool are ranked based on the competition mechanisms enforced in the model, which can favour individuals based on their individual introgression. The process simply consists in presenting males in a given order of introgression to females, so that more competitive ones try to mate first. If no competition is enforced, then the setting “equal” is used and the ranking process is random. Male competition can either favour lower (MED) or higher (ATL) introgressed individuals.

☞ **Female Preference.** This process allows for the implementation of a demonstrated lineage-based behavioural difference involved in pre-zygotic reproductive isolation: female preference for phenotypic dissimilarity (Gil et al., 2015). In this process, multiple systems can be implemented, with female preference expressed based on male phenotype and female genotype³.

Female preference can be absolute or relative. Absolute preference is when the female preference function is scaled to the maximum possible range of variation for male phenotype, whatever the male phenotypic variation she has access to. Relative preference is when the female preference function is scaled on the accessible range of male phenotypic variation for the female. In that case, the range is calculated using the phenotypic variation sampled during the above-mentioned process to reflect the actual OSR available to females. Note that the first option implies that female preference is context-independent, and the female will not discriminate strongly between two close phenotypes. The second option is extremely context-dependent: if a female meets only two males and they have a very close phenotype, she will nevertheless discriminate among them very efficiently.

³ We implemented a relation based on the genotype of the female. In reality, the relation is between both male and female phenotypes.

For absolute preference, *male phenotype* is equal to males' individual introgression while for relative preference, *male phenotype* depends on the minimum and maximum introgression value (*Min* and *Max*, Equation 3 – 9) observed in a female mating pool.

$$\text{Male phenotype} = \frac{\text{Male Individual Introgression} - \text{Min}}{\text{Max} - \text{Min}} \quad (\text{Equation 3 – 9})$$

Three preference models are proposed in MEDITERRANEA:

☞ **Non-genetic preference** (Figure 3 – 19, Equation 3 – 10): Preference is universal when all females express the same preference, independent of their own genotype. It is directed toward either MED or ATL male phenotype.

$$\text{Non – genetic preference} = \text{Intercept} + \text{Slope} * \text{Male phenotype} \quad (\text{Equation 3 – 10})$$

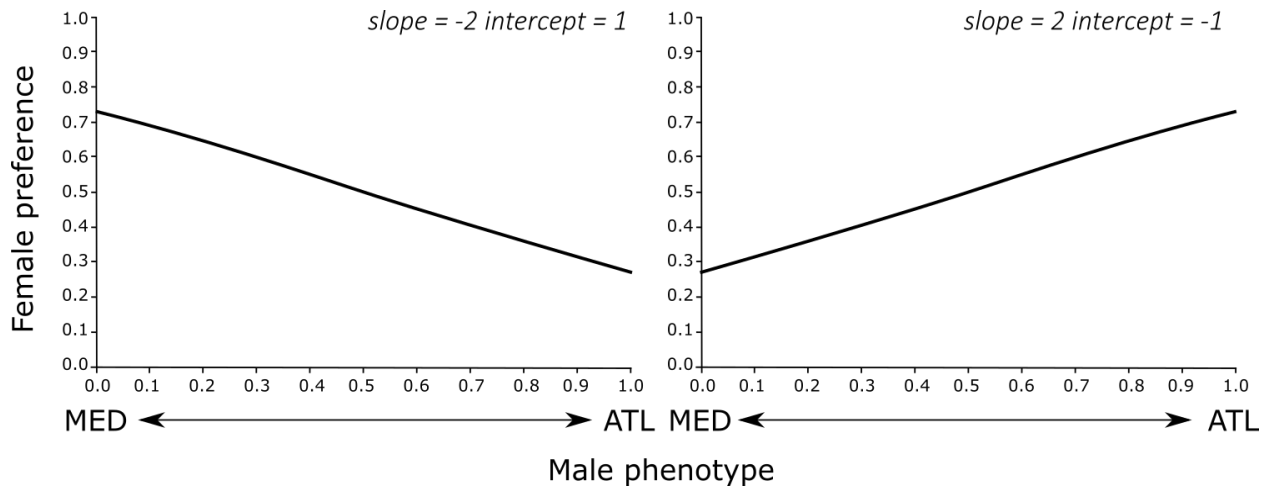


Figure 3—19: Representation of non-genetic preference with all females expressing a preference for either MED (left) or ATL (right) males.

☞ **Genetic dependent preference** (Figure 3 – 20, Equation 3 – 11): Preference is expressed as a function of female individual introgression. It can be set in two ways: (i) preference is positively correlated with female introgression – the ATL lineage is, therefore, more selective – or (ii) preference is negatively correlated with female introgression – the MED lineage is, therefore, more selective. In any case, HYB females express an intermediate preference. Preference is then directed toward MED or ATL male phenotype.

$$\text{Genetic preference} = \text{Intercept} + \text{Slope} * \text{Female genotype} * \text{Male phenotype}$$

(Equation 3 – 11)

Female genotype is expressed differently based on which lineage is more selective.

Female genotype = 1 – Female Individual Introgression when the MED lineage is selective.

Female genotype = Female Individual Introgression when the ATL lineage is selective.

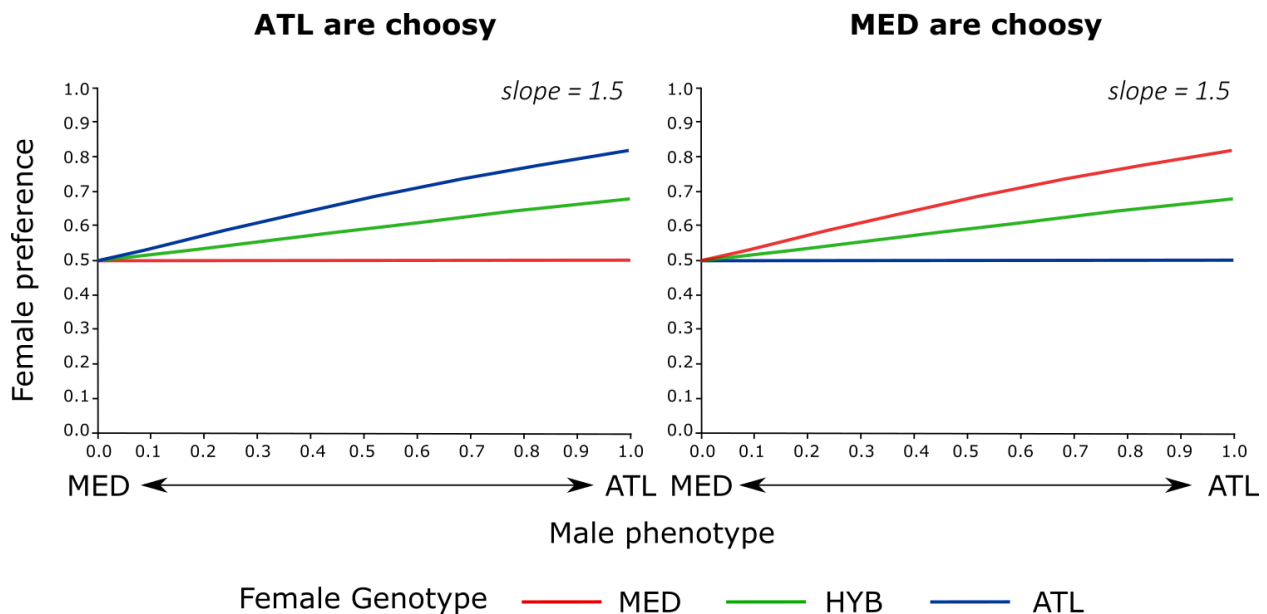


Figure 3–20: Representation of genetic dependent preference. On the left, ATL females express a preference for ATL males, while HYB females express an intermediate preference and MED females are not choosy. On the right, it is the opposite, MED females express a preference for ATL males.

☞ **Homo/heterogamous preference** (Figure 3 – 21, Equation 3 – 12): Preference is respectively expressed for phenotypic similarity or dissimilarity. Hence, preference depends on both, female genotype and male phenotype, and a dissimilarity value is calculated.

$$\text{Homo/heterogamous preference} = \text{Intercept} + \text{Slope} * \text{Dissimilarity value} \quad (\text{Equation 3 – 12})$$

With

$$\text{Dissimilarity value} = |\text{Male Individual Introgression} - \text{Female Individual Introgression}| \quad (\text{Equation 3 – 13})$$

For relative preference, the minimum and maximum dissimilarity values observed in a female mating pool are (*Min* and *Max*) used to calculate a relative dissimilarity value for each male:

$$\frac{|\text{(Male Individual Introgression} - \text{Female Individual Introgression)} - \text{Min}|}{(\text{Max} - \text{Min})} \quad (\text{Equation 3 – 14})$$

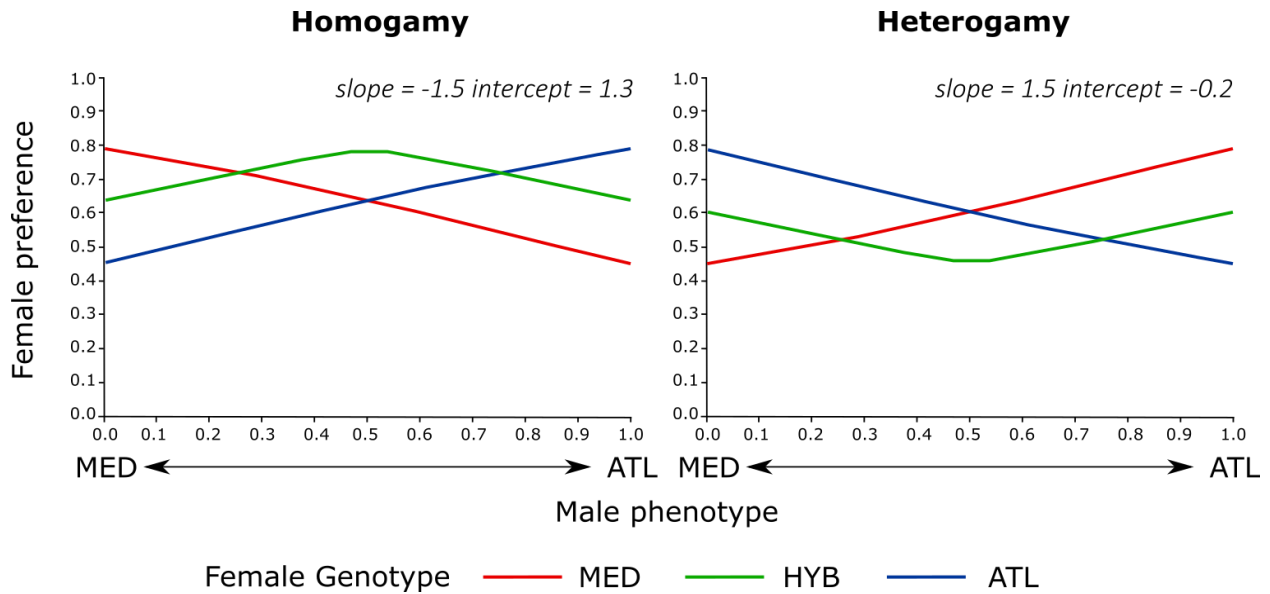


Figure 3—21: Representation of homogamous (left) and heterogamous (right) preferences.

In each model, female preference is always based on male phenotype. The slope of the curve represents the strength of the preference while the intercept could be seen as female choosiness.

Genetic contribution to preference (GCP). In the model, individuals are characterised by genotypic information: individual introgression but phenotypes – based on robe *criteria* – are not implemented. Hence to translate female preference, expressed on phenotype in nature, a coefficient (*GCP*) is used to determine how much of the mating preference is based on individual introgression and will fit the implemented preference curve (based on phenotype). The rest of the mating stays random, with a probability *q* of the mating preference following uniform law probability. This is to account for errors while assessing genotype based on phenotype. Indeed, there could be uncertainties from fish individuals and from experimentations *in natura* on phenotypes assessment. In addition, correlations between phenotype – determined by robe *criteria* (Section 2.1.3, Table 2 – 1) – and genotype are uncertain and have been shown to vary based on samples used (Folio et al., 2021; Gil et al., 2015). GCP is therefore an omnibus way to control the strength of genetically based preference.

Females choice to mate with a male based on her preference curve will then depends on a probabilistic random draw with the following probability:

$$\rho = \frac{\text{genetic contribution} * \left(\frac{e^{\text{Preference}}}{1 + e^{\text{Preference}}} \right) + ((100 - \text{genetic contribution}) * q)}{100} \quad (\text{Equation 3 – 15})$$

If the value drawn is below mating will happen, otherwise, it will not.

☞ Lastly, if **no mating system** is informed, all females will choose to mate with a given male randomly, with a 50% chance to accept mating with any males, independently of their phenotype.

Fertilisation. Spawning and fertilisation happen when a female accepts to mate with a male. Females produce a certain number of eggs. Egg number depends on females' body size and fecundity (*coefficient* and *exponent*) since bigger females tend to produce more eggs (Lobon-Cervia et al., 1997). The number of eggs laid depends however on the female's spawning count (which is set to 2 by default). Fertility will also be controlled by habitat quality for reproduction in the reach and predation – *i.e.* egg cannibalism. Indeed, in the model, females have to split their available gametes between mating events when they decide to mate multiple times (set up to twice a year). They also lay fewer eggs when habitat quality for reproduction is low since spawning substrate availability and quality can influence female investment in reproduction (Heggenes, 1988). Finally, fewer eggs are fertilised when egg cannibalism occurs, as satellite males, females or unsuccessful mates may be present around the spawning site to predate on eggs (Aymes et al., 2010). In the model, it is considered a random event, which effect is based on a randomly drawn variable α ranging between 1 (no cannibalism) and 5 (maximum cannibalism pressure).

$$nEggs = fecundity\ coefficient * (10 * body\ size)^{fecundity\ exponent} * \frac{reproduction\ factor}{(\alpha * spawning\ count)}$$

(Equation 3 – 16)

The number of eggs produced during fertilisation will be added to the hatch created during this time step in that reach, along with maternal and paternal IDs involved in mating.

3.3.7 Fishing

The effect of recreational fishing can be simulated in the model. At initialisation, the user decides on the settings of this fishing process (*Figure 3 – 22, Appendix B: Table 5*). It can step in at different months and it is applied repeatedly every year on those selected months. Fishing pressure is defined as a monthly

additional mortality rate applied to the population (this is not an individual process). This mortality rate varies based on fishing regulations in place in given areas – reaches in the model. Four types of different fishing zones have been defined:

- ☞ “Standard” reach where fishing is allowed at its maximal rate within catch size(s) limits.
- ☞ “Active reserve” reach where fishing is allowed but limited to a certain amount of fish per angler. For this modality, we assume that the fishing mortality will be twice lower than the mortality applied in the standard areas.
- ☞ “No-kill” reach where fishing is allowed only on a catch and release mode. Here we assume a low residual mortality rate, as catch-and-release is known to cause some mortality (Bartholomew & Bohnsack, 2005).
- ☞ “Full reserve” reach where fishing is banned.

This mortality can then only be applied to individuals of a certain size as some size regulation can be implemented. Upper and lower catch size limits are set per reach and the user specifies whether fishing pressure is applied between, above or below these given size limits. Fishing regulation and catch size limits are informed per reach in the initial data file.

During this fishing process, several individuals randomly sampled within size limit regulations will be removed from the simulation every month when fishing is allowed. This number is the product of the mortality rate applied by the number of individuals present in a given area at a given time step.

It is important to notice that these fishing settings will be applied throughout the entire simulation, as this fishing process will happen repeatedly every year. Other options (*Section 3.4.2*) are available to simulate punctual fishing pressure, such as electric fishing.

Fishing pressure

Fishing periods

<input type="checkbox"/> November	<input checked="" type="checkbox"/> May
<input type="checkbox"/> December	<input checked="" type="checkbox"/> June
<input type="checkbox"/> January	<input checked="" type="checkbox"/> July
<input type="checkbox"/> February	<input checked="" type="checkbox"/> August
<input type="checkbox"/> March	<input checked="" type="checkbox"/> September
<input checked="" type="checkbox"/> April	<input type="checkbox"/> October

Legal size options

Fishing below minimum size

Fishing between legal sizes

Fishing above maximum size

Fishing mortality rate per regulation

Standard reach :

Active reserve reach :

No kill reach :

Full reserve reach :

Ok Cancel Help

Figure 3—22: Graphical user interface for classic fishing pressure. The user can decide on which month fishing will happen, catch size regulation and mortality rates related to fishing regulation.

3.3.8 Individualisation

The individualisation process is a modelling operation where fish grouped in a hatch are turned into individuals – *i.e.* fish objects. As a reminder, hatch objects are built right after fertilisation and serve as a collection object where the parental contribution and number of eggs produced are stored, for delayed instantiation into individualised fish objects, so to reduce memory consumption in the simulations. In the present study, this process will happen at a given age for hatches: 8 months, when fish are still juveniles.

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The number of fish left in the Hatch at that age will be the number of individuals created in the model (*Figure 3 – 3*). During that process, each individual will be given a genome, determined based on their maternal and paternal genome – available through parental contribution. This is supported by genetic libraries that will allow the random transmission of an allele from each parent at each *locus* (*Figure 3 – 6*). Since there are no linkages between the seven loci, alleles for each *locus* are transmitted independently. Finally, the trait value – individual introgression – will be calculated and attributed to all newly individualised fish. Hatches characteristics – information on hatching and emergence, or age and body size – are transferred to each individual created while other characteristics, specific to individuals, such as sex or spawning age, are either randomly determined or set by default.

3.3.9 Temperature model

Temperature is a required environmental variable in MEDITERRANEA. Indeed, on the one hand, it affects individual embryonic development (*Section 3.3.1*), as well as growth (*Section 3.3.3*). On the other hand, it dictates genotype-by-environment interactions involved in post-zygotic isolation (*Section 3.3.2*). Therefore, the model generates a first set of 12 temperatures, one per month, using either informed empirical data – when water temperature data are available – or a temperature model. Monthly temperatures will be updated based on the climatic model enforced.

The temperature model uses a periodic function to simulate temperature based on altitude since altitude is among the best predictors of river temperature in the Mediterranean area (Daigle et al., 2016). Managers can also easily inform this variable. In addition, preliminary analyses on river empirically measured water temperatures in the Haute-Savoie area (*Appendix C*) indicate that temperatures vary based on altitudes. This variation also appears to be season dependent. Overall, in winter, temperatures vary less with altitudes than in summer. This temperature model also allows for the implementation of a

climate effect to simulate climate change, such as a gradual increase in temperatures throughout the years. Temperature is calculated for each reach based on their given *altitude* and on a daily time step, as follows:

$$temperature = (A0 + A1 * altitude + A2 * days) + \sin\left(2 * \pi * \frac{(days - phase)}{365}\right) + (B0 + B1 * altitude + B2 * days) \quad (Equation 3 - 17)$$

The sinusoidal function takes π , a *phase* corresponding to the first day of simulation – *i.e.* 1st September – that values 245 (Julian days) as the intercept value must be met there, and *days*, which is the current day number the temperature is calculated for. *Days* represent a cumulative value, calculated over years to allow for the implementation of a climate change effect.

The temperature model requires base value parameters (the base value (*B0*) as well as altitude (*B1*) and climate (*B2*) effect on that base value) to which an amplitude effect is added (amplitude parameters: sea level amplitude (*A0*) as well as altitude (*A1*) and climate (*A2*) effect on amplitude). Other additional and optional climatic parameters, to calculate an overall noise on mean temperature and its variance, are available but not considered here in this manuscript.

To avoid negative values and to fit observed patterns of water temperature, the sinusoidal model is broken in winter. The *temperature* value initially calculated is modified so that water temperature decreases slower in winter. This takes place when the temperature is below or equal to 4°C.

$$\curvearrowright temperature < 0 \quad \rightarrow \quad temperature = 0$$

$$\curvearrowright temperature \leq 4 \quad \rightarrow \quad temperature = 0.125 * temperature^2 + 2$$

Temperature value is not allowed to go below 2°C since it would delay development and causes emergence to potentially happen after July, which would never happen in reality (Scimabio Interface, Com. Pers.).

Based on daily temperatures, the model will then calculate monthly-cumulated temperatures in degree-days and monthly-mean temperatures in degree-Celsius. The evolution of temperature – using monthly mean values – based on altitudes can be visualised in the user interface (*Figure 3 – 23*).

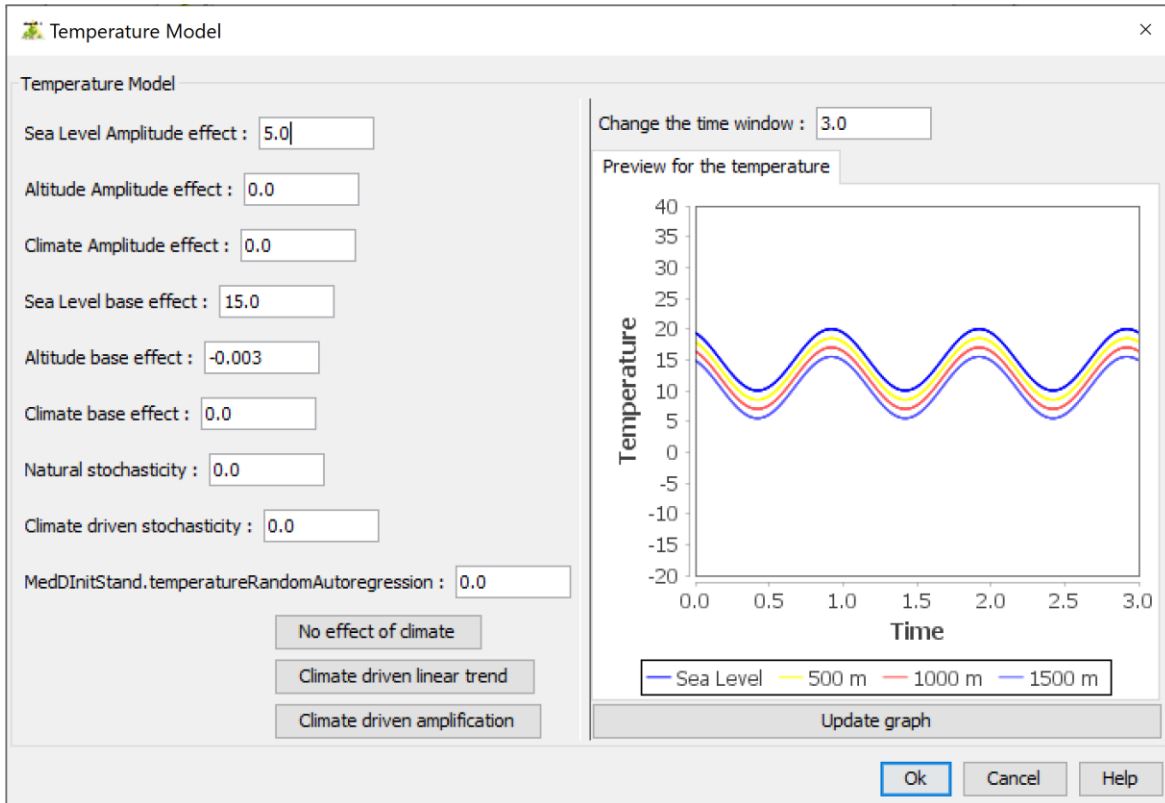


Figure 3—23: Graphical user interface for the setting of the temperature model. The user can modify each parameter. Some pre-set buttons can be created to implement an already define temperature model. Yearly water temperatures can be visualised as a function of various altitudes (sea level, 500m, 1000m and 1500m).

3.4 SIMULATING MANAGEMENT STRATEGIES

The MEDITERRANEA model allows the implementation of “interventions” during any simulation to simulate various impacts on the demo-genetic dynamics. These interventions are used to represent the effect of management strategies or natural events on the evolution of demography and diversity. They

can be punctual or repeated throughout time and affect individuals – referred to as population modifications – or habitats – referred to as habitat modifications. Punctual interventions will happen only once, after being called in the simulation, while repeated interventions will be set to happen X times with a certain frequency for a certain duration. An intervention can be called at any time step but the first one.

3.4.1 Habitat modifications

Connectivity management. This intervention is used to represent a dam or barrier modification, removal or construction. It consists in modifying upstream or downstream weir passability (*Figure 3 – 24, left*). This modification can be done on one or multiple weirs at a time.

Habitat management: quality modification. To mimic an improvement or degradation in habitat quality for survival or reproduction, the user can change the value informing on reaches habitat quality, respectively: carrying factor and reproduction factor (*Figure 3 – 24, right*). Modification in habitat quality for survival will change the maximum carrying capacity allowed in a given reach. Modification in habitat quality for reproduction will affect reproductive movement decisions as well as females' fecundity – the number of eggs produced. This modification can be done on one or multiple reaches at a time.

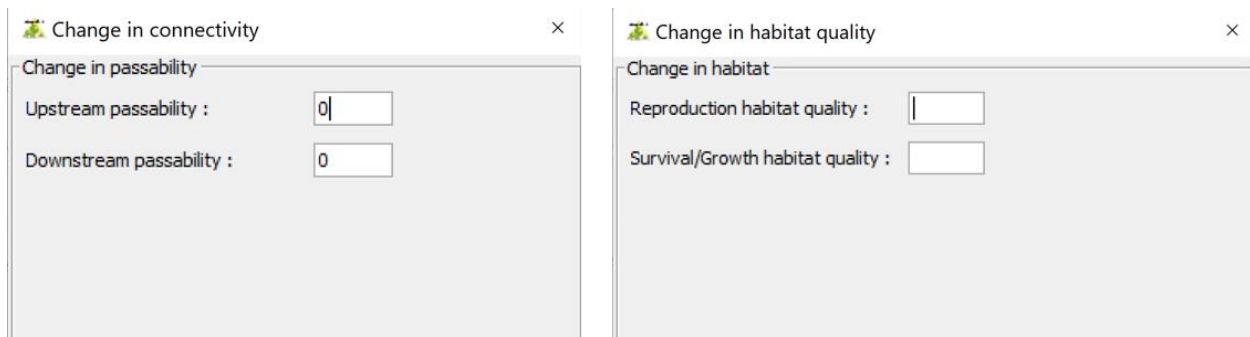


Figure 3—24: Graphical user interface for managing connectivity (left) and habitat quality (right). The user simply specifies a new value for each weir or reach state variable.

3.4.2 Population modifications

Fishing intervention. Various fishing interventions can be carried out in the model: punctual selective fishing or recurrent fishing to simulate the effect of electric fishing, or selective removal for example. Selective fishing can be based on age, size, individual introgression or a combination of all factors. In the graphical interface, the user can just interactively remove a certain amount of individuals knowing the exact number of individuals in each category (*Figure 3 – 25*). Recurrent fishing resembles the classic fishing process that mimics recreational fishing. It can be used to add additional, recurrent, but timed fishing regulations. The number of times this intervention happens and its frequency in years has to be specified.

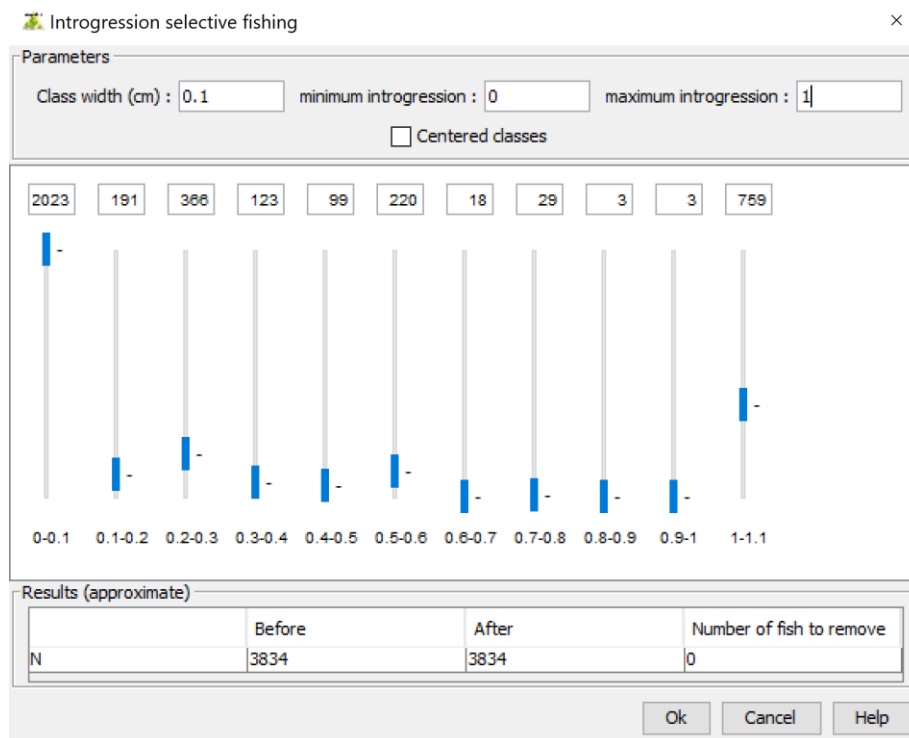


Figure 3—25: Graphical user interface for selective fishing based on individual introgression. The number of individuals available in each category of introgression can be visualised. The user can just move the cursor to decide how many individuals are to be removed in each category.

Fish translocation. Fish translocation is used to move individuals from one reach to another. The method takes a minimum and maximum size as well as a minimum and maximum individual introgression value. This allows transferring individuals based on specific characteristics to implement measures such as the translocation of native individuals. Information on sampled reach and translocated reach are required, as well as the number of individuals to be transferred. The user interface allows for multiple translocation events to happen simultaneously – originating from different sampled reaches (*Figure 3 – 26*).

Origin reach	Available sample	Desired sample	Destination reach
1	559	0	NA
2	321	0	NA
3	411	0	NA
4	340	0	NA
5	0	0	NA

Figure 3—26: Graphical user interface for fish translocation. The user can see how many fish is available in each reach and indicate the number of fish to move and their destination reach.

Fish introduction. To mimic fish introduction, the interface allows the user to upload an extra data file in the model, containing only individuals. Individuals from this new file will be added to the population, in a reach determined based on their current reach ID – informed in the file.

Hatch addition or removal. Hatch removal is used to represent full nest mortality, potentially due to nest scouring. The intervention simply consists in applying a given mortality rate to hatches.

Hatch addition is used to implement fry stocking. It consists in introducing a large number of young individuals (generally ~ 6 months) – grouped in hatches (up to 8 months) in the model. The user indicates the density of individuals stocked per hectare. In addition, some information has to be specified to create these hatches: age, body size, if hatching and emergence have happened yet, as well as average individual introgression – usually 0 or 1 as it is done using native or non-native fry in the MED/ATL context. This intervention can be done on one or multiple reaches at a time and one hatch is created per reach.

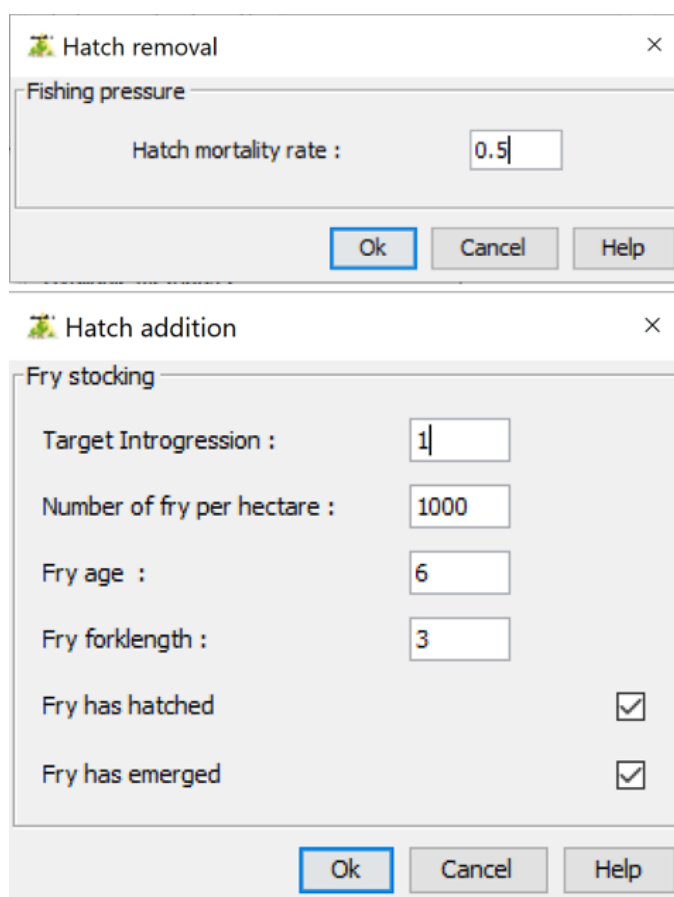


Figure 3—27: Graphical user interface for hatch removal and hatch addition.

3.4.3 Viability analyses

This intervention allows for simulating catastrophic mortality events, such as annual or decennial floods and consists of applying a high mortality rate to the population (*Figure 3 – 28*). Months during which the mortality rate should be applied can be specified, as well as its yearly frequency. Two different mortality rates can be set, one for adults and sub-adults and one for juveniles as they may not be affected similarly by such catastrophic events since they do not share the same habitats (Kaspersson et al., 2012). Studying population viability usually represents managers' first step in management decision-making. Scimabio Interface has already used this functionality of the model in interaction with fishery managers for an applied case study to test the viability of an ATL population in the Mechet River.

The screenshot shows a dialog box titled "Viability protocol" with a close button (X) in the top right corner. The dialog is divided into two main panels. The left panel, titled "Fishing periods", contains a grid of checkboxes for each month of the year: November, December, January, February, March, April, May, June, July, August, September, and October. The "November" checkbox is checked. Below the grid are two input fields: "Repetitions number" with the value "1" and "Interval length" with the value "1". The right panel, titled "Mortality rate", contains two input fields: "Juvenile mortality" with the value "0" and "Adult mortality" with the value "0". At the bottom right of the dialog are three buttons: "Ok", "Cancel", and "Help".

Figure 3—28: Graphical user interface for the viability protocol. The user can specify the month during which the catastrophic event happened and its frequency – by informing the number of years where it should be applied and the interval length between each event.

3.5 MODEL INITIALISATION AND EVOLUTION

To initialise a simulation, MEDITERRANEA uses an initial data file and a set of initial parameters – for each of its processes – to create an initial step and allow model evolution (*Figure 3 – 29*).

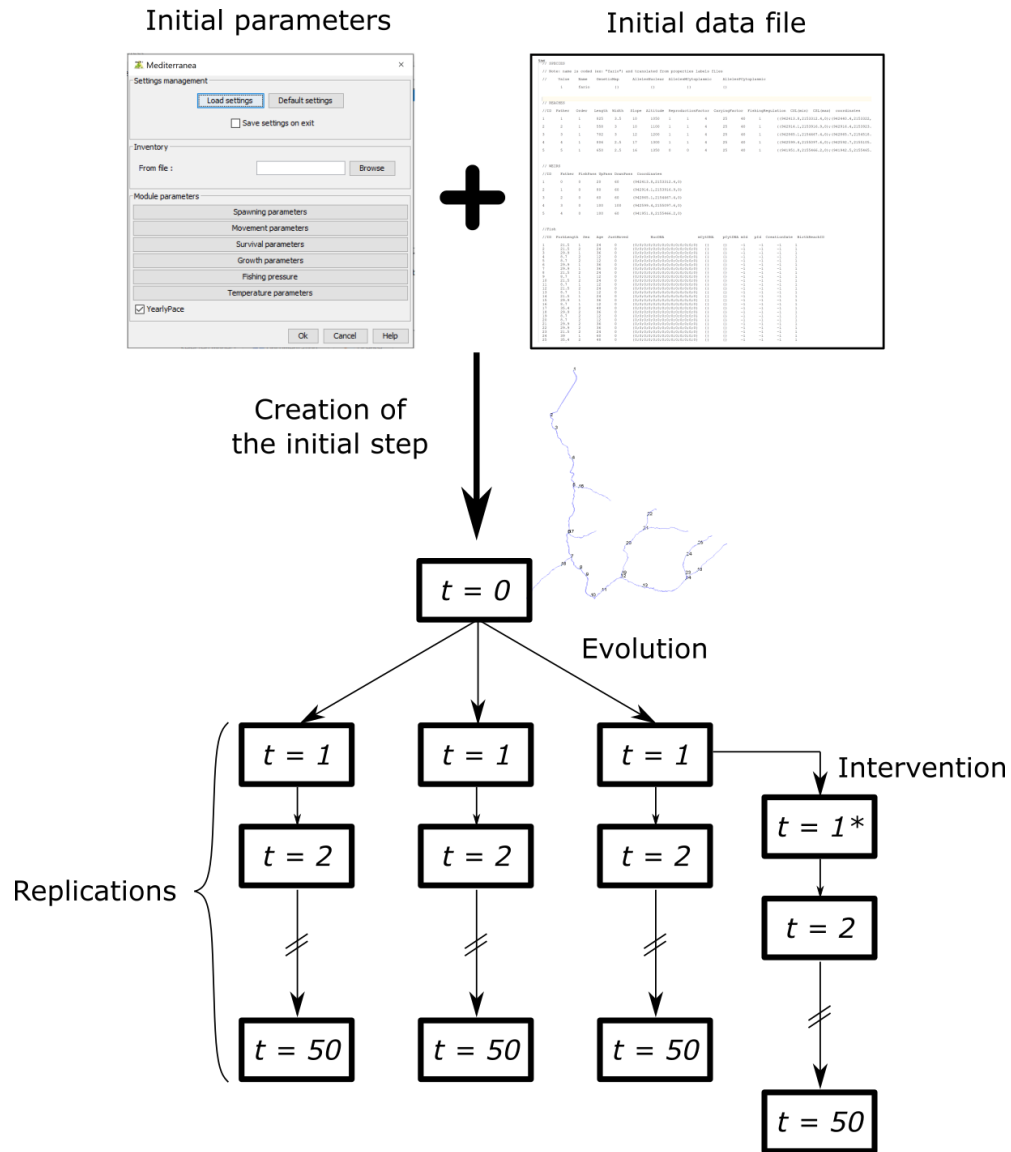


Figure 3—29: Simple representation of the model initialisation and evolution in MEDITERRANEA. The model requires a set of initial parameters and an initial data file to create the initial step ($t = 0$). Multiple trajectories can be run from the same initial step (replications). Interventions can be implemented at any time step, on any replications.

3.5.1 Initial data file

MEDITERRANEA requires initial data on species, habitat – reaches and weirs – and individuals. These data are stored in a single text file: the initial data file (*Figure 3 – 30*), where species data are informed first followed by reach, weirs and finally individuals. Data has to be informed in a specific order so that the model can read them. For species data, the model only deals with one species: *Salmo trutta*. Therefore, no specific information is required (here: *fario*), as the model will directly inform them (genetic map and various allelic effects). For reaches and weirs, initial data are compulsory to build the hydrographic network. These spatial and topological information can be simply prepared using SIG, or manually for small rivers. Reaches data must contain topological information (ID, father ID), physical (length, width, slope, altitude), ecological (reproduction and carrying factor) and management (fishing regulation, catch sizes, specificities) characteristics as well as geographical coordinates (used to visualise the river). For weirs, topology, coordinates and passability characteristics (Fish Pass, Up pass, Down pass) have to be provided. Finally, data for individuals – *i.e.* fish object – gather a specific ID and a variety of state variables that describe phenotypic (sex: 1 is male / 2 is female, body size and age), behavioural (movement status) and genetic (nuclear and cytoplasmic DNA) characteristics as well as parentage (maternal and paternal ID) and birth information (creation date, birth reach ID). Parental IDs and creation date are set to -1 (unknown).

3.5.2 Initial parameters

Initial parameters for each of the previously described processes – survival, growth, movement, reproduction, fishing and temperature model – have to be informed to start a simulation. These parameters will be used throughout the entire simulation and cannot be modified after initialisation. In this manuscript, some of these parameters have been fixed – *i.e.* will not vary among scenarios – as they

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have been calibrated using real data on the MED-ATL complex. Others will be variable among scenarios.

Initial parameters for each process are described in the section where the specific processes are explained

(Section 3.3). The appendix with default parameters also indicates if the parameter is considered fixed or

variable for the present study (Appendix B).

```

5.txt
// SPECIES
// Note: name is coded (ex: "fario") and translated from properties labels files
// Value Name GeneticMap AllelesNuclear AllelesMCytoplasmic AllelesPCytoplasmic
// 1 fario {} {} {} {}

// REACHES
//ID Father Order Length Width Slope Altitude ReproductionFactor CaringFactor FishingRegulation CSL(min) CSL(max) coordinates
1 1 1 825 3.5 10 1050 1 1 4 25 40 1 {(942413.8,2153312.4,0);(942440.4,2153322,
2 2 1 558 3 10 1100 1 1 4 25 40 1 {(942914.1,2153916.9,0);(942916.4,2153923.
3 3 1 702 3 12 1200 1 1 4 25 40 1 {(942865.1,2154467.4,0);(942865.7,2154518.
4 4 1 806 2.5 17 1300 1 1 4 25 40 1 {(942599.4,2155097.6,0);(942592.7,2155105.
5 5 1 650 2.5 16 1350 0 0 4 25 40 1 {(941951.8,2155466.2,0);(941942.5,2155465.

// WEIRS
//ID Father FishPass UpPass DownPass Coordinates
1 0 0 20 60 (942413.8,2153312.4,0)
2 1 0 80 60 (942914.1,2153916.9,0)
3 2 0 60 60 (942865.1,2154467.4,0)
4 3 0 100 100 (942599.4,2155097.6,0)
5 4 0 100 60 (941951.8,2155466.2,0)

//Fish
//ID ForkLength Sex Age JustMoved NucDNA mCytDNA pCytDNA mId pId CreationDate BirthReachID
1 21.5 1 24 0 {0;0;0;0;0;0;0;0;0;0;0;0;0;0} {} {} -1 -1 -1 1
2 21.5 2 24 0 {0;0;0;0;0;0;0;0;0;0;0;0;0;0} {} {} -1 -1 -1 1
3 29.9 1 36 0 {0;0;0;0;0;0;0;0;0;0;0;0;0;0} {} {} -1 -1 -1 1
4 8.7 2 12 0 {0;0;0;0;0;0;0;0;0;0;0;0;0;0} {} {} -1 -1 -1 1
5 8.7 2 12 0 {0;0;0;0;0;0;0;0;0;0;0;0;0;0} {} {} -1 -1 -1 1
6 29.9 1 36 0 {0;0;0;0;0;0;0;0;0;0;0;0;0;0} {} {} -1 -1 -1 1
7 29.9 1 36 0 {0;0;0;0;0;0;0;0;0;0;0;0;0;0} {} {} -1 -1 -1 1
8 21.5 2 24 0 {0;0;0;0;0;0;0;0;0;0;0;0;0;0} {} {} -1 -1 -1 1
9 8.7 1 12 0 {0;0;0;0;0;0;0;0;0;0;0;0;0;0} {} {} -1 -1 -1 1
10 21.5 2 24 0 {0;0;0;0;0;0;0;0;0;0;0;0;0;0} {} {} -1 -1 -1 1
11 8.7 1 12 0 {0;0;0;0;0;0;0;0;0;0;0;0;0;0} {} {} -1 -1 -1 1
12 21.5 2 24 0 {0;0;0;0;0;0;0;0;0;0;0;0;0;0} {} {} -1 -1 -1 1
13 8.7 1 12 0 {0;0;0;0;0;0;0;0;0;0;0;0;0;0} {} {} -1 -1 -1 1
14 21.5 1 24 0 {0;0;0;0;0;0;0;0;0;0;0;0;0;0} {} {} -1 -1 -1 1
15 29.9 1 36 0 {0;0;0;0;0;0;0;0;0;0;0;0;0;0} {} {} -1 -1 -1 1
16 8.7 1 12 0 {0;0;0;0;0;0;0;0;0;0;0;0;0;0} {} {} -1 -1 -1 1
17 35.4 2 48 0 {0;0;0;0;0;0;0;0;0;0;0;0;0;0} {} {} -1 -1 -1 1
18 29.9 2 36 0 {0;0;0;0;0;0;0;0;0;0;0;0;0;0} {} {} -1 -1 -1 1
19 8.7 2 12 0 {0;0;0;0;0;0;0;0;0;0;0;0;0;0} {} {} -1 -1 -1 1
20 8.7 2 12 0 {0;0;0;0;0;0;0;0;0;0;0;0;0;0} {} {} -1 -1 -1 1
21 29.9 2 36 0 {0;0;0;0;0;0;0;0;0;0;0;0;0;0} {} {} -1 -1 -1 1
22 29.9 2 36 0 {0;0;0;0;0;0;0;0;0;0;0;0;0;0} {} {} -1 -1 -1 1
23 21.5 2 24 0 {0;0;0;0;0;0;0;0;0;0;0;0;0;0} {} {} -1 -1 -1 1
24 39 1 60 0 {0;0;0;0;0;0;0;0;0;0;0;0;0;0} {} {} -1 -1 -1 1
25 35.4 2 48 0 {0;0;0;0;0;0;0;0;0;0;0;0;0;0} {} {} -1 -1 -1 1

```

Figure 3—30: Example of an input data file with information on Species, Reaches, Weirs and Fish objects.

Lines starting with ‘//’ are comments and are not considered by the model.

3.5.3 Creation of the initial time step

An initial stand is created using the initial data file and initial parameters set by the user. The hydrographic network is created using the information provided on reaches and weirs. Individuals are distributed among reaches based on their reach of birth. Using parameters from the temperature model or informed empirical data, the first set of 12 temperatures, one per month, is created for each reach. The genetic map for the species is also created as described in genome structure. The initial step is September ($t = 0$).

3.5.4 Model evolution

After the creation of the initial step, the model is ready to run. The evolution of the model is set by the user for a given number of time steps. Multiple simulations can be run from the same initial step. During model evolution, interventions can be applied at each step.

3.6 OVERVIEW OF THE GRAPHICAL USER INTERFACE

The graphical user interface represents all the elements that the user has access to, to interact with the model. To open a model, a new project has to be created and the model specify – here MEDITERRANEA. This leads to a first window divided into three main parts (*Figure 3 – 31*). The first part allows the user to save or load a given set of initial parameters. The second part is where the initial data file, including the hydrographic network and individuals, is loaded. The third part gives access to the initial parameters of the model – ordered by processes.

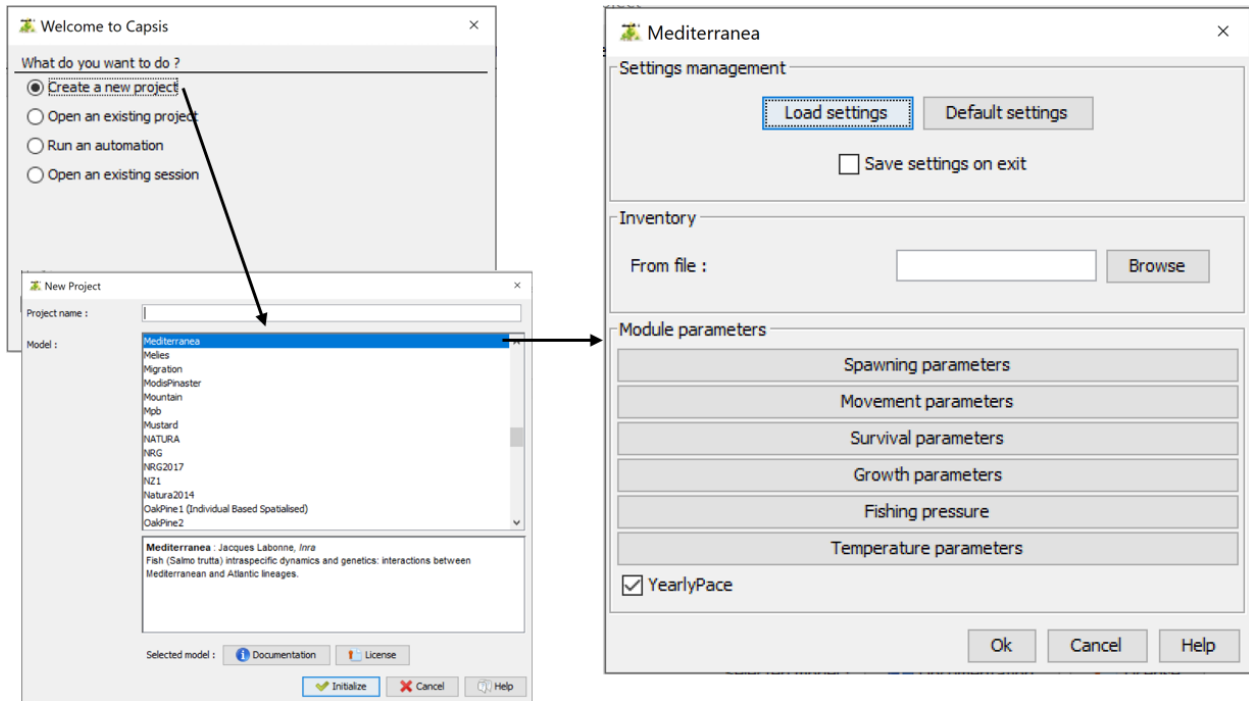


Figure 3—31: CAPSIS-4 graphical interface to initialise the model chosen and MEDITERRANEA first window to load an initial data file and set parameters.

3.6.1 Running simulations

To initialise a simulation, an initial data file has to be loaded. The user can then use default values for initial parameter settings or set his own values. A new project can then start. Simulations always run on a monthly time step but they can be visualised on a monthly or yearly time step.

In the interface an initial step for the project appears – September time step 0. The user can now start the evolution of the model – click <Evolution> - for a given number of time steps. This results in the first trajectory of the project. Each time step can be analyzed and contains every object within the simulation at that given time. Multiple trajectories (or replications), from the same project, can be launched similarly, either from the initial step or from any other intermediate step of the model. *Figure 3 – 32* illustrate multiple trajectories of the same project when visualizing yearly time step – *i.e.* one step out of twelve:

here September. Multiple projects can be started simultaneously in the same session of CAPSIS-4 to directly compare different scenarios with contrasting initial parameters.

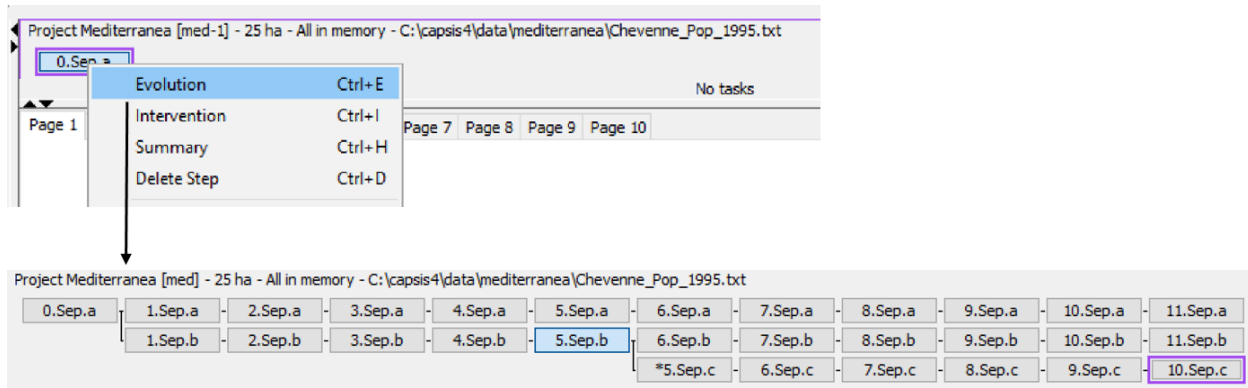


Figure 3—32: MEDITERRANEA graphical user interface showing how to launch model evolution after a project initialisation. Multiple trajectories of the project have been run in this example, as well as one intervention on the last one.

The model interface allows the user to save multiple types of information, such as sets of parameters – when creating a new project – and projects themselves. Each time a project is created, it can be saved independently (Project > Save project) or as part of a session including multiple projects (Files > Save session).

At every time step during a simulation, it is possible to call for an intervention that will affect the current dynamic of the population. A right-click on a time step will lead to <Intervention>. The related dialogue box will propose the different types of actions possible (Figure 3 – 33). Groupers can be used to carry out interventions on a subset of reaches or weirs. Each intervention can be parameterised through a specific dialogue box in the interface. Once the intervention is set, a new trajectory appears with the new modified step (Figure 3 – 32, marked by *). Evolution can then be launched on that new step.

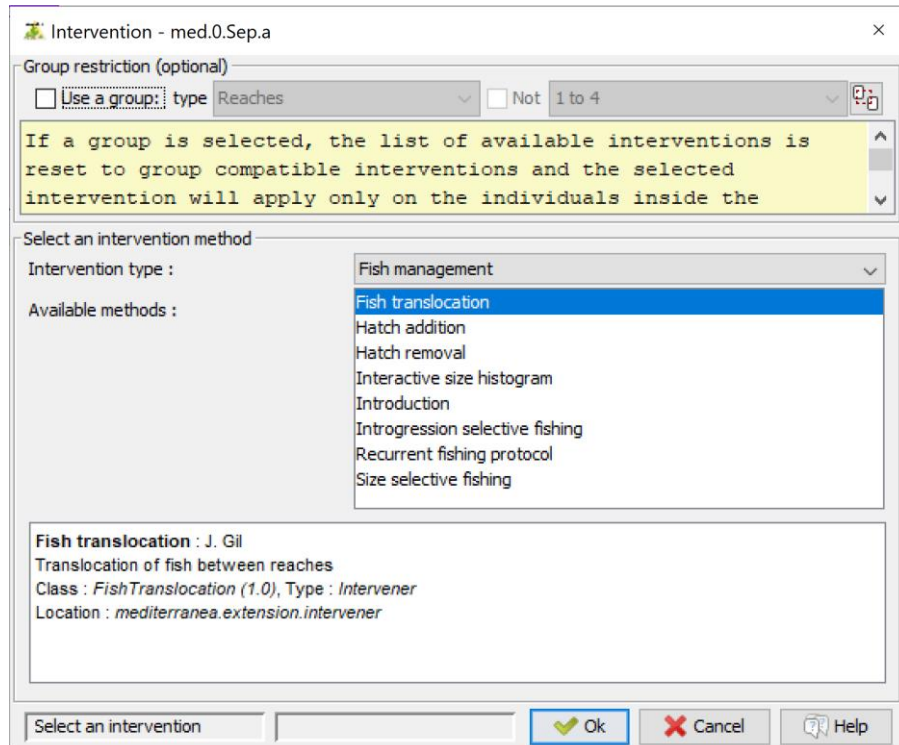


Figure 3—33: Graphical user interface for intervention. The user can choose from many interventions involving either: habitat or connectivity modification, population management or viability analyses.

3.6.2 Observing and analysing simulations

A set of extensions is included in the user interface of MEDITERRANEA. They allow visualisation and analyses of data resulting from simulations. They are accessible on the left of the interface and are divided into two main parts: a graphical part (Chart) and a stand visualisation part (Scene viewer). They can be modified interactively (type of graph, time step ...) and data filtered to only plot a part of the information (some reaches only for example). They are called by time step to visualise a given data at this given time or its temporal evolution up to that time step.

Data extractors. Data extractors are used to analyse graphically a simulation and hence gather various types of data of interest memorised during the simulation. Some are used to visualise temporal data (evolution of: population size, introgression rate, genotypic composition of the population...) while others show the distribution of some variables (Individual age, body size or introgression, reach characteristics ...) at a given time or the relationship between two variables of interests (age and size relationship). Multiple simulations or time steps can be visualised using the same data extractor (click on the step to add and do <control + click>).

Among the most important data extractors, MEDITERRANEA has some on diversity dynamics, demographic dynamics and population characteristics and others on habitat. To follow diversity dynamics, the user can visualise the introgression rate and the genotypic composition of the population (numbers of MED, HYB and ATL individuals) through time, the distribution of individual introgression at a given time step as well as ATL allele frequency per *locus* (differentiating maternally and paternally inherited alleles). To study demographic dynamics and various population characteristics the user can visualise the evolution of population size per life stage, size-at-age relationship or the distribution of size and age at a given time step. Regarding habitat – reaches and weirs, the user can visualise the evolution of temperature per reaches and reaches information on slope, mean width, altitude-temperature relationship...

Types of graphical representation. CAPSIS-4 allows for four different graphical representations of data: lines plot, scatter plot, bars plot and cumulative areas (*Figure 3 – 34*). All available data extractors can use these different representations. Graphs can then be saved to JPG or PNG format. Data can also be saved in a table. Right-clicking on graphs gives access to different options of data visualisation, as data can be filtered by groups (of individuals, reaches or weirs) based on various grouping variables. Colours can also be modified.

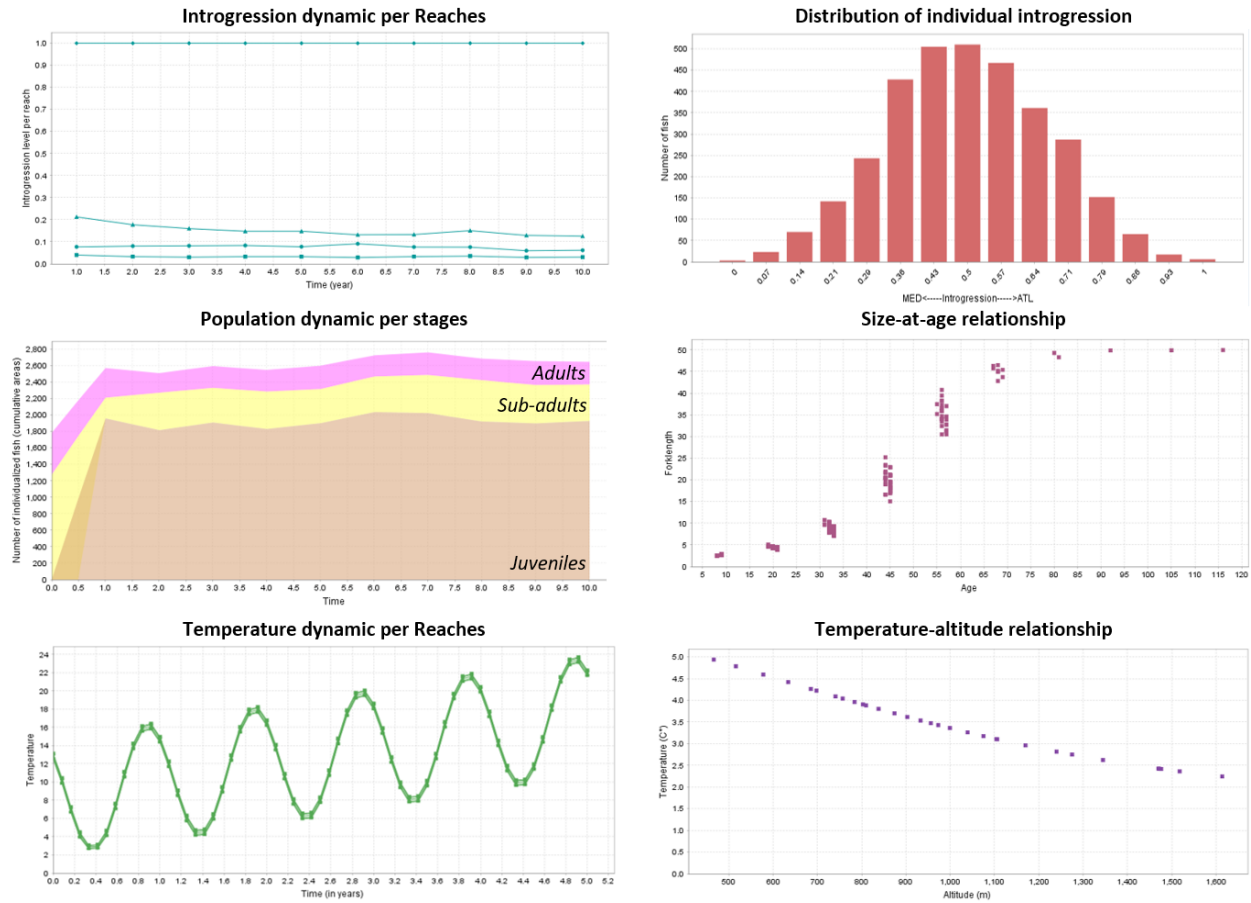


Figure 3—34: Example of various graphical representations provided by CAPSIS-4 software for MEDITERRANEA.

Scene viewer. In the stand visualisation part, the hydrographic network and the information of the different objects in the model – reach, weir, individual or hatch – can be visualised at each time step. Mediterranean viewer offers a two-dimension representation of the hydrographic network where reaches and weirs are delimited (Figure 3 – 35). Some of their characteristics can be shown on the river map. The user can click on each object constituting the river (reaches and weirs) and access all its information (states variables, as well as other related objects – such as individuals located in a particular reach – for which related information can also be accessed).

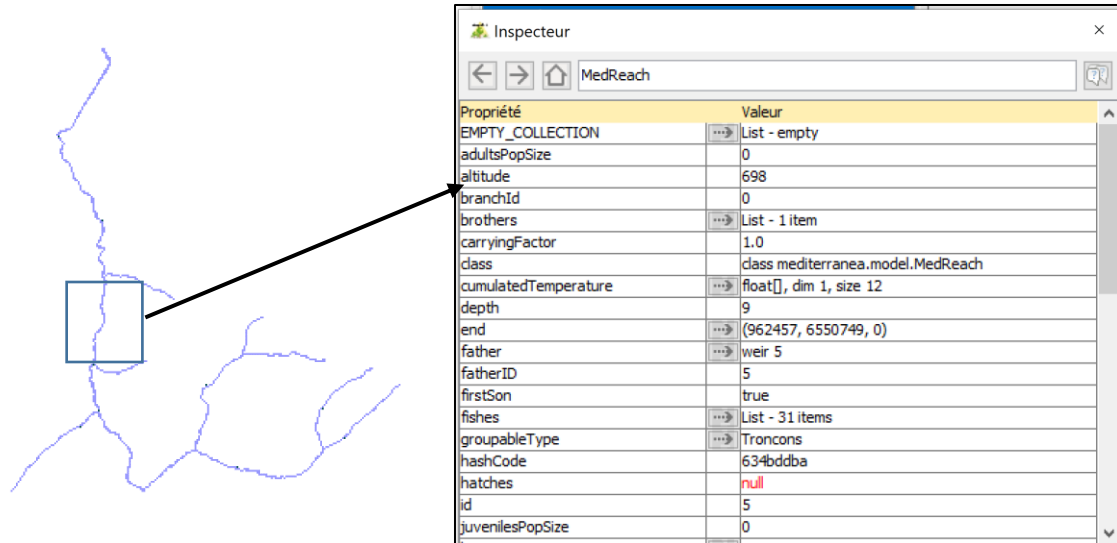


Figure 3—35: Representation of a hydrographic network in MEDITERRANEA – here the Borne River. Objects information (reaches and weirs) can be directly accessed through this viewer.

Groupers. They are often used when the user wants to analyze sub-parts of the data, using filters on three main objects of the simulation: individuals, reaches and weirs. Those filters allow the user to choose objects based on the value of one of its state variables, such as Boolean values (true or false), numerical intervals or directly by selecting a specific object (ID). For example, the user can follow the dynamic of a subset of reaches only (directly chosen by ID or based on a specificity such as fishing regulation) or that of a certain type of individuals (females, juveniles...). He can also create a group of individuals within a group of reaches. Groups can be “dynamic” or “static”. Dynamic groups can evolve through time, meaning that the composition of the group can change through time as long as the filtering condition is matched. A dynamic male group will hence show at each time step male individuals. Static groups will not change through time, meaning that they will be made of the same objects – such as individuals – every time. A static male group will only represent the males present in the population at a given time step. This type of filter can be useful when following the evolution of a specific cohort.

3.7 MODEL PURPOSES

Using this modelling framework, I will address the specific objectives of my PhD, which are:

- To measure the relative importance of the two experimentally assessed EEMs – heterogamous female preference and GxE interactions on embryonic survival – on the evolution of diversity dynamics and demography in various environmental contexts (Chapter 4).
- To evaluate the efficiency of various management practices while considering these EEMs and some variations in important ecological factors – such as temperature (Chapter 5).

CHAPTER 4

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4 MEDITERRANEA: A TOOL TO MEASURE THE ROLE OF ECO-EVOLUTIONARY MECHANISMS

In the MED-ATL hybridization complex, some eco-evolutionary mechanisms (EEMs) driving hybridization have been explored in natural environments to understand observed heterogeneous patterns of diversity. On the one hand, despite long allopatric isolation, no pre-zygotic barriers have evolved between the lineages. Instead, (Gil et al., 2015) unravelled patterns of heterogamous preference with female preference generally aimed at dissimilar male phenotypes. During secondary contact, such a mating system could enhance hybridization between both lineages. On the other hand, even after more than a century in sympatry, lineage-related differences in fitness can still be observed in some environmental conditions. Indeed, maternal gene-by-temperature interaction appears to be one of the main drivers of embryonic survival up to hatching (Folio et al., 2021). Temperature contrasts could therefore influence the persistence of a post-zygotic reproductive barrier between the lineages.

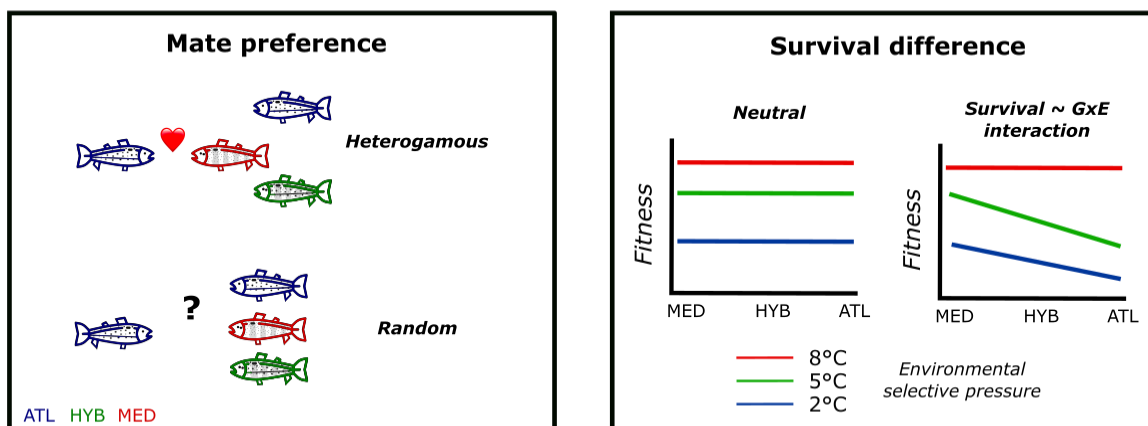
Such EEMs are likely to have a strong influence on the evolution of diversity. However, acknowledging their existence is insufficient to grasp their actual role in hybridization and diversity dynamics. One has to project and calculate how much these mechanisms will interact with the other ecological, genetic, and demographic drivers, including human interventions. This chapter will aim at evaluating the actual role and relative importance of heterogamous preference and GxE interactions on embryonic survival in driving the evolution of diversity and demography, with and without considering interventions of fisheries managers. DG-ABM provides an operational framework to test the fate of these two gene pools under different eco-evolutionary scenarios, as (i) it realistically simulates interactions between individuals, giving rise to demographic and genetic processes, such as allelic transmission and (ii) it allows for the implementation of complex eco-evolutionary relationships, such as mate preference behaviour and

lineage dependent survival, mediated by environment. Such models also enable the implementation of management practices, which can interfere with EEMs and hence diversity dynamics.

4.1 OBJECTIVES

In this Chapter, MEDITERRANEA, which mimics the brown trout life cycle, will be used to compare trajectories of diversity dynamics and demography in the MED-ATL hybridization complex when implementing, or not, heterogamous preference and/or gene-by-temperature (referred to as GxE) survival difference (Figure 4 – 1). Diversity dynamics will include the population introgression rate and the evolution of population genotypic composition – *i.e.* proportion of MED, HYB and ATL individuals –, as well as the distribution of individual introgression at specific time steps – to differentiate between hybrids. Demography will mainly focus on the evolution of population size through time and the age class structure – juveniles, sub-adults and adults.

Testing the actual role of the empirically measured eco-evolutionary mechanisms...



... on the evolution of diversity dynamics and demography

Figure 4–1: Simplified representation of the eco-evolutionary mechanisms implemented in MEDITERRANEA and chapter 4’s main goals.

- ☞ In the first section, I will investigate the evolution of diversity dynamics under various eco-evolutionary scenarios, over long- and short-time scales (relative to management practices, so respectively > 20 years and < 20 years), in a very simplified and theoretical case study of first secondary contact (*Figure 4 – 5, A*). I will initially focus on the influence of (i) heterogamous preference, (ii) GxE interactions and (iii) temperature contrast on the evolution of diversity dynamics and demography. Then, as both EEMs may have opposite effects, one potentially favouring hybridization and the other native diversity, I will also investigate the impact of heterogamous preference on the potential selection mediated by GxE interactions. I will discuss those results in regard to the model specificities and theoretical knowledge of these mechanisms.
- ☞ Then, I will turn to more complex case studies, based on real and documented situations, where management practices have been carried out to restore brown trout populations and/or conserve the MED lineage (*Figure 4 – 5, B*). On the one hand, I will evaluate the impact of management practices on the evolution of diversity dynamics while considering the same eco-evolutionary scenarios. I will investigate whether these mechanisms play a similar role in the evolution of diversity when considering specific case studies – compared to the simple one. Indeed, as they might interact with many ecological and environmental variations (landscape features, spatial variation in temperature, management practices...) it is important to evaluate how they will act in a specific context and whether some other parameters might influence their impact. On the other hand, as punctual genetic and demographic data are available, before and after the implementation of management practices in these case studies, I will compare available empirical data to simulation data to determine whether the inclusion of evolutionary-based mechanisms improves or degrades the ability of the model to predict the empirical findings.

A. Simplified case study		
<ul style="list-style-type: none"> - <i>First contact in a single reach</i> - <i>No environmental variations</i> - <i>No movement</i> - <i>Fixed temperatures</i> - <i>Equal frequencies: 50% MED - 50% ATL</i> 	<p style="text-align: center;">Role of mating preference?</p> <p style="text-align: center;">Role of selection driven by temperature?</p> <p style="text-align: center;">Impact of heterogamous preference on selection?</p>	
B. Real case studies		
<ul style="list-style-type: none"> - <i>Complex hydrographic networks</i> - <i>Environmental variations</i> - <i>Individuals movement</i> - <i>Variable temperatures</i> - <i>Unequal initial frequencies</i> 	<p style="text-align: center;">Similar role for eco-evo mechanisms?</p> <p style="text-align: center;">Influence on management practices?</p> <p style="text-align: center;">Proximity to reality?</p> <p style="text-align: center;">Differences?</p>	
<i>Case study 1: The Chevenne Creek</i>	<i>Case study 2: The Borne River 1988</i>	<i>Case study 3: The Borne River 2004</i>

Figure 4—2: Overview of chapter 4's case studies and main problematics.

This will help identify the relevant mechanisms – and related ecological contrasts – that influence the most the evolution of intraspecific diversity and hybridization between the lineages. This should allow telling whether EEMs really matter for the management of hybridization and intraspecific diversity. If so, knowledge regarding such mechanisms could help develop eco-evolutionary-based approaches to manage intraspecific diversity when populations have been admixed or are at risk of admixture. For example, information on spatiotemporal variations of key environmental factors, such as temperature could be crucial to build future suitable management strategies for intraspecific diversity.

4.2 DEFINITION OF THE ECO-EVOLUTIONARY SCENARIOS

4.2.1 *Main eco-evolutionary scenarios implemented*

The neutral scenario. The neutral scenario assumes no mating preference or survival differences between the MED and the ATL lineages. Default parameters are used for both lineages and all individuals should undergo similar processes independently of their genotype. Random preference will be applied with a 50% chance to mate with any males, no matter their phenotype. Embryonic survival will not be dependent upon maternal genotype.

The heterogamous preference scenario. (*Also referred to as heterogamy for more simplicity on graphical representation*). This scenario assumes heterogamous preference: female preference is based on phenotypic dissimilarity, wherein females prefer males showing contrasted phenotype in relation to their own phenotype, following (Gil et al., 2015) findings. *Figure 4 – 3* displays the female preference curve implemented in the model, as a function of male phenotypes, for each female genotype. However, the phenotype is not explicitly represented in our model. Yet the correlation coefficient between the genetic markers allowing distinguishing between lineages and phenotypic variation is estimated to be around 0.35 to 0.7 depending on the sources (Aparicio et al., 2005; Folio et al., 2021; Scimabio Interface additional data). We, therefore, assumed that 35 % of the decision of the female was based on the male genotype, whereas the other 65% were random (following *Equation 3 – 15*).

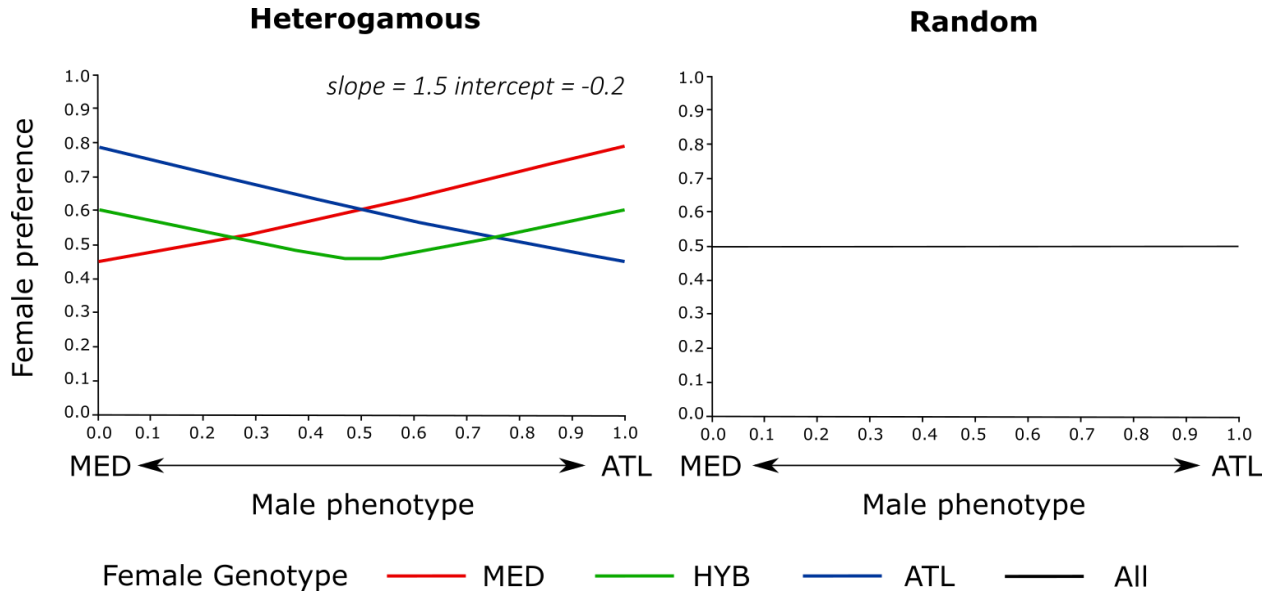


Figure 4—3: Female heterogamous and random preference curves implemented in the model. The heterogamous preference function is implemented with a GCP at 35% and shows a preference for dissimilarity as a function of male introgression.

The genotype-by-environment interactions scenario. (Also referred to as GxE for more simplicity on graphical representation). This scenario assumes a genotypic-based fitness difference, wherein embryonic survival is depending on a maternal gene-by-temperature interaction. Post-zygotic survival is hence implemented as a function of the maternal genotypic score and mean winter temperature experienced up to hatching. Parameter values have been chosen so that the survival curve of each genotype approximately fits the survival observed in natural environments (Folio et al., 2021). At an 8°C temperature, there is no difference in survival between eggs with different maternal genotypes. As water temperatures get colder, offspring with MED maternal genotype have an increasingly higher survival compared to offspring with ATL maternal genotype. Survival curves in various temperature conditions are represented in figure 4 – 4 as a function of maternal genotype. Paternal genotype effects were not accounted for, since they appeared to be minor compared to maternal effects (Folio et al., 2021).

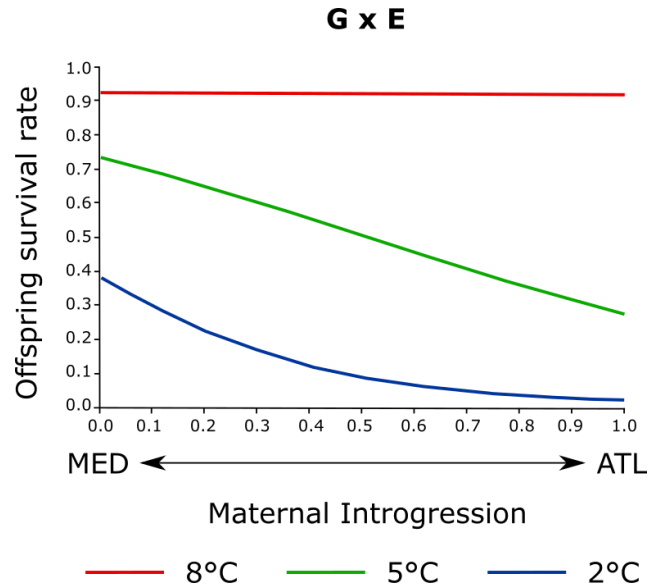


Figure 4—4: Offspring survival curve implemented in the model at hatching as a function of maternal introgression for various modalities of temperature and scenarios considering $G \times E$ interactions.

The heterogamy + $G \times E$ scenario.

This scenario assumes that both potential EEMs driving hybridization apply: pre-zygotic (using the above-described heterogamous mating preference) and post-zygotic (using the above-described maternal genotype-by-environment interaction). This scenario will be used to investigate the relative role of the two mechanisms on intraspecific diversity dynamics.

4.2.2 Sensitivity analyses

Since these pre and post-zygotic isolation mechanisms have only been studied in a specific environment (Folio et al., 2021; Gil et al., 2015), I will analyse the model sensitivity to variation in pre- and post-zygotic isolation parameters.

Heterogamous preference.

Sensitivity analyses were performed by changing the genetic contribution to the preference (GCP, *i.e.* the percentage of the choice that was based on the genetic

dissimilarity between the female and the male) while keeping the same shape for the preference curve (*i.e.* same slope and intercept, *Figure 4 – 3*). Knowing that observed correlation between phenotype and genotype may vary within samples and populations, we tested scenarios where 35% (correlation observed in Aparicio et al., 2005 & Gil et al., 2015), 50% (correlation observed in general data on Haute-Savoie, Scimabio Interface Expertise), 70% (correlation observed in Folio et al., 2021) and 100% of the choice followed the heterogamous preference curve.

GxE interactions. Model sensitivity analyses were performed by conducting a factorial design simulation to investigate how variations in GxE strength combined with different winter temperatures influence the evolution of intraspecific diversity. The strength of GxE interactions was either low (*Figure 4 – 5, A*), medium (*Figure 4 – 4*) or high (*Figure 4 – 5, B*).

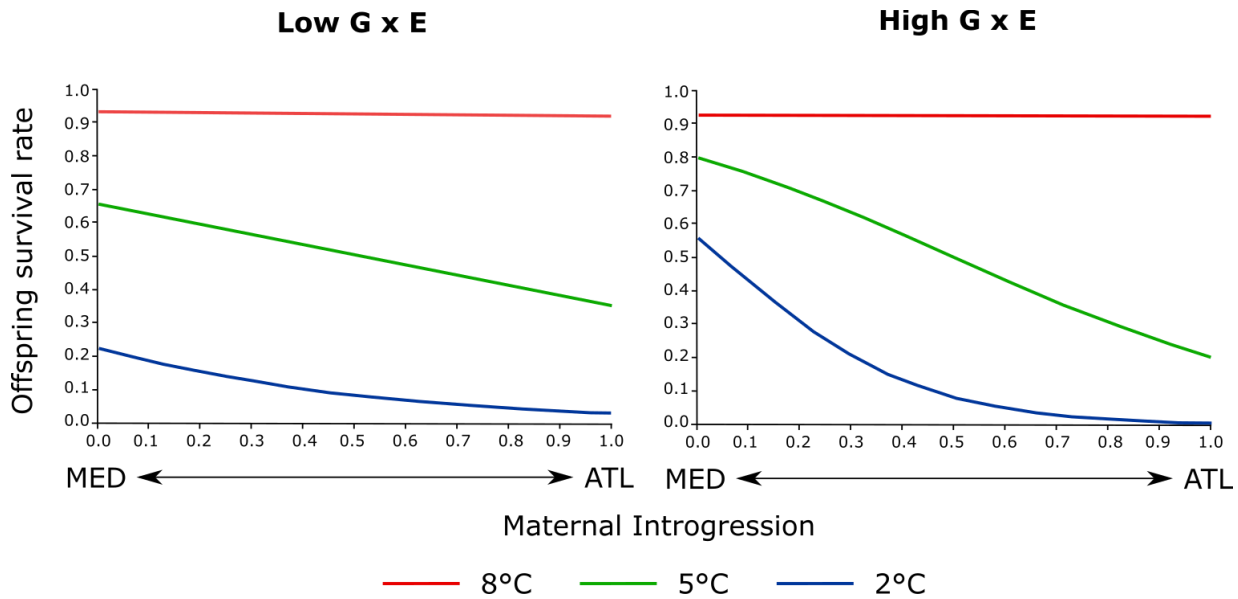


Figure 4—5: Survival curves as a function of maternal introgression for various temperatures and when the strength of G x E selection is considered low or high.

4.3 EXPLORING VARIOUS ECO-EVOLUTIONARY SCENARIOS IN A BASIC CASE STUDY OF FIRST SECONDARY CONTACT

This first section will use MEDITERRANEA to explore the potential role of both EEMs implemented in the model – *i.e.* mate preference behaviour and gene-by-temperature survival – on the evolution of intraspecific diversity. To do so I will follow diversity dynamics in a simple case study of first contact between the ATL and the MED lineages. Here, to avoid as many confounding ecological effects as possible, the environment will be as simple as possible even if yet unrealistic. Therefore environmental variables that may affect population dynamics – such as connectivity, temperature or fishing regulation – will be, either fixed, discarded or removed. In this context, I will use my simulation framework to investigate the role of (i) mate preference behaviour – with a focus on heterogamous preference, (ii) gene-by-temperature survival applied to embryonic survival, as well as (iii) the relative effect of each factor on the evolution of intraspecific diversity. Following first contact, one would expect that a heterogamous preference would increase and/or speed up the rate of hybridization, as mating between dissimilar mates – of each lineage – will be favoured. However, this is only expected to be true during the early time step when pure individuals are still dominant in the population. Prediction for heterogamous preference when a population mainly consists of a variety of HYB individuals is less straightforward. Regarding demography, heterogamous preference might lead to a different outcome compared to random preference. Indeed, heterogamous preference strength varies between 0.45 to 0.8 based on phenotypic dissimilarity whereas random preference strength is always set at 0.5. Based on the level of dissimilarity involved in mating, this may cause populations' mating success to vary. As survival – a fitness component – is a strong determinant of short and long-term population dynamics, gene-by-temperature selection should favour the increase of the advantageous genetic variation – here MED alleles inherited maternally only. The higher the selective pressure is – here lower temperature – the more native diversity should be favoured over time.

4.3 Exploring various eco-evolutionary scenarios in a basic case study of first secondary contact

Knowing that embryonic survival is only dependent upon maternal genetic variation when both barriers are considered hybrid individuals originating from the MED maternal lineage might be favoured.

4.3.1 Simulations settings

Initial ecological settings. A very simple ecological setting will be used to describe the environment so to avoid any confounding effects. Hence, the hydrographic network will only contain one reach of 5000m² – 1000 metres in length and 5 metres in width – to discard the acknowledged role that connectivity and movement have on population dynamics (Fronhofer & Altermatt, 2017; He et al., 2019; Labonne et al., 2008). All quality parameters for carrying capacity and reproduction are set at the maximum, and maximum density is set at approximately 40 ind.100m⁻². Fishing regulation is set on full reserve all along the simulation. Only settings for temperature and EEMs will vary among simulations based on the scenario. All other parameters are set by default.

Initial population. To simulate first contact between both lineages, the initial data file contains an equal number of pure MED and pure ATL individuals – here 1000 individuals for each lineage – with an equal and balanced sex ratio. All individuals are introduced as adults or sub-adults in the model with age starting from 21 months as they are introduced in September – birth month is hypothesised to be December. This will allow the majority of individuals to mature during the first mating season.

Temperature settings. Temperatures are informed per month with only two values: a mean winter temperature from November to April and a mean summer temperature from May to October. This simplification will allow us to test the impact of gene-by-temperature post-zygotic isolation on embryonic survival at hatching while knowing the exact winter temperature applied. Summer temperature will be

fixed among simulations and is set at 12°C, while winter temperature will vary to test for the sensibility of diversity to the selective pressure exerted by temperature. There will be three modalities for winter temperatures: a low (2.5°C), a medium (5°C) and a high (8°C) modality. As shown in *Figure 4 – 4*, the low-temperature modality is associated with a larger fitness difference between the lineages while the high-temperature modality is not associated with any differences.

Simulation framework. The same initial data file is used for all simulations and 20 simulations – replicates – are run per scenario. Each simulation starts in September and is run over 100 years to track the evolution of diversity dynamics and demography over a long period under the four eco-evolutionary scenarios described above.

4.3.2 The role of heterogamous preference

4.3.2.1 Evolution of diversity dynamics under random vs heterogamous preference

Whatever the mating preference considered – random or heterogamous preference – diversity dynamics evolved similarly over time. The population rate of introgression (*Figure 4 – 6*) was stable, and its mean value was around the initial value of 0.5. The mean introgression rate seemed slightly lower (~ 0.47) for simulations including heterogamous preference compared to random preference (~ 0.5). However, confidence intervals overlapped more and more over time, suggesting that heterogamous preference might not influence introgression dynamics.

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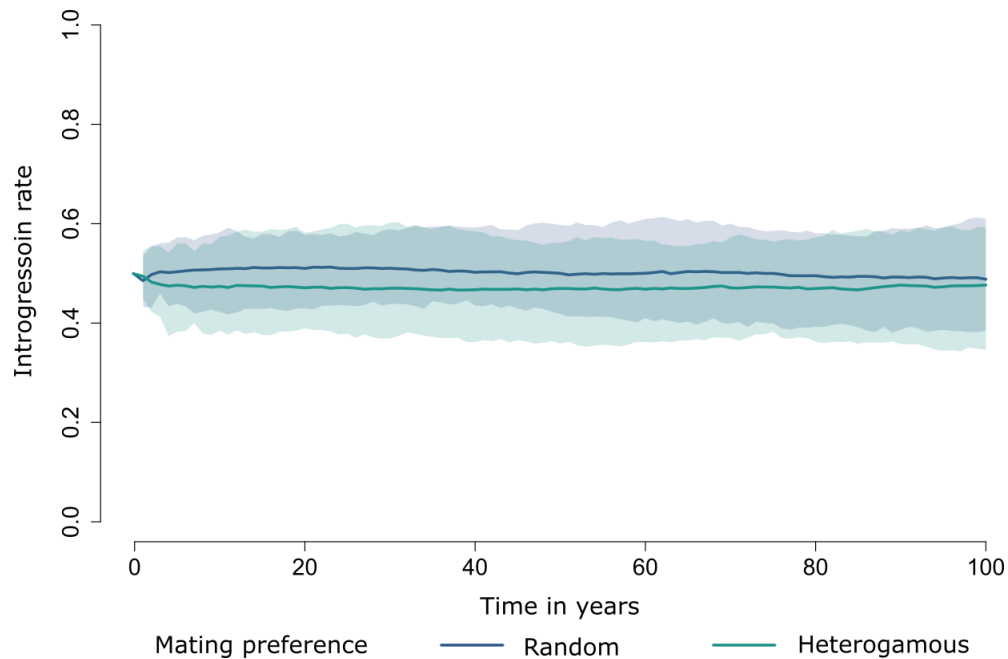


Figure 4—6: Evolution of introgression rate over a hundred years considering random versus heterogamous preference (GCP = 35%). Solid lines represent mean values averaged over 20 simulations while polygons are 95% credible intervals.

Despite a stable introgression rate, the composition of the population (Figure 4 - 7) – MED, HYB and ATL – changed rapidly over the first time steps. Indeed, a rapid decrease of pure genotypes – MED and ATL – was observed within the first 10 years, up until their extinction (Figure 4 - 7, from 1000 to 0). Meanwhile, HYB individuals were created. Therefore, random and heterogamous preferences led to the same outcome at the same pace: a population exclusively made of HYB individuals. However, differences can be observed between both scenarios when focusing on the distribution of individual introgression at early time steps (Figure 4 - 8).

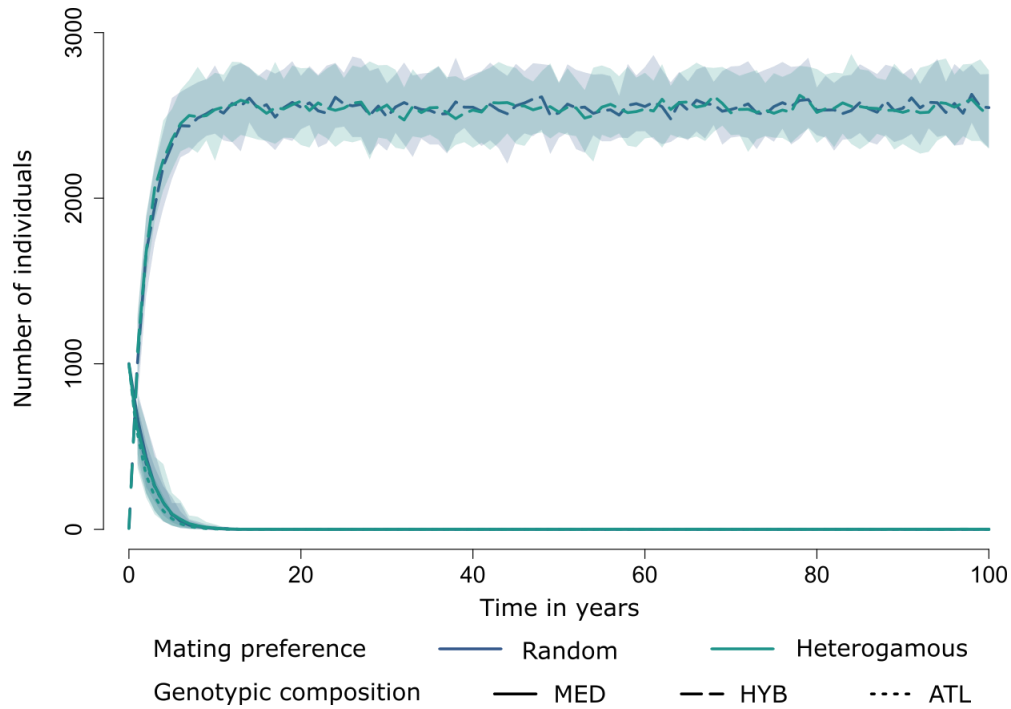


Figure 4—7: Evolution of the genotypic composition of the population – proportions of MED (full lines), HYB (dashed line) and ATL (dotted line) genotypes – over a hundred years considering random versus heterogamous preference (GCP = 35%). Solid lines represent mean values averaged over 20 simulations while polygons are 95% credible intervals.

During the first time step (Figure 4 – 8, $t = 1$), heterogamous preference led to the creation of more HYB individuals compared to random preference (a mean of 1075 vs 1000 individuals). Heterogamous mating was, therefore, slightly more frequent initially. Along that, numbers of pure genotypes were also lower when considering heterogamous preference (600 vs 670 individuals for MED, 580 vs 610 individuals for ATL), suggesting that homogamous mating might be less frequent. However, differences between scenarios remained small, and confidence intervals were sometimes overlapping. In addition, this slight difference rapidly faded away with the creation of a wide range of HYB – less (< 0.5) and more (> 0.5) highly introgressed.

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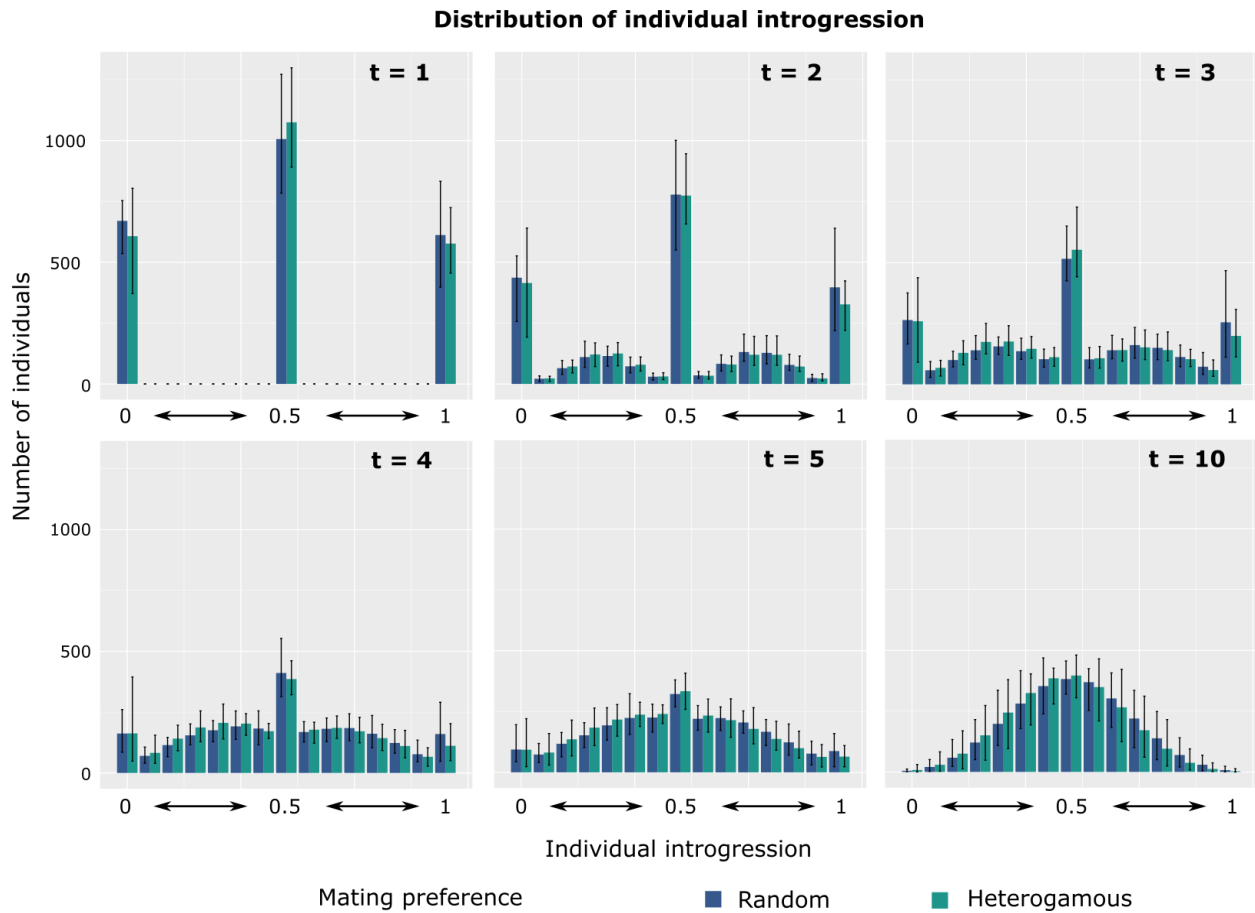


Figure 4—8: Distribution of individual introgression during early time steps considering random versus heterogamous preference ($GCP = 35\%$). Rectangular bars represent the mean number of individuals per class of individual introgression while error bars are 95% CI.

Overall, both scenarios homogenised very early with the distribution of individual introgression forming a bell shape centred on 0.5 (Figure 4 – 8, $t = 10$). This distribution stayed stable over the long term for both scenarios (Figure 4 - 9), with a final distribution still centred on 0.5. It is interesting to note that, for the heterogamous scenarios, more MED individuals were found in time step 2 compared to ATL individuals (Figure 4 – 8, 414 vs 327 individuals), which may explain the fact that the population introgression rate was slightly lower than 0.5 initially (Figure 4 – 6). The initial composition of the population and random

processes that affect genotype frequencies might therefore play an important role in the evolution of diversity dynamics.

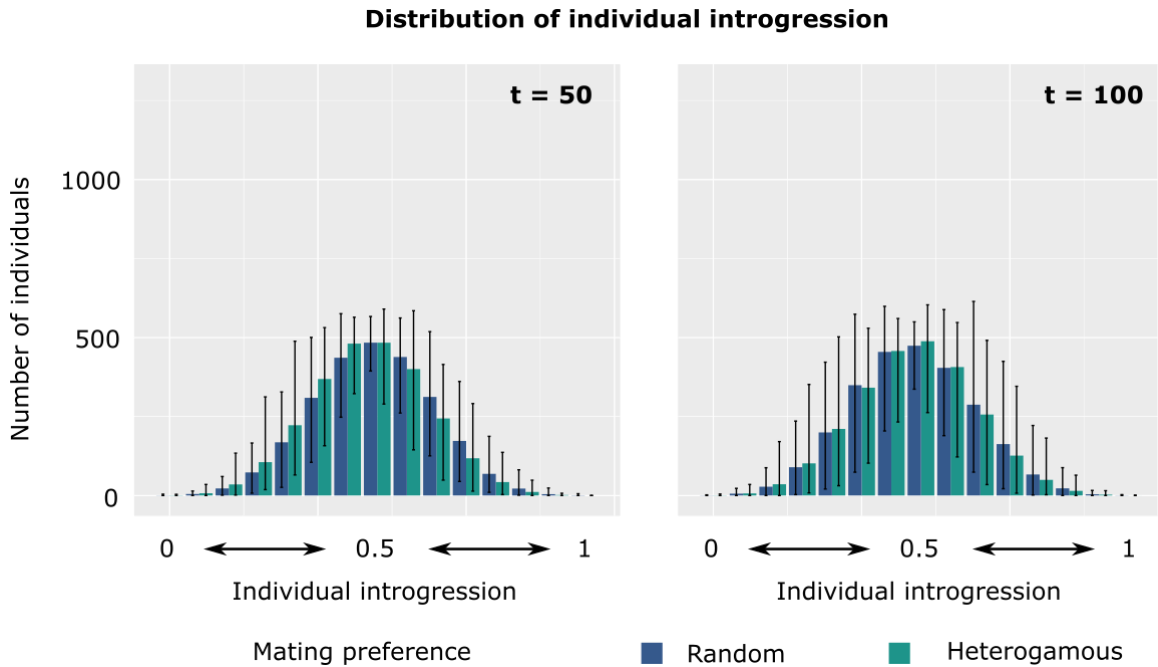


Figure 4—9: Distribution of individual introgression after 50 and 100 years of evolution considering random versus heterogamous preference (GCP = 35%). Rectangular bars represent the mean number of individuals per class of individual introgression while error bars are 95% CI.

4.3.2.2 Evolution of demography under random vs heterogamous preference

Demography – *i.e.* population size and age class structure – was stable over time (Figure 4 – 10). The number of juveniles varied around 2000 individuals with small pics each year, indicating a small variability in yearly reproductive success. Sub-adults and adults dynamics were smoother, as mortality applied at each stage (stage-specific and density-dependent mortality) controlled for the number of individuals recruited to the next life stage. The number of individuals recruited at sub-adult stage was more than four times lower than the number of juveniles. Similarly, the number of adults was twice as low as the number

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of sub-adults. Overall, demography was similar for both scenarios, suggesting that heterogamous preference does not seem to affect the mating success of the population.

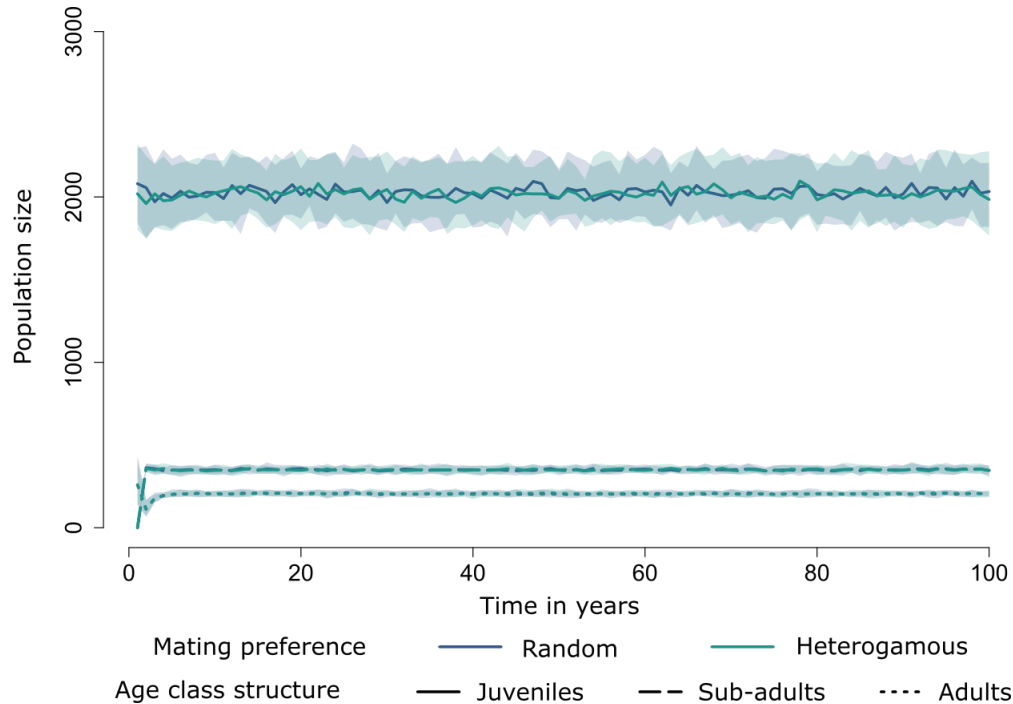


Figure 4—10: Evolution of demography structured per age class – juveniles (full lines), sub-adults (dashed line) and adults (dotted line) – over a hundred years of evolution considering random versus heterogamous preference (GCP = 35%). Lines represent mean values averaged over 20 simulations while polygons are 95% credible intervals.

Heterogamous preference, implemented with a GCP of 35%, appears to have very little impact on diversity dynamics and demography over the long term. Heterogamous preference might slightly influence the outcome of first secondary contact (1st time step only) – with more mating involving MED and ATL individuals. However, its effect seems to fade away when HYB individuals are created, as heterogamous preference might not matter anymore when the population is entirely composed of very similar HYB individuals.

4.3.2.3 Sensitivity analyses on the genetic contribution to preference (GCP)

Sensitivity analyses were performed on the value of GCP implemented in the model to account for variability in the potential correlation between phenotype and genotype. They also allowed evaluating whether the lack of effect was due to the low contribution of the heterogamous preference curve to the mating decision (only 35% vs 65% random).

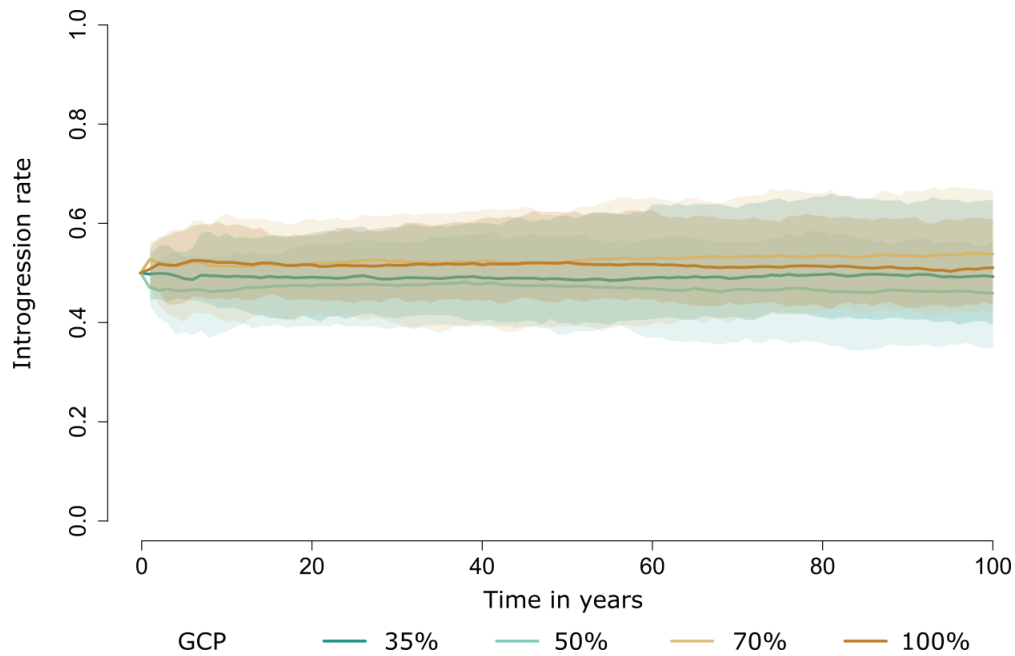


Figure 4—11: Evolution of introgression rate over a hundred years considering heterogamous preference with various values of GCP. Solid lines represent mean values averaged over 20 simulations while polygons are 95% credible intervals.

Looking at introgression and genotype proportion, variations in GCP did not influence significantly the evolution of introgression rate (Figure 4 – 11: slight variations of mean values around 0.5 between [0.48, 0.53], and overlapping CI) nor that of the genotypic composition of the population (Figure 4 – 12).

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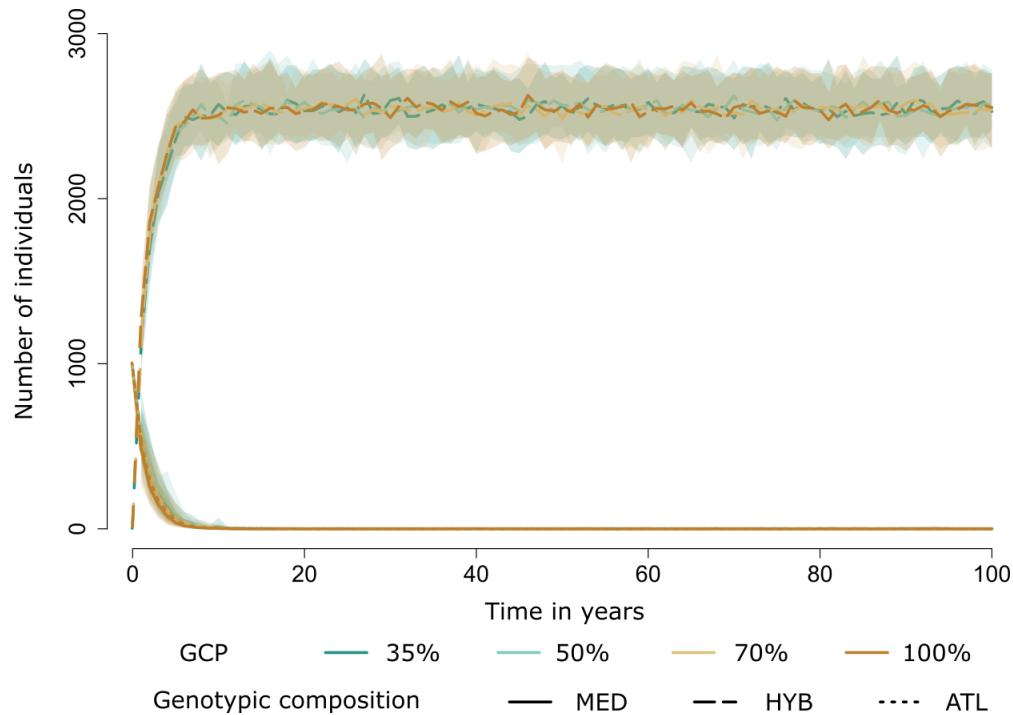


Figure 4—12: Evolution of the genotypic composition of the population – proportions of MED (full lines), HYB (dashed line) and ATL (dotted line) genotypes – over a hundred years considering heterogamous preference with various values of GCP. Solid lines represent mean values averaged over 20 simulations while polygons are 95% credible intervals.

However, the distribution of individual introgression during first contact (Figure 4 – 13, $t = 1$) showed that the higher the value of GCP is, the more HYB individuals are created during the first time step (going from 1140 to 1290 individuals), confirming that heterogamous mating might be more frequent. Following the creation of HYB, this slight difference among scenarios started to fade away. Nevertheless, the final distribution of individual introgression (Figure 4 – 13, $t = 100$) highlighted few differences in the bell shape of the distribution, but no effects appeared to be significant as distributions all remained centred on 0.5 with large and overlapping confidence intervals. Convergence for such patterns might not be reached with 20 replicates considering the amount of stochasticity that remains in the mating decision (Section 3.3.6).

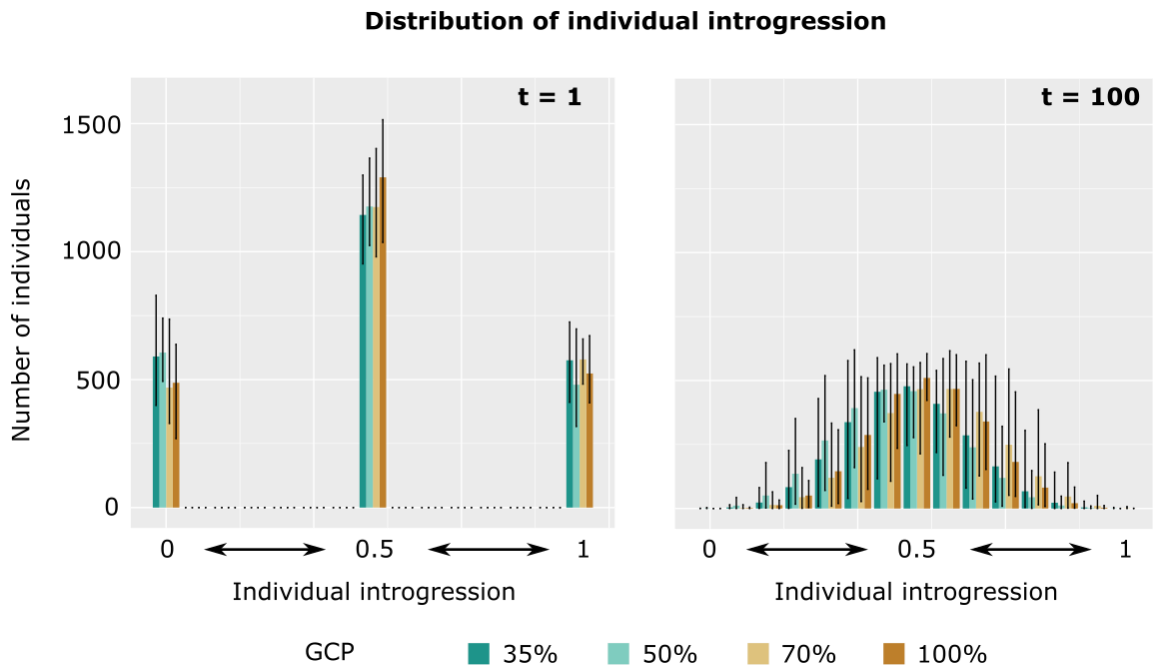


Figure 4—13: Distribution of individual introgression after 50 and 100 years of evolution considering heterogamous preference with various values of GCP. Rectangular bars represent the mean number of individuals per class of individual introgression while error bars are 95% CI.

4.3.2.4 Discussion

Effect on diversity. These results suggest that heterogamous preference might play a very little role in the evolution of intraspecific diversity. Indeed, despite the implementation of a higher genetic contribution to preference (CPG) – up to 100%, the effect of mating preference on diversity dynamics over the long term remained marginal. In fact, the predicted patterns were quite variable when testing different values of GCP, suggesting that random processes might strongly influence the outcome of diversity dynamics.

Heterogamous preference only appears to influence the outcome of the first contact by leading to the creation of more HYB individuals initially. During a first contact, only pure genotypes – MED and ATL –

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encounter each other. Since female preference is based on a scale of phenotypic dissimilarity, it is easier to visualise the effect of heterogamous preference in such contexts, where only the two extreme values of dissimilarity can be found - entirely dissimilar mates (MED-ATL) or entirely similar mates (MED-MED or ATL-ATL). Indeed, when heterogamous preference is applied, the strength of female preference is almost twice as high for entirely dissimilar mates (~ 0.8) compared to entirely similar mates (~ 0.45), meaning that when GCP is considered at its maximum, heterogamous mating is twice as likely to occur compared to homogamous mating. Whereas, when random preference is considered, heterogamous mating and homogamous mating have equal chances to occur.

However, throughout time, with the creation of a wide range of hybrids and the disappearance of pure genotypes, it becomes more and more difficult to envision and predict the effect of such preference. Indeed, after only a few years of evolution, the population homogenises and is mainly composed of highly similar HYB individuals. Considering that female preference is absolute (*i.e.*, its strength is expressed between the minimum and maximum theoretical dissimilarities [0 to 1]), heterogamous preference might not be expressed as much in that context, as when extremely dissimilar phenotypes can be encountered (*Section 3.3.6: see absolute vs relative preference*).

Mating stochasticity.

In our model, despite the implementation of a preference function, the outcome of mating remains the result of a combination of stochastic factors including available genotypic variation and mating decision (*Section 3.3.6*). On the one hand, mating can only occur within mature individuals located in the same reach at a given time step, which will be determined by a variety of processes, all partly stochastic (survival, movement ...). Therefore, mate choice is likely to be variable in space and time since population composition may vary. Moreover, a stochastic sampling routine in the model – independent of phenotypes or genotypes – determines the mating pool available to a given

female at a given time step, making initial encounters and pairing entirely random. In other terms, the preference strength and GCP only increase or decrease the chances of certain types of mating being successful, but they are entirely only conditioned to the fact that an encounter occurs. Additionally, the ultimate mating decision results from a random draw in a binomial process, even if the value of GCP governs the probability of this process.

All of this makes the outcome of mating at the population level challenging to predict, despite the implementation of a specific mating preference, such as heterogamy. For instance, ultimate mating success will strongly depend on stochastic events and the structure of the population (Klug & Stone, 2021). Indeed, chance may play an important role in determining mating success and has been shown to influence the strength of sexual selection mechanisms (Jennions et al., 2012; Sousa & Westneat, 2013; Sutherland, 1985). However, the relative effect of chance may vary with other factors, such as OSR and frequency of advantageous phenotypes (Klug & Stone, 2021). It is therefore difficult beforehand to predict how various factors will influence mating processes (Jennions et al., 2012), even when there is evidence of some sexual selection mechanisms (Hubbell & Johnson, 1987; Sutherland, 1985).

It also proves that knowing the existence of a mechanism - here heterogamous mating - and even having quantified its strength in nature does not allow making intuitive predictions on the influence of such mechanisms in the general eco-evolutionary trends of a population. The DG-ABM approach typically helps us to project the effect of such mechanisms in the complexity of life cycles, space, inter-individual interactions and heredity, and the outcome may somewhat differ from our initial expectations.

A very specific context. The present simulations were tuned to envision a rather theoretical population, with a large number of spawners and a specific initial population structure - an equal

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proportion of MED and ATL individuals and an equal OSR. Considering this context, it is not entirely surprising that random preference also led to extensive hybridization, since the initial chance of dissimilar individuals encountering was high, and progressively became higher with time as parental genotypes rarefied. In reality, many situations may occur where both OSR and phenotypic availability are contrasted. In such situations, a specific mating preference may have a greater influence on diversity dynamics. Indeed, the relative effect of chance on mating success may vary depending on OSR and frequency-dependence effects, causing sexual selection to operate more or less in certain contexts (Jennions et al., 2012; Klug & Stone, 2021). In addition, the strength of sexual selection arising from behavioural processes has been shown to change with the environmental and social context (Cotton et al., 2006; Gauthey, 2014).

For example, if one phenotype is more frequent, despite random preference, mating should be biased toward that common phenotype, as it should be encountered more often due to chances. On the opposite, heterogamous preference might advantage the rare phenotype, when encountered, due to negative frequency dependence effects (Kokko et al., 2007; O'Donald & Majerus, 1988). Understanding if, and when, stochastic events covary with biological factors of interest is important to determine in which cases we might expect sexual selection to be relatively important in shaping evolution (Klug & Stone, 2021).

The importance of representing mating interactions. As reproductive interactions are known to drive evolutionary dynamics (Maan & Seehausen, 2011), explicit representation of sexual interactions remains important in any case, despite the lack of apparent effects on diversity dynamics in this context. This is particularly important when considering adaptive processes. Indeed, mate choice could have more effect on diversity dynamics and demography in cases where the trait under sexual selection is also under natural selection (Chevalier et al., 2020; Thibert-Plante & Gavrillets, 2013). It could also play an important

role when sexual selection acts in a different direction compared to other factors of selection (Andersson, 1994), especially when it opposes natural selection (Ellers & Boggs, 2003; Labonne & Hendry, 2010; A. K. Schwartz & Hendry, 2006). Mating is an important process creating the diversity available for selection to occur on. In addition, considering the dynamic aspect of mating systems is important when studying population demography. Indeed, in certain contexts, mating behaviour may play a crucial role in determining the density threshold for population persistence as it may affect the overall fitness and growth of the population (Berec et al., 2018).

Take home message: When considering only heterogamous preference, the effect on diversity dynamics and demography is close to nothing in our model and the conditions simulated.

4.3.3 The role of GxE interactions on survival

4.3.3.1 Evolution of diversity dynamics under neutral vs GxE survival

Now turning to a possible source of post-zygotic isolation mechanism – GxE interactions on embryonic survival in relation to water temperature –, very clear and divergent results can be observed in our simulations, conditional on the presence or absence of GxE interactions. When implementing GxE interactions on embryonic survival, the introgression rate (*Figure 4 – 14*) did not stabilise and decreased continuously over time, reaching approximately 0.1 after a hundred years of evolution. Conversely, it remained stable and centred on 0.5 for the neutral survival scenario. The confidence interval was rather low, which implies that the implementation of GxE interactions has a rather strong effect, making the result more predictable.

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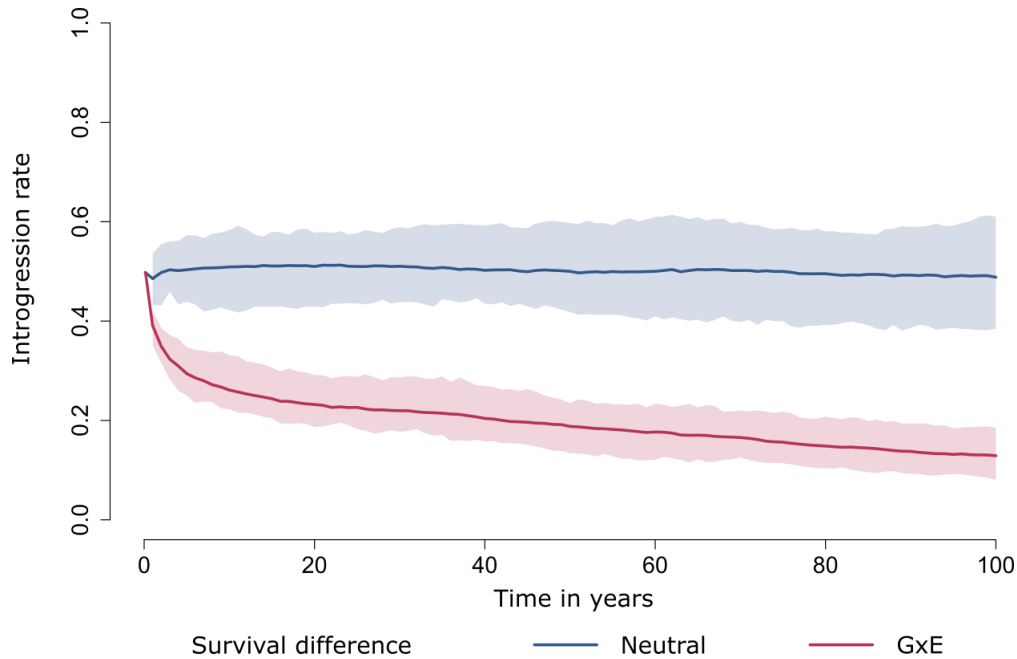


Figure 4—14: Evolution of introgression rate over a hundred years considering neutral versus GxE interactions on embryonic survival (medium strength) applied at 5°C. Solid lines represent mean values averaged over 20 simulations while polygons are 95% credible intervals.

Focusing on genotype proportions (Figure 4 – 15), the composition of the population changed rapidly over the first time steps for both scenarios, with the number of HYB going up fast while that of pure native genotypes was going down. While both scenarios led to a population mainly composed of HYB individuals after a hundred years, the implementation of GxE interactions allowed for the maintenance of some pure MED genotypes. Moreover, the increase of HYB individuals in the population was lower compared to the scenario implementing neutral survival. The numbers of HYB and MED individuals did not stabilise after 20 years. The number of HYB began to decrease slowly but continuously, whereas the number of MED individuals rose at the same pace.

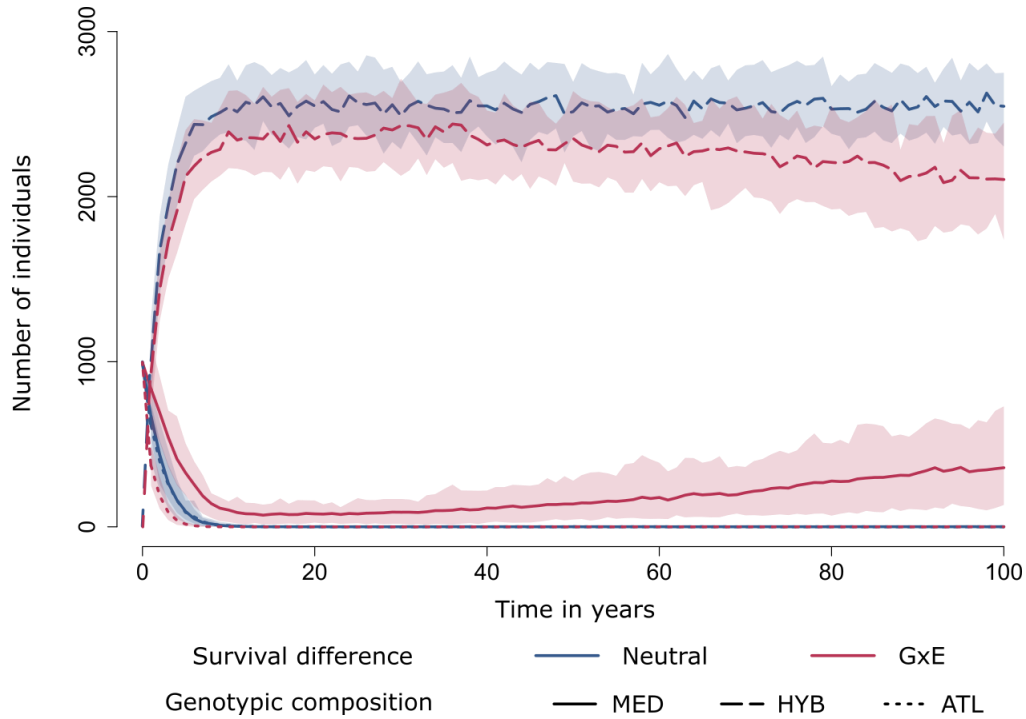


Figure 4—15: Evolution of the genotypic composition of the population – proportions of MED (full lines), HYB (dashed line) and ATL (dotted line) genotypes – over a hundred years considering neutral versus GxE interactions on embryonic survival (medium strength) applied at 5°C. Solid lines represent mean values averaged over 20 simulations while polygons are 95% credible intervals.

The distribution of individual introgression in the population provided a deeper insight into this pattern (Figures 4 – 16 & 4 – 17). Indeed, when first contact occurred (Figure 4 – 16, $t = 1$) a large number of F1 HYB were initially created for both scenarios. However, with the creation of a wide range of HYB individuals, distributions diverged progressively over time (Figure 4 – 16, $t = 10$; neutral: centred on 0.5, GxE: centred on 0.2). Scenarios implementing GxE interactions selected for low introgressed HYB individuals (<0.5). In addition, compared to the neutral survival scenario, a higher number of pure MED individuals was found at each time step while the number of ATL individuals diminished faster.

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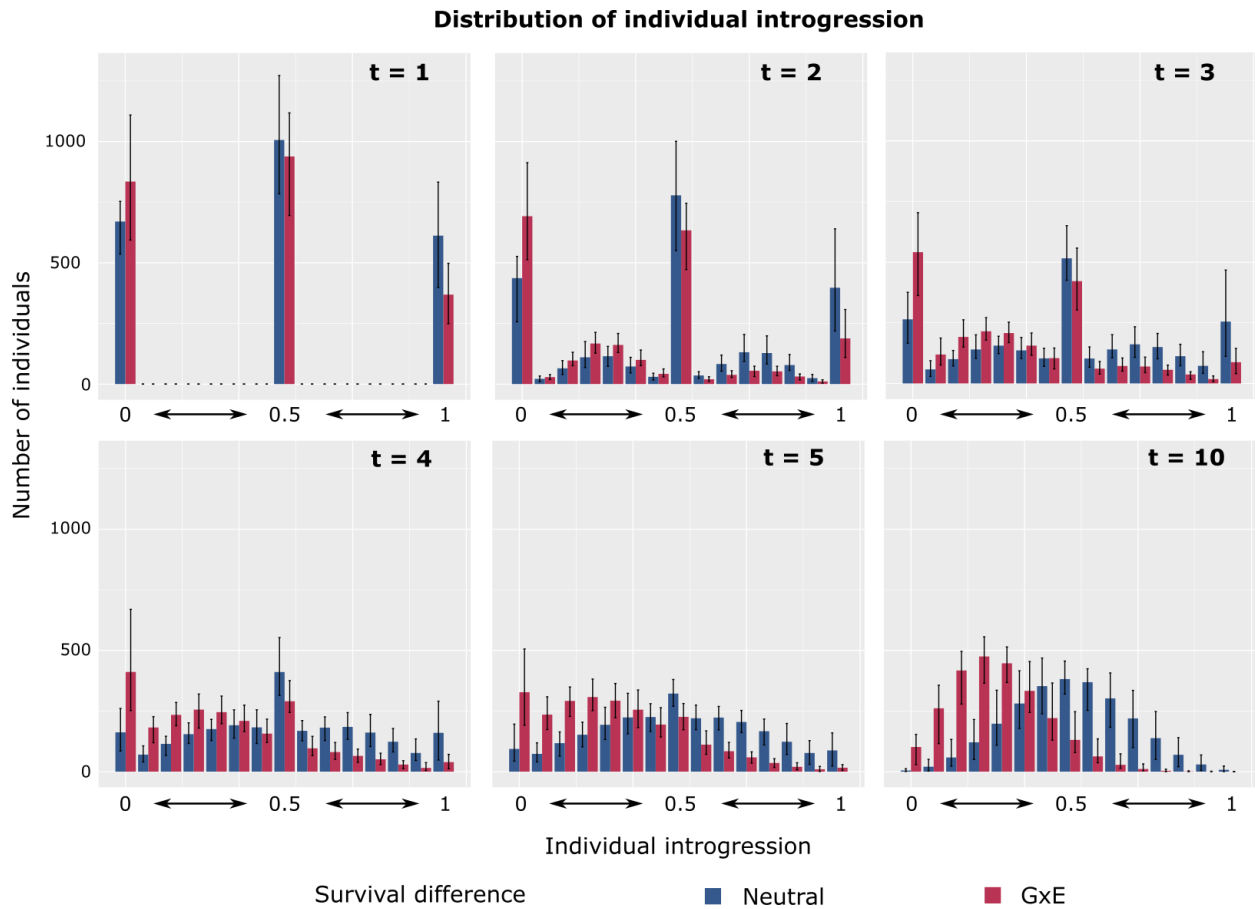


Figure 4—16: Distribution of individual introgression during early time steps considering neutral versus GxE interactions on embryonic survival (medium strength) applied at 5°C. Rectangular bars represent the mean number of individuals per class of individual introgression while error bars are 95% CI.

The distribution of individual introgression stabilised fast for the neutral survival scenario while it continued shifting toward lower values of introgression (*Figure 4 – 17*, distribution centred on 0.28 at = 50 vs 0.14 at $t = 100$) for the GxE survival scenario. Alongside this shift the number of MED individuals increased (*Figure 4 – 17*, ~ 125 at $t = 50$ vs ~ 370 at $t = 100$). Overall, diversity dynamics seem to stabilise rapidly when survival is similar for all genotypes whereas it is still evolving after a hundred years when GxE interactions are implemented.

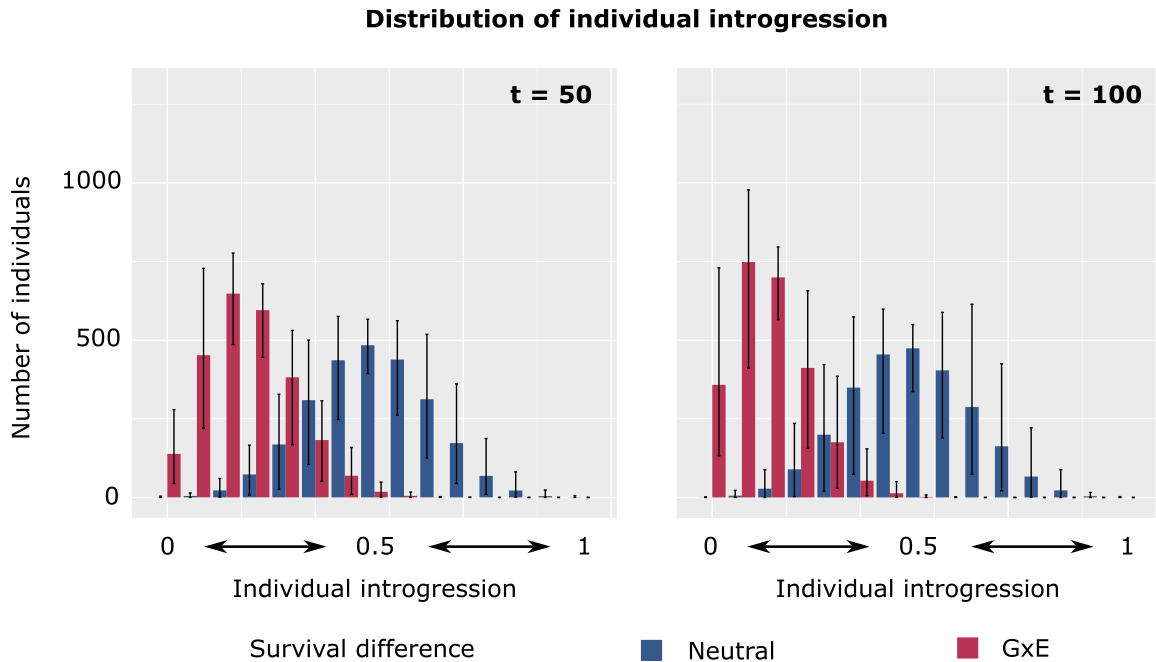


Figure 4—17: Distribution of individual introgression after 50 and 100 years of evolution considering neutral versus GxE interactions on embryonic survival (medium strength) applied at 5°C. Rectangular bars represent the mean number of individuals per class of individual introgression while error bars are 95% CI.

4.3.3.2 Evolution of demography under neutral vs GxE survival

Demography – *i.e.* population size and age class structure – was stable over time (Figure 4 – 18). However, a slightly lower number of juveniles was observed for the scenario implementing GxE interactions (~ 2000 vs 1900). Sub-adults and adults dynamics remained similar among scenarios, suggesting that GxE interactions only affect juvenile dynamics but not recruitment to the other life stages.

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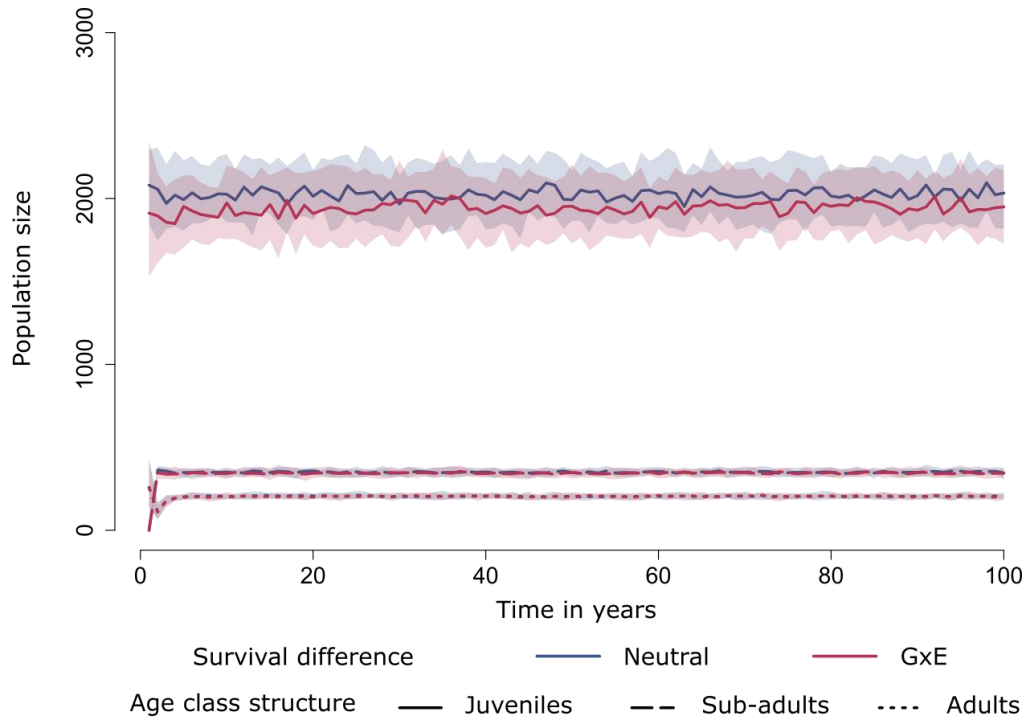


Figure 4—18: Evolution of demography structured per age class – juveniles (full lines), sub-adults (dashed line) and adults (dotted line) – over a hundred years of evolution considering neutral versus GxE interactions on embryonic survival (medium strength) applied at 5°C. Lines represent mean values averaged over 20 simulations while polygons are 95% credible intervals.

G x E interactions, applied at 5°C, appear to impact diversity dynamics and demography over short and long terms. Indeed, GxE interactions influenced the genotypes selected for the next time step by favouring offspring originating from MED females. However, *prior* to selection, initial context (50% MED & 50% ATL) and random mating initially led to the creation of a large amount of F1 HYB individuals. Throughout time, as selection favoured maternally inherited MED alleles, the distribution of individual introgression was progressively biased toward lower values of introgression, leading to an important and continuous decrease in the population introgression rate. The population only appeared to go through a transitory state where HYB individuals were created. Indeed, the selection of MED alleles over time allowed for a slow but progressive increase of MED individuals. GxE interactions also led to lower juvenile population

size, because a part of the population – offspring from the ATL maternal lineage – have lower survival at hatching. This difference was erased during recruitment to the next life stage.

4.3.3.3 Sensitivity analyses on the strength of GxE interactions and temperature

Sensitivity analyses were performed on the strength of GxE interactions (low, medium or high, *Figure 4 – 4, section 4.1.1 & Figure 4 – 5, section 4.1.2*) combined with various winter temperature modalities (2.5, 5 and 8°C) in order to account for possible variations in selective pressure experienced. This allowed evaluating the relative importance of ecological variations, such as temperature, and GxE strength on diversity dynamics and demography.

The strength of GxE interactions had a clear effect on diversity dynamics and demography. This effect was highly controlled by the winter temperature. For the high temperature modality – 8°C – GxE strength did not influence diversity dynamics nor demography, since differences in survival among genotypes are almost null at that temperature (*Figure 4 – 4, section 4.1.1 & Figure 4 – 5, section 4.1.2*). For all three GxE scenarios, HYB individuals were rapidly created and parental genotypes fully disappeared before 10 years (*Figure 4 – 20*). Introgression rates were stable (*Figure 4 – 19*) and distributions of individual introgression were centred on 0.5 (*Figure 4 – 21*). These scenarios are therefore equivalent to the neutral survival scenario.

For the other temperature modalities, – 2.5 and 5°C – GxE strength had a strong impact on diversity dynamics. For all scenarios, the introgression rate decreased over time (*Figure 4 – 19*), but the decrease was steeper and faster when the temperature was lower – at 2.5°C compared to 5°C – and when the strength of GxE interactions was higher.

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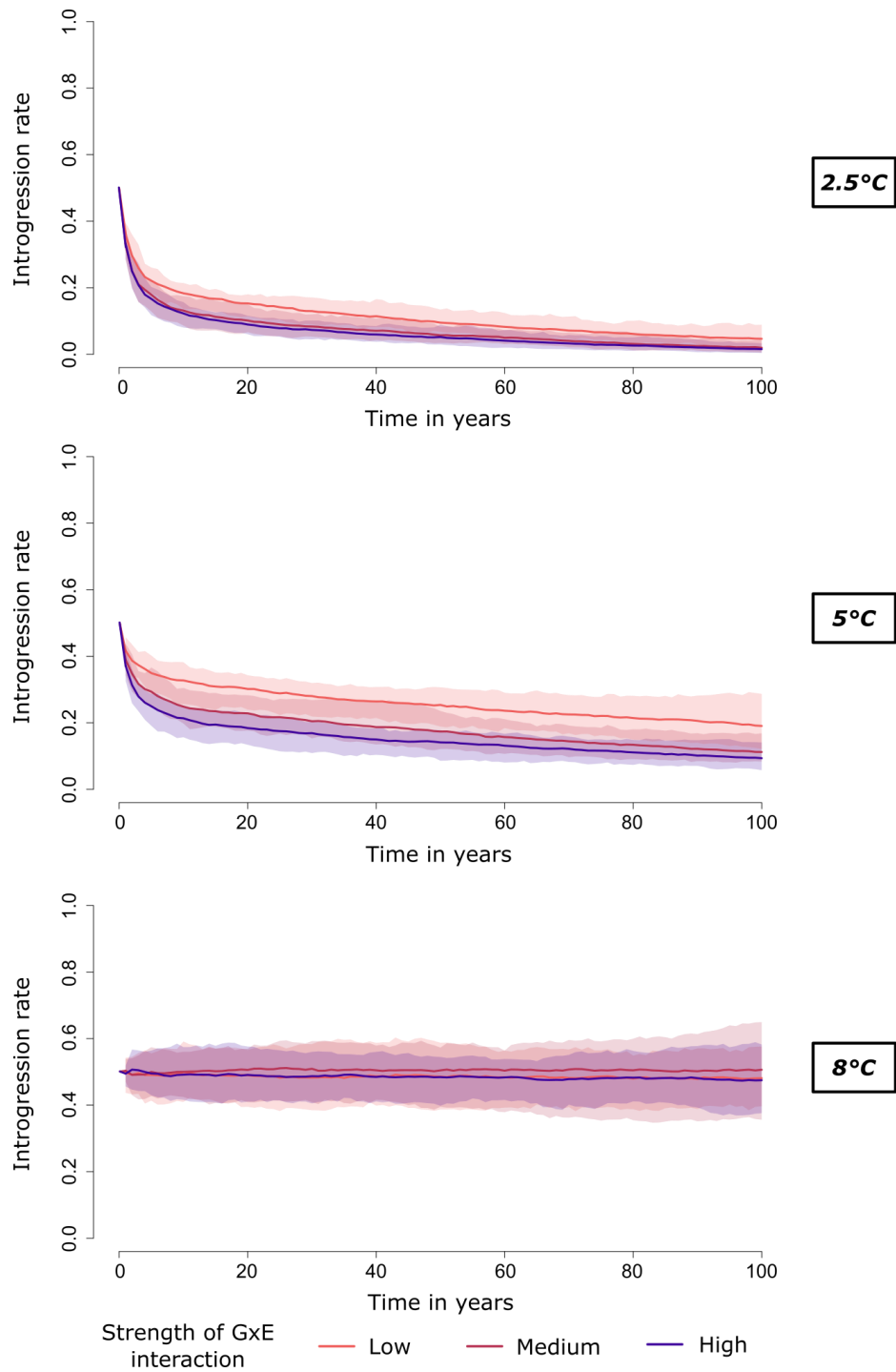


Figure 4—19: Evolution of introgression rate over a hundred years considering various strengths of GxE interactions on embryonic survival, applied at low (2.5°C), medium (5°C) and high (8°C) temperatures. Solid lines represent mean values averaged over 20 simulations while polygons are 95% credible intervals.

However, for the lower temperature, one can notice that introgression dynamics were similar for the medium and the high modality of GxE interactions. Introgression rates reached almost 0 after a hundred years in both cases, suggesting that selective pressures experienced through temperature were strong. This is because differences in survival implemented at lower temperatures are the highest (*Figure 4 – 5, section 4.1.2*).

The evolution of genotypes proportion (*Figure 4 – 20*) highlighted more differences among scenarios and confirmed the combined effect of GxE interactions and temperatures on diversity dynamics. The shift observed in MED and HYB dynamics happened faster when GxE strength was higher and even more so when the temperature was lower. Indeed, comparing GxE scenarios at 2.5°C, the extent of the shift can be visualised within a hundred years. MED individuals took over HYB individuals faster when the strength of GxE interactions was higher – respectively at $t = 55$, $t = 62$ and $t = 95$ for the high, medium and low modalities. Overall, the initial creation of HYB individuals was slightly slower and then decreased faster, while conversely, the decrease in MED individuals was slower and then increased faster, especially when high GxE interactions were implemented. At 5°C, the strength of GxE interactions also affected genotypes proportion but differences appeared lower as the shift happened at a slower rate – because differences in survival implemented are lower (*Figure 4 – 5, section 4.1.2*). Meanwhile, the disappearance of ATL individuals happened at the same rate since the survival of ATL females' offspring is low in any case.

For all scenarios, even the fastest one, the genotypic composition of the population was unstable and still evolved after a hundred years, suggesting that selective pressure enforced by GxE interactions might ultimately lead to a MED population, in the simulated conditions. This pattern was confirmed by the distribution of individual introgression (*Figure 4 – 21*), which shifted faster when GxE interactions were stronger and even more so when temperatures were lower. For example, at 2.5°C the distribution was already biased toward 0 at $t = 50$ years whereas it took longer at 5°C since the distribution was still not centred on 0 – but 0.07 – at $t = 100$, and this for all GxE modalities.

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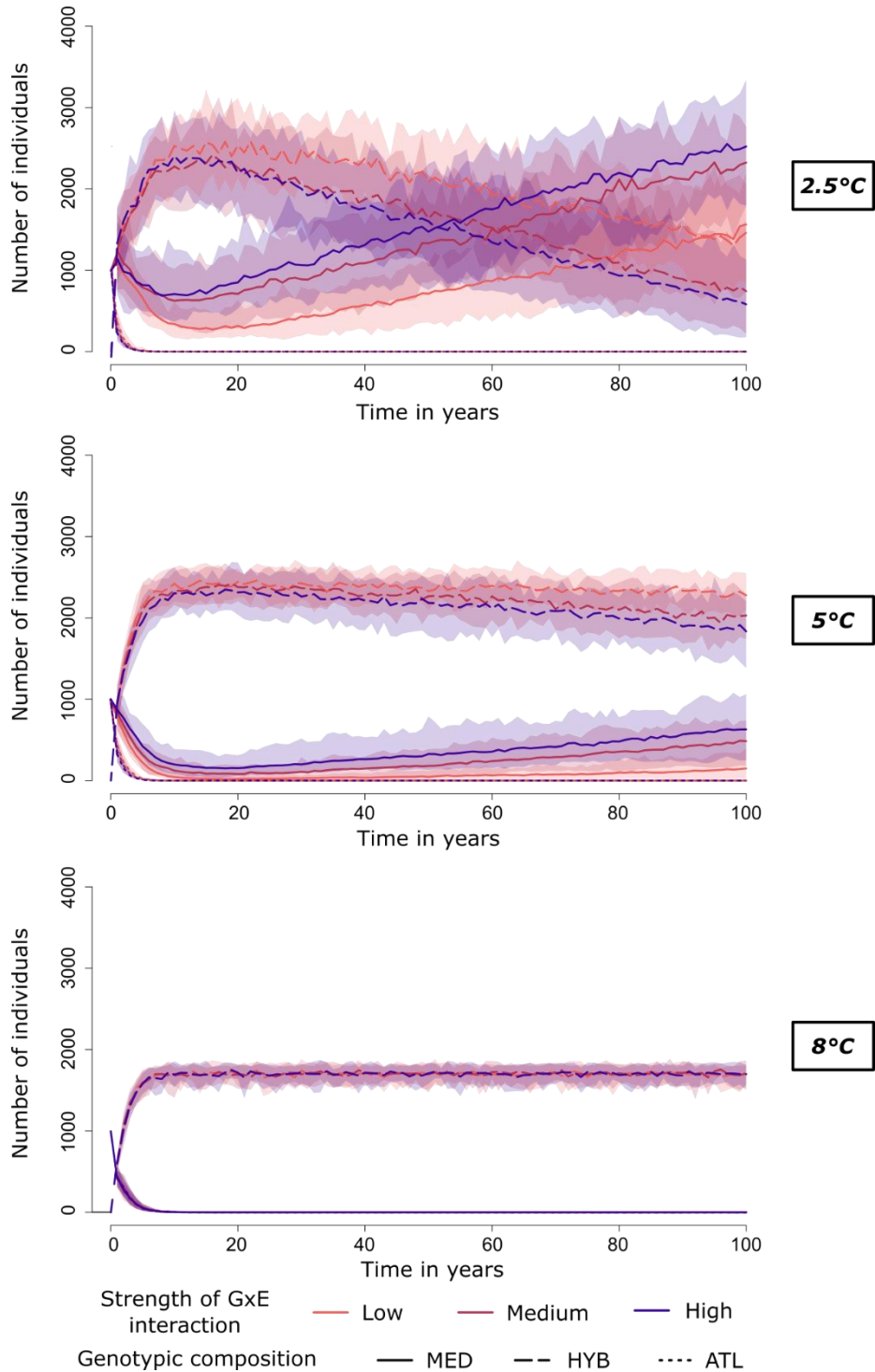


Figure 4—20: Evolution of the genotypic composition of the population – proportions of MED (full lines), HYB (dashed line) and ATL (dotted line) genotypes – over a hundred years considering various strengths of GxE interactions on embryonic survival, applied at low (2.5°C), medium (5°C) and high (8°C) temperature. Solid lines represent mean values averaged over 20 simulations while polygons are 95% credible intervals.

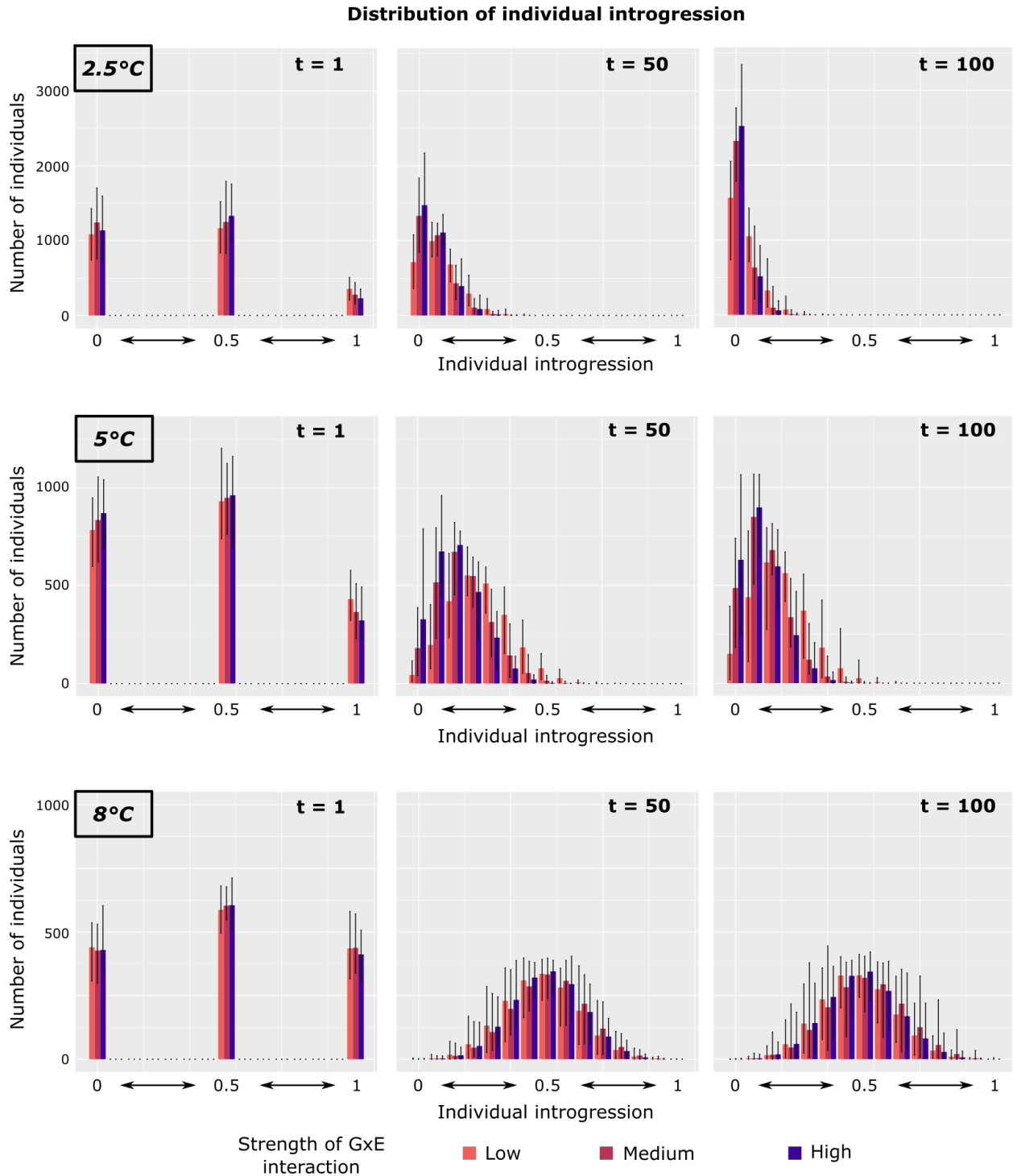


Figure 4—21: Distribution of individual introgression during first contact ($t = 1$) and after 50 and 100 years of evolution considering various strengths of GxE interactions on embryonic survival, applied at low (2.5°C), medium (5°C) and high (8°C) temperature. Rectangular bars represent the mean number of individuals per class of individual introgression while error bars are 95% CI.

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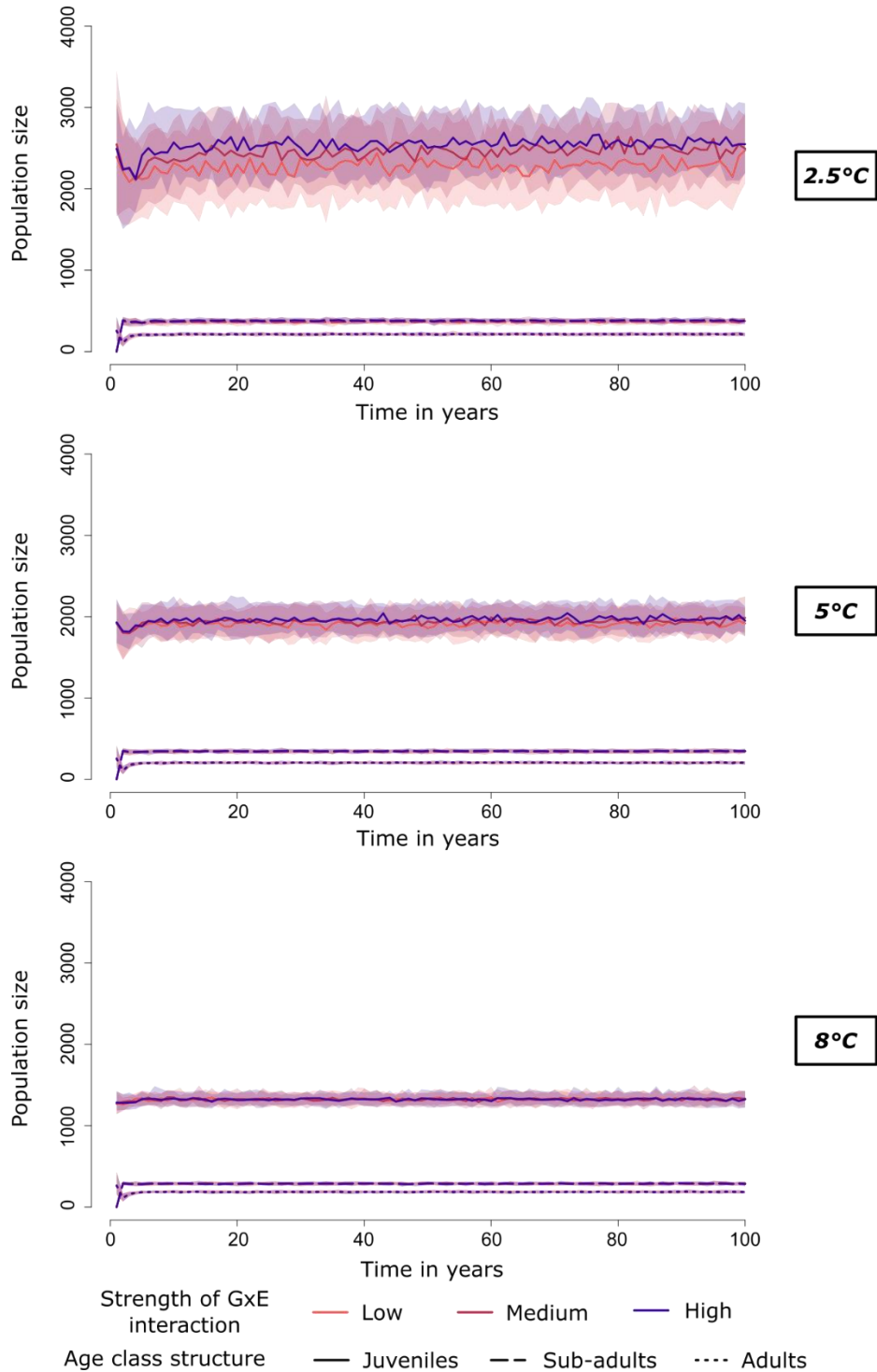


Figure 4—22: Evolution of demography structured per age class – juveniles (full lines), sub-adults (dashed line) and adults (dotted line) – over a hundred years of evolution considering various strengths of GxE interactions on embryonic survival, applied at low (2.5°C), medium (5°C) and high (8°C) temperature. Lines represent mean values averaged over 20 simulations while polygons are 95% credible intervals.

Temperature modality highly influenced demography (*Figure 4 – 22*). Indeed, population size was higher for the lower temperature, and even more so for juveniles. In addition, at 2.5°C, the number of juveniles was the highest for the highest strength of GxE interactions. This could be explained by the survival differences implemented at different temperatures and for various strengths of GxE interactions. Indeed, to increase the survival difference between both lineages, offspring survival is generally higher for MED females when selective pressure is higher, while it is lower for ATL females (*Figure 4 – 5, section 4.1.2*). This allows the optimal fitness of the population to be higher when selective pressures are higher.

4.3.3.4 Discussion

Effect on diversity. The above-described results indicate that the implementation of GxE interactions on embryonic survival – a fitness component – had a strong influence over the evolution of intraspecific diversity on short but also long time scales. Indeed, the fitness differences implemented appear to select against ATL alleles over time – and hence for MED alleles.

However, selection only acts on alleles transmitted maternally, as survival differences are implemented based on maternal genotype (*Section 3.3.2*). Therefore, there might be some room for potentially maladapted ATL genes to be transmitted *via* paternal inheritance. This may partially explain the shifting patterns of genotype distribution observed, where HYB individuals were initially created following secondary contact, before being purged out of the population very progressively. Despite the “random” transmission of paternal alleles, the proportion of ATL alleles in the population kept decreasing – decrease in introgression rate and continuous shift toward lowly introgressed HYB individuals – suggesting that selection was strong enough to eliminate ATL alleles, over the long term at least. As offspring survival depends on the proportion of ATL alleles carried by females, selection favours offspring from MED or lowly introgressed females, thereby progressively increasing the rate of MED alleles in the population, but also

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in males, which will ultimately accelerate the decrease of ATL alleles in the population. The creation of hybrid individuals, therefore, appears to be a compulsory but only transitory stage, where a substantial genetic load is created, since selection cannot act directly on paternally inherited alleles. This indicates that it is important to follow evolution over the long term and not just over a few years. Over the long term, this selection results in patterns of directional selection (Futuyma, 2009), since an extreme phenotype is selected against (ATL) while the other extreme is selected for (MED), as indicated by the shift in individual introgression toward one end of the spectrum.

Types of natural selection⁴. Wallace (1975) identified two types of natural selection, which can have different effects on population dynamics: soft selection and hard selection (Bell et al., 2021).

☞ “Soft selection occurs when the absolute fitness of an individual depends on its trait value relative to that of other conspecifics with which it interacts (*i.e.* the phenotypic composition of the population).” Soft selection often occurs when competition over a limited resource occurs – such as for territories or mating partners; it is, therefore, density and frequency-dependent. As a result, it will influence the composition of the population but will not incur a demographic cost.

☞ “Hard selection occurs when the absolute fitness of an individual depends on its absolute trait value and is independent of the phenotypic composition of the population.” Hard selection is density and frequency independent and can incur a demographic cost on the life stage where selection occurs, potentially impacting population dynamics.

⁴ Arguments are from Bell et al., 2021; and definitions are directly extracted from Box 1 Glossary.

Our results point toward patterns of hard natural selection involving an abiotic factor – temperature. Indeed, individuals' fitness is here independent of the population genetic composition but only depends on the fitness associated with the trait value – individual introgression – for a specific temperature. Therefore, effects on demography and potentially population dynamics are to be expected.

Effects on demography.

The implementation of GxE interactions had a slight impact on population dynamics, as it slightly decreased the number of juveniles. However, this effect did not translate into a decrease in population growth, as other life stages were not impacted. This is not surprising, since hard selection often results in reduced survival or reproductive success in the life stage where it is applied, but does not always influence population dynamics (Bell et al., 2021). This may have multiple explanations. First, selection may be too weak to influence population growth significantly (Bell et al., 2021). However, considering the impact of selection on diversity dynamics, this is unlikely to be the case. Second, the life stage affected by selection may have little influence on population growth (Mills, 2013). This is also unlikely here since juveniles' survival will affect recruitment in fish populations. Alternatively, it could be explained by mechanisms of compensatory selection, where selective mortality at one life stage can be compensated partially or entirely later on (Bell et al., 2021). Indeed, hard selection can be expected to increase mean fitness in subsequent generations (Fisher, 1930), or to be compensated for under the effects of density-dependence (Ratikainen et al., 2008; Reed, Gienapp, et al., 2015). For example, focusing on selection happening early on in life, more juveniles are produced compared to what can be recruited in the population (one of Darwin's observations that led to natural selection). Therefore, hard selection may only remove this excess from the population. However, by acting on a specific genotype, hard selection reduces its proportion in the population, thereby changing the composition of the population, but without specifically affecting demography, if sufficient diversity is available.

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In our context, where both MED and ATL diversity was initially available, selection, by removing deleterious ATL alleles, may have resulted in an increase in the mean fitness of the population over generations. Indeed, as MED alleles were more transmitted over time and ATL alleles decreased in frequency, the population genetic structure changed and was progressively made of more and more advantageous phenotypes, thereby increasing the population fitness. Sometimes such mechanisms of compensatory selection may even increase population growth (Abrams, 2009; McIntire & Juliano, 2018). It appears to be the case here when higher selective pressures are implemented. Indeed, results of sensitivity analyses indicated that higher selective pressure actually resulted in higher population size, as stronger selection more rapidly selected for advantageous MED alleles, thereby leading to a higher mean fitness of the population.

In a different context of diversity – where only ATL diversity will be available – such patterns of GxE interactions could have had stronger and more visible consequences on population growth. Indeed, increased mortality or reduced fertility may incur a demographic cost and thereby affect population dynamics (*sensu* Haldane, 1957). For instance, in an ATL population, low juvenile survival might result in reduced recruitment. As mean population fitness will remain low throughout generations, there might not be room for compensatory mechanisms, thereby resulting in a decline in population size.

Evidence of an eco-evolutionary dynamic. The implementation of GxE interactions on survival created an eco-evolutionary loop, affecting both diversity (evolution) and population (ecology) dynamics. However, the demographic influence of evolutionary responses to selection might not always be visible and can lead to a type of cryptic eco-evolutionary dynamics (M. Kinnison et al., 2015). Indeed, in our case, in response to hard selection, evolution eliminated alleles that may have caused reduced fitness,

potentially maladaptation; which otherwise could have led to a population decline. Understanding the links between natural selection and population dynamics is central to eco-evolutionary dynamics (Carroll et al., 2007; Hendry, 2017) and responses to anthropogenic changes caused by disturbances, climate change or management practices (Pelletier et Coltman, 2018).

Speed of selection. The implementation of stronger selective pressures – through modification in GxE strength or temperature – appeared to result in stronger and hence faster selection. Indeed, the higher fitness differences were between the advantage (MED) and the disadvantage (ATL) phenotype in a specific environment, the faster the elimination of ATL alleles and the directional selection was. The strength of selection is highly related to differences in individuals' fitness. In other words, considering Darwin's idea of natural selection, the more one genotype is advantaged over the other; the faster natural selection will act in favour of that genotype, as it will transmit more alleles to the next generation (Darwin, 1859). It is the case in our model where differences in fitness increase with an increase in the strength of GxE interactions and/or a decrease in temperature (*Figure 4–5, section 4.1.2*). The consideration of the fitness landscape associated with a trait undergoing such directional selection is important to understand the immediate effects of selection on demography. Indeed, in a population, the mean fitness will decrease progressively as the mean trait value gets further away from the optimal phenotype (Bell et al. 2021).

Temperature variations. The selective pressure exerted by temperature greatly influenced the evolution of diversity dynamics. Indeed, the lower temperature was, the shorter the transitory stage of hybridization was and the faster the effects of directional selection could be seen, as the distribution of the trait was more rapidly biased toward MED phenotypes. This suggests that considering variation in ecological parameters that may drive natural selection is essential to predict the evolution of diversity dynamics.

4.3 Exploring various eco-evolutionary scenarios in a basic case study of first secondary contact

Ecological parameters, such as temperature, are often varying in space and time, thereby consistently driving variation in selective environments, which could potentially be linked to adaptation (Carroll et al. 2007). With the increasing impact of climate change on natural environments (Pelletier & Coltman, 2018), considering the ecological context in which natural selection occurs is crucial to understand its influence on contemporary evolution and demography (Bell et al. 2021). Indeed, changes in environmental conditions may consistently alter the balance between gene flow and natural selection, potentially influencing adaptive divergence but also population dynamics (Garant et al., 2007; Hendry, 2017; M. T. Kinnison & Hairston Jr, 2007). For example, despite potential hybridization, local adaptation may still occur in environments where the forces of selection exceed the homogenizing effects of gene flow (Garant et al. 2007), which appears to be the case in our context.

The direction of selection. In this specific case study, patterns of selection were quite clear and directional, as selective pressure and fitness differences were constant in time. However, changes in selective pressure may change the strength and direction of selection, potentially generating different and more fluctuating patterns of diversity over time. Indeed, in reality, selection and evolution fluctuate in direction, as it is often tracking environmental conditions, making that small changes may rarely accumulate in such a long directional trend (Ellner et al., 1999; Gibbs & Grant, 1987; Grant & Grant, 2002, 2006; N. G. Hairston & Dillon, 1990). For example, in our case selection against ATL alleles might be slowed down, or even prevented if temperatures were to increase since fitness differences will be reduced.

Take home message: The maternal genotype-by-temperature interaction over embryonic survival is structuring diversity dynamics and demography in the conditions simulated in our model.

4.3.4 The relative importance of heterogamous preference considering GxE interactions on survival

When implemented separately and compared to a neutral scenario (respectively random preference and neutral survival), GxE interactions on survival seem to play a structuring role in the evolution of diversity, over short and long time scales, while heterogamous preference barely has any influence. However, evaluating the combined effect of both mechanisms remains important, especially considering that heterogamous preference and GxE interactions on survival are opposite forces. While one favours hybridization, the other selects MED diversity. Therefore, implementing heterogamous preference in addition to GxE interactions could modify the rate of selection by influencing the genetic variance available for selection. Given the role of heterogamous preference and GxE interactions implemented alone, I suspect it might slow down selection. This section aims at investigating the impact of heterogamous preference on the selection resulting from GxE interactions on survival. First, scenarios only implementing GxE interactions were compared to scenarios implementing GxE interactions combined with heterogamous preference – at 35% of GCP. Here the various strengths of GxE interactions were considered – at 5°C only – to evaluate if stronger or lower selective pressures are more or less affected by the implementation of heterogamous preference. Then a sensitivity analysis was conducted on heterogamous preference for medium GxE interactions to evaluate if higher percentages of GCP have a stronger influence on selection.

4.3.4.1 Does heterogamous preference affect the selection mediated by GxE interactions?

The implementation of heterogamous preference while considering GxE interactions influenced diversity dynamics. Its effect slightly differed in intensity, based on the strength of GxE interactions. Indeed, when considering heterogamous preference, the decrease in introgression rate was slower for all three

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modalities of GxE interactions, but even more so for the lower and medium ones (Figure 4 – 23). The same observation could be made regarding genotype proportion (Figure 4 – 24), where the decrease in HYB individuals and the increase in MED individuals were slower. The distribution of individual introgression (Figure 4 – 25) confirmed that heterogamous preference influences the outcome of first contact, with more HYB individuals initially created and fewer MED individuals. After a hundred years of evolution, when GxE interactions were strong, the impact of heterogamous preference on diversity dynamics faded away whereas it was still visible for the medium and lower modalities. Indeed, the introgression rate was still slightly higher (Figure 4 – 23: Low GxE ~ 0.24 vs ~ 0.2 and medium GxE ~ 0.17 vs ~ 0.14) and a shift in the distribution of individual introgression could still be observed (Figure 4 – 25, $t = 100$).

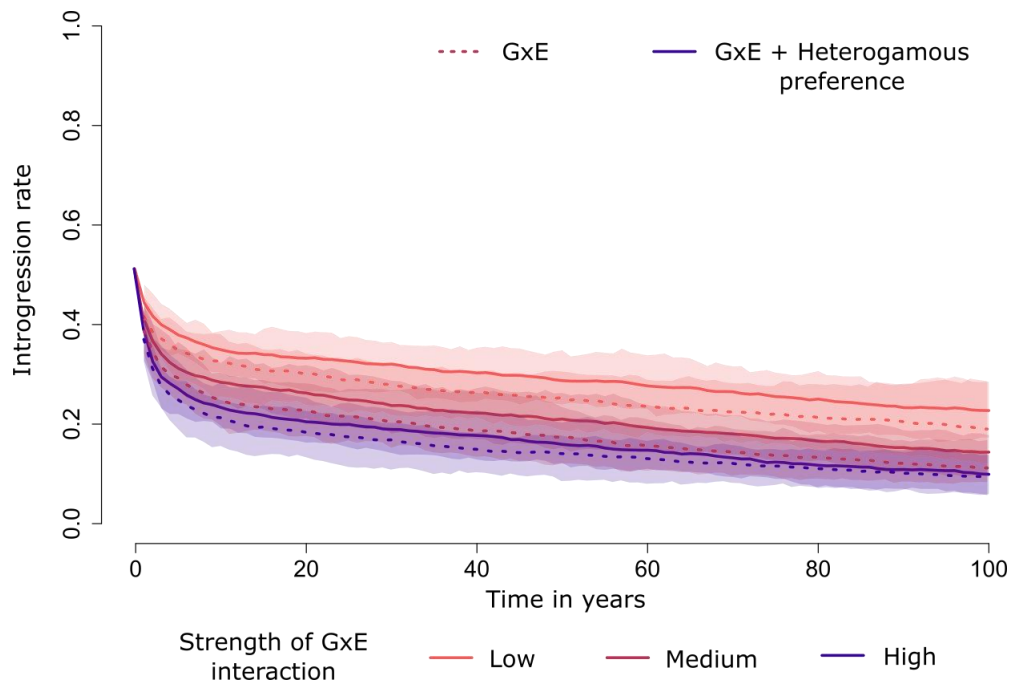


Figure 4—23: Evolution of introgression rate over a hundred years considering various strengths of GxE interactions on embryonic survival applied at 5°C; with (full lines) and without (dotted lines) the implementation of heterogamous preference. Solid lines represent mean values averaged over 20 simulations while polygons are 95% credible intervals.

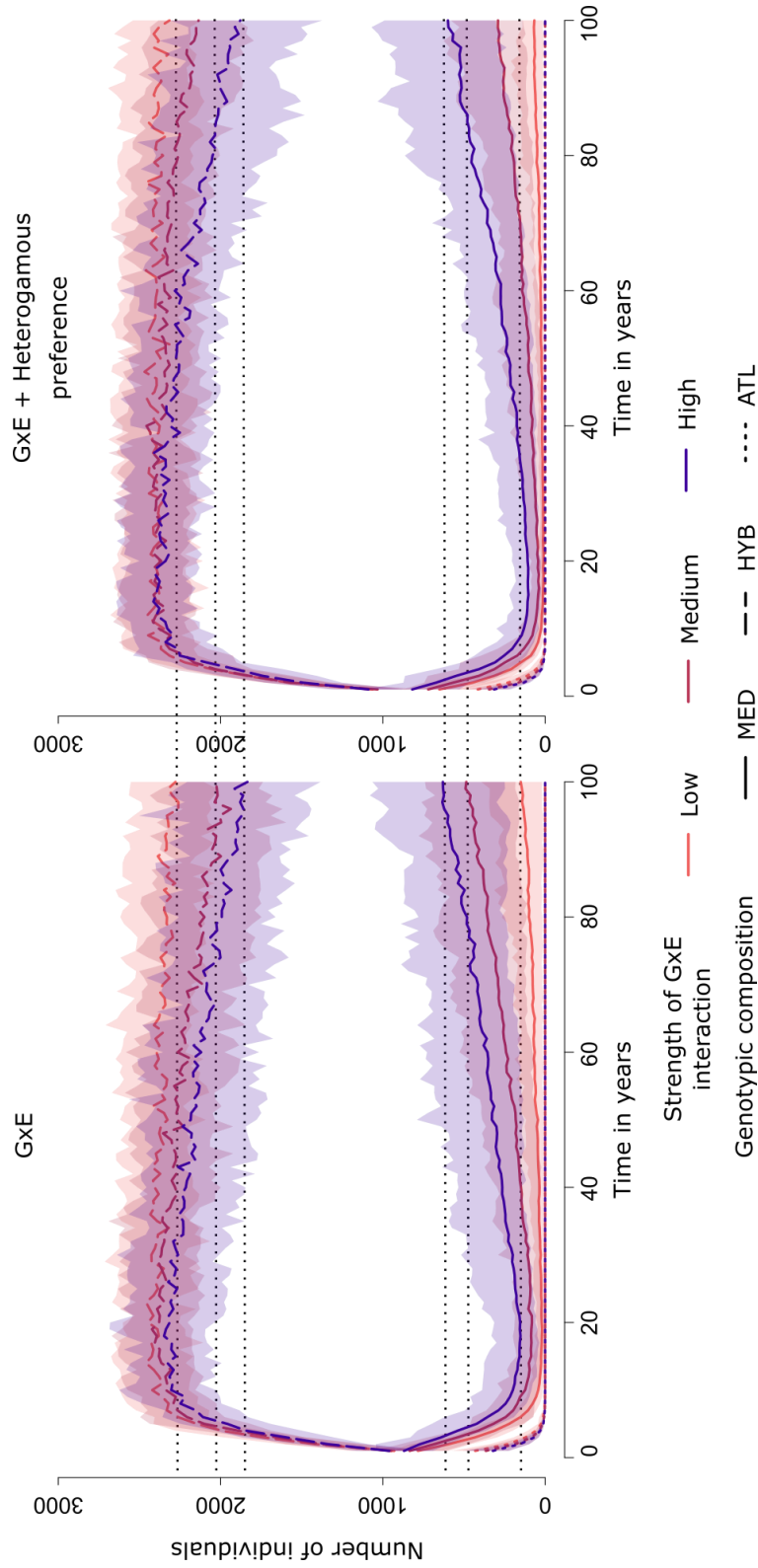


Figure 4—24: Evolution of the genotypic composition of the population – proportions of MED (full lines), HYB (dashed line) and ATL (dotted line) genotypes – over a hundred years considering various strengths of GxE interactions on embryonic survival applied at 5°C; with and without the implementation of heterogamous preference. Solid lines represent mean values averaged over 20 simulations while polygons are 95% credible intervals.

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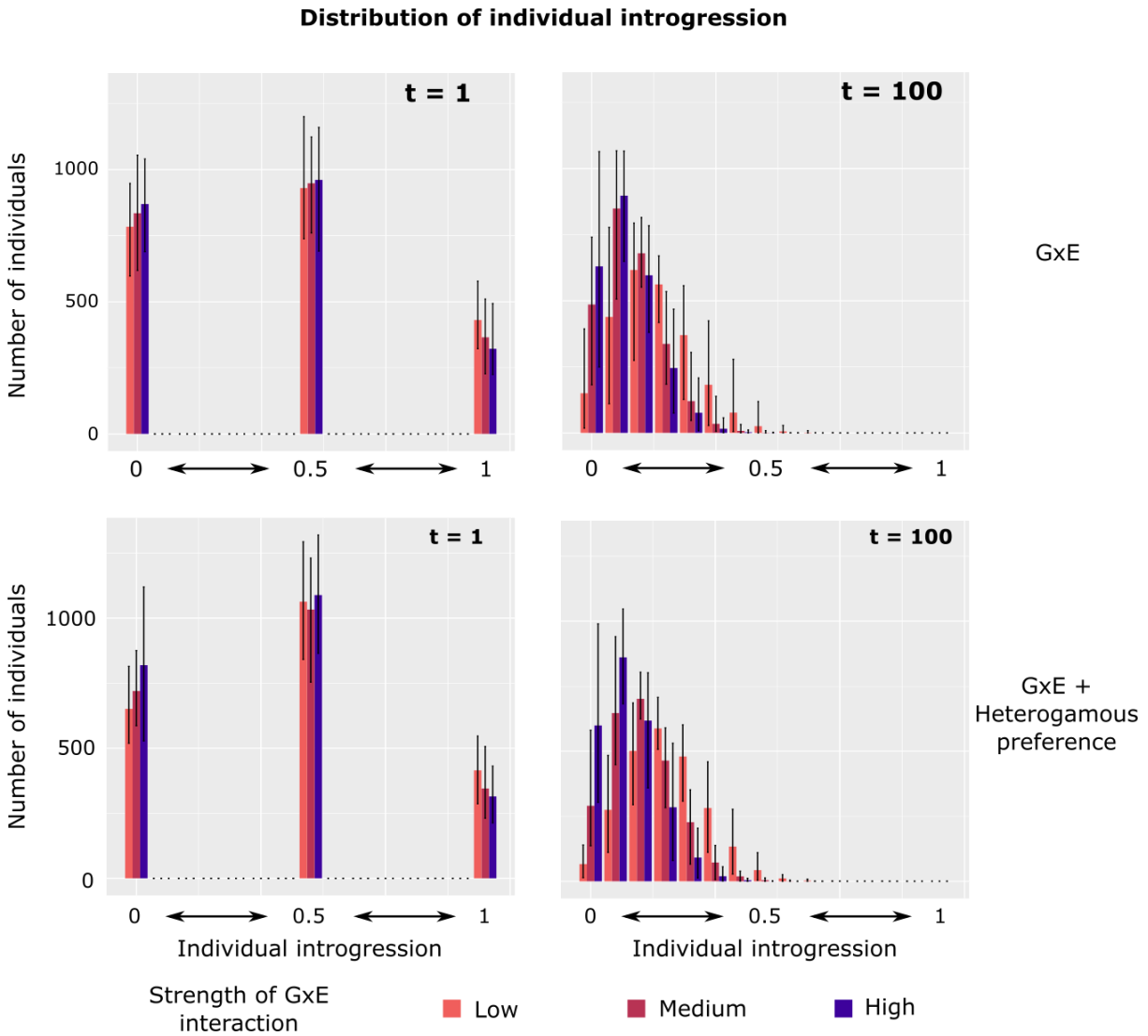


Figure 4—25: Distribution of individual introgression during first contact ($t = 1$) and after 100 years of evolution considering various strengths of GxE interactions on embryonic survival applied at 5°C; with and without the implementation of heterogamous preference. Rectangular bars represent the mean number of individuals per class of individual introgression while error bars are 95% CI.

These results suggest that heterogamous preference slows down selection, and even more so when selective pressure is lower. In other words, stronger selection might be more resistant to the effect of heterogamous preference. However, observed differences remained very low, possibly due to the low value of GCP implemented.

4.3.4.2 Does higher genetic contribution to heterogamous preference have a stronger influence on selection?

When implementing higher values of GCP, a pattern was observed: the more the system was heterogamous, the lower the decrease in introgression rate was (Figure 4–26) and the higher the number of HYB individuals (Figure 4–27) was. Indeed, the distribution of individual introgression during first contact confirmed that higher values of GCP lead to the creation of more and more HYB to the detriment of MED individuals during the first time step (Figure 4–28: at 35% ~ 1000 HYB and ~ 760 MED vs 1150 HYB and 620 MED at 100% of heterogamy).

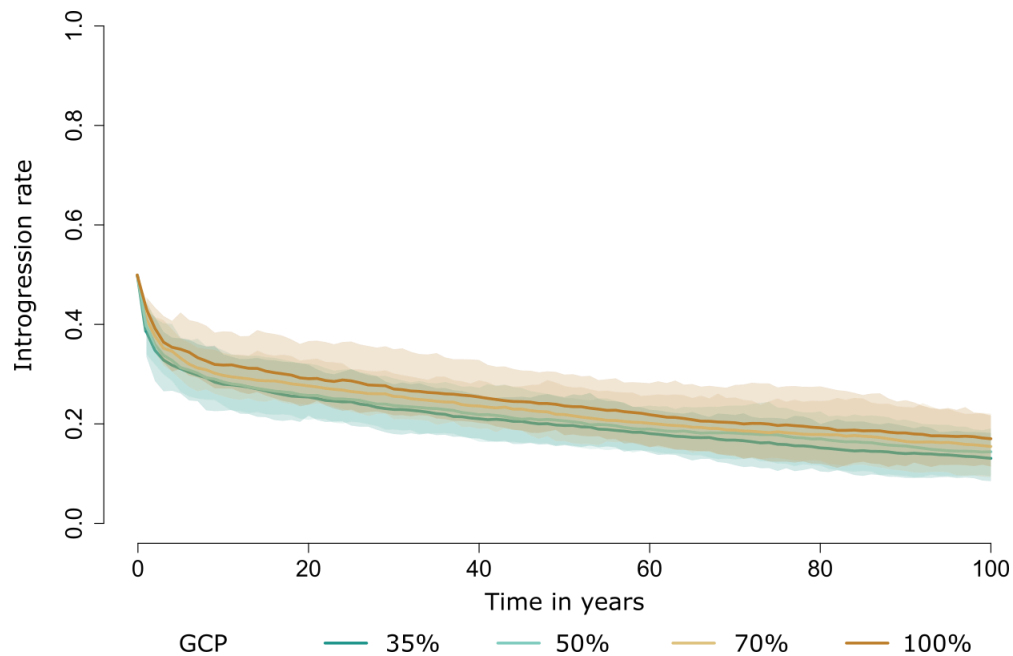


Figure 4–26: Evolution of introgression rate over a hundred years considering medium GxE interactions applied at 5°C and heterogamous preference with various values of GCP. Solid lines represent mean values averaged over 20 simulations while polygons are 95% credible intervals.

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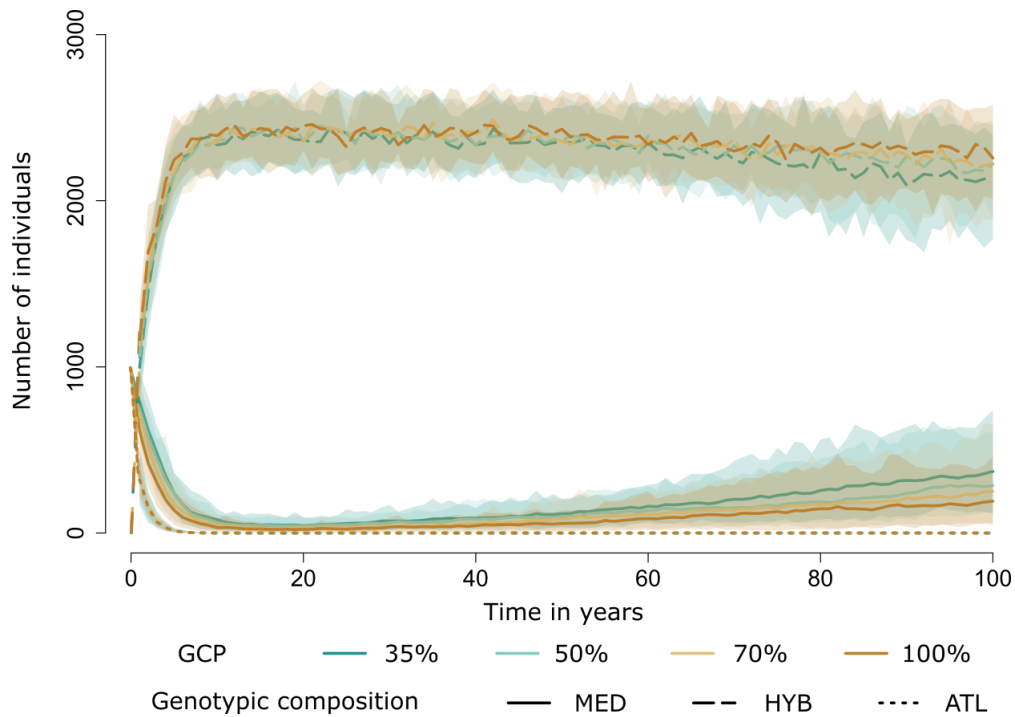


Figure 4—27: Evolution of the genotypic composition of the population – proportions of MED (full lines), HYB (dashed line) and ATL (dotted line) genotypes – over a hundred years considering medium GxE interactions applied at 5°C and heterogamous preference with various values of GCP. Solid lines represent mean values averaged over 20 simulations while polygons are 95% credible intervals.

After a hundred years of evolution, a shift in the distribution of individual introgression could still be observed (Figure 4 – 28: at 35% centred on 0.14 and at 100% centred on 0.21). Moreover, throughout the years, differences in the genotypic composition of the population were progressively accentuated, with the increase in MED individuals being faster for lower values of GCP (Figure 4 – 27). These results suggest that heterogamous preference might slow down the selection of MED individuals, but does not prevent the selection of MED alleles in the population, as observed differences in introgression rate remained very small (Figure 4 – 26: ~ 0.18 à 100% vs ~ 0.14 à 35%).

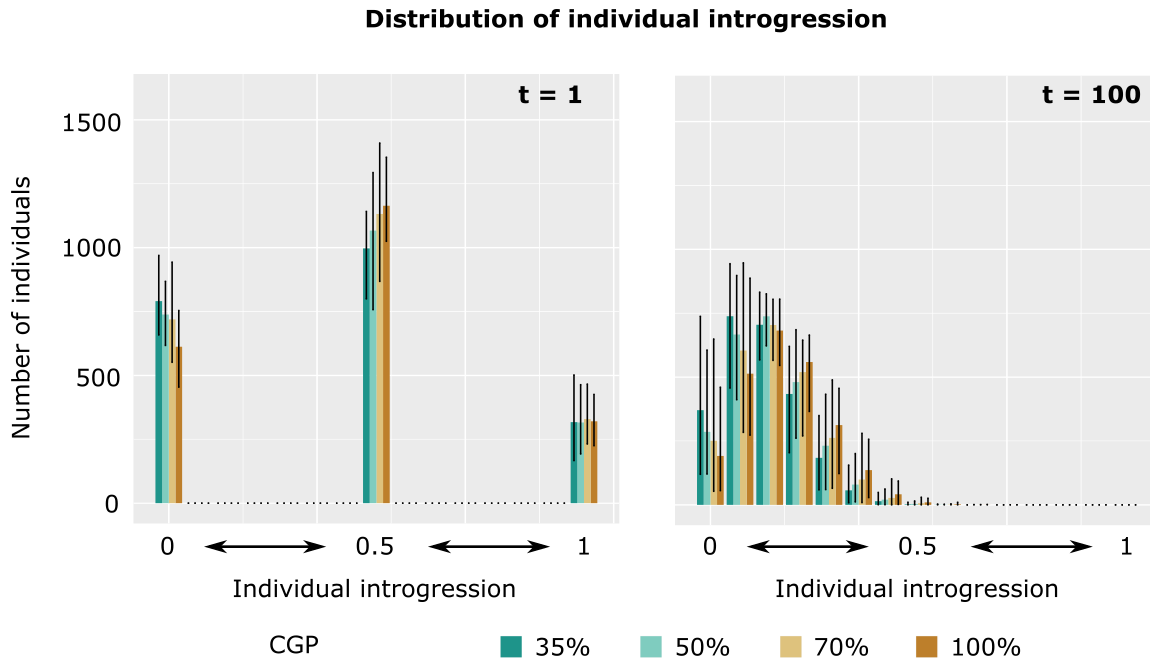


Figure 4—28: Distribution of individual introgression during first contact ($t = 1$) and after 100 years of evolution considering medium GxE interactions applied at 5°C and heterogamous preference with various values of GCP. Rectangular bars represent the mean number of individuals per class of individual introgression while error bars are 95% CI.

4.3.4.3 Discussion

We have seen that while GxE interactions yielded tremendous effects on diversity dynamics, heterogamous mating only had little influence; when both mechanisms were considered independently. However, when considered together, the implementation of heterogamous preference in addition to GxE interactions changed the rate and magnitude of selection. Indeed, the decrease in population introgression rate – so in ATL alleles – and the shift in the distribution of individual introgression – and hence in genotype – were slower. Since selection only acts on maternally inherited alleles, room for maladapted alleles is possible through paternal inheritance. In this context, heterogamous preference accentuates this effect, as the most advantaged females – MED females – will preferentially select for the less adapted phenotype – ATL males; leading to the initial creation of more HYB individuals and a longer

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transitory hybrid stage. Therefore, the implementation of heterogamous preference in addition to GxE interactions participates in creating and maintaining more hybrid polymorphisms associated with a genetic load.

A pleiotropic effect.

GxE interactions and female preference are both coded by the same genetic variation, making our *loci* partially pleiotropic. Indeed, the seven *loci* implemented in the model code for individual introgression. This trait is directly involved in GxE interactions and indirectly in female preference, as it is respectively used as a direct measure of maternal genotype and an indirect measure of phenotype. For the latter, the relationship between an individual genotype and its phenotype will depend on the value of GCP. Consequently, ATL alleles that are disfavoured by natural selection, through maternal genotype, might be favoured by sexual selection, as female preference increases the reproductive fitness of ATL males; thereby countering the effect of natural selection.

Sensitivity analyses.

Natural selection mediated by GxE interactions can be more or less slowed down by heterogamous preference, depending on the strength of selection and the genetic contribution to preference implemented.

On the one hand, stronger selection – higher strength of GxE interactions – appears to be more resistant to the antagonistic effect of heterogamous preference. Indeed, compared to the lower and medium strength of GxE interactions, diversity dynamics were less affected by the implementation of heterogamous preference. This could be explained by the fact that stronger natural selection acts faster to shift the distribution of traits – individual introgression – leaving fewer phenotypes available for sexual selection to act on.

On the other hand, the implementation of higher values of GCP appeared to slow down selection more. This is because the genetic variation coding for natural selection becomes more and more related to the phenotypic variation coding for female preference, exerting the pleiotropic effect mentioned above. Increasing links between trait variation and ecological interactions will increase the importance of evolution to ecological interactions and vice-versa (N. G. J. Hairston et al., 2005).

Antagonism between natural and sexual selection.

In some instances, sexual selection can, indeed, be antagonistic to natural selection (Ellers & Boggs, 2003; Labonne & Hendry, 2010; A. K. Schwartz & Hendry, 2006) and slow down or even prevent populations' mean phenotype from reaching a fitness optimum (Andersson, 1994), sometimes preventing adaptation to occur (Chenoweth et al., 2015). The outcome of such interplay will likely vary based on the relative strength and direction of each selection force (Kasimatis et al., 2019; Labonne & Hendry, 2010). For example, Labonne & Hendry (2010) also showed that sexual selection through female choice could modify the effects of divergent natural selection, but this is depending on the strength of natural selection and the direction of sexual selection. Many authors have argued for the consideration of the role of sexual selection, in addition to natural selection, in shaping the potential for evolution (Labonne & Hendry, 2010; A. K. Schwartz & Hendry, 2006; Svensson & Gosden, 2007).

A form of sexual conflict.

In evolution, this antagonism could have the potential to create a sexual conflict. Indeed, while inheritance from ATL males will have a negative effect on female descendants, through reduced survival of their offspring; it will have a positive effect on male descendants, through potential increased mating success. However, as the autosomal genome is shared between the sexes, the fitness optimum of each sex cannot be reached. Indeed, even if selection can push

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males and females in opposite directions initially (Bonduriansky & Chenoweth, 2009; W. R. Rice & Holland, 1997); after sexual reproduction chromosomal segregation re-arranges autosomal associations across the sexes (Kasimatis et al., 2019). This type of sexual conflict could cause the maintenance of high genetic polymorphisms with a substantial genetic load (Chenoweth et al., 2015; Kasimatis et al., 2019).

Role of natural selection.

However, in our context, the implementation of heterogamous preference did not seem to result in patterns of sexual selection over the long term. Even when considering the highest value of GCP implemented (100%), long-term effects on diversity dynamics remained small. The genetic load created during the hybrid stage was still removed over the long term. Therefore, natural selection is here a much stronger force, as it remains efficient at removing deleterious alleles and still results in patterns of directional selection. In fact, heterogamous preference is indirectly and negatively impacted by natural selection resulting from GxE interactions. Indeed, while it does not affect her reproductive success directly, it reduces her female descendants' reproductive success. This indirect selection explains both: why a transitory hybrid stage is initially possible, but also why selection still acts in the same direction despite the implementation of heterogamous preference.

Role of female preference.

In addition, in our model, female preference is not associated with any direct benefits for females, through direct natural selection (Kirkpatrick, 1996). The implementation of a slight fitness advantage conferred to offspring from ATL males, as suggested in Folio et al. (2021), could potentially result in heterogamous preference playing a more structuring role in the evolution of diversity. Indeed, for sexual selection to shape evolution, some additional selective forces operating directly on female preference might be required, as direct selection has been shown to be more effective at driving the evolution of female preference (Hall et al., 2004; Qvarnström et al., 2006).

The balance of the forces between natural and sexual selection is always important to consider when studying the evolution of diversity, as both have the potential to drive evolution, potentially in an antagonistic way. Particularly, in a management context, their consideration is crucial as they might interact with management practices to drive evolution, sometimes in unpredictable ways. In addition, each situation should be considered unique. Indeed, context could influence the relative roles of these EEMs in driving diversity dynamics, as it will determine population structure and ecological interactions, thereby potentially affecting eco-evolutionary dynamics differently.

4.4 EXPLORING VARIOUS ECO-EVOLUTIONARY SCENARIOS IN MORE COMPLEX CASE STUDIES

The previous part gave us a grasp of the potential role played by each of the eco-evolutionary mechanisms (EEMs) – *i.e.* mate preference behaviour and GxE interactions on embryonic survival – implemented in the model, independently and combined. Now, turning to more complex case studies, I will use MEDITERRANEA to evaluate whether their role is similar when considering more complex hydrographic networks, where various environmental parameters (temperature, population structure but also landscape features such as connectivity) and management practices could interact to also influence diversity dynamics and demography. To do so, I will use three real case studies, where some indicators of diversity and demography had been monitored before and after the implementation of management practices. I will compare the evolution of diversity dynamics and demography under the four main eco-evolutionary scenarios defined in *section 4.1.1*. Sensitivity analyses will be presented for mechanisms of interest only.

- ☞ My first aim will be to explore how the EEMs influence the outcome of management practices and point out relevant parameters (ecological parameters, landscape features, and initial population structure/composition) that may interact with these mechanisms to influence diversity and demography in each context.
- ☞ My second objective will be to compare the available empirical data to our simulation data and check whether the inclusion of these EEMs improves or degrades the ability of the model to predict the empirical findings.

As winter temperature is influencing post-zygotic embryonic survival, we will simulate each scenario under two temperature models, considering warmer *versus* colder winter temperatures, so to investigate what could have been the role of such selective pressure in shaping patterns of diversity.

CASE STUDY 1:

THE CHEVENNE CREEK

4.4.1 The Chevenne Creek

4.4.1.1 Study site

The Chevenne Creek, a tributary of the Dranse d'Abondance River, is a typical middle-altitude northern French Alpine mountain stream. It is 2.5 kilometres long and ranges between 1 to 4 metres in width. Elevation ranges from 1250 to 1000 metres with a mean slope of 10%. It presents a heterogeneous and fragmented habitat characterised by riffles, cascades, and pools (*Figure 4 – 29*). This stream lies within the geographical range of Mediterranean brown trout with its downstream and median parts harbouring a nearly pure MED population (Largiadèr et al., 1996; Largiadèr & Scholl, 1996; Launey et al., 2003).

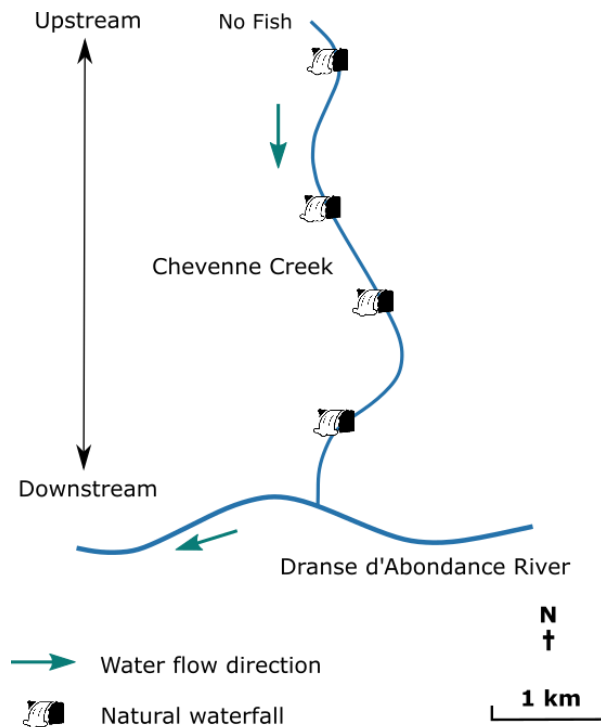


Figure 4—29: Representation and characteristics of the Chevenne Creek, an affluent of the Dranse d'Abondance River. Its unpassable barriers are represented. Figure modified from Caudron and Champigneulle (2011).

4.4.1.2 Historical management

Stocking of brown trout had already begun in 1913 in the Mediterranean area. In the Chevenne Creek, it led to allopatric spatial repartition with the presence of a non-native ATL population in the isolated upper part of the river. The downstream native MED population was initially barely impacted by these practices, but since it was located immediately downstream (Barnetta, 2005); it was threatened by an upstream ATL gene flow. Indeed, downstream migration of ATL trout led to a gradient of hybridization in the intermediate part of the river. As fisheries managers became more aware of the importance of conserving native populations and intraspecific diversity they became interested in the conservation of remaining native brown trout populations to protect well-adapted local populations. Therefore, several management practices were carried out to preserve this native population (Figure 4 – 30).

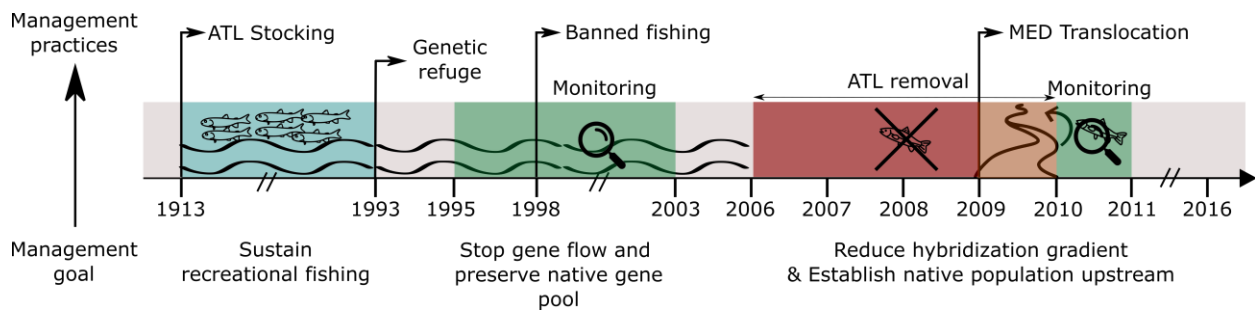


Figure 4—30: Management history timeline for the Chevenne Creek.

A genetic refuge (GR) – where all stocking practices are stopped – was set in 1993 and angling was banned in 1998. However, the upstream ATL population persisted despite years without stocking and genetic analysis indicated that the admixture pattern between the MED and the ATL lineages had not changed significantly (25 to 20%) within 10 years without stocking and angling (Caudron & Champigneulle, 2011). Therefore, from 2006 to 2009, non-native ATL individuals were removed from the upper part of the river

4.4 Exploring various eco-evolutionary scenarios in the Chevenne Creek

by electrofishing, in order to stop this gene flow. Each year two electrofishing samplings were carried out and all trout that had been caught were removed from the river. The removal efficiency was estimated per year based on the number of trout caught and estimated population size per stage: juveniles (or young of the year), sub-adults and adults. Caudron & Champigneulle (2011) monitored the evolution of demography and genetic diversity in the Chevenne Creek following these management strategies.

Following ATL removal, MED individuals sampled from the nearly pure native downstream population (<1% introgression) were translocated upstream to establish a native population upstream and reduce the intermediate gradient of hybridization (Caudron & Champigneulle, 2011). In total 105 MED brown trout of variable size were transferred in the upper part of the river stretch (*Figure 4 – 31*). Dynamics of colonisation and change in genetic diversity were then monitored in 2016 to evaluate the effectiveness of these strategies in restoring a native MED population in the Chevenne Creek (*Scimabio Interface data*).

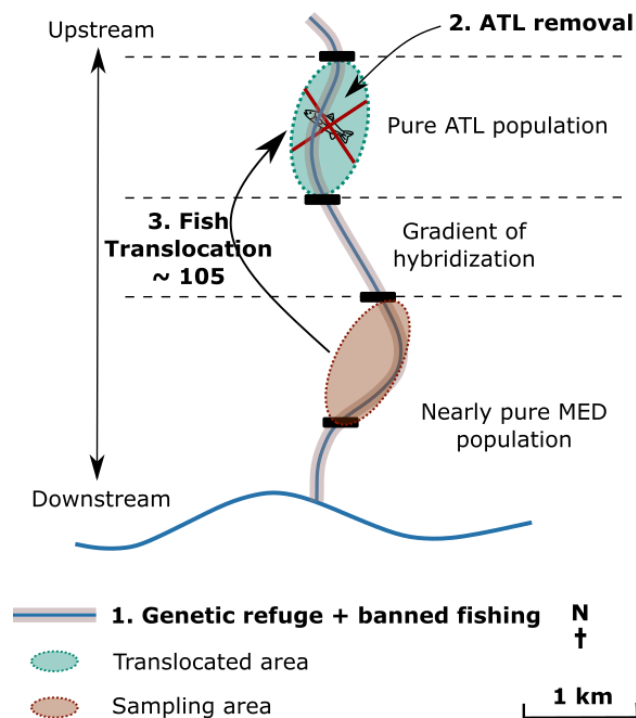


Figure 4–31: Spatial representation of management practices carried out on the Chevenne Creek from 1993 to 2009.

4.4.1.3 Simulation protocol

Hydrographic network. In MEDITERRANEA, the Chevene population is considered a close population, as there is no connectivity represented with the downstream Dranse River. The hydrographic network is explicitly represented by a succession of 5 reaches and 5 weirs defined based on the topology of the Chevenne Creek (*Figure 4 – 32*). Four of the five weirs represent the Chevenne partially passable waterfall barriers (*Figure 4 – 29*). Reaches and weirs state variables are informed by the Chevenne physical characteristics (*Appendix D: Table 1 & 2*).

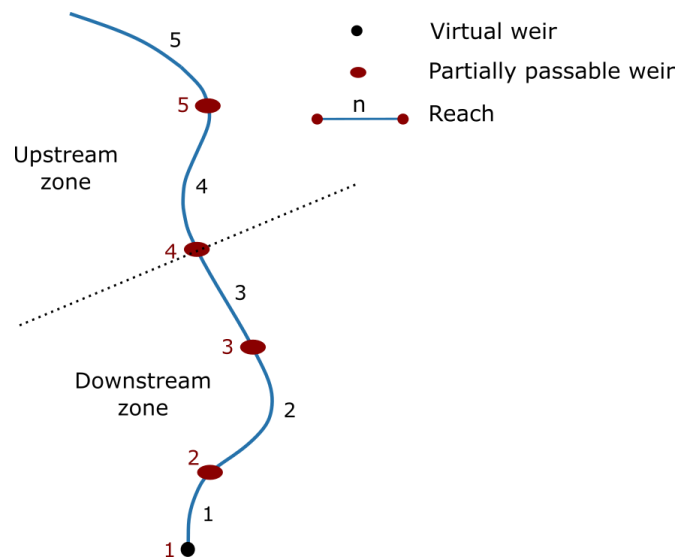


Figure 4—32: Representation of the Chevenne Creek in MEDITERRANEA. It is made of a succession of reaches and weirs. Reach and weir numbers are represented.

Parameters settings. Each hydrographic network can be characterised by its own densities. Therefore, parameters informing and controlling for maximum density are set based on observational data (*Scimabio Interface data*). For the Chevenne Creek observed density is around 3000 individuals per hectare ($K_{maxE} = 1.8$). The rest of the parameters used in the simulations are set by default.

4.4 Exploring various eco-evolutionary scenarios in the Chevenne Creek

Temperature models. As temperature influences GxE selection and potentially diversity dynamics, two temperature models were used. The first temperature model was calibrated based on temperature data informed by *Scimabio interface*. Yearly temperatures are overall more buffered with warmer winter temperatures and lower summer temperatures (*Figure 4 – 33*). The second model is based on data from Daigle et al. (2016), where a few temperatures were available for the Chevenne. Yearly temperatures are overall more fluctuating with colder winter temperatures and warmer summer temperatures (*Figure 4 – 34*).

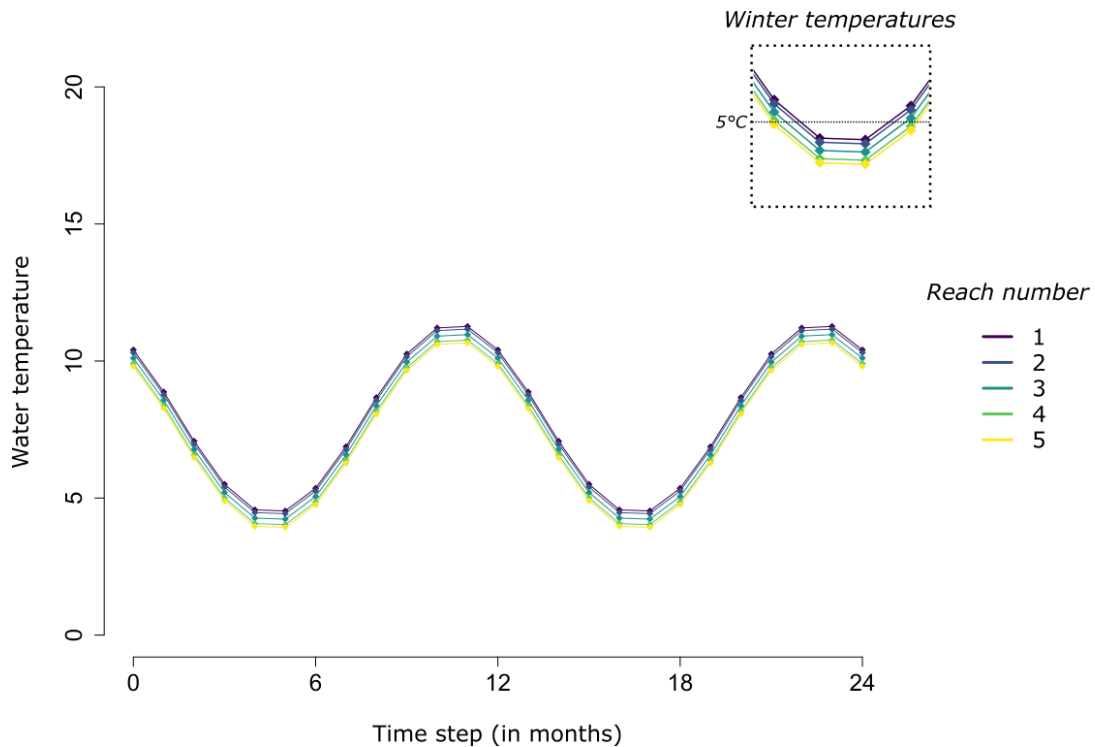


Figure 4—33: Buffered temperature model (warmer modality) used for simulations carried out on the Chevenne Creek. One water temperature is calculated per reach each month. A zoom of winter temperatures shows the temperature from December to March.

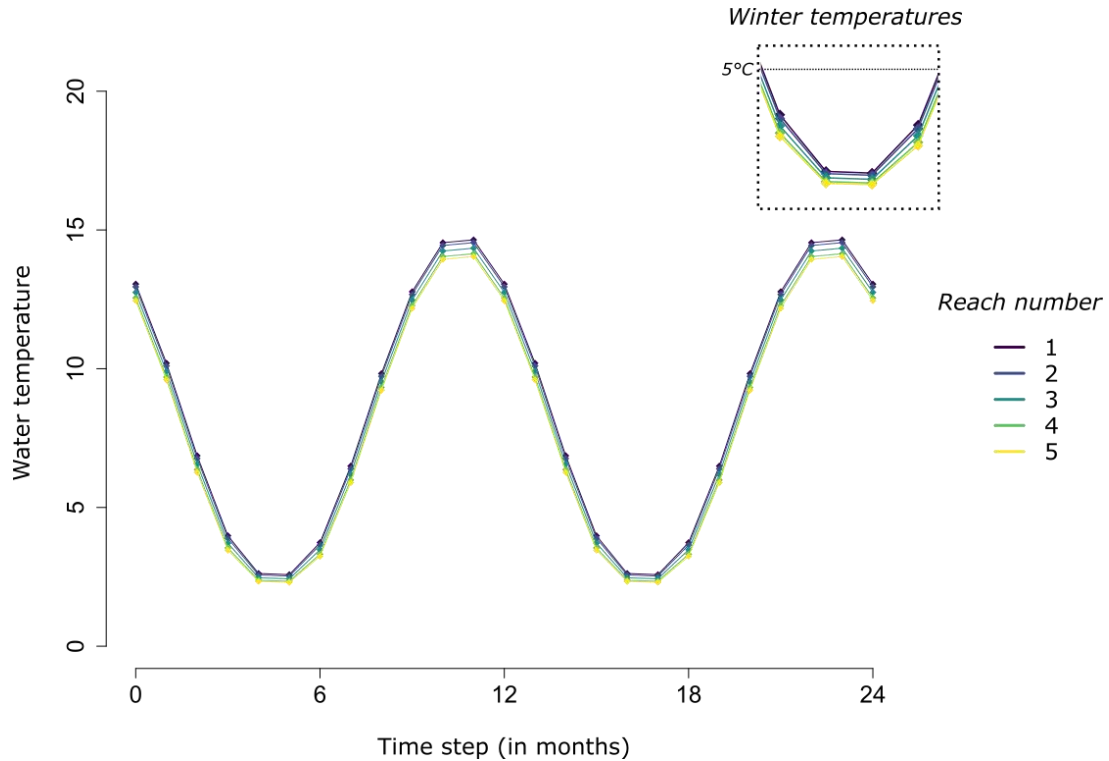


Figure 4—34: Fluctuating temperature model (colder modality) used for simulations carried out on the Chevenne Creek. One water temperature is calculated per reach each month. A zoom of winter temperatures shows the temperature from December to March.

Simulations. All simulations – with the same initial parameters – are replicated 15 times. To stabilise population dynamics and obtain a realistic initial population – population size stabilisation, fitting distributions of individual state variables, creation of hatches and juveniles – the model is run for ten years *prior* to starting the case study. The actual scenario then starts at $t = 11$, in 1995 when the first genetic data are available, to 2016 when the last genetic data are available. Genotypic distribution for the initial population is based on observed genotypic distribution per section, informed by Scimabio Interface. From $t = 11$ to $t = 21$ – hence from 1995 to 2005 – the model simulates the GR strategy. Fishing is also banned from the river. From $t = 22$ to $t = 25$ – hence from 2006 to 2009, ATL removal is simulated by simply removing individuals from reach 4. The probability of being removed is stage-dependent – juvenile, sub-

4.4 Exploring various eco-evolutionary scenarios in the Chevenne Creek

adult, adult – and defined per year (*Table 4 – 1*) to match the removal efficiency described in Caudron and Champigneulle (2011). Finally, at $t = 25$ so in 2009, 105 individuals are transferred from reach 2 to reach 4, considering a variety of sizes and based on individual introgression. To match the sample of individuals transferred, 70% of individuals were pure MED and 30% were allowed to be slightly introgressed – four ATL alleles maximum. Diversity dynamics and demography were recorded for three sections of the river (*Figure 4 – 35*) – the downstream zone, the intermediate zone and the upstream zone. Most results represent the mean value of all the simulations as well as a 95% confidence interval.

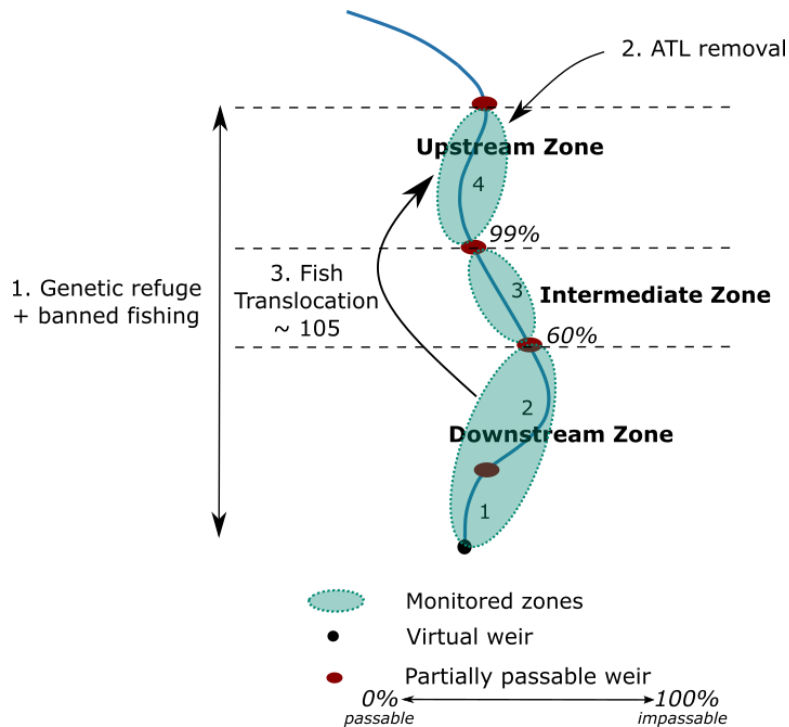


Figure 4—35: Representation of the management strategies in MEDITERRANEA and delimitation of the three zones monitored – the downstream zone, the intermediate zone and the upstream zone. Weir passability is indicated between zones of interest.

Table 4-1: Removal efficiency of ATL brown trout implemented in the model based on the values obtained each year for the three age classes. The first value given is the probability of removal informed in the model and in brackets are the depletion estimates calculated by Caudron & Champigneulle (2011).

	Juveniles	Sub-adults	Adults
2006	80% [71 – 91]	76% [67 – 85]	98% [96 – 100]
2007	93% [87 – 100]	95% [91 – 100]	100%
2008	87% [74 – 100]	100%	100%
2009	96% [92 – 100]	75% [50 – 100]	100%

4.4.2 Evolution of diversity dynamics and demography in the Chevenne Creek

Following the implementation of various management strategies – GR, ATL removal and MED translocation – I monitored the evolution of diversity dynamics and demography in each zone of the Chevenne Creek. As a reminder, diversity dynamics include the evolution of introgression rate and genotypic composition as well as the distribution of individual introgression. Demography focuses on population size and age class structure. As results are numerous, I will not go through all the results for all zones but only target those of interest.

4.4.2.1 Evolution of introgression

In the downstream and intermediate zones, introgression rates were very low (*Figure 4 – 36*, < 0.2) and mainly remained stable over time. For the colder temperature modality, introgression was lower for scenarios implementing GxE interactions compared to neutral survival scenarios. This indicates that selection mediated by GxE interactions always acts and that its effect can be seen even in cases where ATL alleles are rare in the population. In the downstream zone, there was a very slight increase in introgression for scenarios implementing neutral survival. Meanwhile, in the intermediate zone, there was a small decrease in introgression for all scenarios during model stabilisation. This pattern could simply

4.4 Exploring various eco-evolutionary scenarios in the Chevenne Creek

be due to individual movement as the downstream zone might get some individuals from the intermediate zone – likely to be introgressed and hence increase the introgression rate – and conversely, the intermediate zone might get some individuals from the downstream zone – likely to be pure and hence decrease introgression. In addition, the implementation of management practices did not seem to affect introgression dynamics in these zones. This could be explained by the fact that, in the model, the intermediate zone did not seem to be highly influenced by an upstream ATL gene flow, as it might have been the case in reality. A possible explanation is to look at the value given to weir passability (*Figure 4 – 35*), which is very high (99/100) between the upstream and intermediate zone, and lower (60/100) between the downstream and intermediate zone, allowing more gene flow to happen from downstream than upstream. To obtain a more realistic gene flow – that would match that observed in reality – sensitivity analyses on the values given to weir passability should be conducted.

In the upstream zone, following the implementation of the GR strategy (from year 11 to year 21), the introgression rate remained very high for neutral survival scenarios while it decreased progressively for scenarios considering GxE interactions (*Figure 4 – 36*). In these scenarios, despite low passability, MED individuals – or lowly introgressed HYB – that managed to move upstream might have been selected. During the ATL removal (from year 21 to year 25), introgression rates decreased rapidly over the years for all scenarios – close to zero, as most individuals were removed from the river stretch – ATL as well as HYB individuals. The introgression rate then rapidly stabilised at very low levels after MED translocation. With the implementation of GxE interactions, the introgression rate decreased more rapidly and to slightly lower rates. Overall, for all zones, at warmer temperatures, the implementation of EEMs did not appear to impact much introgression dynamics, whereas it had a stronger influence at colder temperatures, as observed differences in introgression rates were higher.

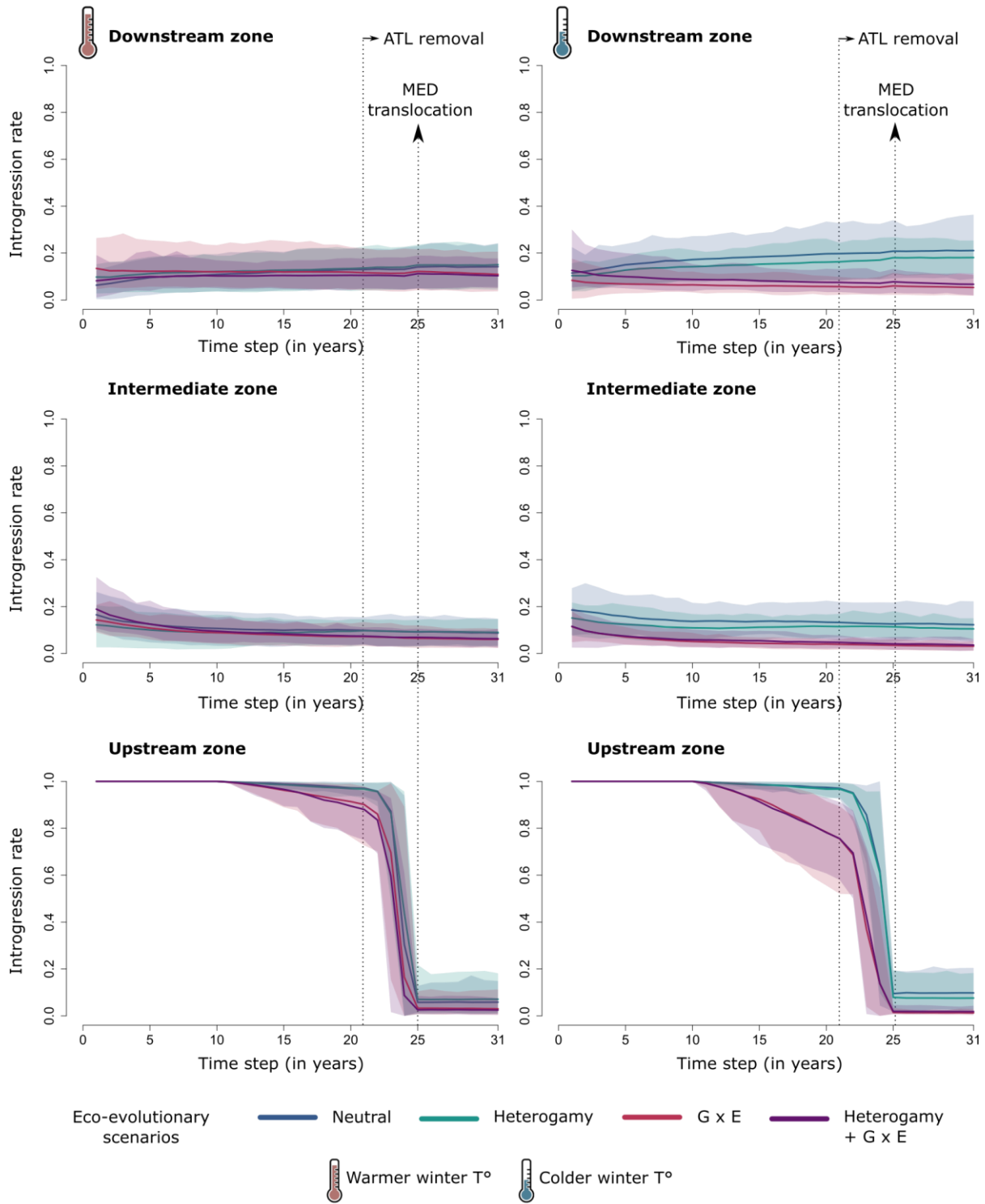


Figure 4—36: Evolution of the population introgression rate over 31 years in each zone of the Chevenne Creek. Trajectories are represented for each eco-evolutionary scenario and temperature modality. The time step during which some management practices were implemented is indicated.

4.4 Exploring various eco-evolutionary scenarios in the Chevenne Creek

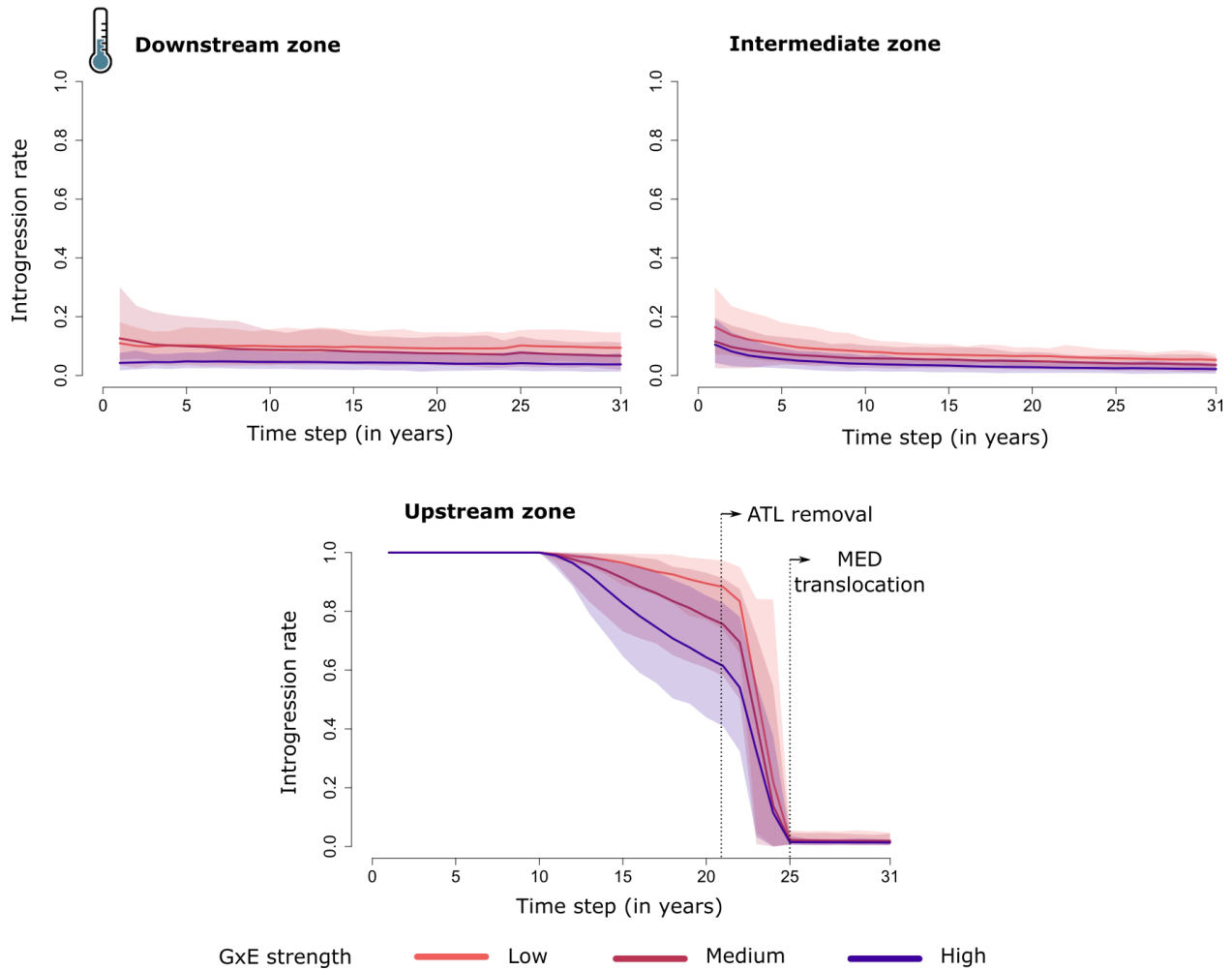


Figure 4—37: Evolution of the population introgression rate over 31 years in each zone of the Chevenne Creek. Trajectories are represented for various strengths of GxE interactions and the cold temperature modality. The time step during which some management practices were implemented is indicated.

Sensitivity analyses on GxE interactions.

The strength of GxE interactions also influenced the evolution of introgression in the Chevenne Creek (Figure 4 – 37). In the upstream zone, the higher the strength of GxE interactions was, the higher and stronger the decrease in introgression rate was following the implementation of the GR and ATL removal. The introgression rate reached approximately 0.9 for the low, 0.75 for the medium and 0.62 for the high strength of GxE interactions just before ATL removal

(Figure 4 – 37, $t = 21$). After full ATL removal and MED translocation, all scenarios ultimately led to the same rate of introgression (close to 0), which was to be expected considering ATL removal. In the downstream and intermediate zone, the introgression rate also decreased with higher GxE interactions, but observed differences between scenarios were lower, as the introgression rate was initially very low already. These results suggest that there is always room for selection to act, even slightly, when some ATL alleles are still segregated in the population.

Management practices were implemented to protect the intermediate zone from an alien gene flow and to replace the upstream ATL population with a native MED population. However, in the simulations, results indicate that the intermediate part was not affected by an upstream gene flow, as it is the case, in reality, no matter the eco-evolutionary scenario considered. On the contrary, the gene flow from downstream appeared to influence the evolution of introgression in that zone. Consequently, the management practices implemented did not affect the intermediate nor the downstream zone. Therefore, the following results will only focus on diversity dynamics in the upstream zone where management practices combined with various eco-evolutionary scenarios led to different outcomes.

4.4.2.2 *Genotypic composition of the population in the upstream zone*

In the upstream zone, the population was initially composed of ATL individuals with a lower population size observed when considering GxE interactions (Figure 4 – 38). The implementation of the GR strategy was associated with an increase in the number of HYB individuals while the number of ATL individuals decreased. This pattern was very slight for neutral selection scenarios and very pronounced when GxE interactions were implemented – steeper and faster. ATL removal led to a high decrease in population size, as most individuals were removed from the ATL zone.

4.4 Exploring various eco-evolutionary scenarios in the Chevenne Creek

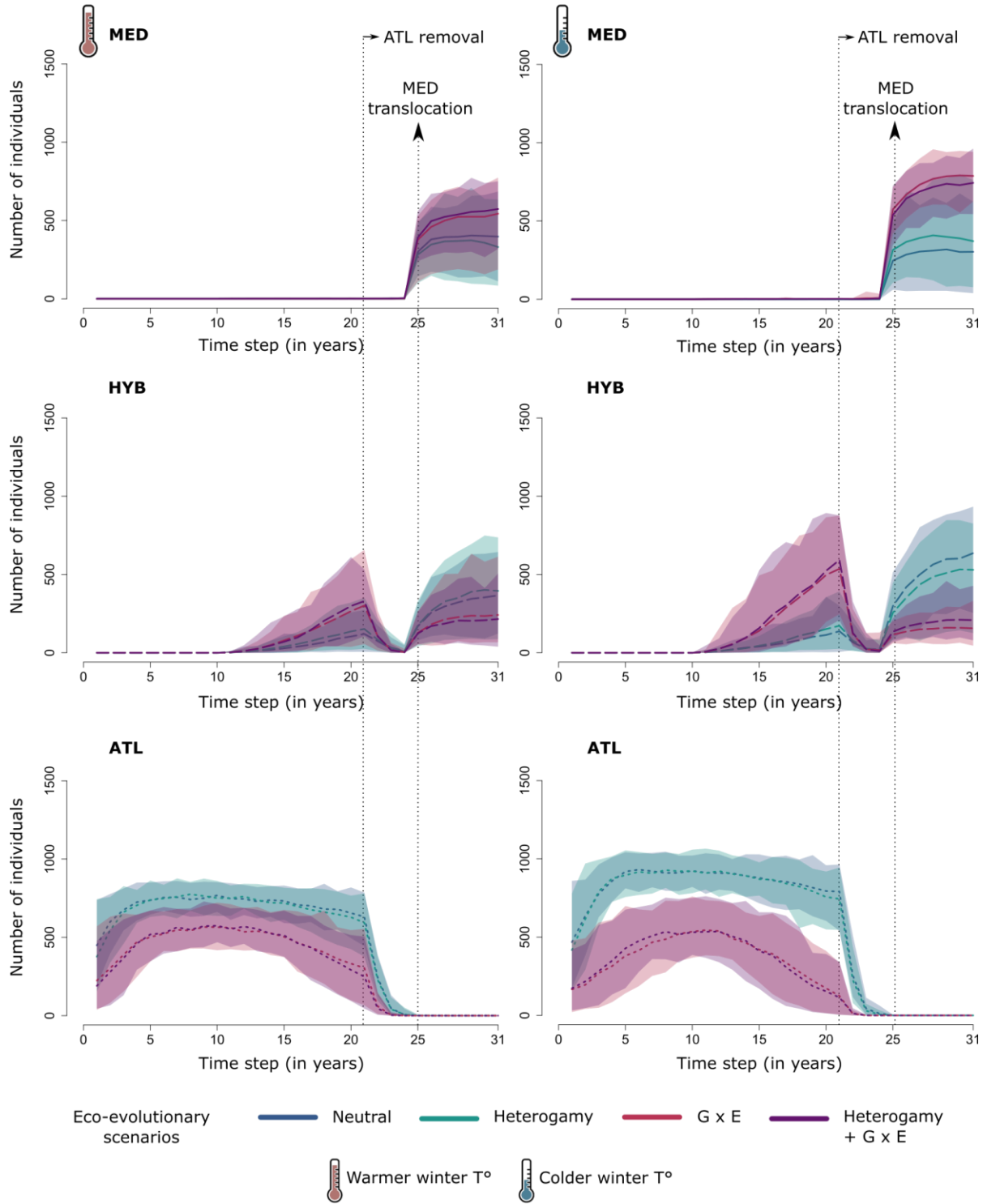


Figure 4—38: Evolution of the genotypic composition of the population over 31 years in the upstream zone. Trajectories are represented for each eco-evolutionary scenario and temperature modality. The time step during which some management practices were implemented is indicated.

Finally, following MED translocation, the numbers of MED and HYB individuals increased (*Figure 4 – 38*). This increase was different based on the survival scenario implemented. When GxE interactions were considered, more MED individuals and fewer HYB individuals were found in the population while it was the other way around when considering neutral survival. Temperature modality affected the differences observed between neutral and GxE survival scenarios, with more pronounced differences observed at colder temperatures.

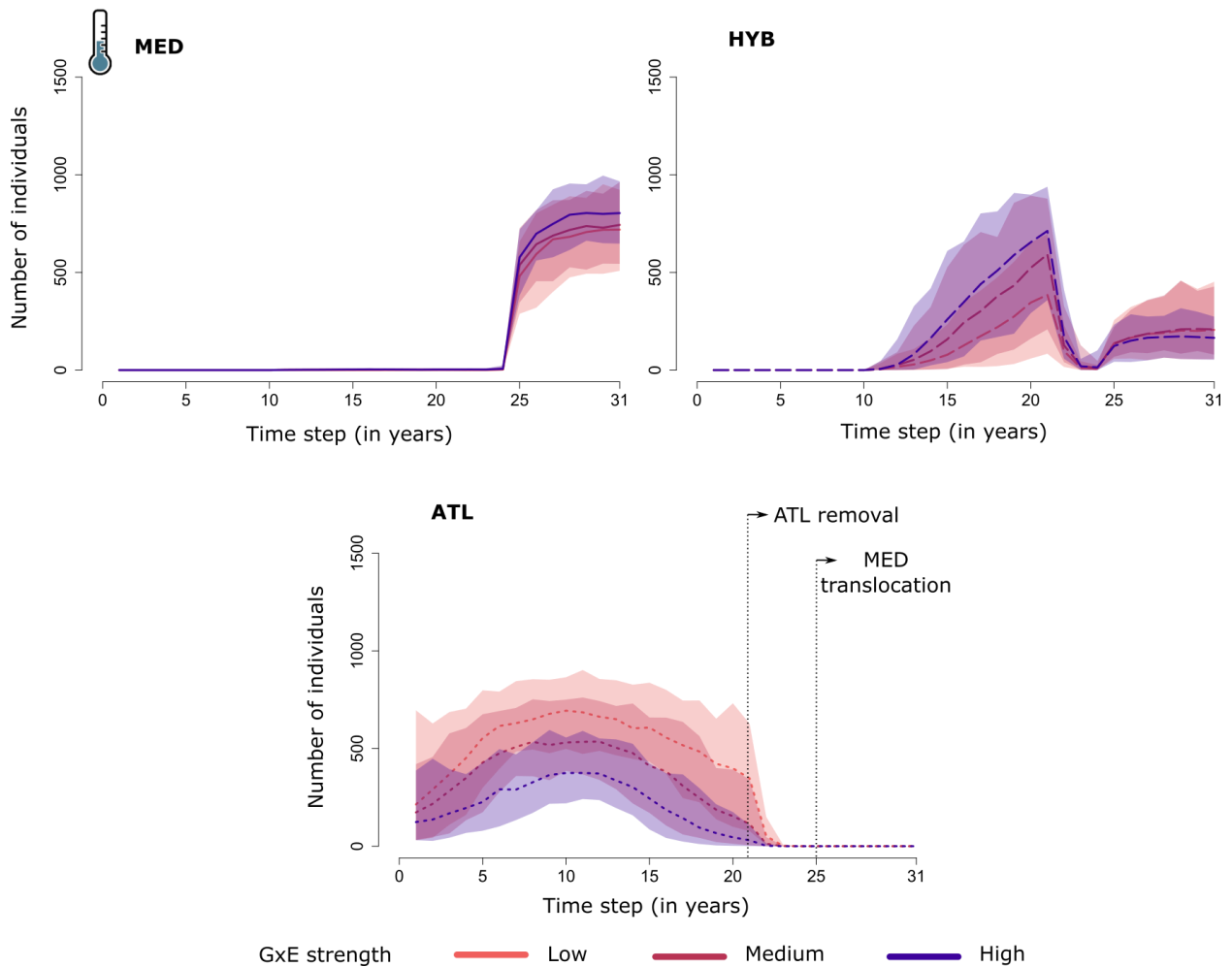


Figure 4—39: Evolution of the genotypic composition of the population over 31 years in the upstream zone. Trajectories are represented for various strengths of GxE interactions and the cold temperature modality. The time step during which some management practices were implemented is indicated.

4.4 Exploring various eco-evolutionary scenarios in the Chevenne Creek

Sensitivity analyses on GxE interactions.

The strength of GxE interactions had a significant impact on the genotypic composition of the population. Population size at equilibrium in the upstream zone stabilised at lower values when higher GxE interactions were implemented (*Figure 4 – 39*, at $t = 10$ years, ~ 350 individuals for the high vs ~ 500 individuals for the medium vs ~ 650 individuals for the low modality). The decrease in the proportion of ATL individuals, following the implementation of the GR strategy then happened at the same speed. Meanwhile, the number of HYB individuals increased faster for the higher modality of GxE interactions before ATL removal. Then following MED translocation, higher GxE strength led to a higher increase in the number of MED individuals, while the increase in HYB was slightly lower.

4.4.2.3 Distribution of individual introgression in the upstream zone

Ten years after the implementation of the GR strategy ($t=21$), a wide range of highly introgressed HYB were created when GxE interactions were implemented, whereas a large number of ATL individuals were still found in the population otherwise (*Figure 4 – 40*). Even fewer ATL individuals were found considering GxE interactions and the colder temperature modality. Ten years after MED translocation ($t=31$), the distribution of individual introgression switched toward MED individuals as ATL individuals had been previously removed. More HYB individuals were found when considering neutral survival scenarios, while GxE interaction scenarios favoured MED individuals. Again, this pattern was more pronounced at colder temperatures.

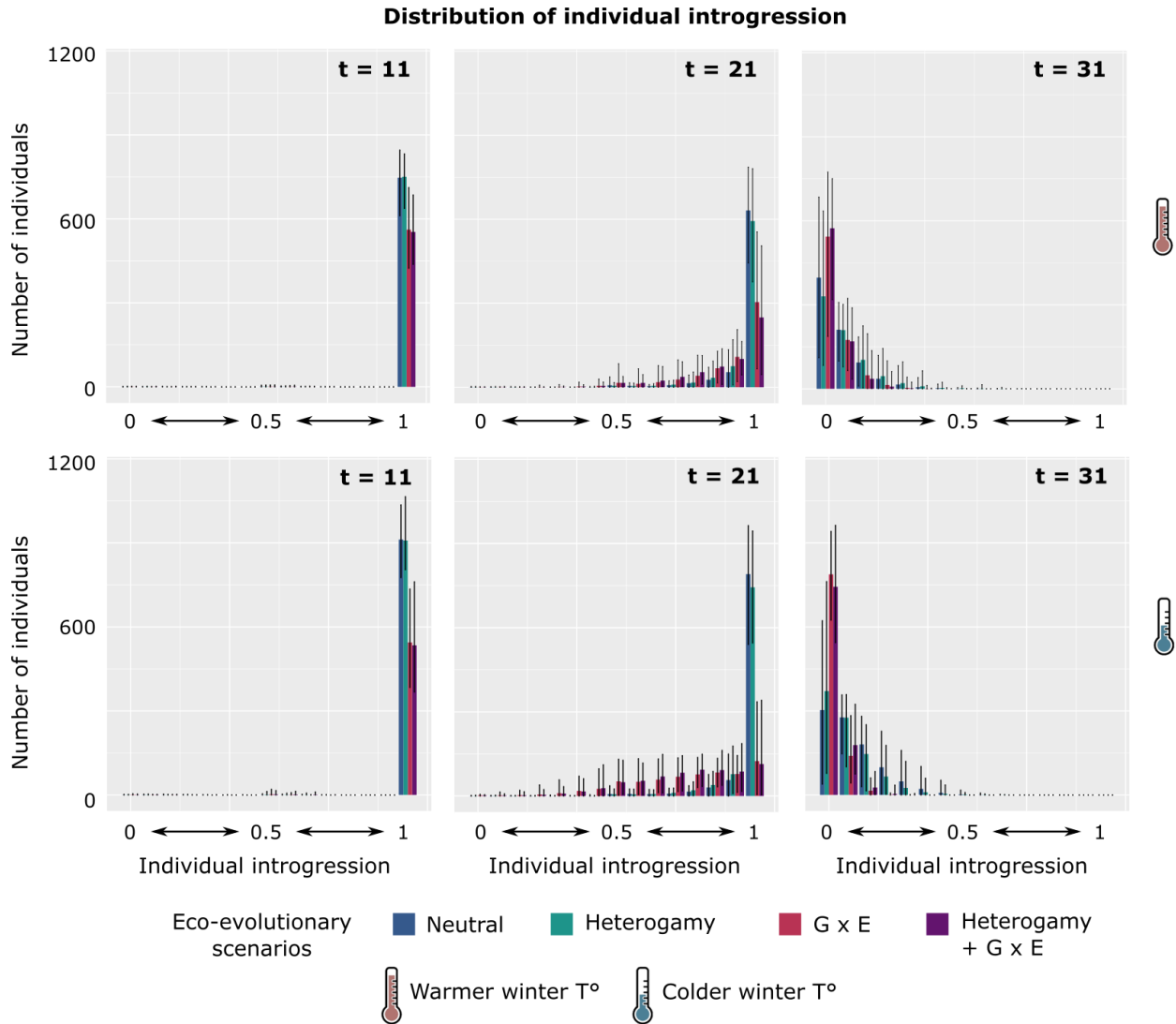


Figure 4—40: Distribution of individual introgression just before the implementation of the GR strategy ($t = 11$), 10 years after and before ATL removal ($t = 21$) and at the end of the simulation, after ATL removal and MED translocation ($t = 31$). Distributions are represented for each eco-evolutionary scenario and temperature modality.

4.4.2.4 Evolution of demography: total population size

In the downstream and the intermediate zone, population size mainly remained stable over time except at $t = 25$, where a slight decrease in population size in the downstream zone was observed due to MED sampling for translocation (Figure 4 – 41).

4.4 Exploring various eco-evolutionary scenarios in the Chevenne Creek

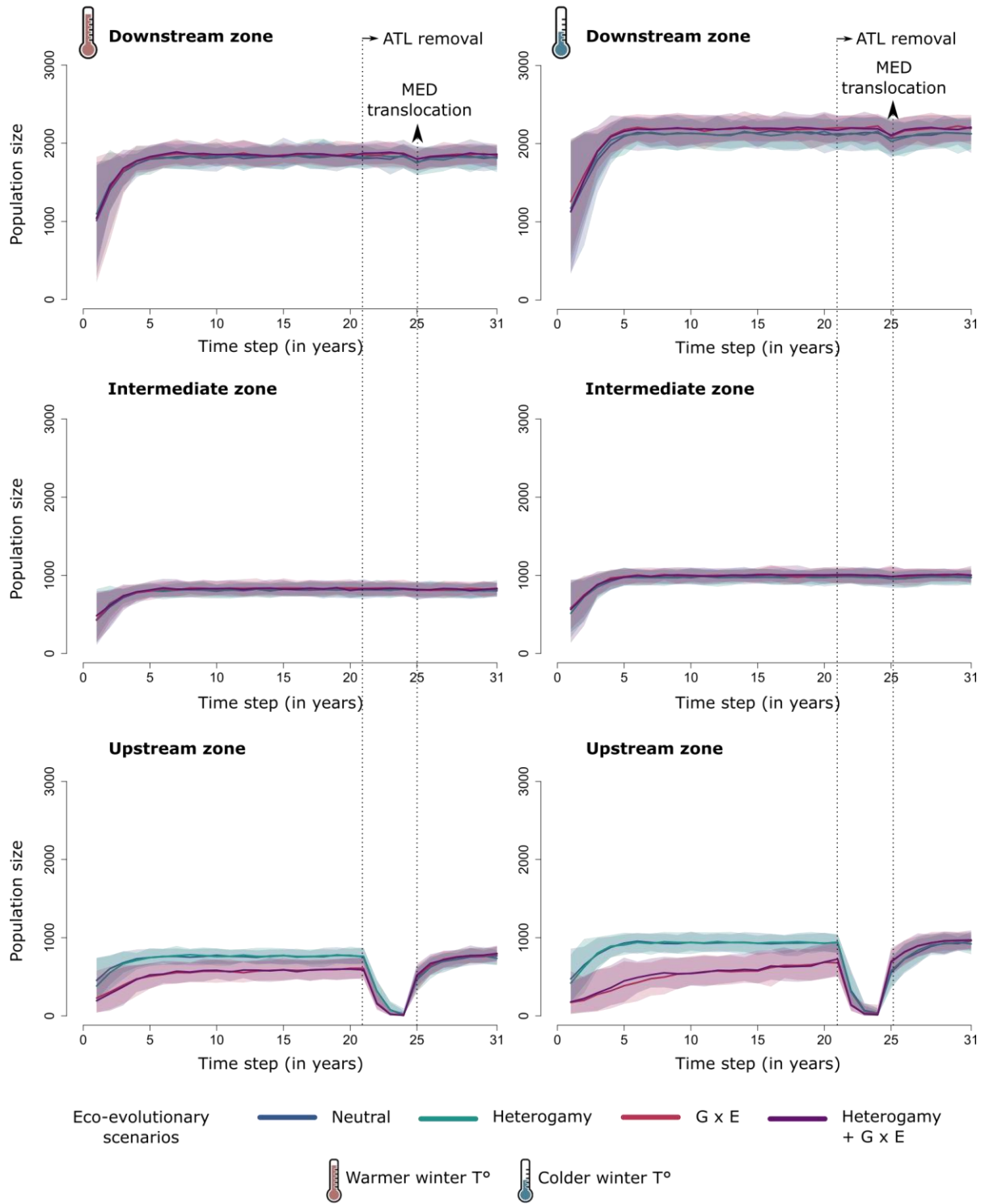


Figure 4—41: Evolution of population size over 31 years in each zone of the Chevenne Creek. Trajectories are represented for each eco-evolutionary scenario and temperature modality. The time step during which some management practices were implemented is indicated.

Management practices and eco-evolutionary scenarios led to variation in demography mainly in the upstream zone (*Figure 4 – 41*). Population size was initially lower when GxE interactions were implemented, and even more so at colder temperatures. With the implementation of the GR strategy, population size increased progressively, but only at colder temperatures. At that temperature, higher selective pressure might cause selection to be stronger, favouring the gene flow from the intermediate part. The resulting progressive increase in MED alleles might then allow the population mean fitness to increase. Following ATL removal, population size decreased for all scenarios. It then increased back up with the translocation of MED individuals. This increase was stronger for GxE interaction scenarios, as population size was higher after MED translocation compared to before ATL removal. In addition, the population size was slightly higher at colder temperatures for all scenarios. This could potentially result from a model bias on survival, as survival is initially higher for lower stages of life (eggs vs larvae vs juveniles), which last longer at colder temperatures (*Section 3.3.1 & 3.3.2*).

4.4.2.5 Evolution of population size per age class in the upstream zone

Focusing on the evolution of population size per stage in the upstream zone (*Figure 4 – 42*): before ATL removal and translocation, differences in population size between scenarios considering neutral *versus* GxE interactions survival were strong for all three life stages, even more so for juveniles and at colder temperatures. For all scenarios, translocation led to an increase in the number of juveniles, sub-adults and adults and the population size for each stage became similar among scenarios. At colder temperatures, this increase was initially faster when GxE interactions were implemented.

4.4 Exploring various eco-evolutionary scenarios in the Chevenne Creek

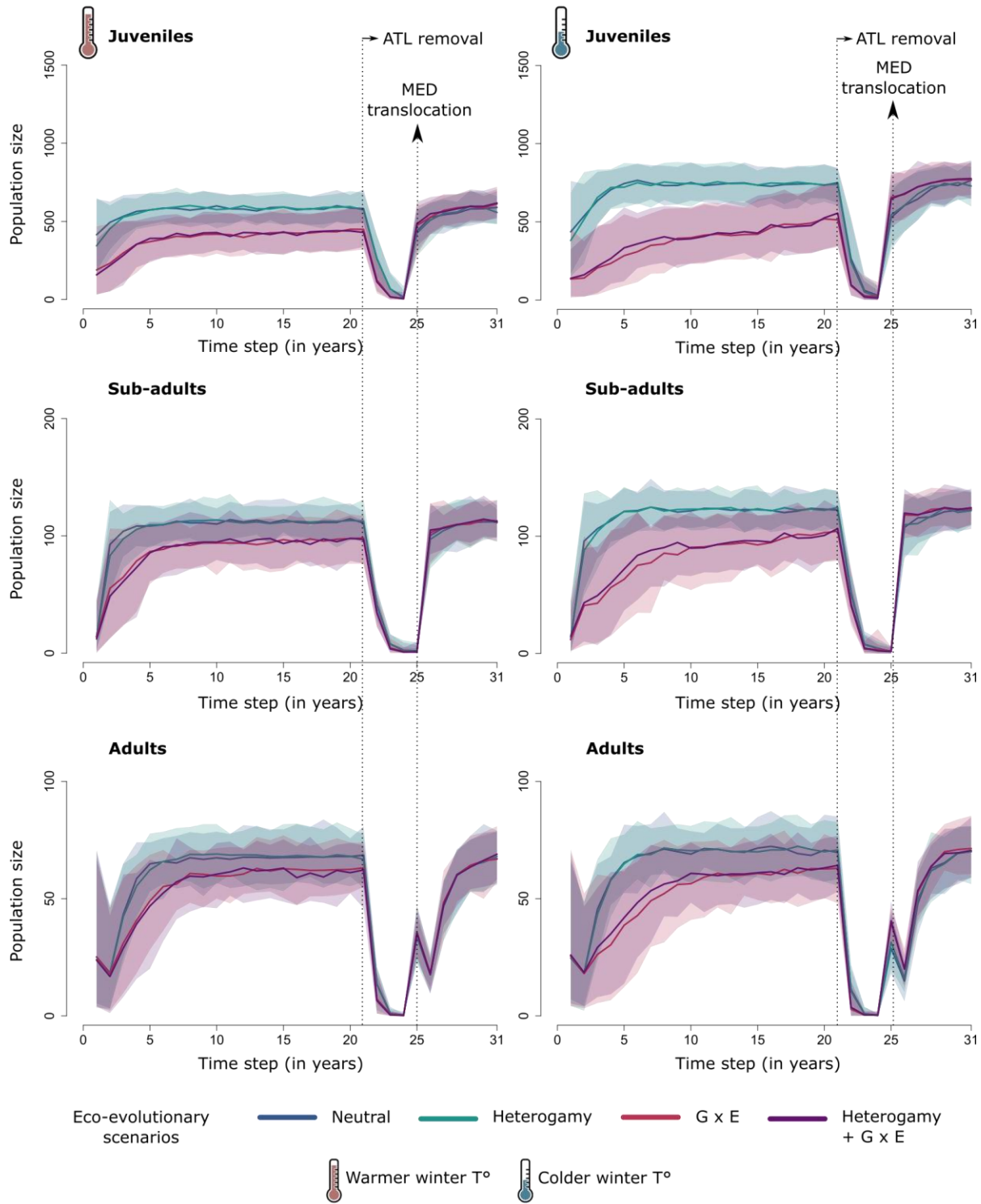


Figure 4—42: Evolution of population size per age class over 31 years in the upstream zone. Trajectories are represented for each eco-evolutionary scenario and temperature modality. The time step during which some management practices were implemented is indicated.

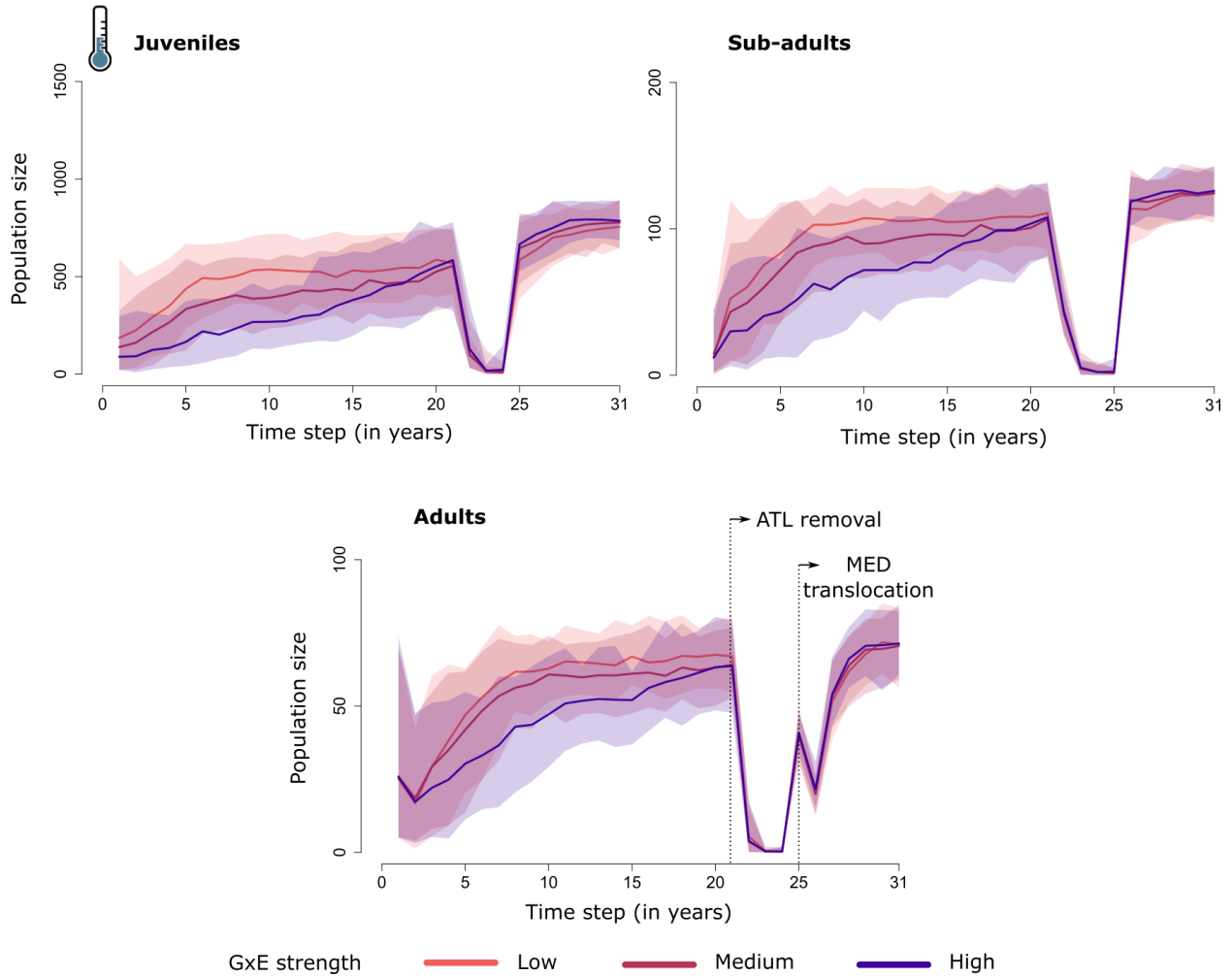


Figure 4—43: Evolution of population size per age class over 31 years in the upstream zone. Trajectories are represented for various strengths of GxE interactions and the cold temperature modality. The time step during which some management practices were implemented is indicated.

Sensitivity analyses on GxE interactions.

The strength of GxE interactions had a significant impact on demography in the upstream zone before ATL removal (Figure 4 – 43). For all life stages, population size after stabilisation was initially smaller for the higher modality of GxE interactions. Following the implementation of the GR strategy, population size increased faster for the highest modality of GxE interactions, leading to the same population at $t = 21$, just before ATL removal. Following MED translocation, population size became the highest for the higher modality of GxE interactions. This is

4.4 Exploring various eco-evolutionary scenarios in the Chevenne Creek

because the mean fitness of a MED population is higher when selective pressures are higher (either through temperature or GxE strength), as MED offspring survival increases while ATL offspring survival decreases (*Section 4.2*).

CASE STUDY 2 & 3:

THE BORNE RIVER

4.4.3 The Borne River

4.4.3.1 Study site

Located in the Rhone River Basin, the Borne River is a mountainous fast-flowing water stream that extends 32 kilometres long and ranges from 2750 to 400 metres in elevation in a 158 kilometres square catchment area. This typical Northern French Alpine stream is characterised by a strong slope (mean value: 3.3%) and lies within the geographical range of Mediterranean brown trout, native to the area (Bernatchez et al., 1992; Guyomard, 1989; Launey et al., 2003). Multiple artificial and natural impassable barriers fragment this river, causing isolated populations of brown trout that cannot disperse. Three artificial ones are located in the mainstream. Barriers one and three (Figure 4–44) are old watermill dams with small impassable waterfalls (2-3 metres high) and barrier two is a small hydroelectric dam (9 metres high). Two natural impassable waterfalls (4 & 5) are located in the tributaries of the Borne River.

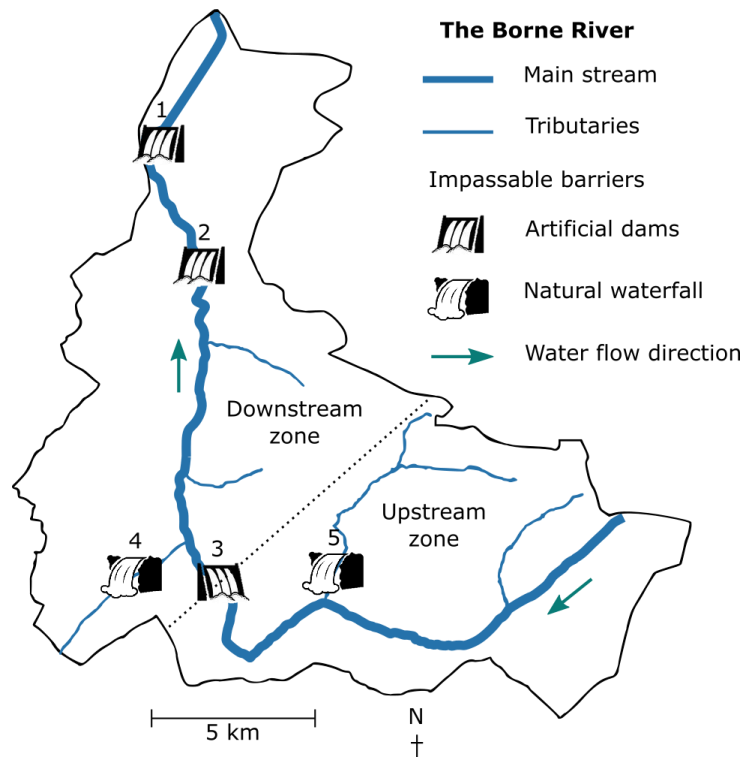


Figure 4—44: Representation and characteristics of the Borne River with the mainstream and its tributaries. Main fragmentations that represent impassable barriers are represented.

In the Borne River, habitat quality is considered good for both reproduction – *i.e.* spawning ground – and carrying capacity of brown trout, even though some upstream areas limits population settlement due to upstream pollution (skiing tourism and cattle wintering). However, such steep and fast-flowing streams are characterised by harsh conditions, such as flash floods, which can have a direct impact on habitat structure and harshly affect brown trout populations. Flash floods happen periodically (decennial, centennial ...) and can be of variable magnitude. In the Borne, discharge can range from two $\text{m}^3.\text{s}^{-1}$ (annual average flow) to more than $200 \text{ m}^3.\text{s}^{-1}$, with a decennial flood value of $75 \text{ m}^3.\text{s}^{-1}$. In July 1987, the Borne River experienced a major flooding event (the "Grand Bornand disaster"), expected to occur every 400 years. A violent storm caused the river to flood in the upper part of the catchment area with discharge values superior to $200 \text{ m}^3.\text{s}^{-1}$. This flood scoured the entire upstream area and wiped out all brown trout populations located upstream of dam 3 (*Figure 4 – 44*). Downstream populations were also severely affected with all redd scoured and only a small proportion of the population remaining. To restore a viable population along the Borne River, stocking was highly intensified following this flood.

4.4.3.2 *Historical management*

Stocking of brown trout had already begun in 1913 (*Figure 4 – 45*) when a hatchery was created nearby (Vizille, Isère), with 20 000 fry yearly stocked. This number gradually increased and peaked after the flood in 1989, reaching 1 000 000 introduced fry. To help restore brown trout populations and counter the damage caused by the catastrophic flood, stocking was at its highest in 1989, 1990 and 1991. Genotypic studies on microsatellite *loci* Str541 and Str591 in the Vizille hatchery indicated that the introduced strain belonged to the ATL lineage of brown trout (Launey et al., 2003). Stocking happened every year up until 2004 all along the Borne River with 4-5 cm juveniles usually introduced before summer, when hydrological stream conditions were stable (*Figure 4 – 46*).

4.4 Exploring various eco-evolutionary scenarios in the Borne River

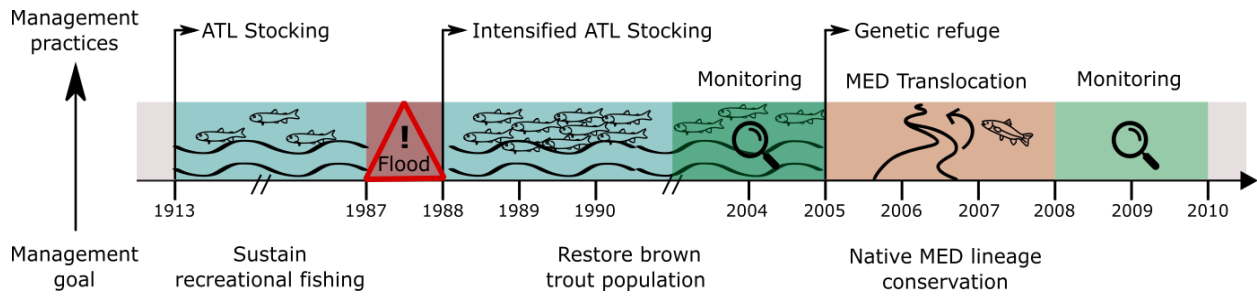


Figure 4—45: Historical management timeline for the Borne River. Management goals and practices are represented.

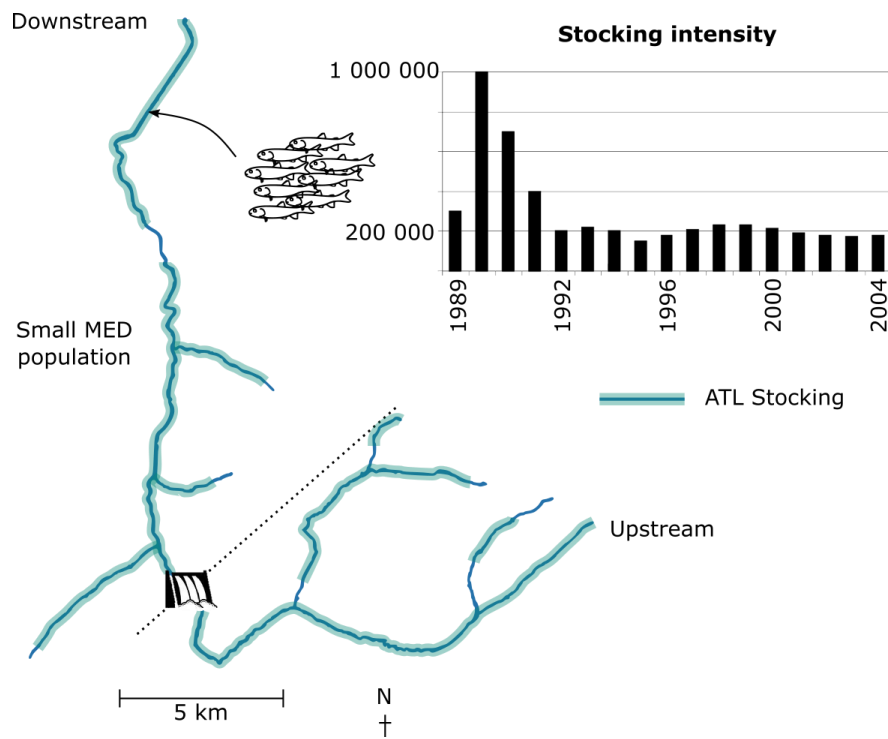


Figure 4—46: Spatial representation of stocking practices carried out on the Borne River from 1913 to 2004. The number of fish released throughout the Borne between 1988 and 2004 is indicated (Figure from Caudron et al., 2009).

In 2002, Caudron et al. (2009) started investigating the evolution of demography and genetic diversity – *i.e.* introgression rate – as well as the contribution of restocked fish to stage 0+, in both upstream and

downstream areas of the Borne River. Genetic and demographic monitoring revealed the presence of a thriving and almost pure native MED population downstream (43-55 fish.100m⁻²) with a very low introgression rate (~ 10%), despite the ongoing stocking effort with ATL strains from 1988 to 2004. In the upstream area, however, introgression rates were very high (ranging from 78 to 100%), where a small non-native population showed very low densities (1-2 fish.100 m⁻²). Marked otolith analyses showed that the majority of fish contributing to stage 0+ upstream were restocked (90-100%), pointing toward a lack of natural recruitment from stocked ATL brown trout. Altogether, these analyses revealed that after the flood the native Mediterranean population was restricted to the lower part (*Figure 4 – 44*, under dam 3) of the Borne River and recovered naturally downstream without hybridizing with stocked ATL individuals, while the population upstream most likely originated from and has been maintained by continuous ATL stocking.

As scientists and managers became more aware of inter and intraspecific diversity, fisheries managers became interested in the conservation of remaining native brown trout populations to protect well-adapted local populations. Therefore, in the Mediterranean area management goals changed toward the conservation of the native MED lineage. In 2005, stocking of ATL brown trout stopped in the Borne River and a GR strategy was implemented to preserve native alleles. Additionally, in order to restore the native MED gene pool upstream and establish a viable population, direct translocation of native wild trout had been implemented for three consecutive years, from 2005 to 2007. In total, 1630 MED brown trout of various age classes were sampled from the downstream area, where introgression rates were very low, and directly translocated to two upstream parts of the river (*Figure 4 – 47*). More trout were translocated in the lower part of the river stretch – respectively 125, 610 and 370 in sector B compared to 135, 282 and 110 in sector A. Recreational fishing was banned from the translocated zone B (*Figure 4 – 47*) and its lower stretch B1 to favour the settlement of the translocated native trout, but not in upper sectors A and A1.

4.4 Exploring various eco-evolutionary scenarios in the Borne River

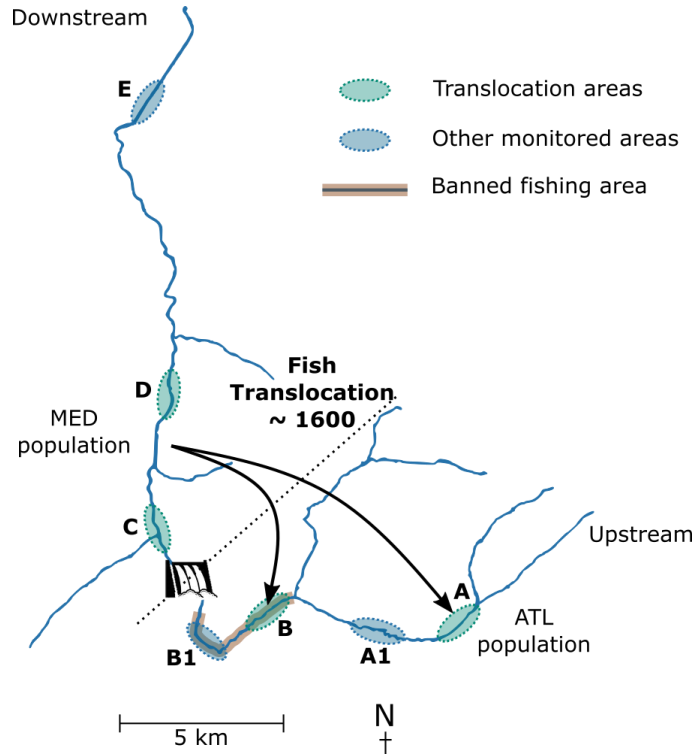


Figure 4—47: Spatial representation of fish translocation practices carried out on the Borne River from 2005 to 2007.

(Caudron, Champigneulle, et al., 2012) monitored the evolution of demography and genetic diversity in the Borne River following these management practices. Five sectors (Figure 4 – 47), three located upstream (C, D and E) and two downstream (A and B), were studied to respectively evaluate the efficiency of the GR strategy and the translocation strategy. Demographic and genetic monitoring were performed in these sectors in 2004, just before the measures and after, in 2008 and 2009. In 2009, genotypic data were also studied in two additional sectors (A1 and B1) located downstream of the translocated sectors (A and B), to investigate the potential migration of introduced trout or their offspring.

4.4.3.3 Simulation protocol

Simulations. All simulations – with the same initial parameters – are replicated 15 times. Most results represent the mean value of all the replications as well as a 95% confidence interval.

Hydrographic network. In MEDITERRANEA, the Borne hydrographic network is explicitly represented by a succession of 31 reaches and 25 weirs defined based on the topology of the Borne River. Five of the 25 weirs represent the Borne impassable barriers (*Figure 4 – 48*). Reaches and weirs state variables are informed by the Borne physical characteristics (*Appendix D: Table 3 & 4*).

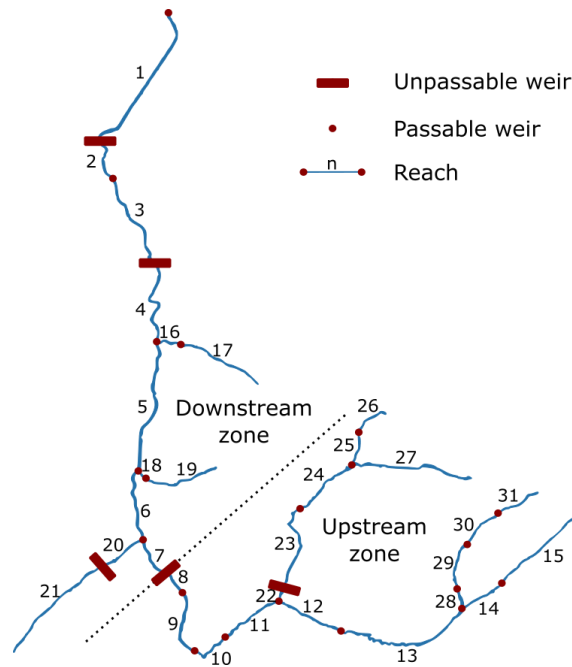


Figure 4—48: Representation of the Borne River in MEDITERRANEA. It is made of a succession of reaches and weirs. Unpassable weirs are marked. Reach numbers are represented.

Parameters settings. Parameters informing and controlling for maximum density are set based on observational data (*Scimabio Interface data*). For the Borne River observed density is around 5000

4.4 Exploring various eco-evolutionary scenarios in the Borne River

individuals per hectare ($K_{maxE} = 3.1$). The rest of the parameters used in the simulations are set by default.

Temperature models. As temperature influences GxE selection and resulting diversity dynamics, we used two temperature models. One has an overall lower winter temperature (Figure 4 – 49), and hence selective pressure might be potentially higher, while the other has an overall higher winter temperature (Figure 4 – 50). To implement these models, observed water temperatures in 2003 and 2010 were used, as yearly water temperature data for the Borne River are scarce.

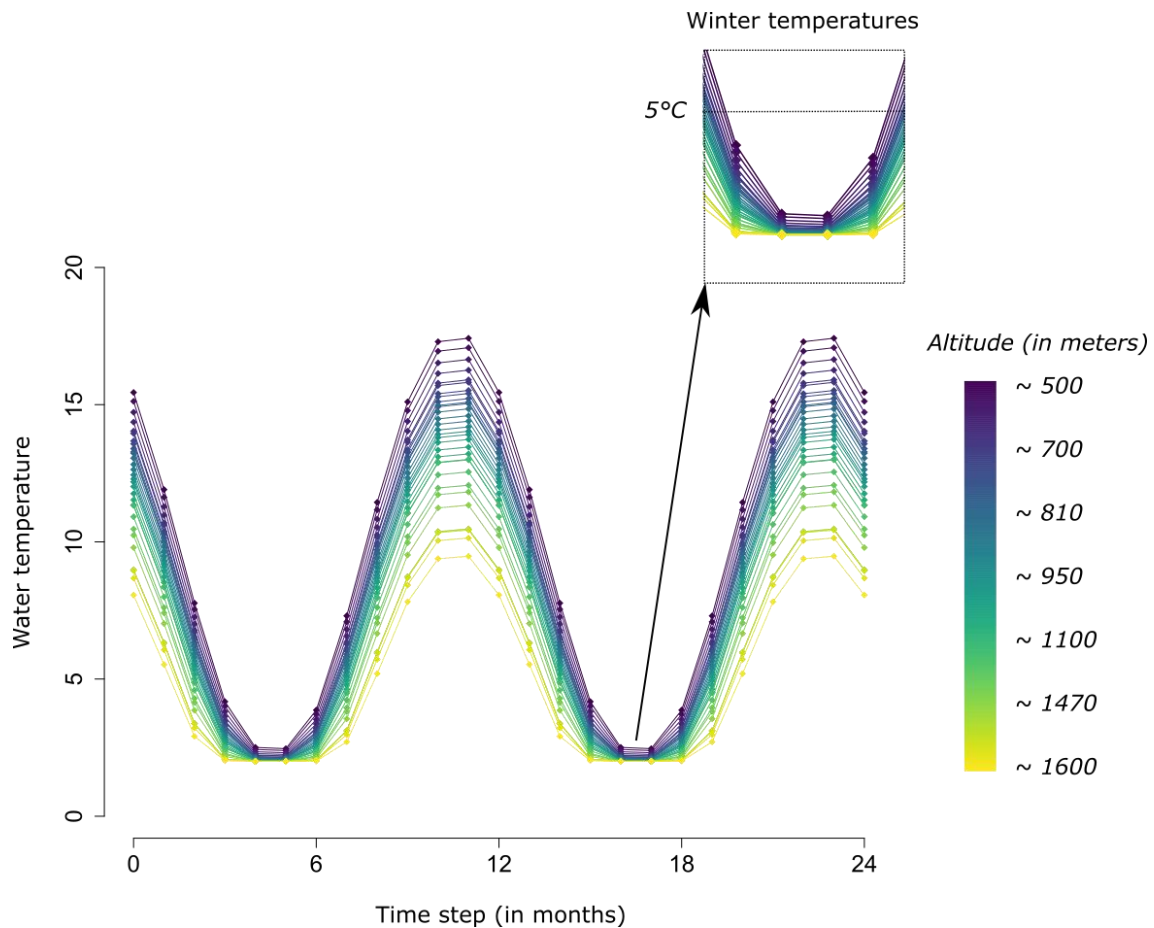


Figure 4—49: Colder temperature model used for simulations carried out on the Borne River. One water temperature is calculated per reach each month based on altitude. A zoom of winter temperatures shows the temperature from December to March.

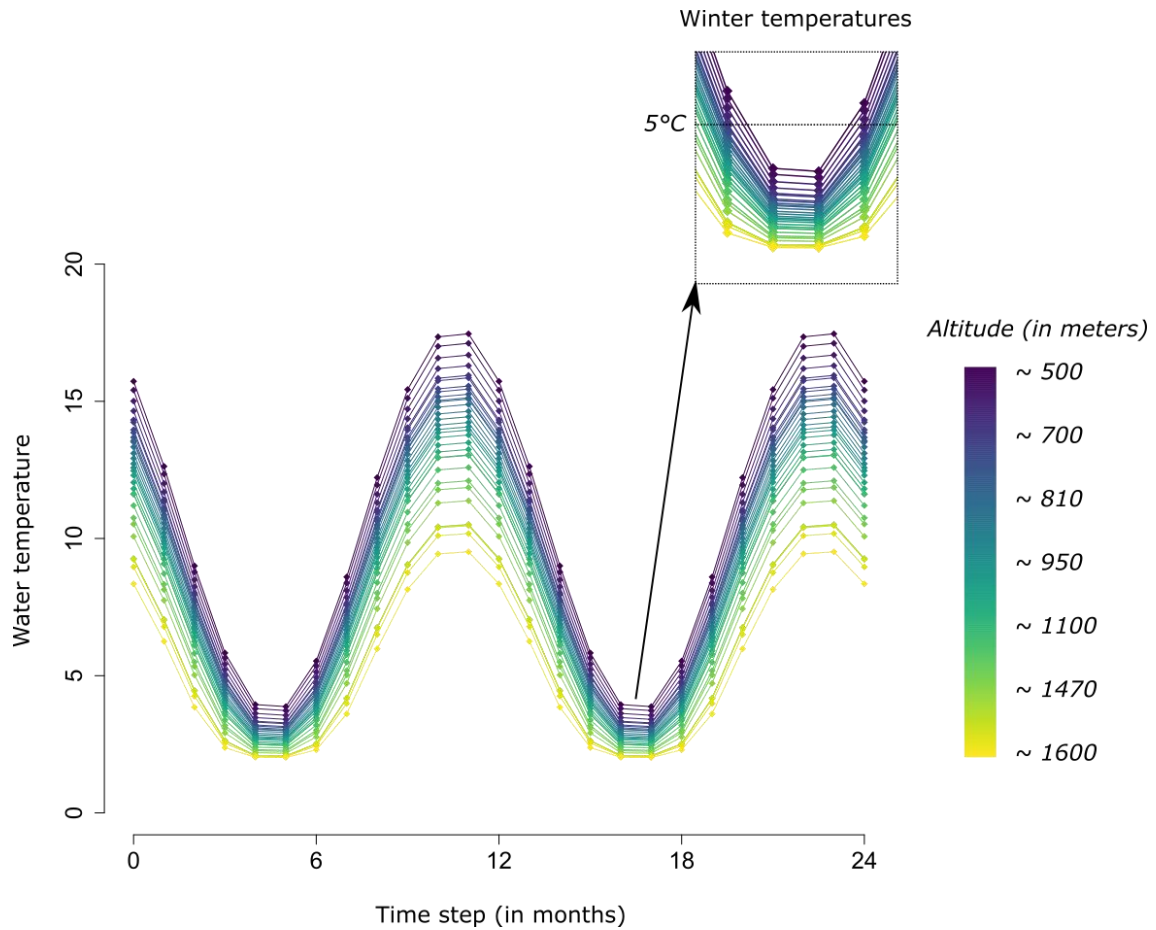


Figure 4—50: Warmer temperature model used for simulations carried out on the Borne River. One water temperature is calculated per reach each month based on altitude. A zoom of winter temperatures shows the temperature from December to March.

Based on its historical management and available data, the Borne River will be used in two separate case studies. The first one will focus on the period going from 1988 to 2004 when ATL stocking took place to restore a devastated brown trout population. The second one will represent the management practices that took place after 2004 to conserve and restore a native MED population all along the Borne River.

CASE STUDY 2:

THE BORNE RIVER

From 1988 to 2004: ATL stocking

4.4.4 Evolution of diversity dynamics and demography in the Borne River during ATL stocking (from 1988 to 2004)

After the devastating flood of the Borne River in 1987, ATL stocking was intensified all along the river to help restore the brown trout population. The first case study aims at simulating the stocking event that took place from 1988 to 2004 to predict its impact on diversity dynamics and demography. Therefore, the simulation will start in September 1987 – time step 0 – right after the flood, and will be run for 17 years. The initial population will be representative of the post-flood devastated brown trout population, with barely any individuals located upstream and a very low-density population of MED individuals downstream. Unlike the other case studies, there will not be any population stabilisation using the model, as our goal is to start with a devastated population without any nests or juveniles. Management practices – *i.e.* intervention – will hence take place directly during year 1 – *i.e.* 1988. Stocking with ATL fry will happen every year, in June (time step 9) from 1988 until 2004 included. A given density of fish per metre square will be added to each reach based on the stocking intensity experienced in that given year (*Figure 4 – 51*). Individuals are added as part of a group of individuals using the intervention “hatches additions” (*Section 3.4.2*). Hatches are added at 6 months old, their mean size is set at 4 cm and their mean introgression at 1 (*Figure 4 – 51*, initial hatch characteristics).

In the simulations, stocking practices in the Borne River only led to the admixture of the MED and the ATL lineages in the downstream section of the Borne River where a small native MED population was present. Hence, diversity dynamics will only be monitored in this part of the river.

4.4 Exploring various eco-evolutionary scenarios in the Borne River 1988

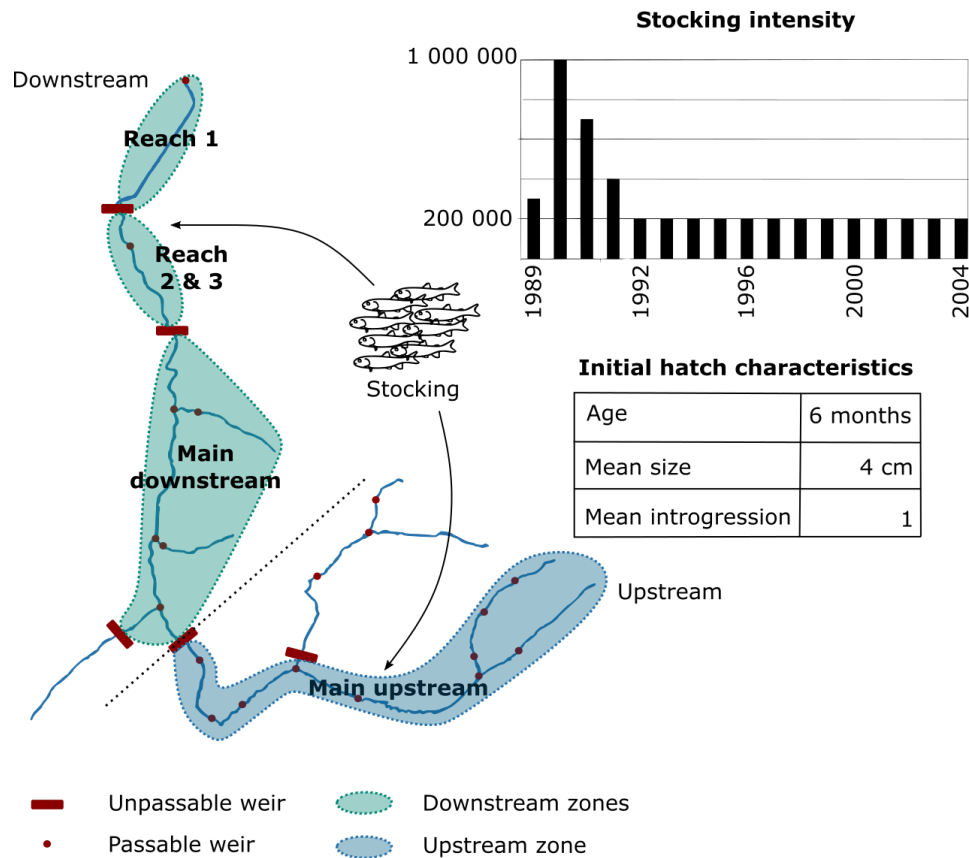


Figure 4—51: Representation of ATL stocking practices carried out in MEDITERRANEA for the Borne River. The zones that will be studied are highlighted in the downstream (green) and upstream (blue) sections. Stocking intensity used in the simulation is represented as the number of individuals stocked in the entire river. Initial hatches characteristics are informed.

4.4.4.1 Evolution of introgression

A clear and continuous increase in introgression level (Figure 4 – 52) – i.e. the percentage of ATL alleles – followed the implementation of stocking practices in the three downstream zones (delimited based on impassable barriers, Figure 4 – 44) and for all eco-evolutionary scenarios. This increase was very steep during the first three years as stocking was more intensive, and then slowed down. Differences among eco-evolutionary scenarios could also be observed, with the scenarios considering GxE interactions leading to a lower and slower increase in introgression rate compared to those that did not.

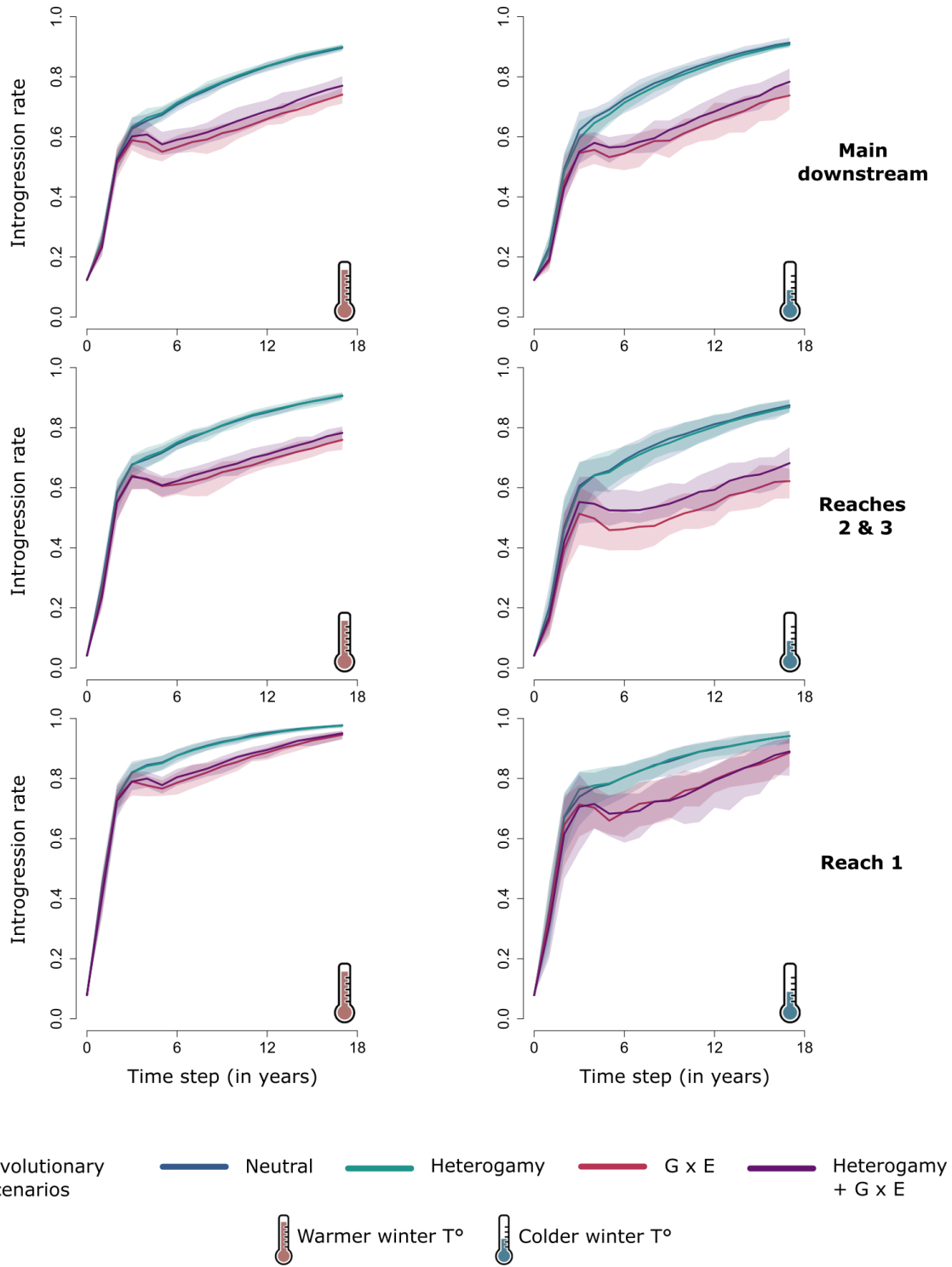


Figure 4—52: Evolution of the population introgression rate in each downstream zone of the Borne River from 1988 to 2004, when ATL stocking took place every year. Trajectories are represented for each eco-evolutionary scenario and temperature modality.

4.4 Exploring various eco-evolutionary scenarios in the Borne River 1988

This was generally true; although observed differences could be more or less pronounced based on the temperature modality and the zone (Figure 4 – 52). In the most downstream zone (reach 1), the introgression rate went up the highest, to approximately 0.97 versus 0.95 when considering or not GxE interactions at warmer temperatures, and up to approximately 0.95 versus 0.88 at colder temperatures. For the two other zones, observed differences among scenarios were more consequent (> 0.1) as the introgression rate did not go above 0.8 when implementing GxE interactions whereas it was superior to 0.9 otherwise. For these zones, when implementing heterogamy in addition to GxE interactions, one can notice that it led to a slightly higher rate of introgression, especially at colder temperatures and for the zone including reaches 2 and 3 (0.69 vs 0.62), where introgression level remained lower compared to the other zones. However, apart from that, the implementation of heterogamy barely had any impact on introgression dynamics, as confidence intervals mainly overlapped.

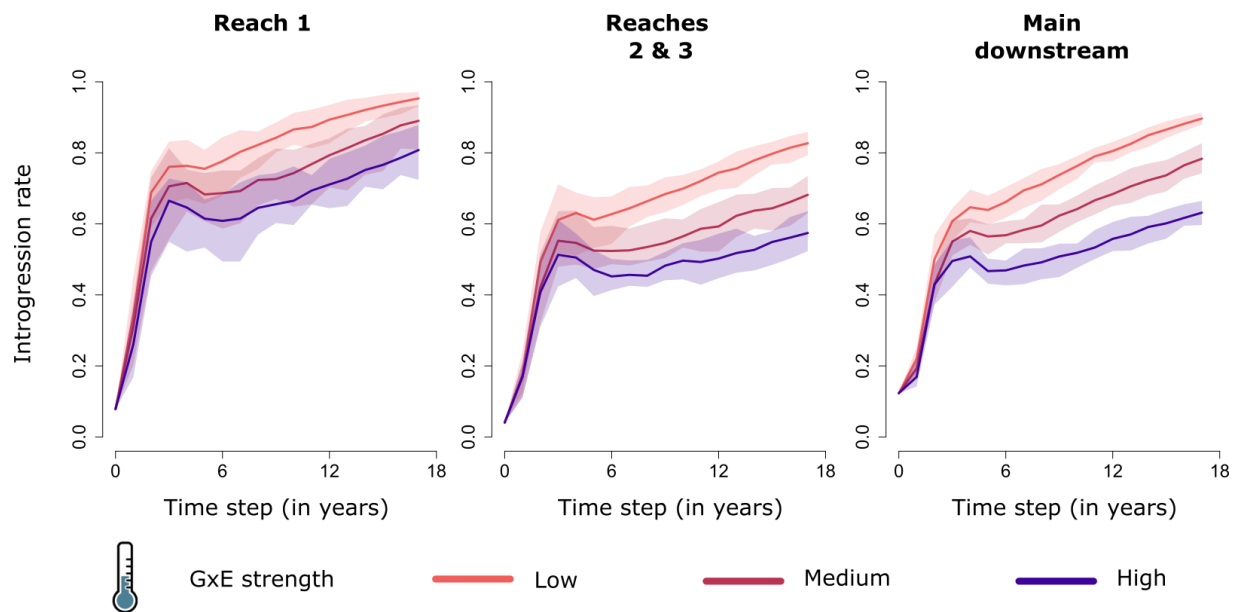


Figure 4—53: Evolution of the population introgression rate in each downstream zone of the Borne River from 1988 to 2004, when ATL stocking took place every year. Trajectories are represented for various strengths of GxE interactions and the colder temperature modality.

Sensitivity analyses on GxE interactions.

The strength of GxE interactions also influenced the evolution of introgression (*Figure 4 – 53*). Overall the higher the strength of GxE interactions was, the lower and slower the increase in introgression rate was. For example, in the main downstream zone, the introgression rate reached approximately 0.9 for low, 0.78 for medium and 0.62 for high strength of GxE interactions. However, the extent of this effect was mediated by the zone in which the introgression rate was followed. Introgression dynamics were less influenced by differences in GxE interactions in reach 1 compared to the other zones.

Overall, temperature modalities, zones and strength of GxE interactions influenced the speed and intensity of increase in introgression rate, but patterns of introgression dynamics remained similar. Therefore, the following results will only focus on one of the zone: the downstream area.

4.4.4.2 Genotypic composition of the population

Before the implementation of stocking, the downstream population was mainly composed of a low number of pure MED individuals, due to the flood (*Figure 4 – 54*). As population size was initially very low, the numbers of MED, HYB and ATL individuals increased rapidly within the first three years. However, with the continuous implementation of stocking, the number of MED individuals then decreased rapidly, until the extinction of the MED lineage, while more HYB individuals were created. Meanwhile, after a rapid increase, the ATL lineage also experienced a small decrease in population size as the intensity of stocking decreased after four years. However, with continuous stocking of ATL individuals, their number then slowly increased back up, while the number of HYB individuals started decreasing. Only small differences in the genotypic composition of the population were observed among eco-evolutionary scenarios. The implementation of GxE interactions led to a lower proportion of ATL individuals and a slower

4.4 Exploring various eco-evolutionary scenarios in the Borne River 1988

disappearance of MED individuals for both temperature modalities. For colder temperatures, it also led to a slightly lower number of HYB. Barely any differences could be observed when heterogamy was implemented – both with and without GxE interactions – as confidence intervals mainly overlapped.

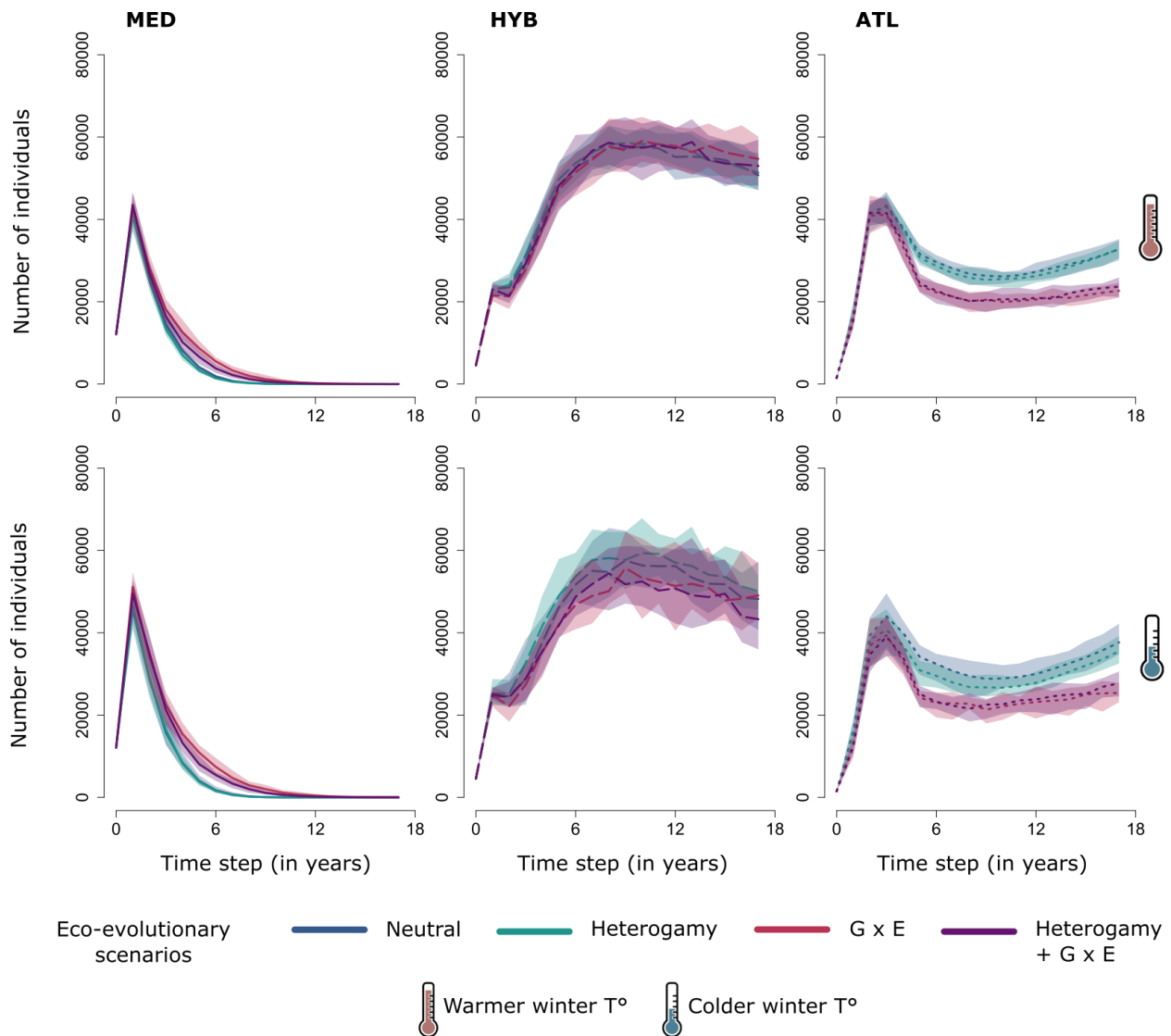


Figure 4—54: Evolution of the genotypic composition of the population in each downstream zone of the Borne River from 1988 to 2004, when ATL stocking took place every year. Trajectories are represented for each eco-evolutionary scenario and temperature modality.

Sensitivity analyses on GxE interactions. The strength of GxE interactions had a significant impact on the genotypic composition of the population (Figure 4–55). Higher GxE strength led to a slower decrease in the number of MED individuals and a stronger increase in the number of HYB. For ATL individuals, their number was initially lower and increased back up more slowly.

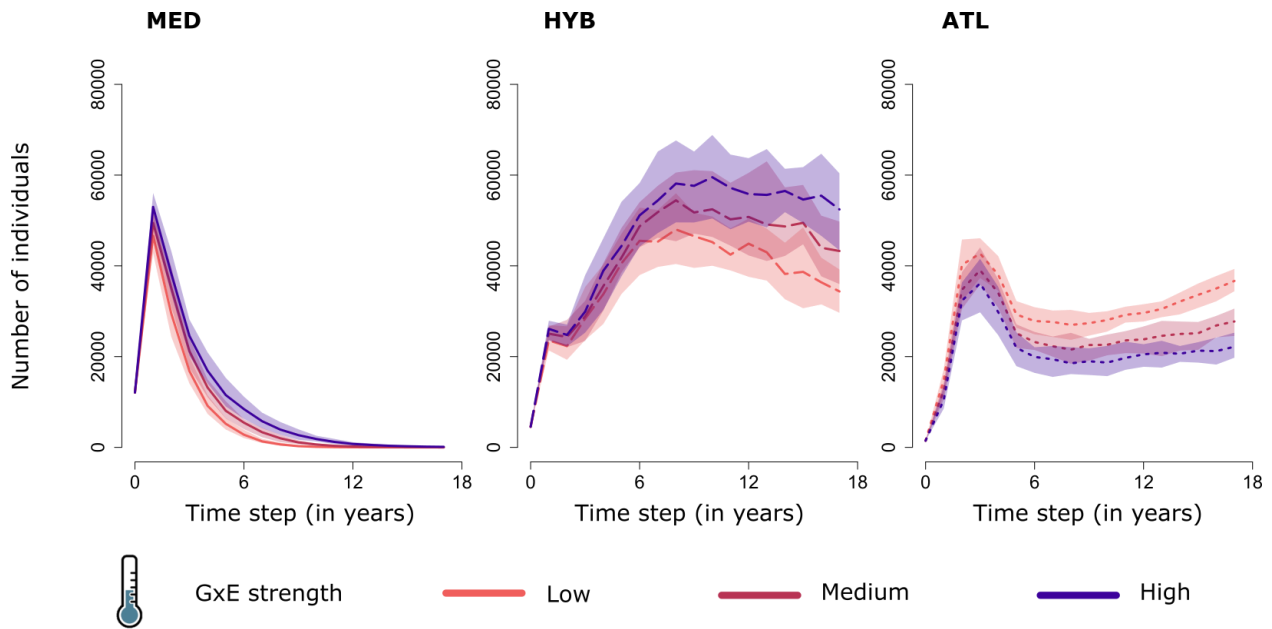


Figure 4–55: Evolution of the genotypic composition of the population in each downstream zone of the Borne River from 1988 to 2004, when ATL stocking took place every year. Trajectories are represented for various strengths of GxE interactions and the colder temperature modality.

4.4.4.3 Distribution of individual introgression

The initial distribution of individual introgression indicated that the population was composed of a low number of pure MED individuals and a few lowly introgressed HYB. No differences were initially observed among scenarios (Figure 4 – 56). However, after years of stocking, the final distribution of individual introgression was very different based on the implemented eco-evolutionary scenarios. For neutral and heterogamous scenarios, the distribution was biased toward pure ATL and highly introgressed individuals, whereas when GxE interactions were implemented, the distribution was different. While ATL individuals

4.4 Exploring various eco-evolutionary scenarios in the Borne River 1988

remained a majority, they were less numerous (~ 20 000 vs 30 000). In addition, the distribution of individual introgression for HYB individuals shifted and was centred on a lower value of introgression (0.64 at colder temperatures and 0.71 at warmer temperatures).

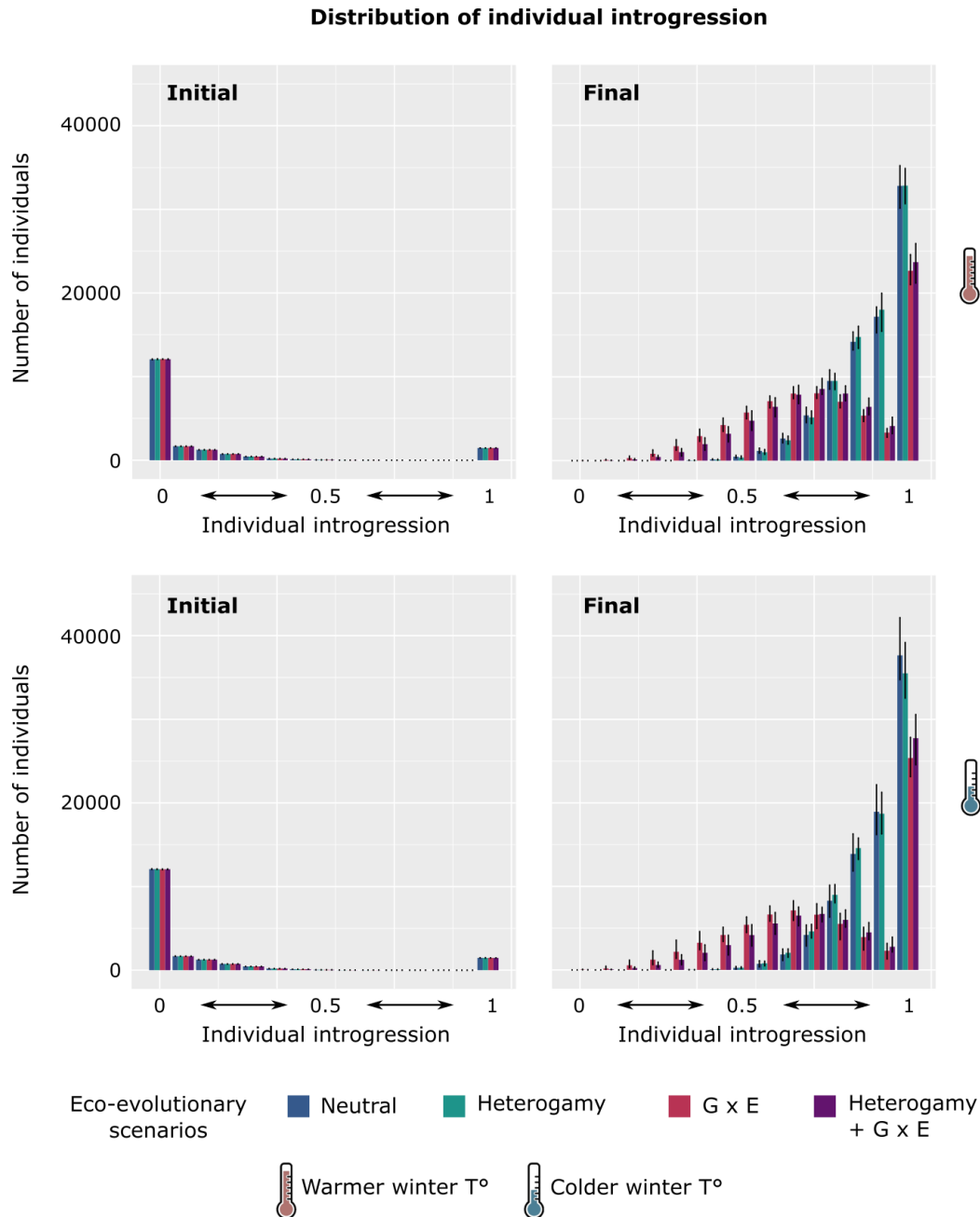


Figure 4—56: Distribution of individual introgression in 1988 when stocking started (initial) and in 2004 it ended (final). Distributions are represented for each eco-evolutionary scenario and temperature modality.

4.4.4.4 Evolution of demography: total population size

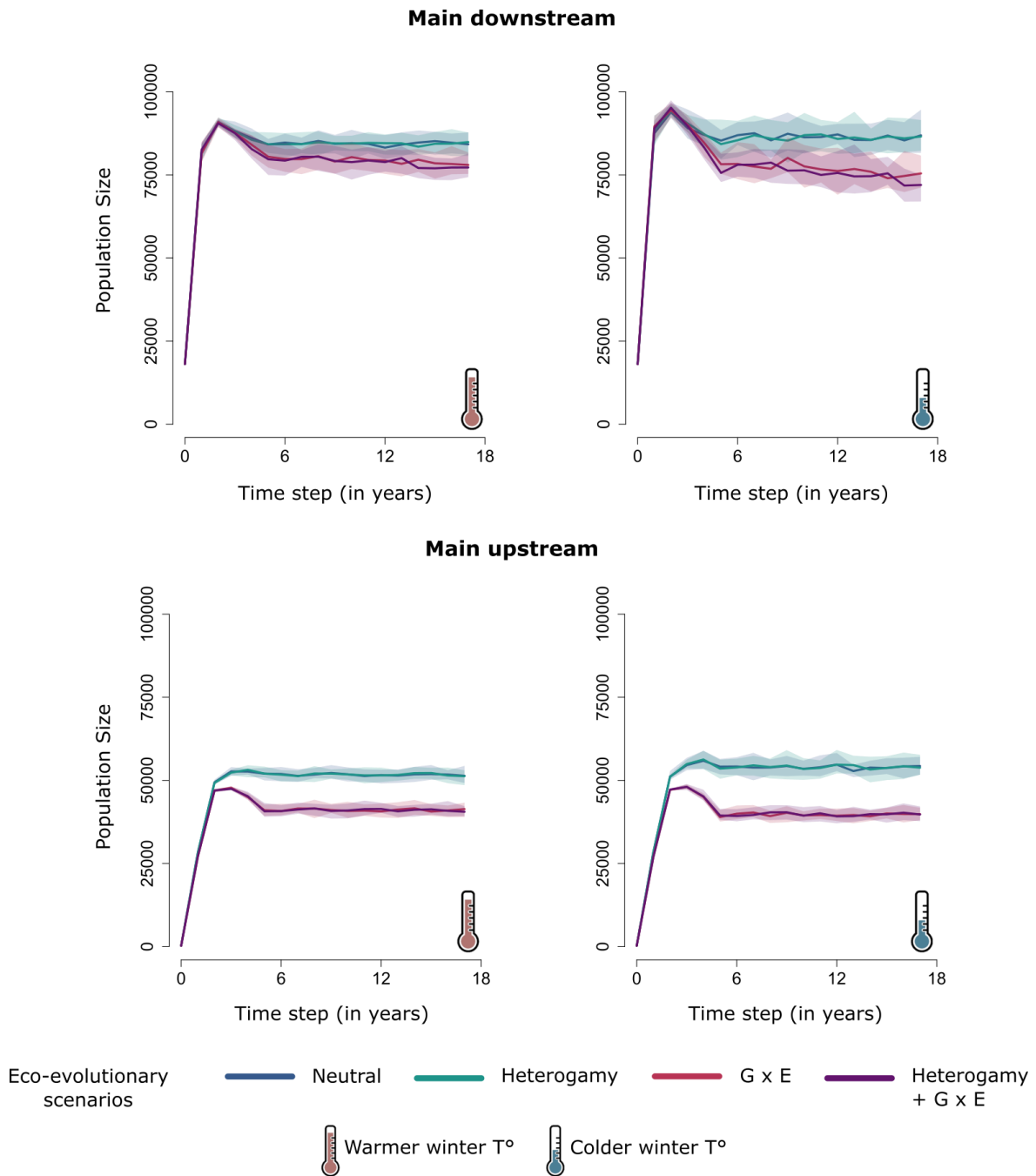


Figure 4—57: Evolution of population size in the main downstream and main upstream parts of the Borne River from 1988 to 2004, when ATL stocking took place every year. Trajectories are represented for each eco-evolutionary scenario and temperature modality.

4.4 Exploring various eco-evolutionary scenarios in the Borne River 1988

The implementation of stocking practices over the years led to a rapid increase in population size, upstream and downstream of the Borne River (*Figure 4 – 57*). However, population size at equilibrium was influenced by the implementation of GxE interactions and to a lesser extent by temperature modalities. Indeed, in the main upstream zone, scenarios considering GxE interactions reached a significantly lower population size at equilibrium ($\sim 40\,000$ vs $55\,000$ individuals), with colder temperatures leading to a slightly higher difference in population size among scenarios. Comparatively, in the main downstream zone, the implementation of GxE interactions seemed to influence population size more slowly and progressively. There, population size did not reach an equilibrium. Indeed, while differences among scenarios were initially low, there was a slight and continuous decrease in population size over the years for scenarios implementing GxE interactions. This decrease was more pronounced at colder temperatures.

CASE STUDY 3:

THE BORNE RIVER

Starting from 2004: MED translocation

4.4.5 Evolution of diversity dynamics and demography in the Borne River following MED translocation (from 2004)

In 2004, after the last stocking event, studies indicated that an almost pure and thriving MED population had settled downstream of the Borne River, below dam 3, whereas a small non-native population showing very low densities was located upstream. This second case study aims at simulating the management practices that took place after 2004, and which aimed at restoring a viable MED population upstream, as well as conserving the downstream MED population. This case study will therefore start in 2004, just before the first management practice took place. The initial population is made of pure MED and very low introgressed HYB downstream and only pure ATL individuals upstream. To stabilise population dynamics and obtain a realistic initial population – stable population size, age and size distribution, creation of hatches and juveniles – the model is run for ten years *prior* to the start of the case study. Hence time 10 will represent the year 2004 and intervention for management practices will take place just after. From $t = 11$ to $t = 13$, we simulated three consecutive years of translocation. Translocation zones (sampling and translocated areas) in the model are based on reaches delimitation and match the location of the actual area. *Figure 4 – 58* indicates the corresponding translocation reaches as well as the other monitored areas. Each year, and for each section, the number of translocated trout was similar to that done in reality. Therefore, 1630 individuals were also transferred in the model. To match the sample of individuals transferred, 80% of individuals were pure MED and 20% were allowed to be slightly introgressed – 4 alleles maximum. To match all the management practices that took place during this period, fishing was also banned from the translocated zone B and B1 (*Figure 4 – 58*).

In the simulations, MED translocation only led to the admixture of the MED and the ATL lineages in the upstream section of the Borne River. Hence, diversity dynamics will only be monitored in this part of the river.

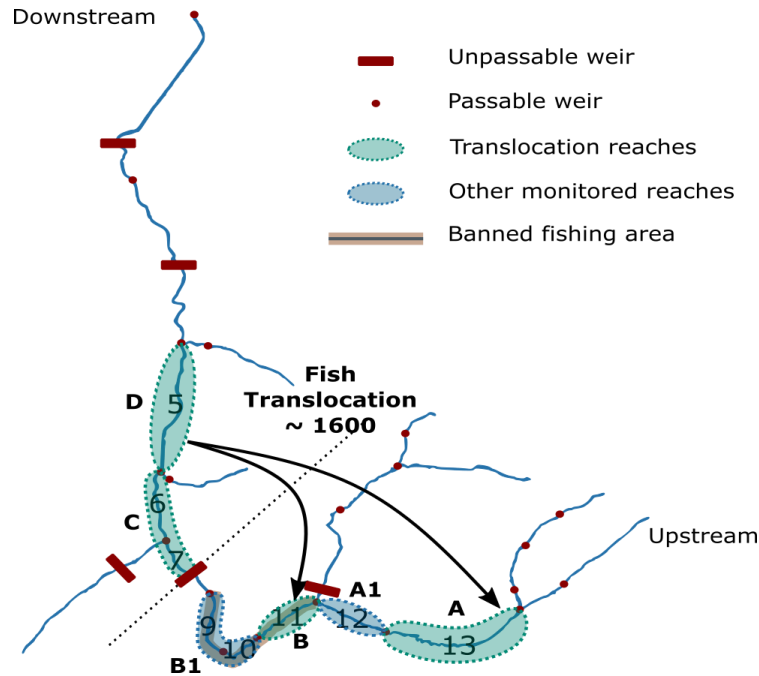


Figure 4—58: Spatial representation of fish translocation practices carried out in MEDITERRANEA based on the structure of the Borne River.

4.4.5.1 Evolution of introgression

Following translocation, the introgression rate decreased (*Figure 4 – 59*) in the translocated zones (A and B) but also in the adjacent zones (A1 and B1), suggesting that movement allowed for the homogenisation of the population upstream (Upstream zone: entire upstream population). The extent of this decrease was highly influenced by the implementation of GxE interactions but not by heterogamous mating. For scenarios without GxE interactions, the introgression rate stabilised rapidly – around 0.95 – after a small decrease during the translocation period. Temperature modality and zone did not have any influence over this dynamic. For scenarios considering GxE interactions, a steep decrease in introgression was associated with the translocation, followed by a slower and continuous decrease. This decrease appeared faster in zones A and A1, which reached slightly lower rates of introgression than zones B and B1. Colder temperatures also led to a stronger decrease in all zones.

4.4 Exploring various eco-evolutionary scenarios in the Borne River 2004

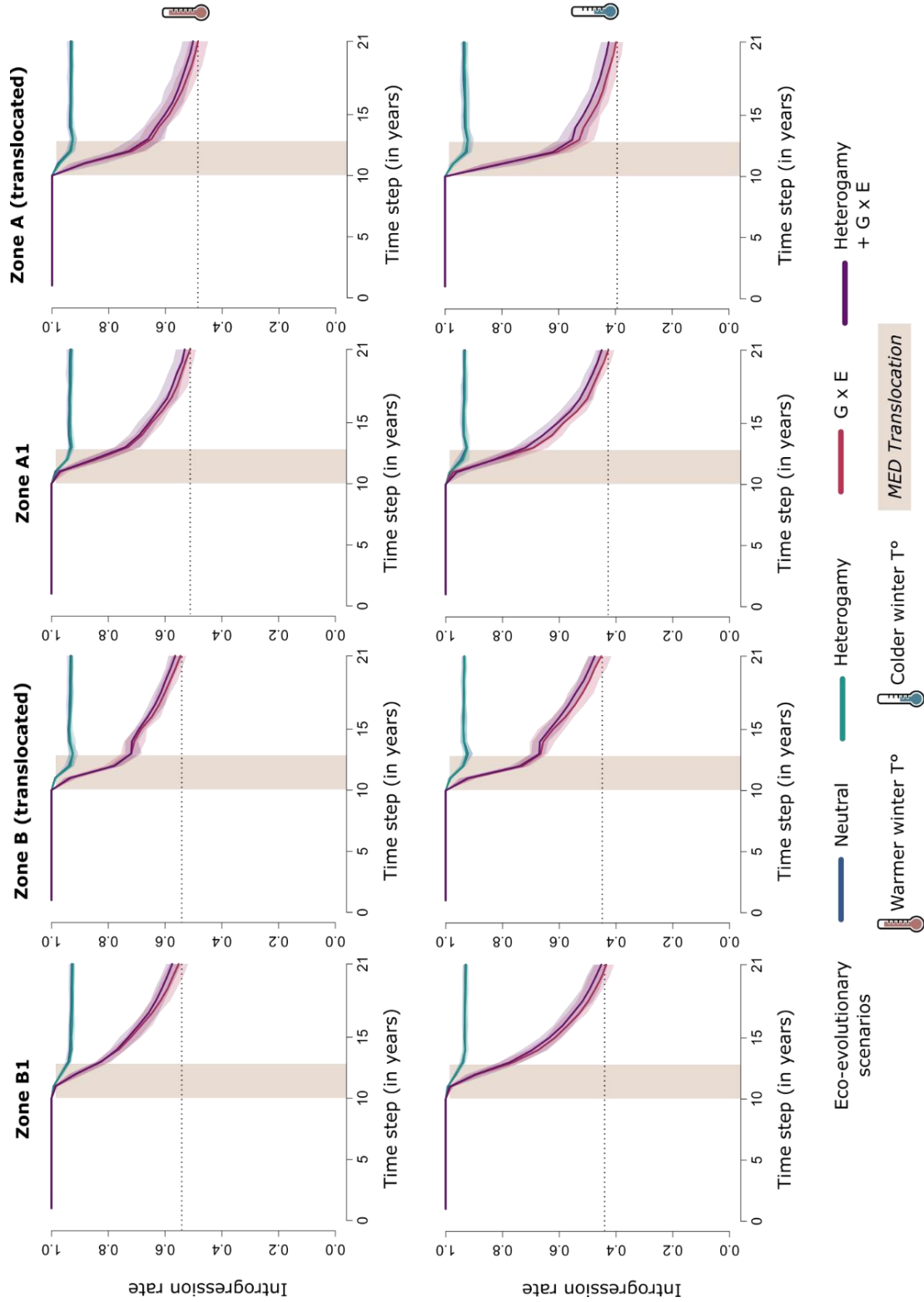


Figure 4—59: Evolution of the population introgression rate in each upstream zone of the Borne River that were monitored. The years when management practices took place are highlighted. Trajectories are represented for each eco-evolutionary scenario and temperature modality.

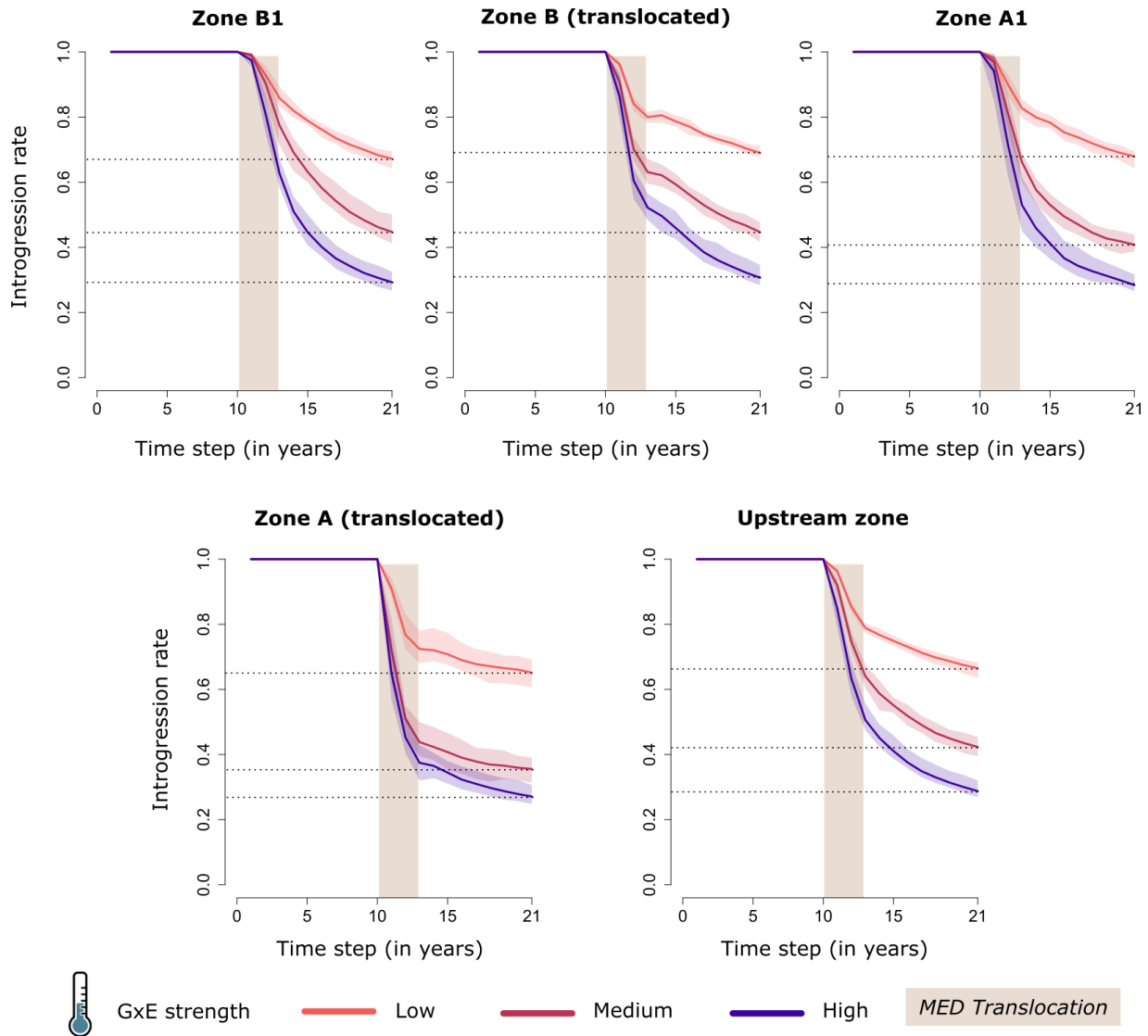


Figure 4—60: Evolution of the population introgression rate in each upstream zone of the Borne River that were monitored. The years when management practices took place are highlighted. Trajectories are represented for various strengths of GxE interactions and the colder temperature modality.

Sensitivity analyses on GxE interactions. The strength of GxE interactions also influenced the evolution of introgression (Figure 4 – 60). Overall the higher the strength of GxE interactions was, the higher and stronger the decrease in introgression rate was. In the upstream zone, introgression rates reached approximately 0.66 for low, 0.42 for medium and 0.28 for high strength of GxE

interactions. However, the influence of the strength of GxE interactions was slightly different based on the zone. Going from downstream to upstream (*i.e.* from zone B1 to A), observed differences in final introgression progressively became higher between the low and medium strength of GxE interactions. On the contrary, it became lower between the medium and high strength of GxE interactions, as selective pressure became even more pronounced upstream, where altitude was higher and hence temperature lower.

Overall, the evolution of introgression was quite homogenous in the upstream section. Therefore, the following descriptions will only focus on the entire upstream population.

4.4.5.2 Genotypic composition of the population

Following MED translocation, the number of HYB individuals increased while that of ATL individuals decreased (*Figure 4 – 61*). The number of MED individuals only increased during the translocation, but rapidly decreased back to zero, for all scenarios. Again, GxE interactions had a strong influence over the genotypic composition of the population while heterogamous preference did not. When implementing GxE interactions, the increase in HYB number was higher and faster for both temperature modalities. While the speed of the decrease in the number of ATL individuals appeared similar, the initial value at equilibrium was lower, and even more so at colder temperatures. In these scenarios, this decrease ultimately led to the disappearance of ATL genotypes.

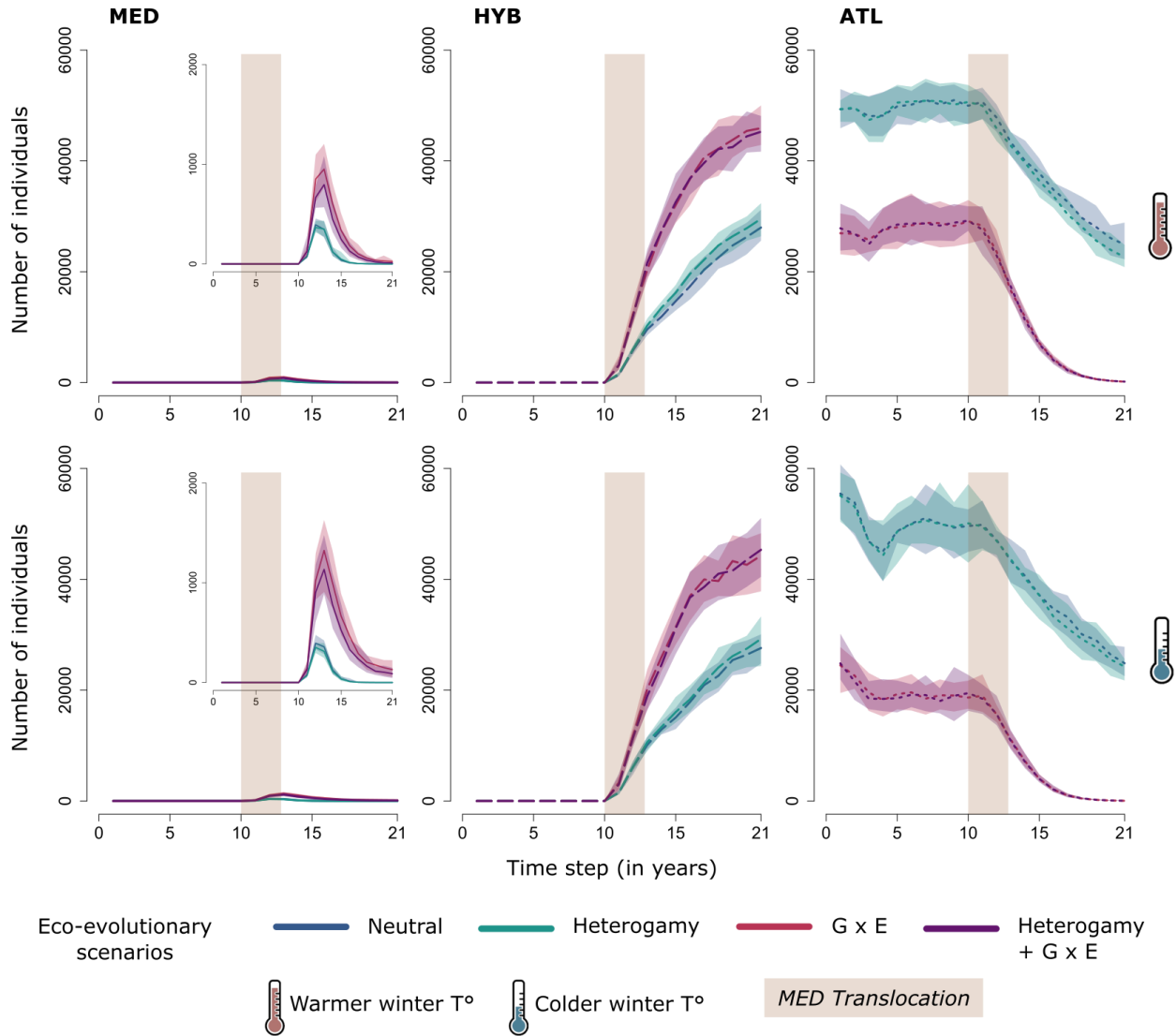


Figure 4—61: Evolution of the genotypic composition of the population in the upstream zone of the Borne River. The years when management practices took place are highlighted. Trajectories are represented for each eco-evolutionary scenario and temperature modality.

Sensitivity analyses on GxE interactions. The strength of GxE interactions had a significant impact on the genotypic composition of the population (Figure 4 – 62). For MED individuals, higher strength of GxE interactions led to a higher initial increase in population size, which then decreased when translocation stopped, to finally stabilise around 1000 individuals (high modality). For ATL individuals, a lower

4.4 Exploring various eco-evolutionary scenarios in the Borne River 2004

population size was observed initially; hence ATL genotypes disappeared faster (at $t = 16$ for the high, $t = 17$ for the medium and $t > 21$ for the low modality of GxE interactions). Meanwhile, the increase in the number of HYB individuals was faster and higher.

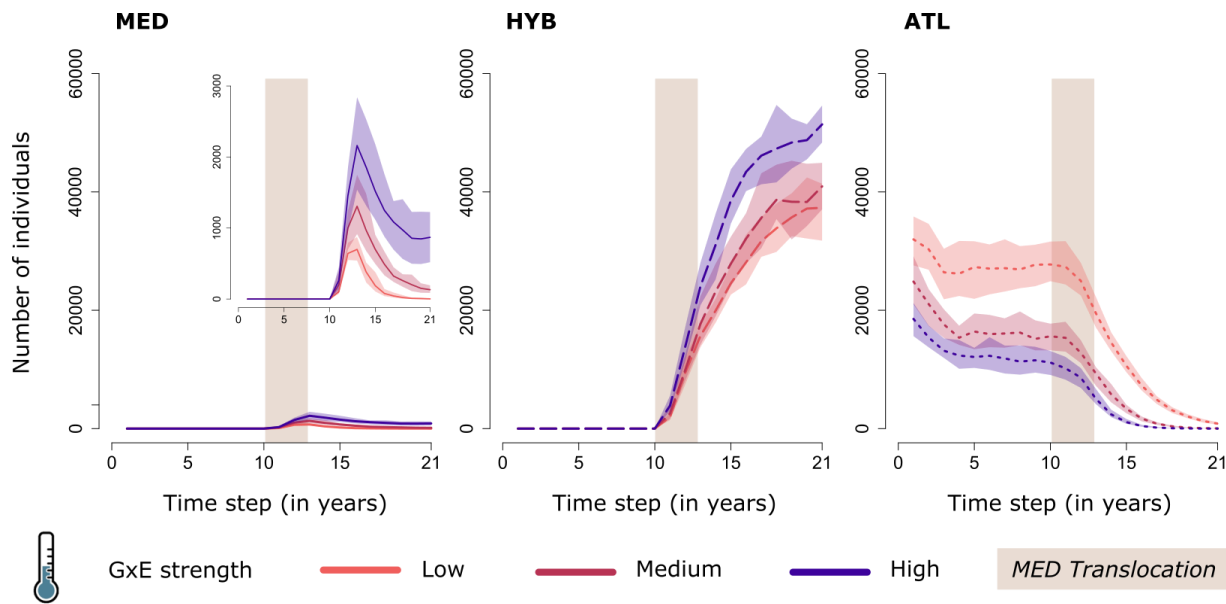


Figure 4—62: Evolution of the genotypic composition of the population in the upstream zone of the Borne River. The years when management practices took place are highlighted. Trajectories are represented for various strengths of GxE interactions and the colder temperature modality.

4.4.5.3 Distribution of individual introgression

The distribution of individual introgression for HYB individuals indicated that during translocation (Figure 4 – 63), a large number of F1 hybrid individuals were created, especially for the scenario including GxE interactions. After three years of translocation, when GxE interactions were considered a wider range of HYB individuals were created with the presence of both lowly and highly introgressed HYB individuals. Colder temperatures led to a higher proportion of lowly introgressed HYB. There was a clear shift in the final distribution of individual introgression between scenarios considering or not GxE interactions (Figure

4 – 64). The implementation of GxE interactions led to a hybrid distribution centred on 0.5 and 0.42 for warmer and colder temperature modalities, whereas it was highly biased toward high values of introgression otherwise (0.93).

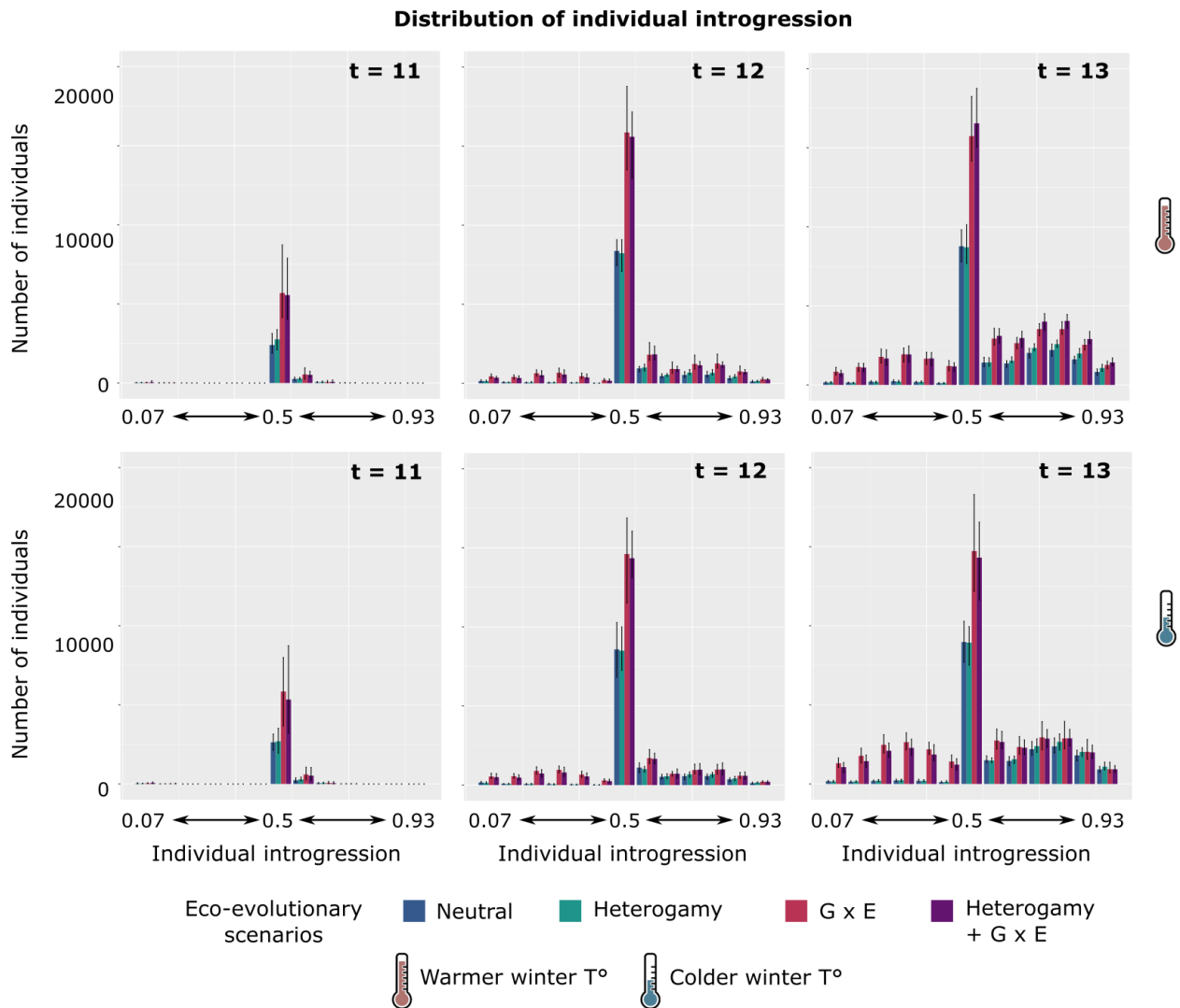


Figure 4—63: Distribution of individual introgression during MED translocation (from 2005 to 2007). Distributions are represented for each eco-evolutionary scenario and temperature modality.

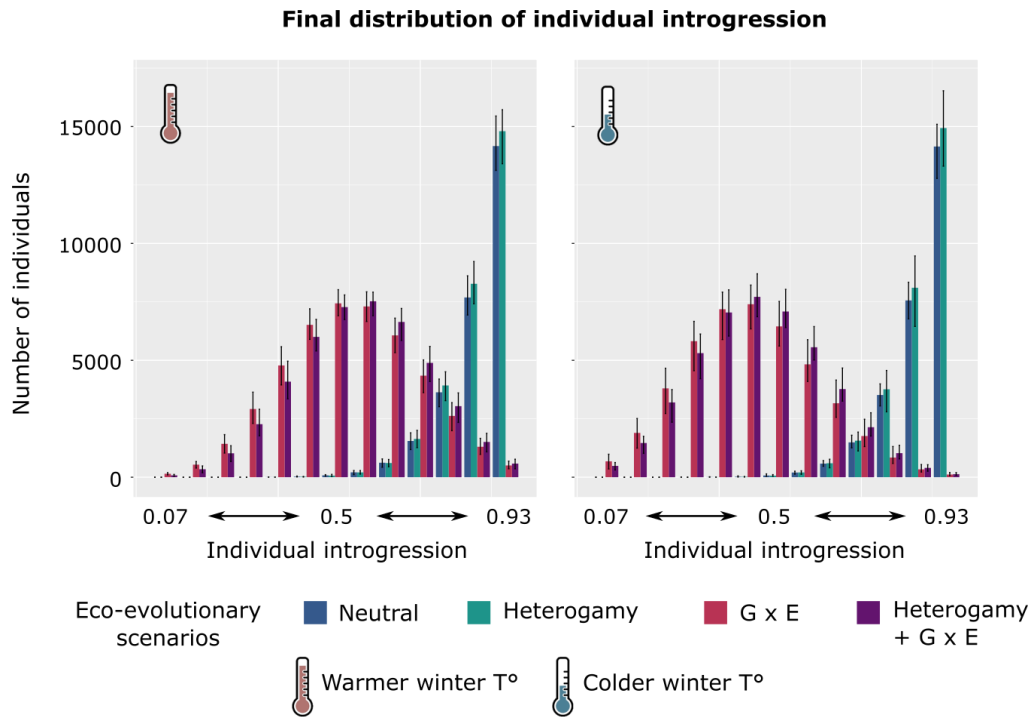


Figure 4—64: Distribution of individual introgression at the end of the simulation (in 2015: 8 years after MED translocation, $t = 21$). Distributions are represented for each eco-evolutionary scenario and temperature modality.

4.4.5.4 Evolution of demography: total population size

Before translocation, population size at equilibrium was highly influenced by the implementation of GxE interactions and by the temperature modality (Figure 4 – 65). Scenarios implementing GxE interactions had a lower population size (~ 30 000 vs 50 000) and even more so at low temperatures (~ 20 000 vs 50 000). For those scenarios, the implementation of translocation led to a stronger and continuous increase in population size, almost reaching the same population as neutral and heterogamous scenarios after ten years of evolution. This increase was steeper and faster for lower temperatures, as both modalities ultimately reached the same population size at $t = 21$ (~ 45 000).

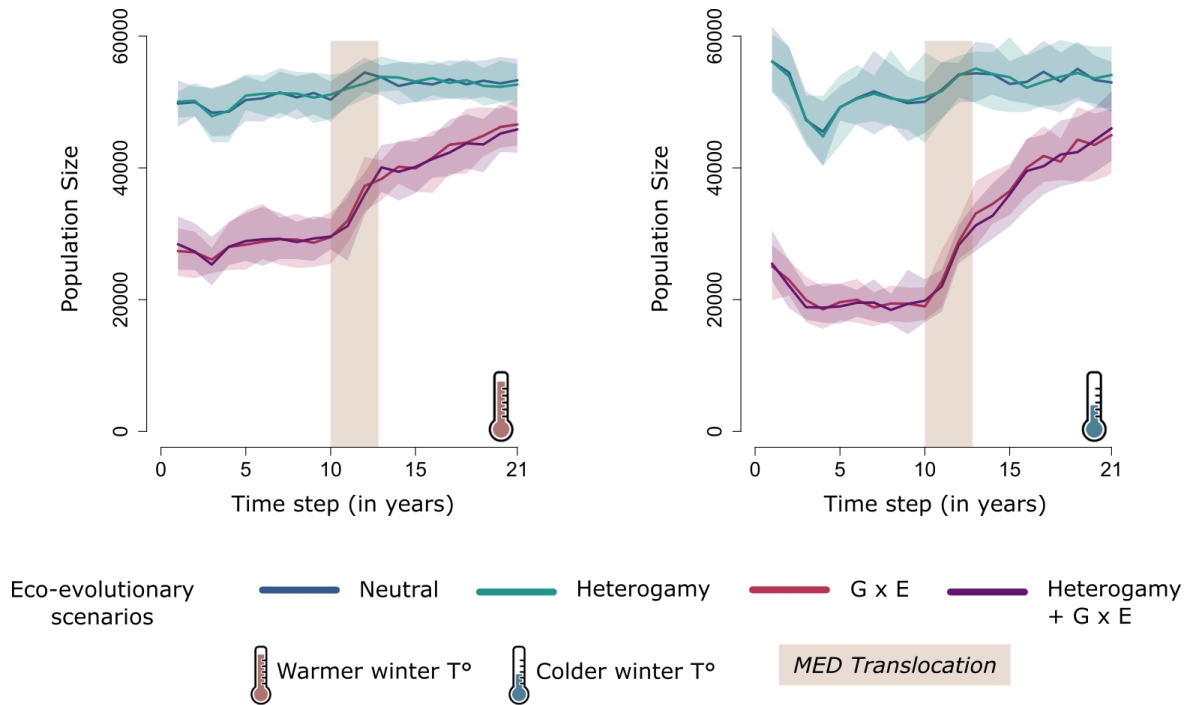


Figure 4—65: Evolution of population size in the upstream zone of the Borne River. The years when management practices took place are highlighted. Trajectories are represented for each eco-evolutionary scenario and temperature modality.

4.4.5.5 Evolution of population size per age class

Focusing on the evolution of population size per stage, before translocation, differences in population size between scenarios decreased, when going from juveniles to adults (Figure 4 – 66). Translocation mainly led to an increase in the numbers of juveniles and sub-adults for scenarios considering GxE interactions, where population sizes were initially much lower. It resulted in a significant increase in adults for all scenarios. For each stage, when GxE interactions were considered, the observed increase in population size, following translocation, was faster for colder temperatures (initially associated with lower population sizes).

4.4 Exploring various eco-evolutionary scenarios in the Borne River 2004

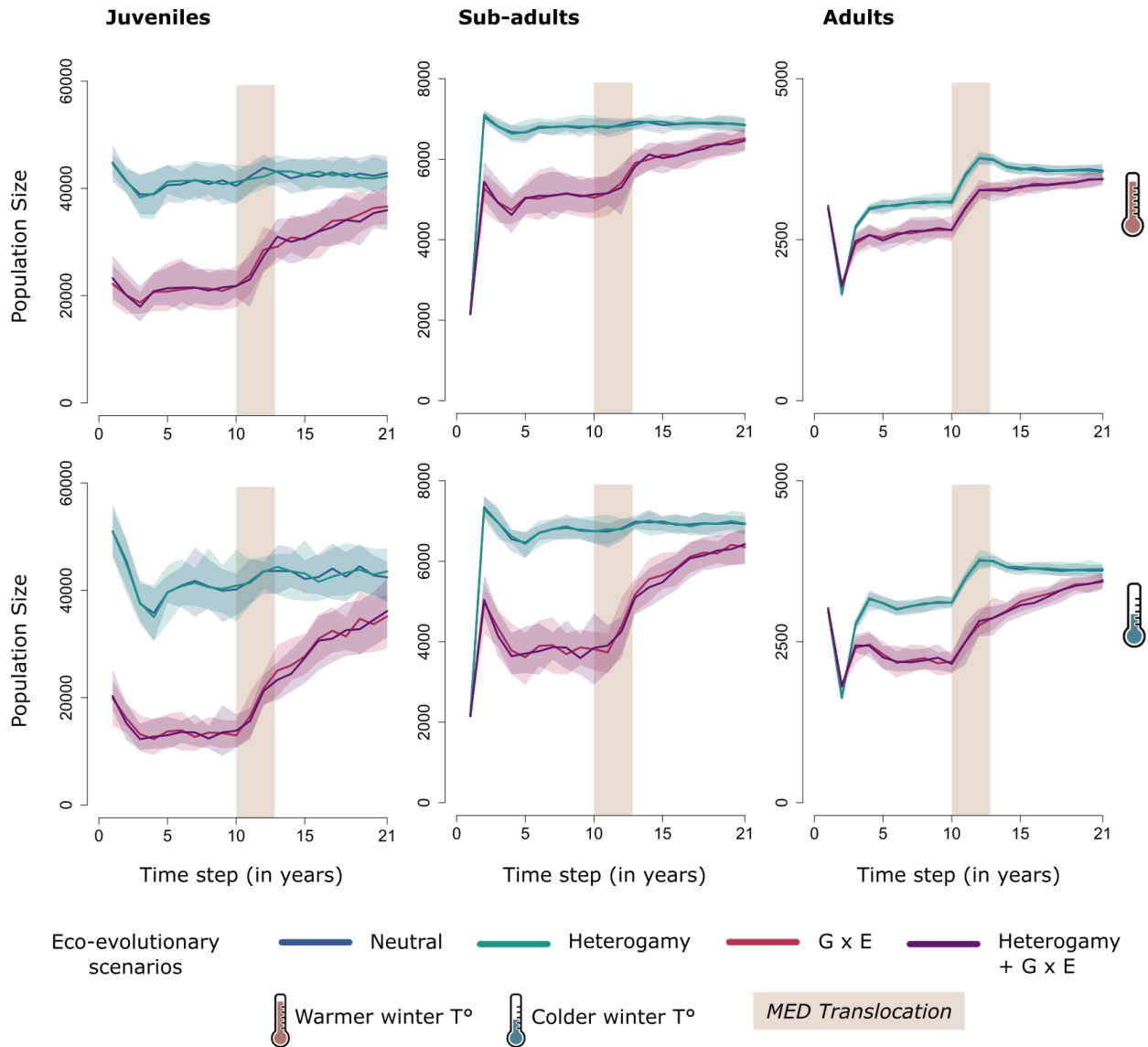


Figure 4—66: Evolution of population size per age class in the upstream zone of the Borne River. The years when management practices took place are highlighted. Trajectories are represented for each eco-evolutionary scenario and temperature modality.

Sensitivity analyses on GxE interactions. The strength of GxE interactions had a significant impact on demography (Figure 4 – 67). The stronger GxE interactions were the higher the increase in population size was, so that, following translocation, population size became the highest for the highest modality of GxE interactions. This pattern was observed for all three life stages but was more pronounced for juveniles.

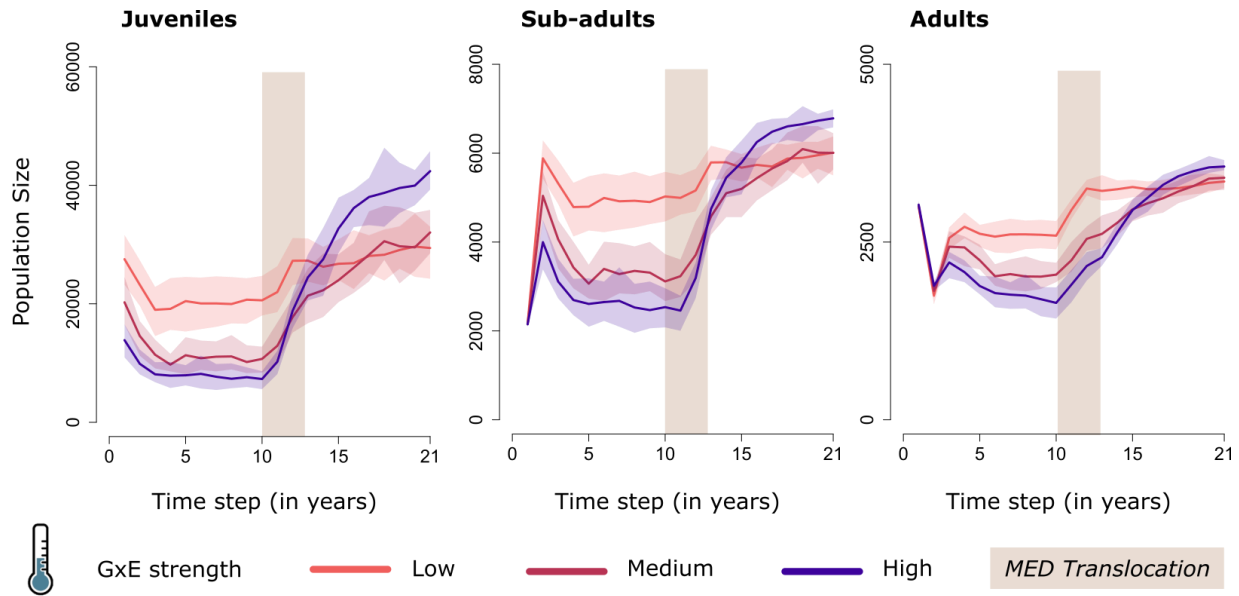


Figure 4—67: Evolution of population size per age class in the upstream zone of the Borne River. The years when management practices took place are highlighted. Trajectories are represented for various strengths of GxE interactions and the colder temperature modality.

***COMMON DISCUSSION TO ALL CASE
STUDIES***

4.5 DISCUSSION ON THE ECO-EVOLUTIONARY MECHANISMS

Our simulations based on real case studies demonstrated that management practices could have strong eco-evolutionary consequences by influencing the evolution of diversity and demography. Specifically, I showed that the outcome of each management practice was, to some extent, influenced by the various eco-evolutionary scenarios (*Section 4.1.1*) implemented. Similarly to the results obtained in the basic case study, heterogamous preference had very little impact on diversity dynamics. On the opposite, GxE interactions drove the evolution of diversity, thereby playing a crucial role in determining the outcomes of management practices. Overall, simulations on real case studies indicate that the EEMs tested - heterogamous preference and GxE interactions on survival - have the same impact on diversity dynamics and demography no matter the environmental and ecological context.

4.5.1 *Heterogamous preference*

Contradictory to our prediction (*Section 4.2.2: Discussion*), heterogamous preference does not appear to influence much more diversity dynamics in a more specific context where population structure differs (Klug & Stone, 2021) – different initial genotypic frequencies. Indeed, biased genotypic frequencies – in favour of ATL individuals for example in the “Borne2004” scenarios – did not cause the rare phenotype to be more successful – frequency-dependent sexual selection hypothesis (O’Donald & Majerus, 1988) – as trajectories considering random or heterogamous preference did not differ. No matter the mating preference, the genotype found in higher frequency will reproduce the most. Indeed, given how males are randomly sampled from the population to undergo mating events during the reproductive season (*Section 3.3.6*), the mating system is bound to be related to the frequency of each genotype in a linear way – *i.e.* the more of one specific genotype there is in a population, the more it will reproduce.

This suggests that reproductive interactions might not always drive evolutionary dynamics (Maan & Seehausen, 2011). However, it is not entirely surprising that heterogamous preference does lead to the same outcome as random preference, as both have the potential to lead to hybridization. A different mating system, for example based on homogamy, could have caused mating preference to play a much more important role in the evolution of diversity by preventing hybridization and enhancing reproductive isolation between lineages. For example, in other species, models have shown that assortative mating played a major role in shaping the genetic differentiation between populations experiencing gene flow (Soularue & Kremer, 2014) and, compared to random mating, could change the genetic variance available for selection (Godineau et al., 2021).

Therefore, in order to evaluate whether it is any mating preference that does not play a structuring role in the evolution of diversity, I carried out simple simulations to check the role of homogamous preference compared to random and heterogamous preference. Results regarding homogamous preference – while considering (*Appendix E*) or not (results not presented here) selection mediated by GxE interactions – were in accordance with another study conducted on salmonids (Nathan et al., 2019). Using a DG-ABM with a hybrid index similar to our measure of individual introgression, they showed that homogamous compared to random preference did not influence the outcome of hybridization between bull trout and Dolly Varden. Despite implementing mating preference in different ways, both our studies indicated that no matter the mating preference considered, all scenarios ultimately result in a system dominated by hybrid individuals at similar rates. Put together, these results suggest that mating preference based on origin does not seem to play an important role in the evolution of diversity dynamics in Salmonids, potentially because it does not appear to lead to specific patterns of mating system. In our model, this could be due to the many stochastic processes also influencing mating. Results comparing the relative effect of heterogamous vs homogamous preference while considering GxE interactions (*Appendix E*)

confirmed the antagonistic effect of heterogamous preference over selection and, conversely, pointed to a synergetic effect of homogamous preference, as it appeared to favour selection.

4.5.2 GxE interactions

As expected, the selection mediated by GxE interactions strongly influences diversity dynamics and demography in interaction with management practices. As observed in the basic case study, selection helped decrease the ATL alleles rate while increasing that of MED alleles. Indeed, compared to a neutral scenario, the implementation of GxE interactions always led to lower rates of introgression following management practices. In the case of the “Borne 1988”, selection slowed down the increase in introgression following ATL stocking, by partially preventing a maladaptive gene flow (Garant et al., 2007). However, as only maternally inherited alleles are under selection, this gene flow is unavoidable, no matter the strength of the GxE interactions implemented. In the cases of the “Chevenne” and the “Borne 2004”, selection favoured a rapid decrease in introgression rate by favouring adaptive gene flow (Garant et al., 2007), following the introduction of adaptive genetic variation in the population (through natural movement and translocation of MED individuals). In these cases, when considering GxE interactions, the implementation of management practices led to patterns of genetic and evolutionary rescue (Carlson et al., 2014; Whiteley et al., 2015). Indeed, *prior* to management, GxE interactions had strong consequences on demography: population size in the upstream section of the Chevenne Creek and the Borne River were initially low. Following the implementation of management practices, a progressive increase in population size was observed, even more so for juveniles, to whom selection directly applied. As management practices combined with selection led to evolutionary changes, – changes in alleles frequency – the mean fitness of the population increased, leading to changes in population dynamics – an increase in population size. Each time, higher strength of GxE interactions led to a higher increase in population size, as the mean fitness associated with MED alleles increased. In addition, as observed in the simple case study, the

implementation of colder temperatures, but also higher strength of GxE interactions also led to a stronger and faster selection against ATL alleles.

These results are in accordance with another study focusing on hybridization between the bull trout and the Dolly Varden indicating that variations in fitness and temperature influence the outcome of diversity dynamics. Nathan et al (2019) explored how variation in temperature based-selection and hybrid fitness relative to either parental species influenced the rate and spatial extent of hybridization. Similar to us, temperature-based selection – favouring one or the other parental species – would affect the speed of hybridization depending on the fitness modality implemented. However, unlike us, different fitness scenarios led to more contrasting results regarding the population genotypic composition. Indeed, hybrid fitness influenced the proportion of hybrids found at the end of the simulation, whereas our scenarios always resulted in the extensive creation of hybrid individuals. Compared to Nathan et al (2019), in our model, hybrid fitness is not directly implemented: only some alleles inherited maternally confers an advantage.

4.5.3 Importance of hybrid fitness

General results on salmonids indicate the importance of hybrid fitness for determining the fate and persistence of parental species (Drinan et al., 2015; Hitt et al., 2003; Muhlfeld et al., 2009; Ostberg et al., 2004; E. M. Rubidge & Taylor, 2004; Seehausen, 2004). In our case, empirical studies on the relative fitness of hybrids are lacking, as we implement only a survival difference based on a linear relationship with maternal genotype. Indeed, empirical results derived from Folio et al., 2021 indicate a survival difference between offspring from the MED and the ATL lineages based on a linear relationship with the maternal genotypic score. However, most crosses involving hybrid parents were missing for various reasons,

meaning that the implemented linear relationship mainly relies on inference from pure or nearly pure parental genotypes – as identified by the microsatellites and SNP markers set used for lineage identification. More studies of hybrid fitness relative to native MED individuals' fitness across various environmental gradients – specifically temperature – would improve our understanding and predictions of the evolution of intraspecific diversity in the MED/ATL complex.

4.5.4 Case studies nuances

Furthermore, the real case studies allowed us to highlight some notable points of interest. The extent of the impact of GxE interactions over diversity dynamics varies among but also within case studies. It appears to be modulated by two main factors: management practices and spatial variation (zones).

On the one hand, by interfering with population composition, management practices can influence the ratio of MED vs ATL alleles found in the population. This could highly influence the speed of selection since more ATL alleles will take longer to eliminate. For example, in the “Borne 1988”, the stocking of a very large amount of ATL fry resulted in a large proportion of ATL alleles to select against, hence slow selection patterns.

On the other hand, results indicate that the strength of selection mediated by GxE interactions can be variable depending on the zone monitored within the hydrographic network. For example, for the “Borne 1988”, GxE interactions barely slowed down the increase in introgression in the most downstream reach (reach 1, altitude ~ 460 metres), compared to the other zones (reach 2 & 3: altitude ~ 520 and 580 metres; “main downstream” zone: altitude ranging from 634 to 1170 metres), where stronger patterns of selection could be observed. Similarly, in “Borne 2004”, the decrease in introgression rate was slightly

faster in zone A and A1, located upstream (altitude ~ 850 metres and 900 metres) compared to zone B and B1, (altitude ~ 960 metres and 1040 metres). In the “Chevenne”, the effect of GxE interactions also appeared larger in the upstream zone, but only before ATL removal. Overall, the general pattern observed is the same for all case studies: the selection mediated by GxE interactions appears to be stronger and faster at higher altitudes. The spatial variations of some important ecological factors, potentially driven by landscape features – among which altitude – may interplay with GxE interactions to drive different strengths of selection.

☞ First, in the model, altitude is the main parameter driving temperature variation in space. Therefore, zones located upstream experience colder temperatures and hence higher selective pressure on ATL alleles and *vice-versa*. Once more, our results highlight the importance of temperature variations in determining the strength of the selection mediated by GxE interactions.

☞ Second, population size and composition could also interplay with selection. Indeed, the ratio of MED and ATL alleles initially found in the population might highly influence the speed of selection. For example, in the “Borne 2004”, in addition to temperature differences, population size was smaller in zones A and A1 compared to B and B1, since population size usually decreases from downstream to upstream as reaches become smaller due to lower average width. This means that fewer ATL individuals were initially present in zone A and A1 when translocation occurred causing variations in the initial ratio of MED vs ATL individuals.

☞ Finally, connectivity might also influence how these differences play out among zones. Indeed, the spatial arrangement of habitats can shape individuals’ and alleles’ movement (He et al., 2019). Comparing the “Borne 1988” to the “Borne 2004”, higher differences in the strength of selection can be observed for the “Borne 1988” compared to the “Borne 2004”. In the “Borne 2004”, as

connectivity is full among zones, there seems to be a strong homogenising effect thanks to gene flow, despite differences in temperature and population composition. For instance, zone A1 and B1, which had not been translocated, presented almost a similar decrease in introgression rate compared to the translocated zones. On the contrary, in the “Borne 1988”, zones are separated by an unpassable barrier preventing any gene flow. The lack of connectivity, therefore, appears to accentuate differences in selection caused by other factors.

Nevertheless, the general pattern of selection resulting from the implementation of GxE always remains the same. This is true independently of the hydrographic network size and structure (one reach, the Chevenne Creek or the Borne River) or the management practices implemented. Selection will always interact with management practices to drive the evolution of diversity in a specific direction. This highlights the robustness of this EEM in structuring diversity dynamics. Contextual factors – management practices, ecological factors and landscape features – only appear to modulate more or less its effect. For instance, the force of the resulting selection can be highly driven by temperature variations, with colder temperatures always leading to stronger patterns of selection. Altogether, our results emphasise the importance of considering temperature variations for management practices. Indeed, such mechanisms, as well as variations in selective pressures – here temperature – should never be discarded when evaluating the potential efficiency of management practices.

4.6 COMPARING SIMULATED TO EMPIRICAL DATA

These more complex case studies are based on real and documented situations, where management practices had been carried out to restore brown trout populations and/or conserve the native MED lineage. On the one hand, some punctual genetic and demographic data are available, before and after

the implementation of management practices. On the other hand, simulations have been replicated, which provides a confidence interval for results; and empirical data can be either in or out of this confidence interval. Therefore, I will compare available data to simulation data to determine whether the inclusion of evolutionary-based mechanisms improves or degrades the ability of the model to predict the empirical findings. This comparison will be based on the distance between simulation predictions and empirical data. I will also discuss the main differences observed in each case study and the potential reasons why.

4.6.1 The Chevenne Creek

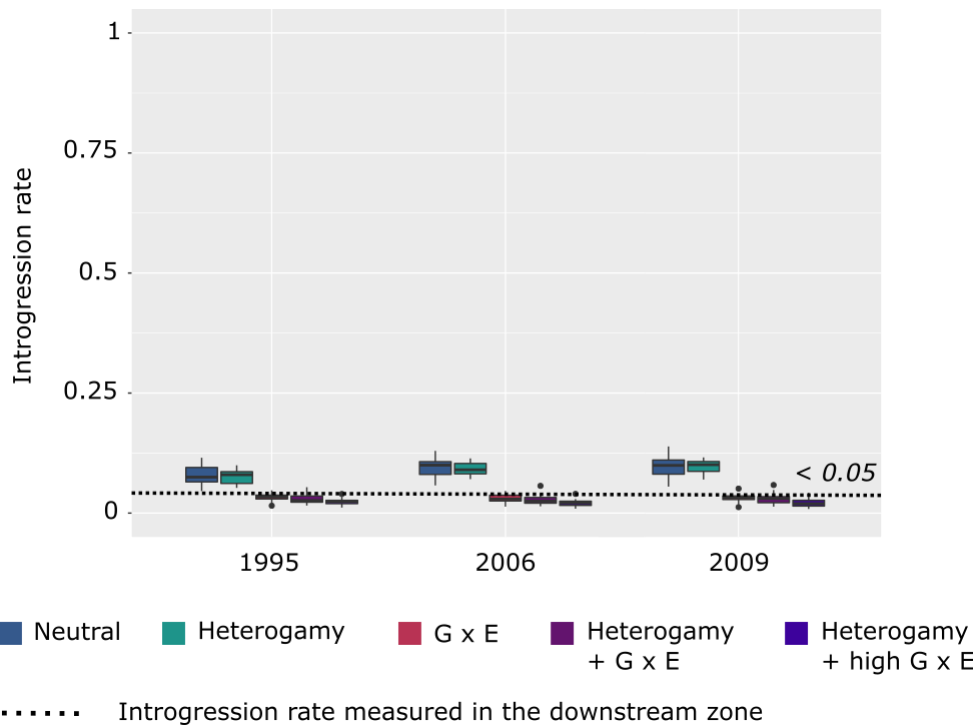


Figure 4—68: Boxplot representing the introgression rate measured for each eco-evolutionary scenario at three given time steps (1995: before the GR strategy, 2006: after the GR strategy, 2009: after ATL removal and MED translocation) in the downstream zone. The dotted line (and value) represents the real introgression rate observed in the downstream part of the Chevenne Creek.

Introgression in the downstream zone. In the downstream zone, the scenarios implementing GxE interactions were closer to the actual introgression rate measured (*Figure 4 – 68*). Indeed, as observed in reality (Caudron & Champigneulle, 2011; Scimabio Interface data), these scenarios led to a rate of ATL alleles inferior to 5% while the other two scenarios resulted in superior values.

Introgression in the intermediate zone. In the intermediate zone, introgression rates observed in the model were far from those measured in reality (Caudron & Champigneulle, 2011; Scimabio Interface data), no matter the scenario considered (*Figure 4 – 69*). In the model, introgression rates were very low and constant over time for all scenarios, considering or not GxE interactions. A lower introgression could be observed owing to the selection mediated by GxE interactions. However, in reality, introgression was initially higher and increased between 1995 and 2006 during the GR strategy. It then remained almost stable during ATL removal (done in the upstream zone). These differences are mainly due to the way individual movement is implemented in the model. First, movement depends on weirs' passability (*Section 3.3.4*). As a reminder, the higher the value is (scaled on 100) the less likely a fish is to pass. The value for weir passability in the model between the intermediate and the downstream zone (60/100) is way lower than between the intermediate and the upstream zone (95/100). Second, in the model parameterisation used, the probability to choose between upstream and downstream movement is balanced ($p = 0.5$ for both, *section 3.3.4*) during the growth season but biased toward upstream movement during the reproductive season. Altogether, this suggests that, in the model, there might be a higher gene flow coming from the downstream zone (MED alleles mainly) compared to the upstream zone (ATL alleles), as movement from upstream might be more limited. However, in reality, studies have indicated that admixture has been occurring in the intermediate zone of the Chevenne Creek (Barnetta, 2005) due to the downstream movement of ATL trout from the upstream zone (Caudron & Champigneulle, 2011).

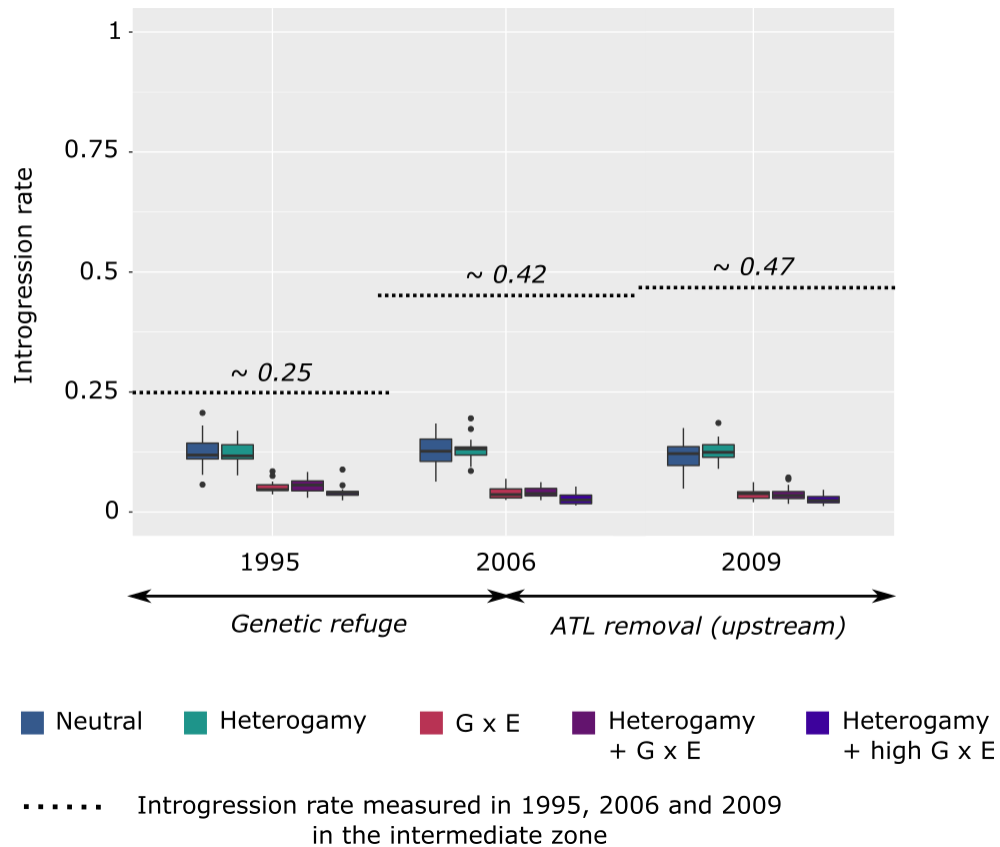


Figure 4—69: Boxplot representing the introgression rate measured for each eco-evolutionary scenario at three given time steps (1995: before the GR strategy, 2006: after the GR strategy, 2009: after ATL removal and MED translocation) in the intermediate zone. Dotted lines (and values) represent real introgression rates measured in the intermediate part of the Chevenne Creek in 1995, 2006 and 2009.

These differences indicate that there is some room for improvement in the model. On the one hand, the transcription of network information might have to be reconsidered. Indeed, the weir passability provided (by scimabio Interface) might not be adequate given the model parameterisation for movement. To fit these values properly, one could use the model to test different weir passabilities and evaluate which value leads to the most adequate patterns of diversity. Replicated on multiple river basins, this could progressively help improve the definition and scale of weir passability. On the other hand, parameterisation for movement might have to be tailored case by case when adequate information is

available. For instance, here the probability for downstream movement during the growth season should be set higher than that of upstream movement in order to fit the observed patterns. In addition, considering downstream-directed water flow, some mechanisms regarding specific downstream movement might be missing in the model, such as juvenile downstream migration (Arawomo, 1981; Tiffan et al., 2012). Indeed, the movement of aquatic organisms can be driven by water flow, but also changes in thermal regimes (Arawomo, 1981; Blanchet et al., 2020; García-Vega et al., 2017), as well as being impacted by river fragmentations (here weirs).

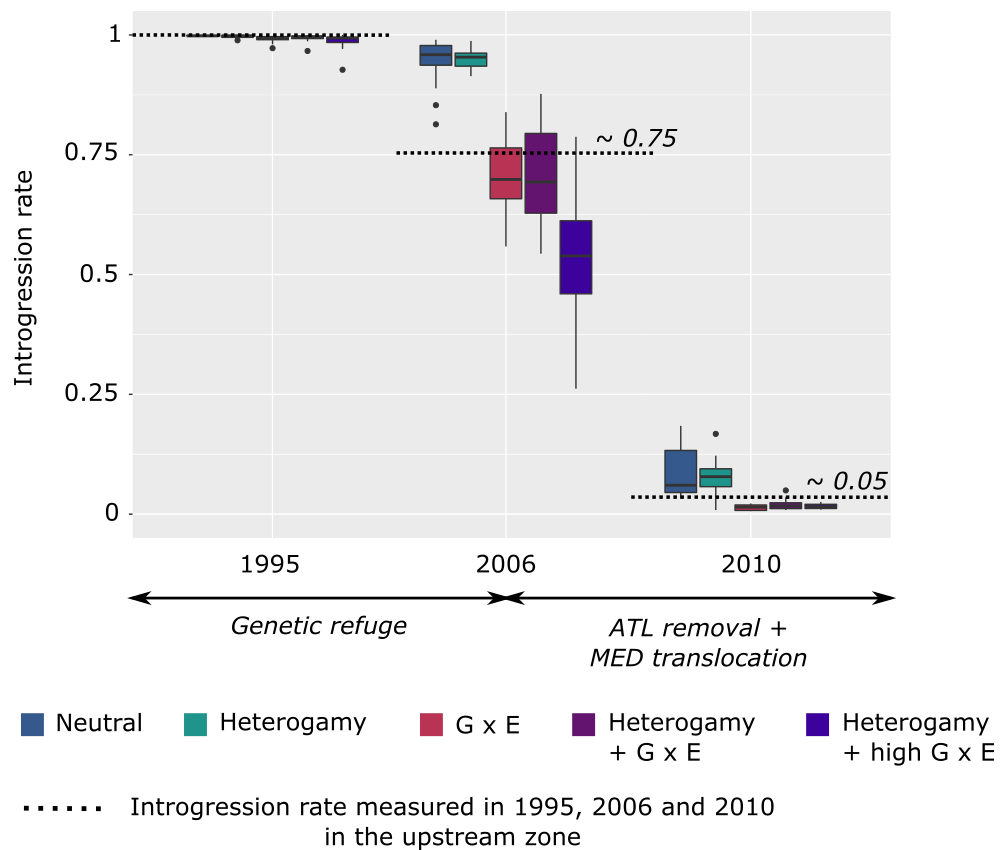


Figure 4—70: Boxplot representing the introgression rate measured for each eco-evolutionary scenario at three given time steps (1995: before the GR strategy, 2006: after the GR strategy, 2010: after ATL removal and MED translocation) in the upstream zone. Dotted lines (and values) represent real introgression rates measured in the upstream part of the Chevenne Creek in 1995, 2006 and 2010.

Introgression in the upstream zone. In the upstream zone, for all simulations, the pattern of introgression rate simulated matches the one observed in reality before and after the implementation of the various management practices (*Figure 4 – 70*; Caudron & Champigneulle, 2011; Scimabio Interface data). Indeed, a decrease in introgression followed the implementation of the GR strategy. This decrease was higher for scenarios implementing GxE interactions, which were closer to reality when a medium strength was implemented. Indeed, stronger GxE interactions led to lower values of introgression rate (~ 0.55) compared to reality (~ 0.75) while the absence of GxE interactions resulted in higher values (~ 0.92). Following ATL removal and MED translocation, while all scenarios led to a significant decrease in introgression rate, the scenarios implementing GxE interactions were slightly closer to reality.

Demography in the upstream zone. In addition, as observed in reality, demography pointed to a self-sustained population located upstream *prior* ATL removal for all scenarios. Similarly, following ATL removal, barely any individuals were left in the population. However, scenarios implementing GxE interactions showed densities closer to reality. Indeed, without GxE interactions, densities were higher in the upstream zone *prior* ATL removal ($\sim 50 \text{ ind.}100\text{m}^{-2}$); whereas it was lower in reality ($\sim 33 \text{ ind.}100\text{m}^{-2}$), and in scenarios considering GxE interactions ($\sim 36 \text{ ind.}100\text{m}^{-2}$).

4.6.2 The Borne River: from 1988 to 2004

Introgression in the downstream section. In the downstream section in 2004, following stocking, introgression rates observed in the model were far from those measured in reality (Caudron et al., 2009), no matter the scenario considered (*Figure 4 – 71*). Indeed, while in reality introgression rate barely increased in the downstream section despite intensive stocking, it did increase a lot in the model. However, one can notice that when GxE interactions were implemented, this increase was lessened, even

more so in reaches 2 and 3 and in the main downstream zone, where actual introgression rates were also lower (respectively ~ 0.1 and ~ 0.07) – compared to that of reach 1 (~ 0.18). While simulated data were getting closer to reality when stronger GxE interactions were implemented, this mechanism alone was not sufficient to properly predict the evolution of diversity. Some additional knowledge related to ATL fry contribution to the population and their relative survival is likely to be missing in the model. First, empirical data indicate that the contribution of ATL fry to stage 0+ in autumn is variable and low (ranging from 0 to 49%, Caudron et al., 2009). Second, despite a medium contribution in some sectors, it appears that they do not contribute much further to the population. Indeed, results from Caudron et al., 2009 indicate that the percentage of stocked ATL trout varied among age classes, and was significantly lower for 3+ individuals (7% only) compared to 1+ and 2+ (respectively 50% and 47%). In addition, considering that ATL trout are more susceptible to angling pressure (J. L. García-Marín et al., 1998; Mezzera & Largiadèr, 2001), the majority of them – which survived to 1+ or 2+ – might have ended up being fished. Finally, studies indicate that domesticated ATL strains have a survival deficit (Caudron & Champigneulle, 2002). In addition, it has been shown that domesticated trout are more prone to predators (Biro et al., 2004) and anglers (Dwyer, 1990). However, all the underlying mechanisms pertaining to this knowledge remain unknown and additional empirical data would be required.

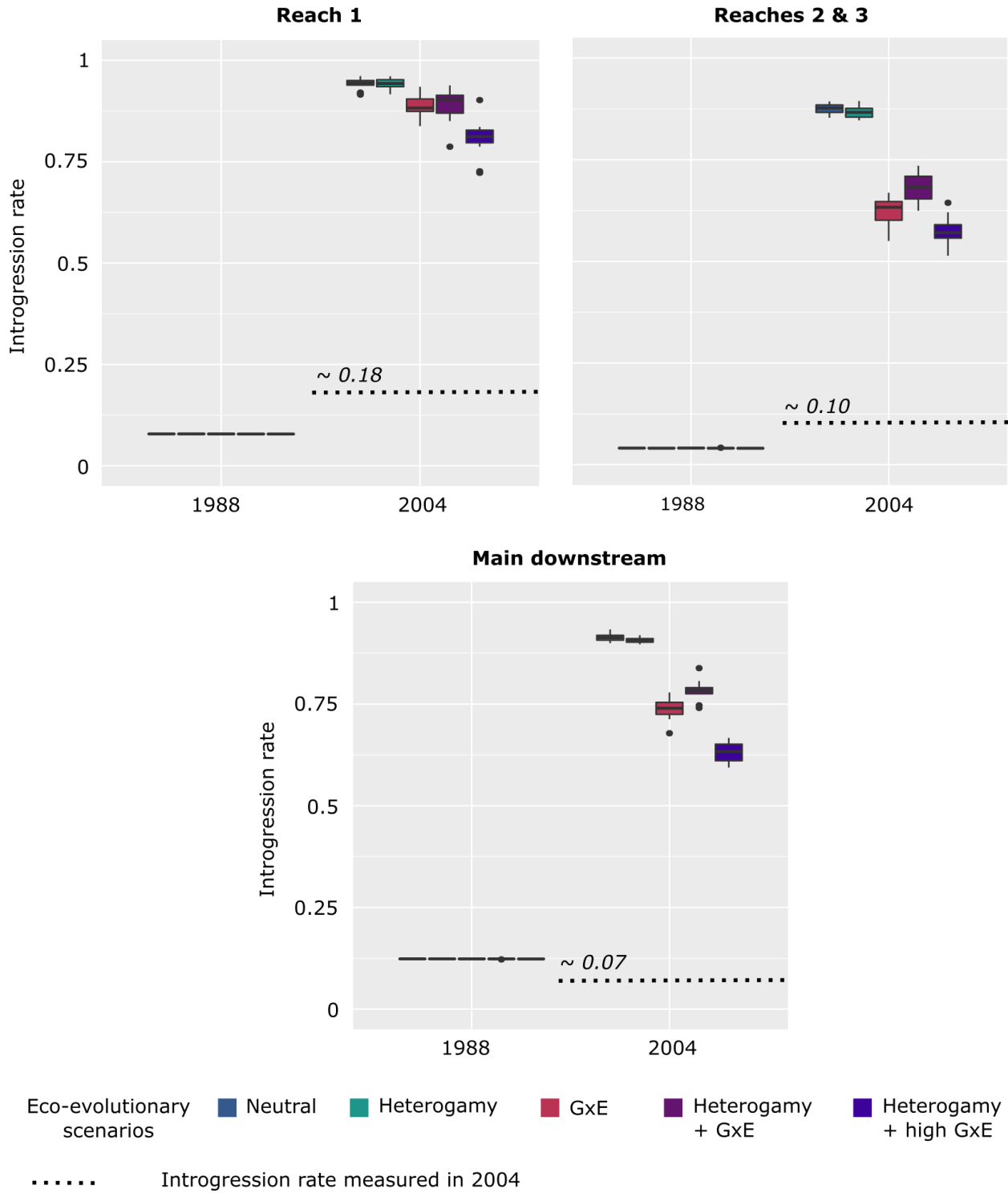


Figure 4—71: Boxplot representing the introgression rate for each eco-evolutionary scenario before and after the implementation of stocking practices for each zone of the downstream part of the Borne River. The dotted line represents the introgression rate sampled in 2004 just before stocking practices stopped.

Demography in the downstream section. Regarding demography, the model overestimated population size in the downstream zone, and even more so without the implementation of GxE interactions. Indeed, densities in the main downstream varied between 60 to 75 ind.100m⁻², whereas empirical data indicate densities around 55 ind.100m⁻² (Caudron et al., 2009). This is likely to result from the way density is managed in the model: either through the parameter KMaxE that deals with maximum carrying capacity in the hydrographic network (*Section 3.3.2*) or through the values of carrying capacity given to each reach (Scimabio Interface data, determined based on reaches quality for resources). Any of these parameters (KMaxE or reach capacity) could have been overestimated. Therefore, more sensitivity analyses should be performed on each parameter to determine which one may affect the most the final densities observed.

Demography in the upstream section. In the upstream section, ATL stocking led to the creation of a self-sustained ATL population in the model no matter the scenario considered (*Section 4.3.4, Figure 4 – 57*). However, in reality, only a very small population maintained by stocking was observed (Caudron et al., 2009). Indeed, densities measured in the upstream zone barely exceeded 14 ind.100m⁻² (just upstream of barrier 3, *Figure 4 – 44*) and were mainly around 1 or 2 ind.100m⁻² (Caudron et al., 2009); whereas in the model, densities varied between 45 to 65 ind.100m⁻² in the upstream sector when considering or not GxE interactions. Stocking was hypothesised to have failed upstream for three main reasons (discussed in Caudron et al., 2009). First, poor water quality could have affected the survival of early developmental stages. Second, high concentrations of ammonium and phosphate were observed, which can result in egg mortality (Massa et al., 1998; Rubin & Glimsäter, 1996). Finally, a small number of females was found upstream, potentially due to angling pressure. Beyond these assumptions, the underlying mechanisms for the observed pattern are still unknown. For example, there are no details of

the links between pollution and viability available during those years (Caudron et al., 2009). Hence, such knowledge could not have been implemented in the model.

4.6.3 The Borne River: starting from 2004

Introgression in the upstream section. In each zone, following the translocation, the pattern of introgression rate simulated matched the one observed in reality (Caudron, Champigneulle, et al., 2012) only for scenarios considering GxE interactions, where a significant decrease in introgression rate could be observed (*Figure 4 – 72*). The introgression rate measured in 2004 indicates a significant decrease in both translocated zones (A and B, respectively down to 0.21 and 0.17) whereas it decreased to a lesser extent in the zones located just downstream (A1 and B1, respectively down to 0.34 and 0.69). On the contrary, in the model, the introgression rate decreased similarly among zones, suggesting a homogenising effect potentially due to movement – with translocated individuals migrating downstream. This could explain why simulated introgression rates were higher in the translocated zone compared to reality, despite the implementation of stronger GxE interactions, whereas it was closer to reality (A1) or even lower (B1) in the zones located downstream.

Genotypic composition in the upstream section. Focusing on the genotypic composition of the population, the simulated results were further away from empirical data (*Figure 4 – 73*; Caudron, Champigneulle, et al., 2012). In reality, in the translocated zones (A and B), associated with the decrease in the proportion of ATL individuals, translocation led to a massive increase in the proportion of pure MED individuals, whereas only a small proportion of HYB was created. In the simulations, no scenarios allowed for such an increase in pure MED individuals. Instead, the proportion of HYB individuals increased while that of ATL decreased, and barely any MED individuals remained.

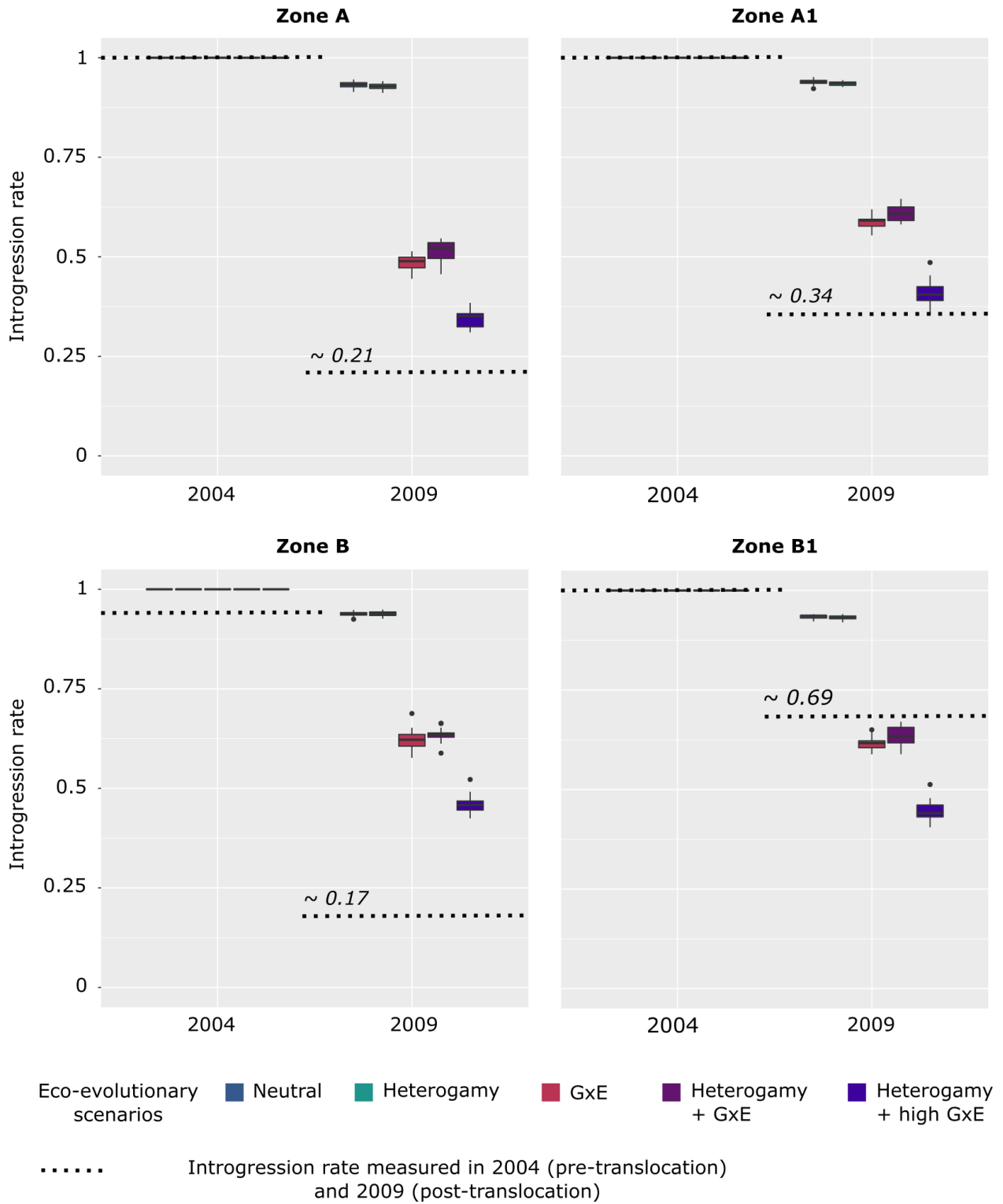


Figure 4—72: Boxplot representing the introgression rate for each eco-evolutionary scenario pre and post MED translocation for each zone monitored in the upstream part of the Borne River. The dotted line represents the introgression rate measured in 2009 after MED translocation.

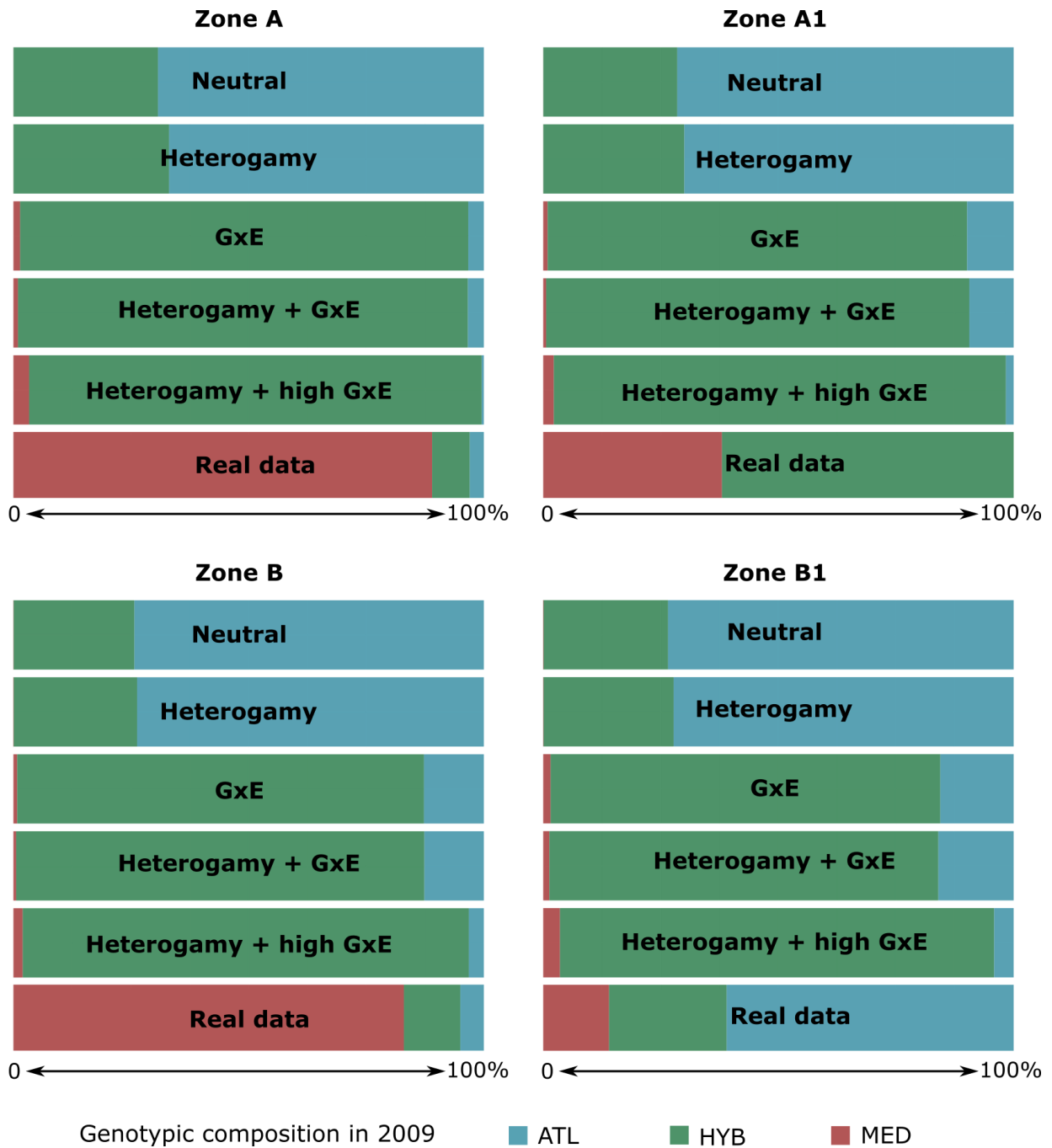


Figure 4—73: Genotypic composition of the population in 2009 for each eco-evolutionary scenario and for real data in each zone monitored in the upstream part of the Borne River.

Nevertheless, the scenarios implementing GxE interactions were still closer to reality when considering the extent of the decrease in ATL individuals. Results were more mitigated among the non-translocated zones. For both, no scenarios could recreate the actual proportion of MED individuals sampled. However, for zone A1, the model also predicted a correct decrease in the proportion of ATL individuals whereas, for zone B1, it overestimated the proportion of HYB individuals compared to that of ATL individuals. These results indicate that when considering GxE interactions, the model always seems to result in full hybridization, whereas in reality many pure MED individuals are sampled. While one may think that this is a failure of the model degrading its ability to predict empirical findings, I suggest that this is related to the number of markers used to discriminate the lineages. Indeed, in reality, a set of only two microsatellites markers (Str541 and Str491, Gharbi et al., 2006) have been used on the Borne River (for the 1988 case study also: Caudron et al., 2009), whereas in the model we implement seven markers (*Section 3.2.2.4*). Therefore, in one case the determination of an individual genotype is based on only four alleles, whereas in the other it depends on 14 alleles. Consequently, there are three chances out of four ($p = 0.75$) to be classified as a hybrid individual in reality *versus* 13 chances out of 14 ($p = 0.93$) in the model. The use of a higher number of markers, in reality, might also have led to a higher proportion of hybrid individuals. Similarly, the implementation of only two markers in the model could easily change the genotypic composition of the population.

Demography in the upstream section. In addition, when GxE interactions were considered, the main demographic pattern was similar to that observed in reality. Indeed, an increase in population size was observed following MED translocation. However, the magnitude of this increase was far from that obtained in reality, mainly because the initial population size was not as low. Indeed, while the selection mediated by GxE interactions helped in reducing population size, it did not entirely prevent recruitment in the model, whereas in reality no self-sustained ATL population was found upstream, as indicated in the

Borne 1988 case study (Caudron et al., 2009). This could not be implemented in the model as underlying mechanisms were and are still missing. Subsequently, in the model, densities only increased by up to two folds within three years in the entire upstream area, whereas in reality, densities increased more and differently between zones. In the translocated zones, densities increased respectively by 6 to 20 folds in zone A and by 20 to 55 folds in zone B (sometimes up to 55 ind.100m⁻², as found downstream). In zones A1 and B1, densities increased way less, up to respectively 13 and 25 ind.100m⁻². In the model, the presence of a self-sustained population upstream could also account for some of the differences observed in introgression rate and the genotypic composition of the population, as more ATL individuals would have been present when translocation happened.

In reality, genetic and demographic effects appeared to be more restricted to the zones where translocation happened (Caudron, Champigneulle, et al., 2012). As already suggested earlier, individual movement, which seems to lead to homogenisation among zones, might influence these results. For instance, in the model, homing movement will make individuals try to go back to their natal reach. As a result, translocated individuals are more likely to migrate downstream for reproduction. There might therefore be more movement in the model compared to reality, which could explain why genetic and demographic effects are more widespread.

4.6.4 Discussion

Altogether, the comparison of empirical data to simulated data indicates that the implementation of GxE interactions enables the model to reproduce the general patterns of diversity dynamics and demography observed in reality for each case study (except in the intermediate zone of the Chevenne Creek), much more than the neutral scenario. In addition, the implementation of stronger GxE interactions and lower

selective pressures seems to drive simulated data closer to reality, suggesting that strong patterns of hard selection may have influenced the evolution of diversity dynamics. However, while simulated data appears closer to reality when considering EEMs, this does not mean it is the right model, or that these specific mechanisms only, led to those patterns. Nevertheless, in reality, the consistent change observed in alleles frequency – from ATL to MED alleles – following management practices across many populations (Gil et al., 2016) does imply that these alleles are beneficial to individual and population fitness and that natural selection might have, indeed, played an important role in structuring diversity dynamics.

Therefore, empirical as well as simulated data point toward strong patterns of hard selection in some environments, while it appears to be less prominent in others. For instance, in the Borne River, the ATL population located upstream was mainly maintained by continuous stocking and collapsed after the implementation of the GR, whereas in the Chevenne a self-sufficient ATL population was naturally maintained.

While for some case studies or zones, the model could reproduce some changes in allele frequency on similar timescales, the magnitude of these changes was less well represented. In addition, demographic patterns were further away from reality. However, the differences observed between simulated and empirical data are not entirely surprising for multiple reasons.

- ☞ First, it remains hard to compare empirical and simulated data, given that empirical data are highly incomplete due to limited sampling and many biases. For instance, depending on the case study, only one or two years of data were available. Sampling was performed very soon after the implementation of management practices and no follow-up was available later on. In addition, data were often collected at some given points of the river stretch and not along the entire section studied, and may not be fully representative of the population.

- ☞ Second, while simulation data are much more complete and comprehensive, they rely on a set of assumptions that were partly verified at most, and that were formulated based on a few empirical data. Indeed, parameter values used for calibrating some sub-models (such as survival and mating preference), were mainly based on general observations made from only one or a few populations, and may not represent the entire MED/ATL hybridization complex. By definition, the model represents an intentional simplification of the processes observed in reality. It does not, and could not have included all the eco-evolutionary forces playing in reality, as it will make it way too complex, but also because much information is still missing on the potential factors driving hybridization.

- ☞ Finally, those differences could arise from differences in temperatures experienced *versus* simulated as variations in temperatures modulate the selection mediated by GxE interactions. For instance, the temperatures used for each case study did not represent actual temperatures experienced in reality. Indeed, water temperature data were not available to implement an actual climatic trend for the years over which management practices took place. Consequently, the temperature model was highly simplified – no climatic trend, *i.e.* the same every year – and only based on the very few punctual data available.

Furthermore, these results highlight the importance of movement processes. Indeed, as dispersal has been acknowledged as central for understanding species distribution among but also within rivers (Tonkin et al., 2018), factors influencing movement in the model might play an important role in the spatial structuration of intraspecific diversity. On the one hand, the mechanisms and factors influencing movement have to be more specific to each case study. A range of values for some parameters, such as movement probability or weirs passibility, could be tested using the model in order to improve their fit.

On the other hand, we may have to consider additional movement processes, such as juvenile downward migration.

CHAPTER 5

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5 MEDITERRANEA: A DECISION-MAKING TOOL TO PROVIDE MANAGEMENT GUIDELINES

The previous chapter investigated the actual role of both empirical eco-evolutionary mechanisms (EEMs) - heterogamous preference and GxE interactions on survival - in structuring the evolution of diversity. Specifically, this was investigated in real case studies, where management practices had been implemented and monitored by managers and scientists. Comparing scenarios considering, or not, these EEMs, we concluded that the selection mediated by GxE interactions could interfere with management practices to modify their outcome. Furthermore, we showed that the implementation of GxE interactions helped improve the predictability of the model, as simulated results were getting closer to reality in most cases. Therefore, these mechanisms cannot be discarded when implementing management strategies, as such knowledge could help in building more efficient and evolutionary-inspired management strategies.

However, simulations in the previous chapter were based on punctual and real case studies, wherein data and knowledge were available. These results alone are not sufficient to infer general knowledge on the importance of such mechanisms for management. Indeed, variations in some ecological factors, such as temperatures, landscape features (hydrographic network size, connectivity, structure...), as well as the ratio and the spatial distribution of genotypes are important to consider. They may modulate the impact of such EEMs on diversity dynamics and hence influence the outcome of management strategy. Therefore, selecting the appropriate strategy adapted to each context is not an easy task.

While further research is required to better understand spatial as well as temporal dynamics of introgression over time, evaluating the effectiveness of management strategies in an adaptive loop remains essential (B. K. Williams, 2011). This can be achieved through modelling, using DG-ABMs

(Lamarins, Fririon, et al., 2022). Hence, by allowing for the consideration of complex ecological and evolutionary processes (Ayllón, Railsback, et al., 2019; Castellani et al., 2015; Lamarins, Hugon, et al., 2022; Nathan et al., 2019), as well as management strategies (Ayllón, Nicola, et al., 2019; Santostasi, Ciucci, et al., 2020) – and their impact on individuals and their interactions, it can represent an efficient prospective-tool to inform decision-making.

5.1 OBJECTIVES

As already described before (*Section 2.2.3*), a few common patterns of diversity have been observed in the Mediterranean area. Similarly, hydrographic networks can be categorised based on their shape and their mean winter temperatures. This information can be pooled and translated into many situations in order to evaluate the impact of various management practices - usually applied in the MED/ATL hybridization complex (Gil et al., 2016) - in some typical situations. These situations, yet unrealistic, would be more generic and may help in evaluating the usefulness of evolutionary enlightened management. For instance, some general dynamics might be observed in certain situations, for example when network connectivity is higher.

Therefore, the aim of this chapter is to simulate various management practices in some of these generic situations while accounting for both EEMs, using MEDITERRANEA. On the one hand, I will compare the evolution of diversity dynamics under various management scenarios (i) to determine whether the management goal is achievable and (ii) to evaluate the relative efficiency of each management strategy. I will also consider whether simulated results corroborate what has been observed in reality following the implementation of these management strategies. On the other hand, I will investigate whether some differences can be observed based on some initial ecological settings - temperature and network

connectivity. This should allow us to provide some general guidelines to managers based on these ecological setups.

5.2 CASE STUDY AND SIMULATION SCENARIOS

5.2.1 Ecological settings

Initial context. For these simulations, I used one of the typical diversity distributions observed in the Mediterranean area (*Section 2.2.3, Figure 2 – 7, situation D*): an allopatric spatial repartition with an ATL population located upstream and a MED population downstream. An allopatric distribution was favoured because conservation strategies are often carried out where nearly pure MED populations are still found (Gil et al., 2016; Laikre et al., 1999) and where the isolated location of ATL individuals will favour the implementation of some selective management practices (Caudron & Champigneulle, 2011). An equal repartition of the population is initially assumed with each population occupying 50% of the geographic range (*Figure 5 – 1*).

Hydrographic networks. Simulations are carried out on two different types of hydrographic networks: a longitudinal rectilinear network with simple ramification *versus* an inverted leaf-shaped dendritic network (*Figure 5 – 1*) in order to test the impact of connectivity (Labonne et al., 2008) on management strategies efficiency. Most topological aspects of each hydrographic network are simplified in order to avoid any confounding effects. Reach characteristics influencing density, such as length, width or carrying factor are similar among reaches, even though upstream parts of rivers are narrower in reality. This is to allow the simulation of an admixture event between downstream MED and upstream ATL populations with the same potential carrying capacity. Both hydrographic networks have the same size and contain 50 reaches of 10 000 metres square – 2000 metres in length and 5 metres in width, to only

test for the effect of connectivity. All quality parameters – carrying and reproduction factor – are set at the maximum and density is set around 30 ind.100m⁻². As the temperature model is based on altitude, altitude is the only parameter to vary between reaches in order to create a temperature contrast from upstream to downstream. For both hydrographic networks, the difference in altitude, between the lower and the higher reach of the river, ranges from 400 metres to 1400 metres. An increase in altitude will be constant from one reach to another within a hydrographic network.

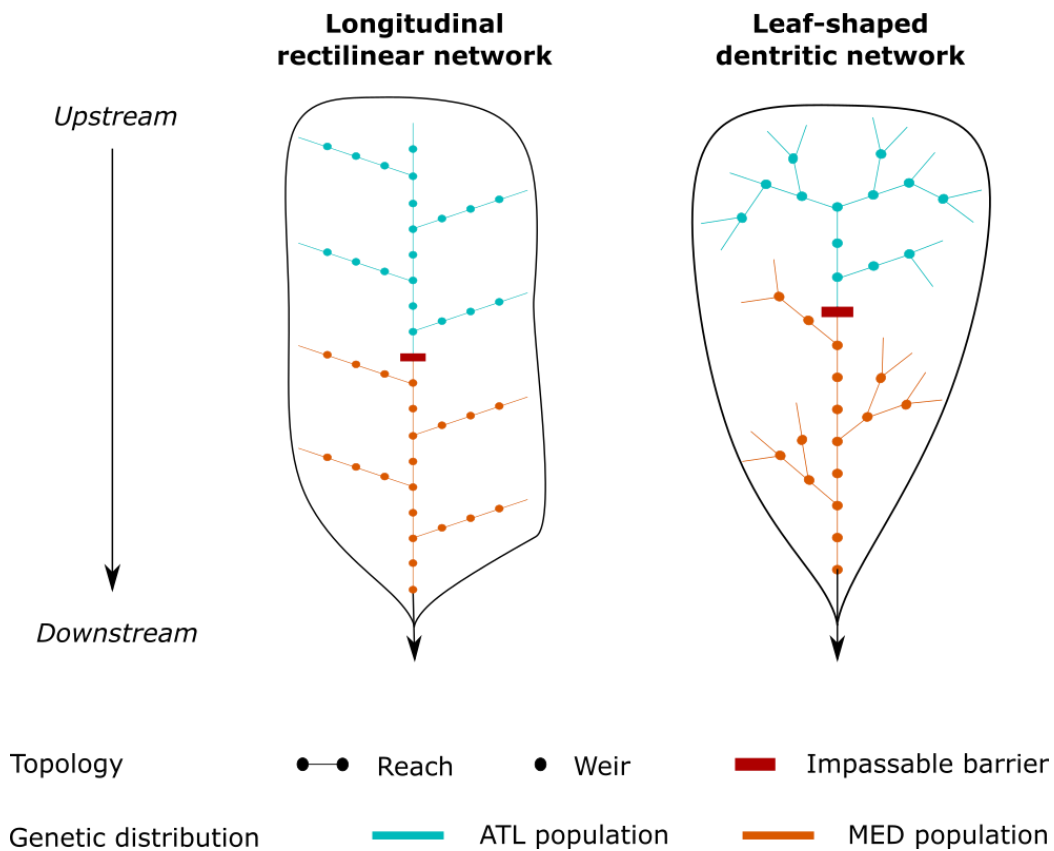


Figure 5—1: Representation of both hydrographic networks under MEDITERRANEA with the shape of the drainage basin and the initial genetic distribution. On each network, a MED population is located downstream and an ATL population upstream each occupying 50% of the geographic range.

Temperature model. The same temperature models are used for both hydrographic networks. However, the topology of each network produces temperature differences between reaches as the dendritic aspect of one network generates more reaches at higher altitudes - the leaf-shaped one. One temperature model will represent a potentially favourable habitat for MED populations with low winter temperatures (*Figure 5 – 2*). Alternatively, the other one will simulate warmer winter temperatures, where all lineages may fare the same (*Figure 5 – 3*).

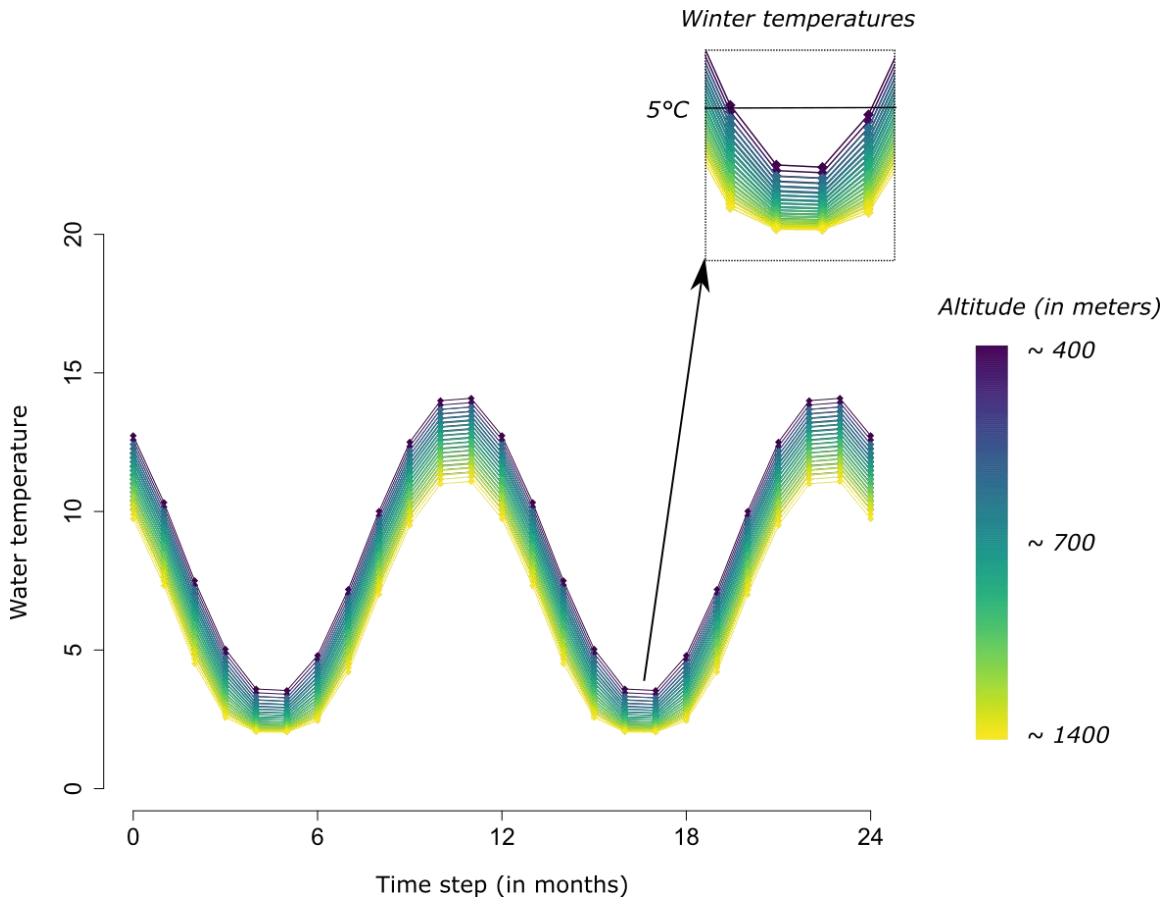


Figure 5—2: Colder temperature model. Water temperature is calculated per reach each month based on altitude. A zoom of winter temperatures shows the temperatures from December to March, which are here always inferior to 5°C. This graph is made using the rectilinear hydrographic network.

Simulation framework. Simulations are replicated 20 times per scenario. Each simulation starts in September and is run over 30 years in order to follow the evolution of diversity dynamics and demography over a long period after the implementation of management strategies. The first 10 years are used to stabilise the model and interventions for management strategies are then implemented ($t = 11$). The results will only focus on two components of diversity dynamics usually investigated by managers – introgression rates and genotypic composition of the population (MED, HYB, ATL) – as well as total population size.

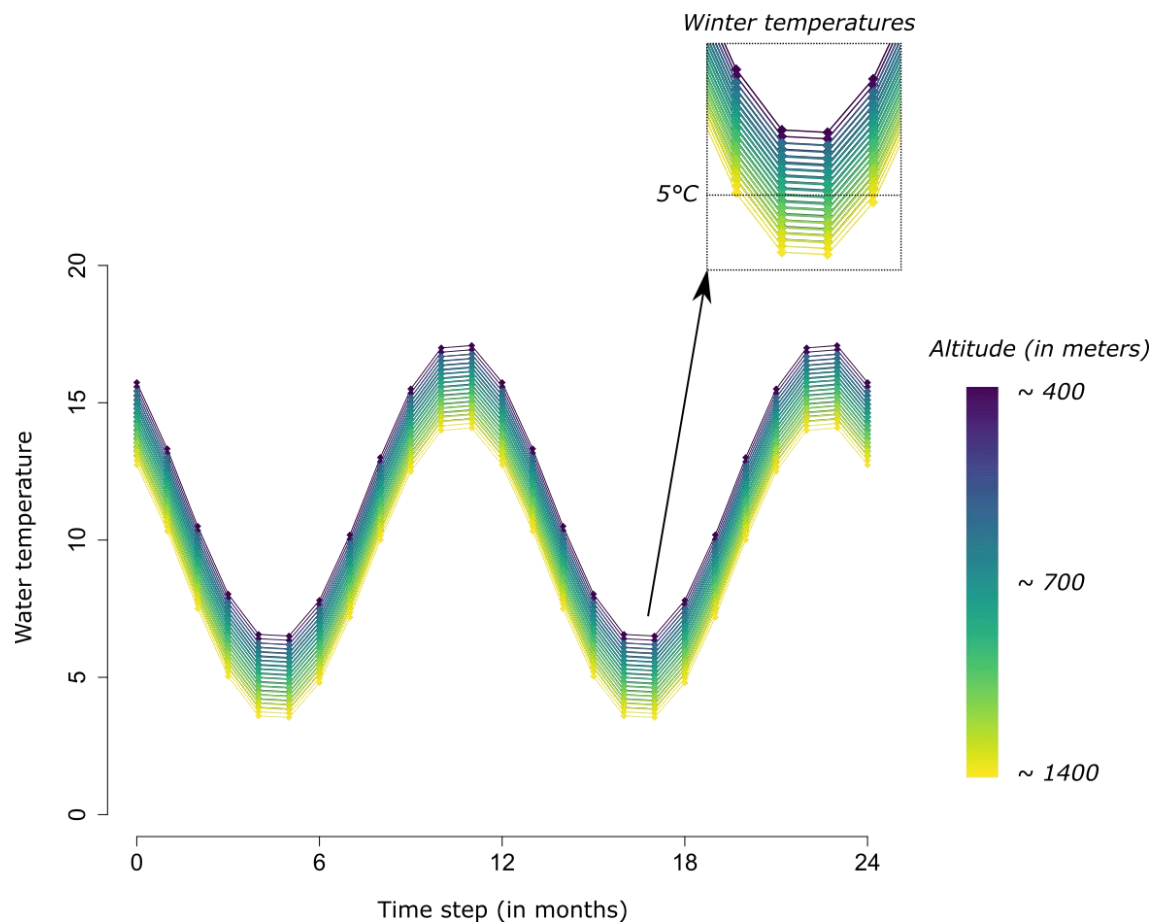


Figure 5—3: Warmer temperature model. Water temperature is calculated per reach each month based on altitude. A zoom of winter temperatures shows the temperatures from December to March, which are often inferior to 5°C. This graph is made using the rectilinear hydrographic network.

5.2.2 Management scenarios

Managers' goal. In this context of allopatric repartition, managers often aim at protecting and restoring a continuous and viable MED population along the river in order to (i) establish a self-sufficient population upstream when the ATL population does not thrive (Caudron, Champigneulle, et al., 2012) and/or avoid an ATL gene flow from upstream that may compromise the MED population (Caudron & Champigneulle, 2011). Over the last 20 years, many management practices have been implemented in order to conserve and restore the native MED gene pool at the population level (Caudron, Champigneulle, et al., 2012; Caudron et al., 2006, 2011; Caudron, Vigier, et al., 2012; Caudron & Champigneulle, 2011; Gil et al., 2016). However, they often lead to the admixture of both lineages. Their impact on the evolution of diversity dynamics should therefore be monitored in order to avoid counter-productive results (Gil et al., 2016).

Management strategies. A few of the most common management practices applied by fisheries managers will be assessed with and without *prior* removal of non-native individuals by electrofishing (Caudron et al., 2011; S. E. Moore et al., 1986; Peterson et al., 2004). Management efficiency will be evaluated for the following strategies (*Figure 5 – 4*): barrier removal, BR (Hart & Poff, 2002; Roni et al., 2002), stocking with native fry, SNF (Caudron et al., 2006; Cowx, 1994; Crivelli et al., 2000; Leitwein et al., 2016) and direct translocation of wild individuals, DT (Caudron, Champigneulle, et al., 2012; Hilderbrand, 2002; Moritz, 1999; Schmetterling, 2003): genitors exclusively (Caudron et al., 2011) or individuals of various ages (Caudron, Champigneulle, et al., 2012). Management scenarios are defined as described in *Figure 5 – 5*. Management strategies implemented are described below:

- ☞ **Non-native ATL removal:** extra mortality is applied to ATL individuals to ensure that 90% of the population has been removed with no genitors left (Caudron & Champigneulle, 2011). As the goal is not to evaluate how long removal might take but only to simulate its outcome, ATL individuals

are removed over one time step just before the implementation of other management strategies. Note that, in the model, removal is perfect; *i.e.* there is no error on genotype assessment.

- ☞ **Barrier removal (BR)**: the impassable barrier between MED and ATL populations is removed to reinstall full connectivity along the river.
- ☞ **Stocking with native MED fry (SNF)**: the ATL zone is stocked with native MED fry for five consecutive years. 6000 individuals are stocked per hectare and per year. Individuals are stocked just before summer in May when they are approximately 5 months old with an initial size of 3 centimetres (Caudron et al., 2006; Gil et al., 2016).
- ☞ **Direct Translocation of wild MED Trout (DT)**: MED individuals from the downstream part of the river are transferred upstream for five consecutive years. A sufficient number of individuals has to be translocated to reflect the genetic composition of the source population (Stockwell et al., 1996) and occupy approximately 10% of the carrying capacity (Hilderbrand, 2002) with at least 100 individuals transferred per introduction event to favour their establishment (Fischer & Lindenmayer, 2000; Minckley, 1995). In addition, it is suggested that fish are introduced along large areas of the river rather than restricted ones to favour the colonisation of the full area (Caudron, Champigneulle, et al., 2012). Therefore, 5000 trout are translocated in five reaches, segregated along the mainstream to cover a larger area (*Figure 5 – 4*), resulting in the transfer of 200 trout per year per reach. Overall, a density of 200 trout per hectare is transferred (calculated based on successful results from the Borne River, Caudron, Champigneulle, et al., 2012). For the translocation of genitors, only individuals above a certain size (~ 20 centimetres) are transferred.

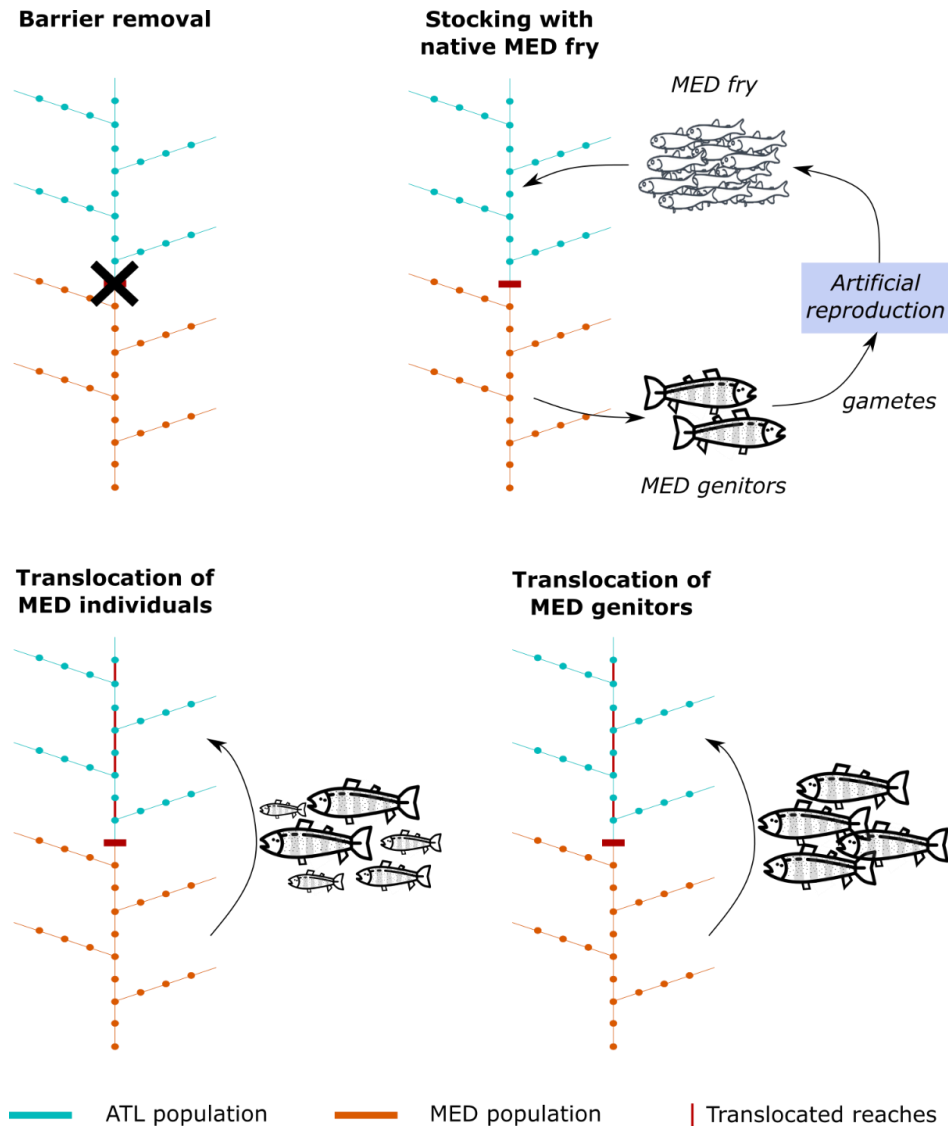


Figure 5—4: Representation of the management strategies assessed. Each practice is tested with and without prior non-native ATL removal.

Management practices efficiency is often measured by evaluating the decrease in population introgression rate. Based on Laikre et al. (1999), populations with an introgression rate of 25% or less are considered as nearly pure native MED populations. Hence, management practices leading to such a decrease will be considered successful. Relative management efficiency will be evaluated based on (i) the time within which such a decrease happened, (ii) the rate of pure MED *versus* HYB and ATL individuals

observed in the population and (iii) the consequences on population size. Therefore, results will focus on diversity dynamics and demography – introgression, genotypic composition and distribution of individual introgression.

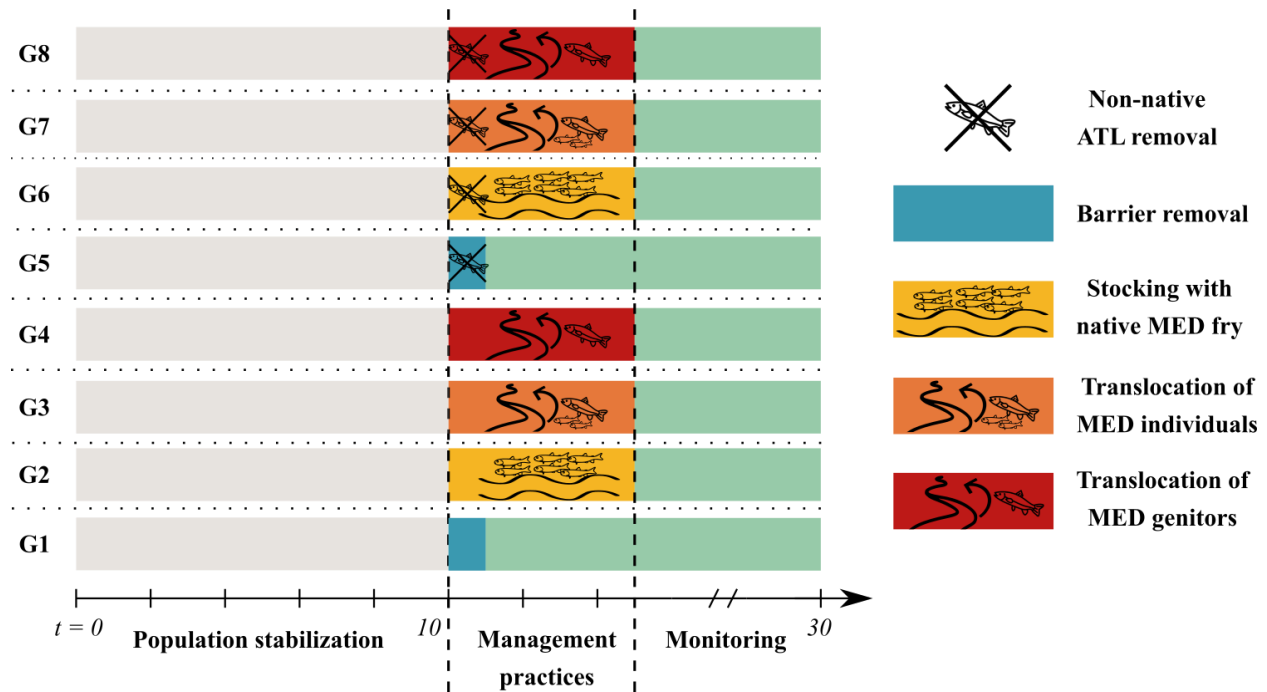


Figure 5—5: Simulations timeline and list of management scenarios (G1 à G8) with implemented strategies.

5.3 EVALUATING MANAGEMENT STRATEGIES EFFICIENCY

5.3.1 Rectilinear network under colder temperatures

5.3.1.1 Evolution of introgression

A clear decrease in introgression rate – the percentage of ATL alleles – followed the implementation of all management strategies (Figure 5 – 6). For most, the decrease was more important when *prior* ATL removal was implemented. The SNF strategy led to the highest decrease going from 1 to 0.2 in one year only, and

to nearly 0 after five years of stocking without *prior* ATL removal. With ATL removal, it went from 1 to nearly 0 in just one year. For both DT strategies – individuals and genitors only – introgression rates decreased less rapidly (from 1 to ~ 0.4 in five years), especially without ATL removal (from 1 to less than 0.2 in five years). The decrease was the steepest during translocation and slowed down afterwards. The BR strategy led to the smallest and most progressive decrease in introgression, which reached respectively 0.35 and 0.7 with and without *prior* ATL removal, five years after the barrier removal.

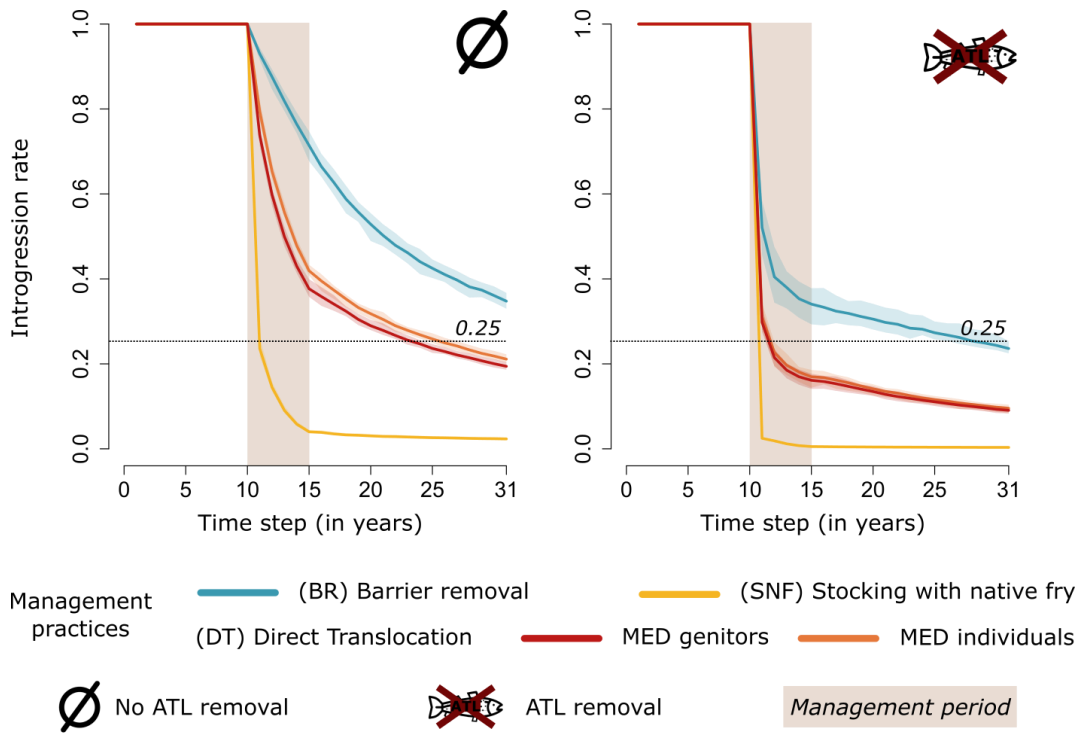


Figure 5—6: Evolution of the population introgression rate in the upstream zone of the rectilinear network for twenty years following the first year of management. Trajectories are represented for each management strategy, with and without *prior* ATL removal under the colder temperature modality.

5.3.1.2 Genotypic composition of the population

After stabilisation (10 years), the upstream area showed an ATL population with a low population size (Figure 5 – 7, less than 30000 individuals), due to the strong selection exerted by GxE interactions at colder

temperatures. Following the implementation of all management strategies, a decrease in ATL genotypes was observed. This decrease was faster following the implementation of the SNF strategy and slower for the barrier removal. Obviously, with the implementation of ATL removal, this decrease was faster and the same for all management scenarios.

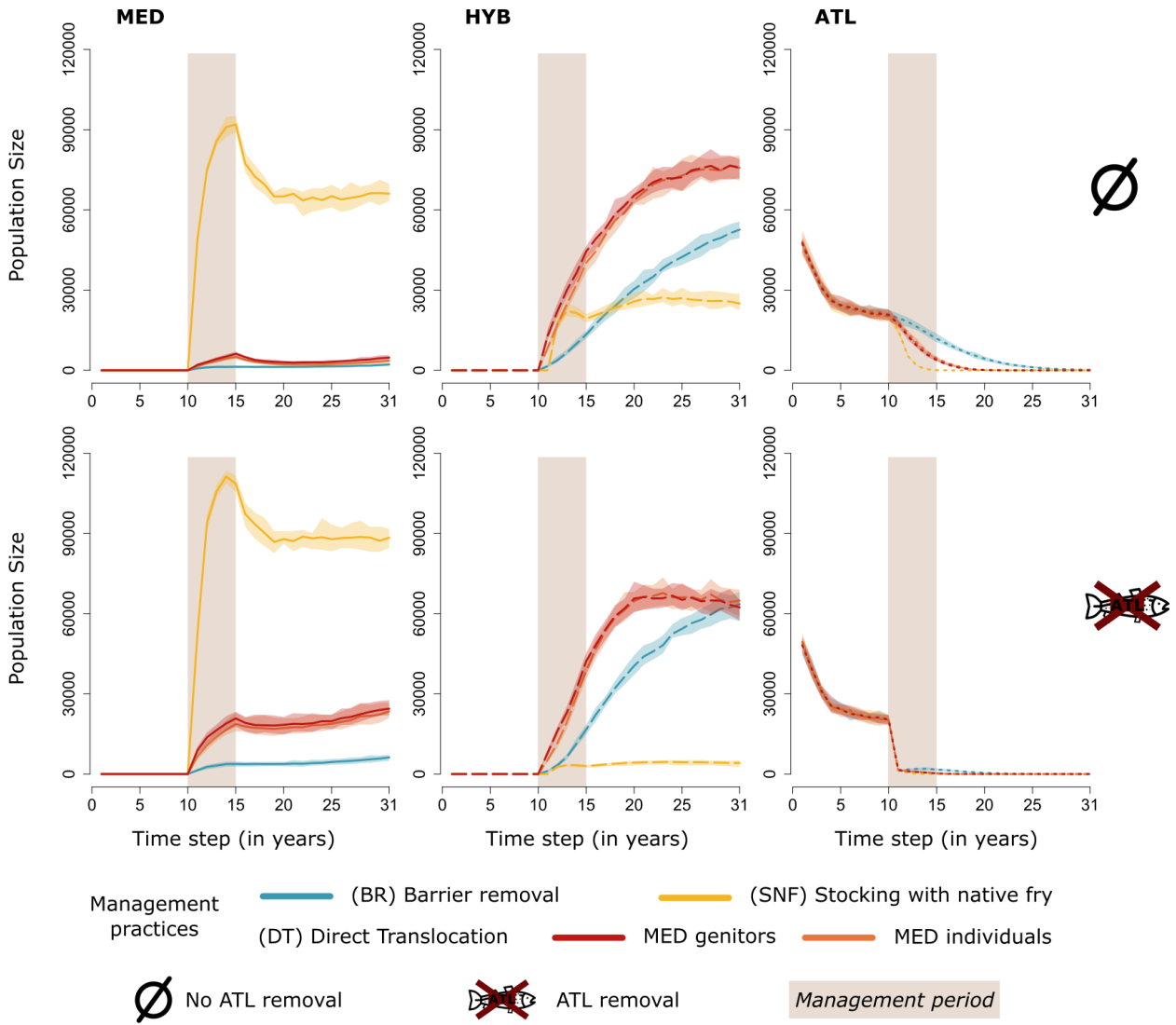


Figure 5—7: Evolution of the genotypic composition of the population in the upstream zone of the rectilinear network for twenty years following the first year of management. Trajectories are represented for each management strategy, with and without prior ATL removal under the colder temperature modality.

For all scenarios, 10 years after the implementation of management practices, ATL genotypes had fully disappeared from the population (*Figure 5 – 7*). Therefore, all management strategies seemed quite efficient in erasing pure ATL genotypes. The SNF strategy was associated with a substantial increase in MED genotype (up to ~ 70000), even more so with *prior* ATL removal (up to ~ 90000) since it reduced the proportion of HYB individuals created (25000 vs less than 5000). Both DT strategies led to the same outcome, with the creation of a large number of HYB individuals and very few MED individuals remaining after translocation, especially without *prior* ATL removal. However, when ATL removal was implemented, the number of HYB started decreasing at $t = 20$ years, while there was a progressive increase in the number of MED individuals. The outcome of the BR strategy was similar but the speed at which HYB individuals were created was slower. In addition, there were even fewer MED individuals. For all management strategies, ATL individuals were easily purged from the population. However, the proportion of MED and HYB individuals varied vastly based on the management strategy implemented. For instance, ATL removal always allowed for the persistence of more MED individuals.

5.3.1.3 Evolution of demography

A subsequent increase in population size followed the implementation of each management strategy (*Figure 5 – 8*, initial population size at $t = 10$: ~ 20000 individuals) – after a small initial decrease following ATL removal. This increase was the fastest and the largest for the SNF strategy. During stocking, population size peaked out as many individuals were stocked (~ 0.6 fry per m^2). After a small decrease, a plateau was observed with a population size of approximately 90000 individuals. For the DT strategies, the increase in population size was more progressive, especially without ATL removal. The increase was the steepest during translocation and then slightly slowed down. A higher population size was reached faster when ATL removal preceded the implementation of DT (~ 65000 vs 55000 just after translocation and ~ 90000 vs 80000 at the end of the simulation). The BR strategy led to the slowest and more progressive increase

in population size. For that strategy, the increase was much faster when ATL removal was also implemented (with ~ 70000 vs without ~ 55000 at the end of the simulation). Overall, different strategies only differed slightly in maximum population size, but highly in their speed to reach it.

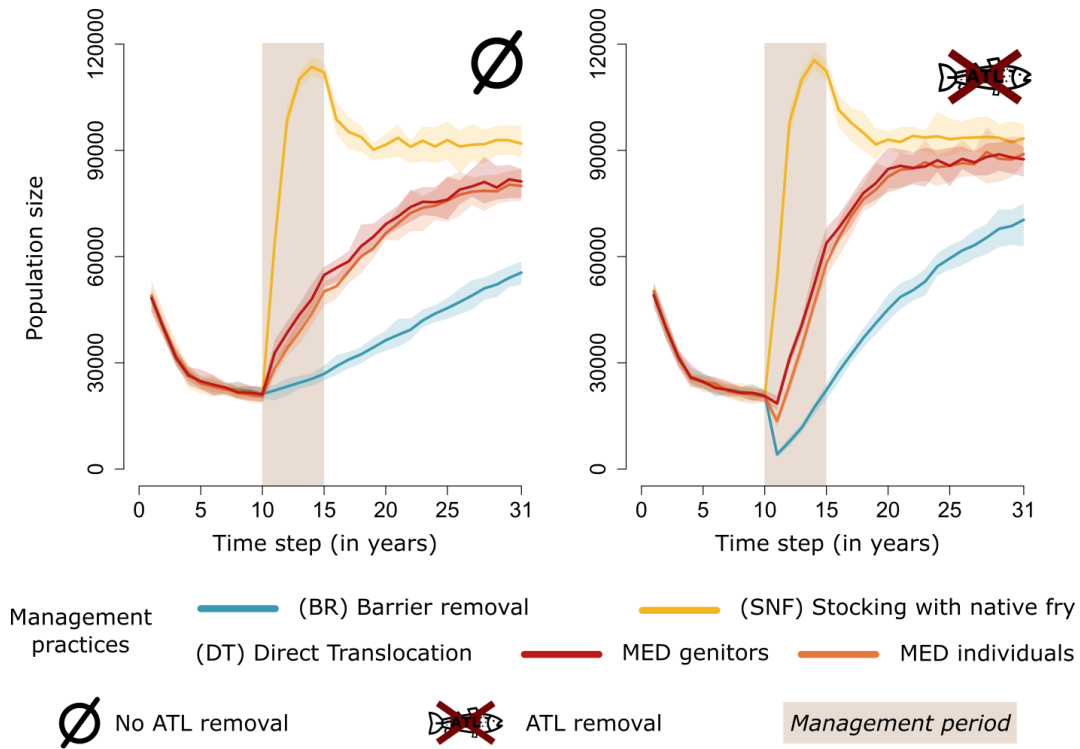


Figure 5—8: Evolution of population size in the upstream zone of the rectilinear network for twenty years following the first year of management. Trajectories are represented for each management strategy, with and without prior ATL removal under the colder temperature modality.

5.3.2 Leaf-shaped network under colder temperatures

5.3.2.1 Evolution of introgression

When implemented in a leaf-shaped network, management strategies also all resulted in a decrease in introgression (Figure 5 – 9). For the SNF strategy, the decrease was the same compared to the rectilinear network, probably because this management strategy was carried out on all the reaches, as native fry

were poured all along the river. For the other management strategies – DT and BR – the decrease in introgression rate was faster and steeper in the leaf-shaped network, especially for the BR strategy. The effect of *prior* ATL removal remained the same: a faster decrease. For the DT strategies, after five years of translocation, introgression reached approximately 0.1 with, and 0.25 without ATL removal. For the BR strategy, introgression rates valued respectively 0.2 with, and 0.5 without ATL removal five years after the barrier removal. These values were way lower than those observed in the rectilinear network.

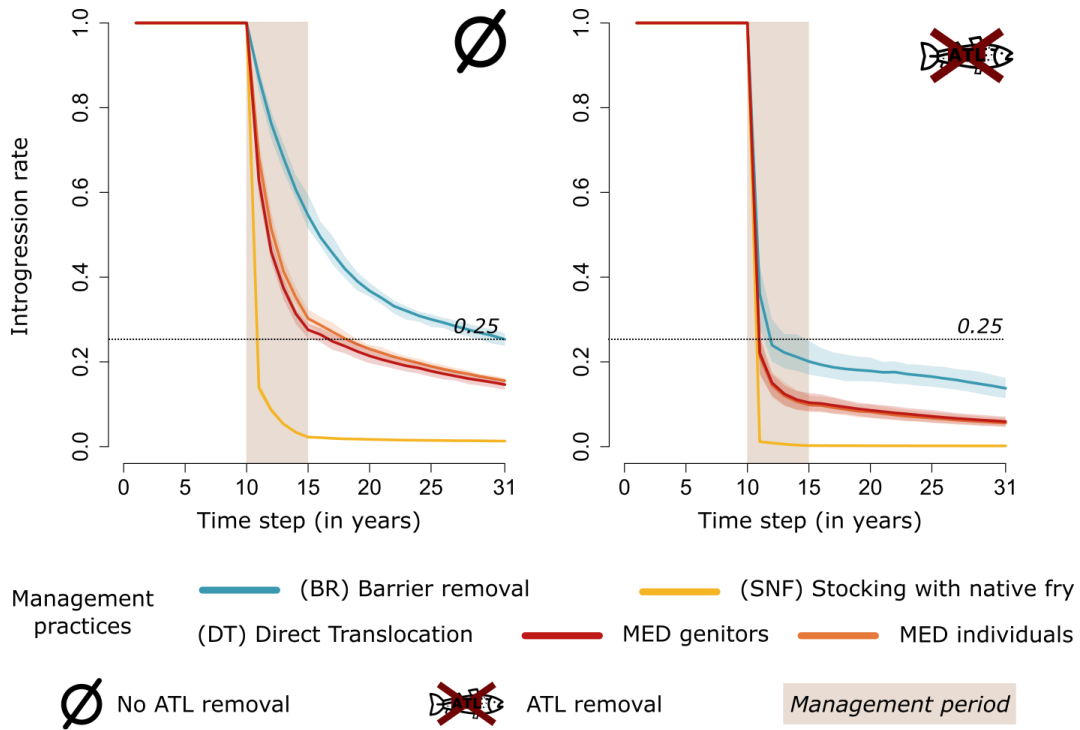


Figure 5—9: Evolution of the population introgression rate in the upstream zone of the leaf-shaped network for twenty years following the first year of management. Trajectories are represented for each management strategy, with and without prior ATL removal under the colder temperature modality.

5.3.2.2 Genotypic composition of the population

In the leaf-shaped network, the composition of the population (Figure 5 – 10), as well as its initial size, slightly varied compared to the rectilinear network. A lower initial number of ATL individuals was found

5.3 Evaluating management strategies efficiency

in the population for the same habitat surface. All management strategies resulted in a slightly higher proportion of MED individuals, which was associated with a lower proportion of HYB individuals, in some cases. In the case of the BR strategy, the increase in the proportion of HYB individuals was slower but ultimately led to the same amount of individuals, while the increase in MED individuals was faster. For both DT strategies, the increase in the proportion of HYB was also slower, but it did not ultimately reach the same amount of individuals – it remained lower.

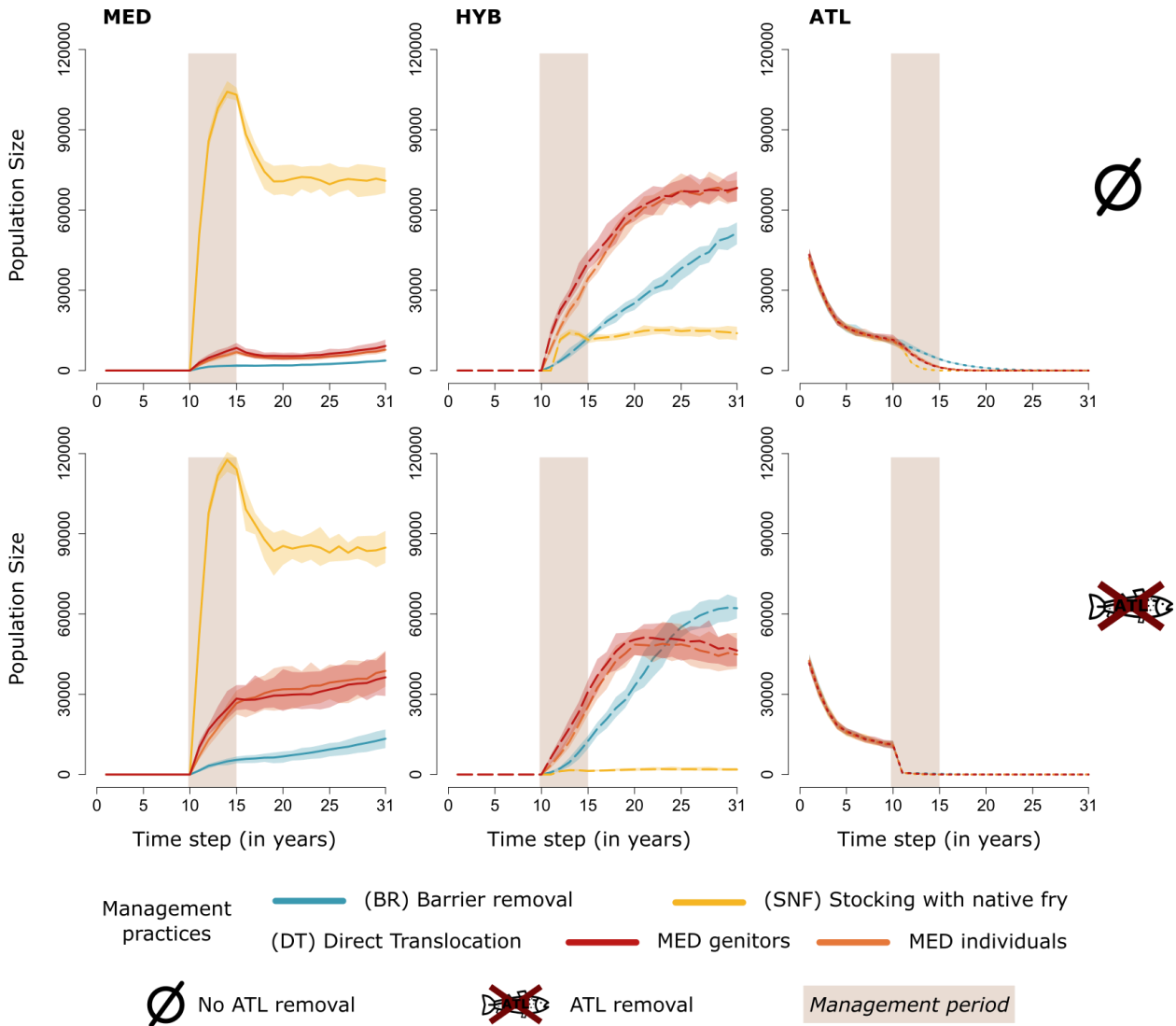


Figure 5—10: Evolution of the genotypic composition of the population in the upstream zone of the leaf-shaped network for twenty years following the first year of management. Trajectories are represented for each management strategy, with and without prior ATL removal under the colder temperature modality.

In addition, when ATL removal was considered, the subsequent decrease in HYB proportion (at t = 20 years) appeared to be slightly faster (Figure 5 – 10). Overall, compared to the rectilinear network, higher connectivity led to a faster decrease in introgression, except for the SNF strategy. For all management strategies, ATL individuals were also removed, but MED individuals appeared to be slightly favoured.

5.3.2.3 Evolution of demography

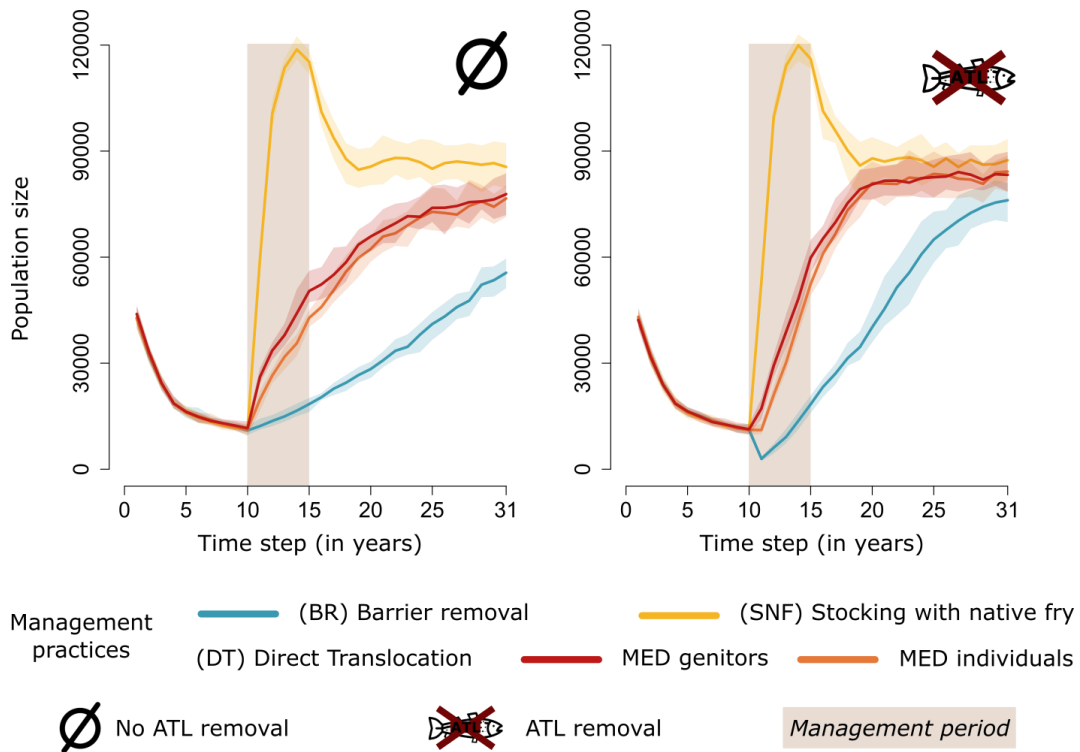


Figure 5—11: Evolution of population size in the upstream zone of the leaf-shaped network for twenty years following the first year of management. Trajectories are represented for each management strategy, with and without prior ATL removal under the colder temperature modality.

In the dendritic network, *prior* to any management strategies, the population size was significantly lower compared to the rectilinear network (Figure 5 – 11, ~ 10000 individuals). However, following management implementation, population size either stayed lower or became higher depending on the management

strategy. For both the SNF and the DT strategies, population size also increased but not as much or as fast as in the rectilinear network. For example, for both DT strategies, the population size reached 80000 individuals with and 75000 individuals without ATL removal (*Figure 5 – 11*) at the end of the simulation (vs respectively 90000 and 80000 individuals in the rectilinear network, *Figure 5 – 8*). Conversely, for the BR strategy population size increased faster and became higher in the dendritic network, and even faster with ATL removal (~ 75000 individuals here, *Figure 5 – 11*; versus 70000 in the rectilinear network, *Figure 5 – 8*). Overall, the leaf-shaped network produced a lower population size compared to the rectilinear network, except for the BR strategy.

5.3.3 Rectilinear network under warmer temperatures

In this section, the same scenarios are investigated in the rectilinear network but using a different temperature regime. This temperature regime shows warmer winter temperatures (*Figure 5 – 3*), around 7°C. Considering GxE interactions, the survival difference between lineages is therefore lower. Hence, the selective advantage associated with the native lineage might diminish or even disappear, which could modify the outcomes of management strategies.

5.3.3.1 Evolution of introgression

A warmer temperature modality changed drastically the outcome of some management practices (*Figure 5 – 12*). For the SNF strategy, the introgression rate still decreased massively during the stocking period up until values of introgression inferior to 0.2, therefore lower than management goals. However, for the DT and BR strategies, introgression rates decreased to a much lower extent, and even more so without *prior* ATL removal. For the DT strategies, introgression rates reached approximately 0.6 with and 0.8 without ATL removal after five years of translocation. Both rates then kept decreasing slower up to

respectively 0.45 and 0.65 at the end of the simulation. For the BR strategy, the introgression rate still decreased progressively but very slowly. Five years after the barrier removal, it had barely decreased below 0.9 considering ATL removal.

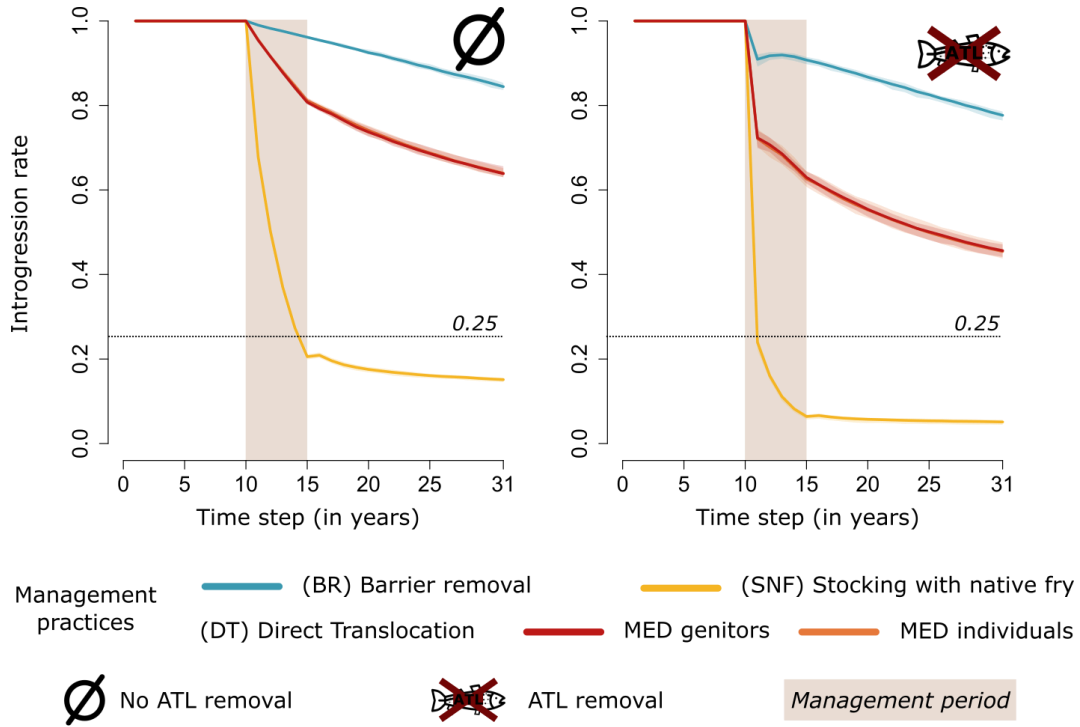


Figure 5—12: Evolution of the population introgression rate in the upstream zone of the rectilinear network for twenty years following the first year of management. Trajectories are represented for each management strategy, with and without prior ATL removal under the warmer temperature modality.

5.3.3.2 Genotypic composition of the population

The ATL population initially located upstream was more than twice bigger when a higher temperature modality was implemented since GxE mediated selection was less strong (Figure 5 – 13). In this context, ATL removal highly decreased the proportion of ATL individuals. However, their number remained high when the other management strategies were implemented. Although all adults were removed, the sub-adults left were able to mature and reproduce during the next time step, as indicated by the subsequent

5.3 Evaluating management strategies efficiency

increase in the proportion of ATL individuals for the BR and DT strategies. Following the implementation of each management strategy, the evolution of the genotypic composition of the population differed compared to scenarios considering colder temperatures, as suggested by the evolution of introgression.

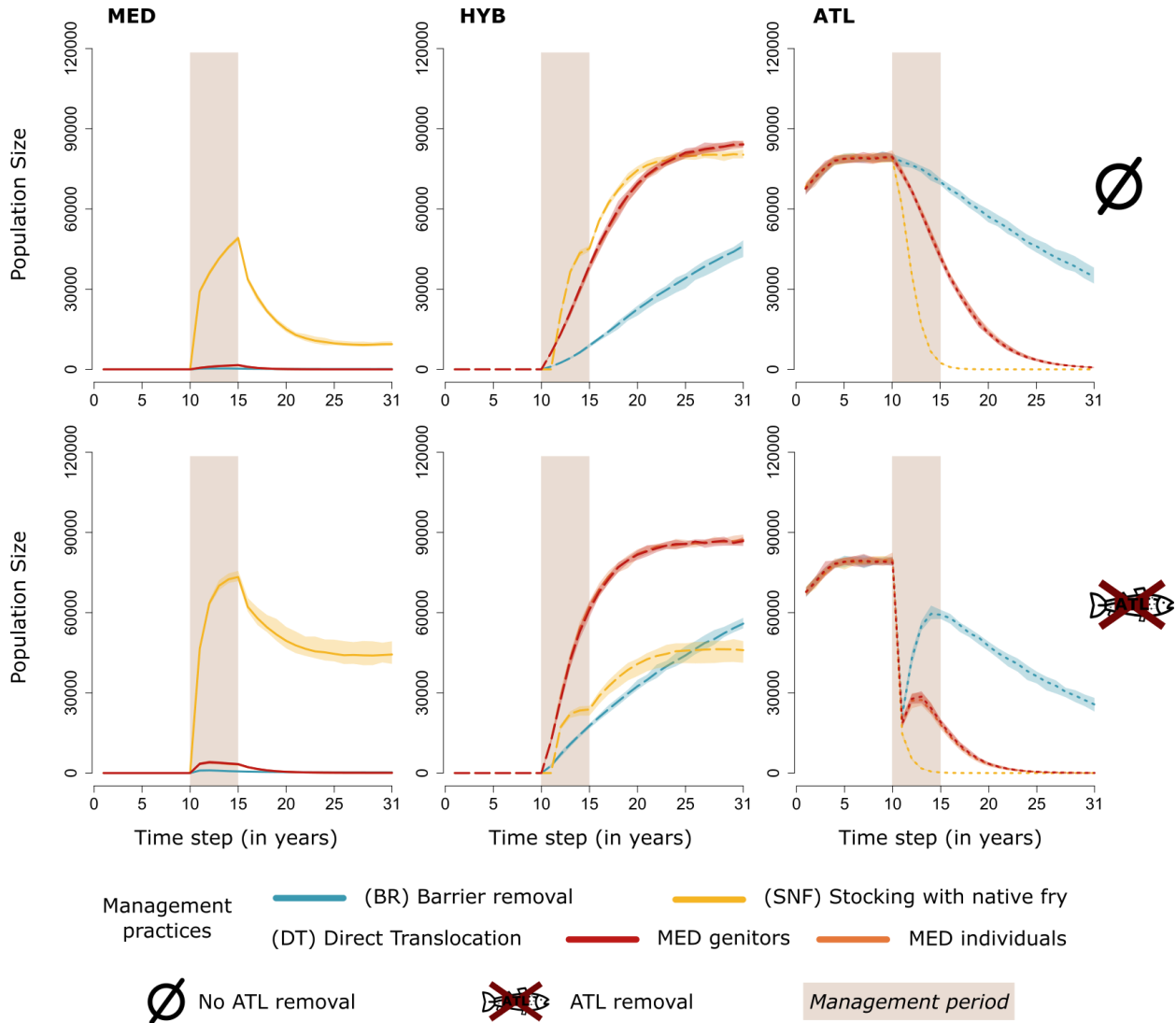


Figure 5—13: Evolution of the genotypic composition of the population in the upstream zone of the rectilinear network for twenty years following the first year of management. Trajectories are represented for each management strategy, with and without prior ATL removal under the warmer temperature modality.

The elimination of ATL individuals took longer as their proportion was initially higher (*Figure 5 – 13*). It remained the fastest for the SNF strategy (within the five years of stocking). However, considering higher temperature, this strategy also led to extensive hybridization, especially without *prior* ATL removal, where a higher proportion of HYB individuals was found (~ 80000 HYB vs 15000 MED at the end of the simulation). Apart from the SNF strategy, here, no other management strategies allowed for the maintenance of pure MED individuals. The DT strategies both led to an overall decrease in the proportion of ATL individuals associated with a continuous increase in the proportion of HYB individuals. Ultimately, the population was exclusively made of HYB individuals (~ 90000 individuals) and this pattern was the same with and without *prior* ATL removal. Finally, for the BR strategy, the decrease in ATL individuals was more continuous and a large proportion of ATL individuals were still found at the end of the simulation, considering or not ATL removal (respectively 30000 and 35000 individuals). Meanwhile, the proportion of HYB individuals increased progressively.

Under this temperature regime, the effects of management strategies were much more contrasted. Most of them (except SNF) were inefficient considering the initial management goal. Indeed, introgression rates did not decrease as much, and more HYB individuals were created.

5.3.3.3 Evolution of demography

Without *prior* ATL removal, population size did not increase as much as when colder temperatures were considered (*Figure 5 – 14*). The increase remained the largest for the SNF strategy, whereas it was very slight for the DT strategies and almost null for the BR strategy. This is because the fitness of ATL populations is not as reduced compared to that of MED populations when winter temperatures are warmer. Considering ATL removal, population size increased significantly for all scenarios, since removal had caused a large initial decrease. Similarly, the increase was the largest for the SNF strategy, followed

by the DT strategy and finally the BR strategy. This could be explained by differences in population mean fitness. Indeed, even if the differences in survival are lower between MED and ATL genotypes in this context, populations with lower introgression rates – *i.e.* a lower proportion of ATL alleles – still have a fitness advantage over populations with more ATL alleles. Overall, under this temperature regime, population size did not increase as much following management strategies as it was not as low initially.

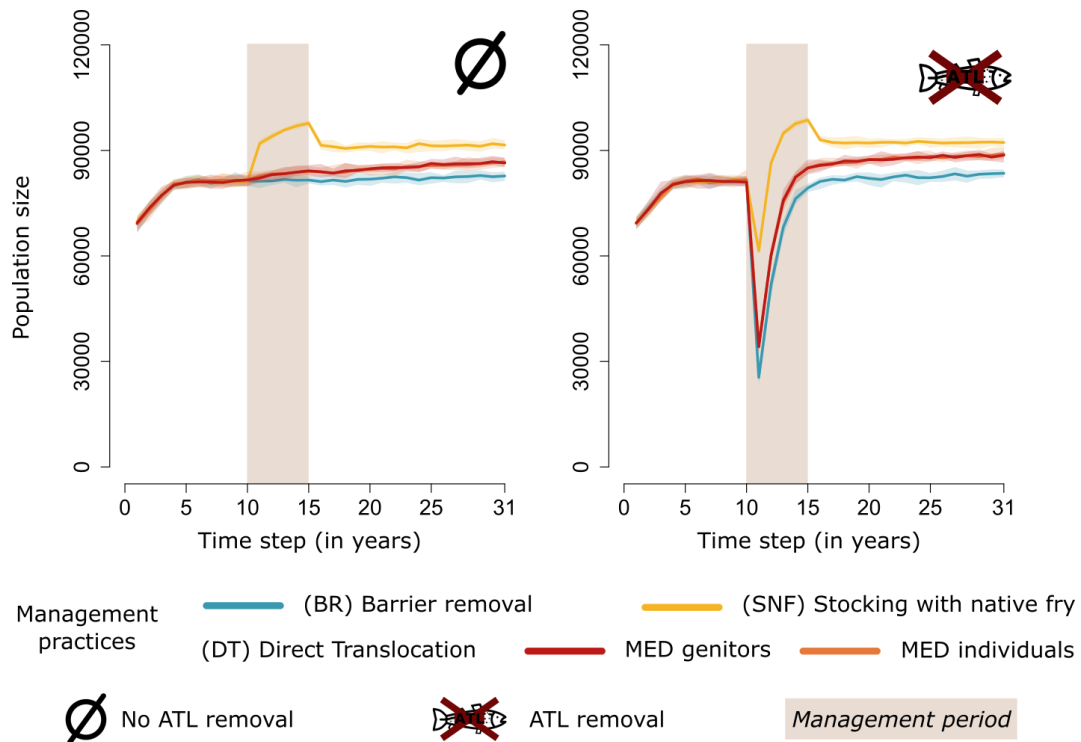


Figure 5—14: Evolution of population size in the upstream zone of the rectilinear network for twenty years following the first year of management. Trajectories are represented for each management strategy, with and without prior ATL removal under the warmer temperature modality.

5.4 DISCUSSION

The different management strategies implemented in the model all influenced diversity dynamics and demography. All management strategies led to a decrease in introgression. In most cases, the strategies

allowed the elimination of pure ATL genotypes, while largely increasing the proportion of hybrid individuals. In favourable temperatures, some management strategies allowed for a small recovery of pure MED genotypes, especially following ATL removal. These changes were observed in a short period – within 5 years following the first implementation. When the initial upstream population size was low, management strategies all led to a significant increase in population size. Around this general pattern, however, there were some nuances in the efficiency of the different management strategies.

5.4.1 Management strategies efficiency in the model

The general goal of managers was the restoration of a nearly pure MED population upstream. Based on the threshold used by managers for nearly pure populations, I consider a management strategy to be successful when the introgression rate is below 25% (Laikre, 1999). If no management strategies proved successful, the management goal is considered unachievable. The efficiency of a management strategy is determined by the speed at which the target introgression rate is reached, as well as genotypic composition. We can therefore also look at the relative efficiencies between management strategies.

Hydrographic networks and temperatures influenced the efficiency of the various management strategies. For instance, despite a generally good efficiency of all management strategies, it appears that target introgression was reached faster in the leaf-shaped network. The downside, however, is that it was accompanied by general lower population sizes.

Furthermore, management strategies' efficiency highly varied based on winter temperatures. For the warmer winter temperature, most of the management strategies were not successful, as target introgression was not reached (except for the SNF strategy). For the lower winter temperature modality

– favourable to the MED maternal lineage – most management strategies were successful as introgression rates ultimately decrease below 25%. Therefore, temperature appears to be the factor influencing most management practices' efficiency in the simulations.

In cases where most management strategies were successful, the relative efficiency of each management strategy differed. The SNF strategy was the most efficient one in the model, as it always led to the fastest and strongest decrease in introgression (nearly 0 within only 5 years). It also allowed for the creation of more MED genotypes compared to HYB genotypes, and led to the highest population size recovery. Considering *prior* ATL removal, this strategy led to the restoration of a nearly pure MED population mainly composed of pure MED genotypes (barely any HYB remained). Both DT strategies - individuals or genitors only - then followed with a rapid decrease in introgression and a significant increase in population size. However, this management strategy was associated with the creation of a majority of HYB individuals. Finally, the BR strategy was not always successful – *i.e.* without ATL removal – and was less efficient as the decrease in introgression and the increase in population size were the slowest. Overall, *prior* ATL removal made all management strategies more efficient as it allowed for the removal of a large proportion of ATL individuals. Specifically for the DT strategies, it resulted in the creation of more MED genotypes. It also allowed for a stronger increase in population size, as it increased the mean fitness of the population – through the removal of low fitness genotype.

5.4.2 Evaluation of each strategy

Each of the management strategies tested here has previously been suggested and potentially implemented in the MED/ATL hybridization complex and/or on other salmonids. Therefore, some knowledge is available regarding their actual efficiency and feasibility in different cases. This knowledge

combined with our simulated results will help us evaluate each management strategy in a cost-effective way.

5.4.2.1 *Barrier removal*

Barrier removal has never been used as a management strategy in the context of MED/ATL hybridization. Indeed, barriers can stop the spread of non-native individuals, when invasive or domesticated individuals pose a threat to native diversity (P. E. Jones et al., 2021). For instance, some management practices rely on, or use, such fragmentation to intentionally prevent the movement of non-native individuals into native populations (“Isolation management”: (Novinger & Rahel, 2003); “Selective fragmentation”: (Rahel & McLaughlin, 2018)). This type of strategy may provide short-term benefits by diminishing the risks of hybridization between divergent gene pools or *taxa* (Novinger & Rahel, 2003).

However, there might be some long-term consequences to such isolation, including vulnerability to stochastic processes, diseases, angling pressure, etc., as well as the loss of genetic diversity (Garcia de Leaniz, 2008; Novinger & Rahel, 2003). Indeed, barriers, such as dams, affect river fragmentation and connectivity (Nilsson et al., 2005) and can restrict the distribution and abundance of salmonids populations (Garcia de Leaniz, 2008). In addition to their impact on animal movements and habitat availability, barriers can also have significant impacts on temperature and hydrological conditions (Hart et al., 2002). Dam removal represents an important management tool for the restoration of rivers (Hart & Poff, 2002) and the restitution of connectivity (Roni et al., 2002).

Therefore, managers often wonder whether barrier removal would be a beneficial strategy allowing for the recolonisation of upstream parts of the river by native individuals. Indeed, increasing the available surface for growth and reproduction could be one of the best ways to restore a self-sufficient population

all along the river and increase population size. However, they also fear that this strategy would lead to deleterious impacts on native populations when a non-native population is present upstream.

Our results give some insight into the impact of this management strategy in such contexts. On the one hand, it suggests that it will likely lead to extensive hybridization upstream when a self-sufficient ATL population is present. Managers who do not wish to be faced with this outcome should therefore avoid this management strategy. On the other hand, barrier removal barely had any impact on diversity dynamics and demography of the downstream population (results not shown). When temperatures were favourable, selection against ATL alleles appeared to be strong enough to counter the homogenising effects of gene flow (Garant et al., 2007). Therefore, such management practices could be used by managers interested in the general resilience of the population, as it will increase stream connectivity and accessibility (Garcia de Leaniz, 2008), thereby favouring the growth of the population. Nevertheless, for long hydrographic networks, recolonisation might take a long time. Additional management strategies could be used to accelerate the settlement of a population.

5.4.2.2 *Stocking with native fry*

The SNF strategy has already been used multiple times in Haute-Savoie (Caudron et al., 2006) and elsewhere (Fernández-Cebrián et al., 2014; Leitwein et al., 2016) to restore native MED populations in the Mediterranean area. While simulations show very promising results, the reality of this management strategy is more nuanced. In reality, while the introgression rate of populations also decreased significantly following the SNF strategy (Caudron et al., 2006, 2011; Gil et al., 2016), it did not translate into a large increase in the proportion of MED genotype, unlike in the model. On the contrary, it led to the extensive creation of hybrid individuals (Caudron et al., 2006, 2011; Gil et al., 2016). In reality, this management strategy was therefore not considered as successful regarding managers' initial goal to

restore a nearly pure MED population with a majority of pure MED genotype (Gil et al., 2016). Nevertheless, from another perspective, one could consider this management strategy as efficient given that it led to the disappearance of the ATL genotype and the establishment of a new lowly introgressed admixed brown trout population. Other studies on salmonids showed the same results and suggested that the introduction of pure native fry can lead to the establishment and restoration of new admixed populations (Hansen et al., 2006; Vincenzi et al., 2008).

However, artificial reproduction in fish farming conditions might still have consequences on individuals' fitness, even if genitors have not been domesticated, and hence influence population dynamics. For instance, crosses are made by human choices and might be biased. In addition, early life stages in artificial conditions might influence development. Furthermore, genomic studies indicate that heterozygote deficiency is found in hatchery strains from both, ATL and MED strains (Leitwein et al., 2016). This study, as well as others (Fernández-Cebrián et al., 2014; Lusardi et al., 2015) suggest that stocking practices – may it be from native or non-native strains – can result in genetic homogenisation and the actual loss of native diversity, thereby affecting the genetic integrity of wild populations.

Given the long-term negative consequences associated with the SNF strategy on native diversity (Fernández-Cebrián et al., 2014; Leitwein et al., 2016; Lusardi et al., 2015), managers should avoid it when the genetic integrity of MED diversity is at risk. For instance, this could be the case when pure MED individuals are found in sympatry with ATL and/or HYB individuals, or when gene flow from an ATL population threatens a MED population. Similarly, if the management goal is to restore nearly pure MED genotypes this strategy should also be avoided, as the likely outcome will be full hybridization. However, for managers only aiming at removing and replacing ATL genotypes, this strategy could still be used, but only if the ATL population is completely isolated.

5.4.2.3 Direct translocation

Direct translocation of MED individuals (Caudron, Champigneulle, et al., 2012; Caudron & Champigneulle, 2011) and MED genitors (Caudron et al., 2011) have been implemented multiple times to manage brown trout intraspecific diversity. Patterns observed in reality following the implementation of DT strategies are very similar to those predicted by the model. Indeed, this strategy always leads to a decrease in introgression; but the genotypic composition of the population varies based on the initial density of ATL individuals. For instance, this strategy has proved very efficient at restoring nearly pure MED populations in sectors where ATL density was low (naturally: Caudron, Champigneulle, et al., 2012; Caudron et al., 2011 or following removal: Caudron & Champigneulle, 2011). On the contrary, when ATL density was higher, it led to admixture between both lineages (Caudron et al., 2011). Comparing the effect of multiple strategies, Gil et al. (2016) identified this strategy as the most efficient one. This could result from the fact that this strategy keeps a large part of the natural processes *in natura*, as translocated individuals have been subject to natural selection, and will be subject to sexual selection. Managers aiming at restoring MED populations should therefore favour this strategy when feasible.

Some conditions were proposed to evaluate the feasibility of translocation. First, the receiving environment should be able to support the introduction of additional individuals in terms of resources and habitats for reproduction (Dunham et al., 2011). Second, the removal of individuals should not endanger the donor population (Dunham et al., 2011). Finally, the density of non-native individuals and their ability to reproduce is crucial to consider, if hybridization is an issue (Gil et al., 2016). When the first two conditions are validated, managers interested in restoring MED genotypes should apply this strategy only when initial ATL densities are low. However, managers interested in the resilience of the species can use this strategy, even when a well-established ATL population is found, as it will lead to large hybridization, thereby increasing the standing genetic variation of the population.

5.4.2.4 *ATL removal*

The removal of non-native individuals through electrofishing has already been used as a management strategy to reduce the density of non-native populations (Caudron & Champigneulle, 2011; Thompson & Rahel, 1996). While it does lead to a significant decrease in population size, removing the entire non-native population remains impossible despite years and years of removal (Caudron et al., 2011; S. E. Moore et al., 1986; Thompson & Rahel, 1996). In the model, even though many ATL individuals remained in the population, ATL removal was an efficient *prior* management strategy, as it allowed increasing the efficiency of other management strategies. It could therefore remain a good strategy *prior* to the implementation of restoration strategies such as translocation (Caudron & Champigneulle, 2011).

However, this strategy can be very costly and laborious (Caudron & Champigneulle, 2011; Meyer et al., 2006; S. E. Moore et al., 1986; Peterson et al., 2004; Shepard et al., 2002; Thompson & Rahel, 1996), as multiple consecutive years of fishing are required. For instance, Caudron & Champigneulle (2011), estimated a cost of 1 500 € per 100 metres of streams. Considering this aspect, ATL removal might only be cost-effective in a small hydrographic network, like in the Chevenne Creek (Caudron & Champigneulle, 2011). In a bigger network, it is likely to be impossible to implement.

In addition, the distribution of genotypes might also be important to consider. This strategy might be easy to implement when native and non-native individuals are in allopatry, as all individuals may just be fished out. However, when they are distributed in sympatry, distinguishing between fish of different origins might be complex.

5.4.3 Network shapes and landscape features

Our results indicated that the shape of dendritic networks influences diversity dynamics and demography. For instance, in the leaf-shaped hydrographic network, introgression rates observed following each management strategy were slightly lower compared to the rectilinear network. This could be explained by two main reasons related to differences in landscape features.

- ☞ On the one hand, connectivity may vary between both hydrographic networks, as the leaf-shaped one has more ramifications compared to the rectilinear one. Such variations in the dendritic aspect of networks might shape animal movement and thereby drive social and sexual interactions among individuals (He et al., 2019). Focusing on dendritic network shapes, such as riverine, Labonne et al. (2008) had already shown a strong correlation between population demogenetics and connectivity. In our case, stronger connectivity, resulting from higher ramifications, might favour movement between reaches, and hence gene flow and genetic rescue following the implementation of management strategies. In fact, using simple simulations, I could observe that the hybridization dynamics varied based on movement probability. Higher movement threshold probability led to faster gene flow. The same should be true if the network structure favours movements through connectivity, and *vice-versa*. In addition, the potential increase in connectivity could also explain the slight decrease observed in population size, as also observed by Labonne et al. (2008).
- ☞ On the other hand, as mentioned in *section 5.2.1*, variations in temperatures among hydrographic networks are to be expected. Indeed, while both networks have the same temperature model and the same range of altitude [400 – 1400 metres], differences will be generated due to their contrasting topology. The leaf-shaped network produces more reaches at higher altitudes. As

higher altitude is associated with lower temperature, this could be a sound explanation for the differences observed.

In our simulations, the number of landscape feature parameters allowed to vary was highly reduced. However, in reality, many landscape features of rivers can influence hybridization dynamics (Nathan et al., 2019) and shapes spatial patterns of diversity (Altermatt, 2013). Consequently, the accumulation of many differences, including shape, dendritic connectivity, size, habitat quality, etc., is likely to generate ample differences in hybridization dynamics among rivers. Managers should consider this when planning their conservation measures, as it can influence the efficiency of management strategies.

5.4.4 The importance of small-scale variations in temperatures

Our results indicated that winter temperatures strongly influence diversity dynamics and demography. Considering warmer temperatures, most management strategies turned out unsuccessful, as the general outcome was full hybridization, with medium to high introgression rates (except for SNF). Therefore, knowledge of temperatures could represent good leverage for managers to guide their decision-making. For instance, a threshold of mean winter temperature could be defined to decide when to consider undertaking any measures at all. Indeed, based on the results from Folio et al. (2021), when the water temperature is above 7.5°C, the maternal MED lineage loses its survival advantage. In such cases, it might be better to do nothing in order to avoid a waste of time and energy, as management goals might be impossible to reach.

In mountain hydrosystems, temperature variation is very heterogeneous at different spatial and temporal scales (Brown & Hannah, 2008; Daigle et al., 2016). For instance, large temperature variations were

observed on the study sites where the empirical study on survival was conducted (Folio et al., 2021). Indeed, the three rivers used were connected but presented contrasted thermal regimes within a few kilometres only. This, in conjunction with temperature-based GxE interactions (Folio et al., 2021), could explain some of the hybridization patterns that are observed in the Haute-Savoie region, and elsewhere. For instance, some pure MED populations appear to have much greater fitness than some pure ATL populations in some river stretches. In contrast, in other stretches, they are extremely vulnerable to introgression and have been extirpated (Gil et al., 2016). Likewise, (Largiadèr & Scholl, 1996) failed to find frequent hybrids in the Doubs population, and concluded to potent reproductive barriers at work there: this could be related to cold temperature.

Therefore, management strategies should be implemented at small spatial scales in order to be adapted the most to local conditions. For this to be possible, managers should consider long-term monitoring of water temperature in some rivers of interest, in order to have adequate information to inform the model and their decision-making. Alternatively, when temperature data are unavailable, a better temperature model could benefit MEDITERRANEA. Indeed, the temperature contrasts observed cannot be summarized by the altitude gradient only: geothermal influence, land cover as well as the distance to source or exposure to wind and light, can also strongly condition water temperature dynamics.

Altogether, the combined effect of dendritic network shapes and climatic variations could interplay to affect the patterns of intraspecific diversity observed in the Mediterranean area, as shown in other species (e.g. Brauer et al., 2018). Hence, managers should always expect differences in management efficiency based on local conditions, especially if they are involved in selection. Considering all these potential factors influencing hybridization dynamics, and consequently management practices, I join others (Allendorf et al., 2001; Bohling, 2016; Genovart, 2009) in the idea that management strategies should always be context-specific.

CHAPTER 6

« L'important n'est pas de convaincre, mais de donner à réfléchir. »

Bernard Werber

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6 GENERAL DISCUSSION

6.1 DO ECO-EVOLUTIONARY MECHANISMS REALLY MATTER FOR MANAGEMENT?

6.1.1 *Thesis objectives*

Empirical studies realised during Jordi Gil's PhD (Gil, 2015), uncovered some eco-evolutionary mechanisms (EEMs) – female heterogamous preference (Gil et al., 2015) and GxE interactions on embryonic survival (Folio et al., 2021) – that could have influenced hybridization dynamics in the Mediterranean area. On the one hand, female heterogamous preference was hypothesised to have catalysed hybridization between both lineages following secondary contact (Gil et al., 2015). This could explain why so many stable hybrid zones are found in this area nowadays (*Section 2.2.3, Figure 2 – 6*). On the other hand, survival differences at the embryonic stage resulting from the maternal genotype-by-temperature interaction could have resulted in post-zygotic reproductive isolation in some environments (Folio et al., 2021). Associated with small-scale spatial variations in temperature, this could explain the spatial heterogeneity observed in introgression (*Section 2.2.3*).

However, there was no actual evidence that these mechanisms were actually influencing the evolution of diversity in that context. Indeed, knowledge about the existence of non-random preference and GxE interactions influencing survival of one life stage is insufficient to actually measure the impact of these EEMs on hybridization and diversity dynamics, over both, short and long time scales. Therefore, the aim of my PhD was to explore the actual impact and consequences of such EEMs in a realistic spatiotemporal framework, in order to assess whether EEMs matter for management or not. To do so, I collected and assembled (i) general knowledge on the brown trout life cycle as well as (ii) the specific knowledge available on the MED/ATL hybridization complex, both ecological and evolutionary, to contribute to the

6.1 Do eco-evolutionary mechanisms really matter for management?

creation of an agent-based demo-genetic modelling framework. This framework – MEDITERRANEA – allowed me to consider: (i) the EEMs potentially influencing the evolution of intraspecific diversity, (ii) their genetic bases, as well as (iii) variations in important environmental parameters. In addition, it allowed simulating (iv) the effects of various management practices. Using MEDITERRANEA, I investigated whether each of these mechanisms acted as we expected them to, based on the empirical findings. More precisely, I aimed at measuring their impact, over short and long time scales, on various case studies to consider how these mechanisms may interact with other ecological, genetic and demographic drivers, including management practices.

6.1.2 EEMs do matter for the management of brown trout intraspecific diversity

In the present thesis, I demonstrated that some EEMs do really matter for the management of intraspecific diversity in the MED/ATL hybridization complex. Indeed, the consideration, or not, of these EEMs in MEDITERRANEA led to interesting and contrasted results regarding diversity dynamics and demography, and even more so when considering management practices.

First, the results of Chapter 4 indicated that the consideration of some, but not all EEMs (documented in the present case) changed the outcomes of diversity dynamics and demography.

☞ On one side, **heterogamous mating preference** barely influenced the evolution of diversity dynamics, no matter the genetic contribution to preference that was implemented, nor the initial structure of the population or any other variations. These results went against our initial prediction that heterogamous preference might catalyse hybridization. While the lack of effect could be explained by the way female preference is implemented in the model (*Section 3.3.6*),

other studies on hybridization in salmonids have also pointed toward little effects of mating preference (Nathan et al., 2019).

☞ On the contrary, **GxE interactions on embryonic survival** highly influenced diversity dynamics and demography. The implementation of this EEM led to selection against ATL alleles inherited maternally. In other words, carriers of MED maternal genes do have a major selective advantage in cold environments, as suggested by Folio et al. (2021). The strength of the selection mainly varied based on plausible variations in temperatures. In addition, in ATL populations, it led to a decrease in population size due to the lack of recruitment resulting from low early life fitness. As already discussed, similar studies on salmonids highlighted the importance of temperature-based selection and fitness in driving hybridization dynamics (Nathan et al., 2019).

Second, the comparison of simulated eco-evolutionary scenarios to empirical data (for real case studies, *Section 4.4.7*) gave some insight into the mechanisms that may have shaped patterns of diversity in the Mediterranean area. Overall, results were closer to reality when the effect of GxE interactions over embryonic survival was implemented. However, more validation – combining simulation and empirical data – is still required to actually confirm that it has been this uncovered mechanism that actually shaped these past patterns of diversity. In addition, while this mechanism could explain qualitatively some of the variations observed; it is not sufficient to predict quantitatively the actual temporal changes in diversity. Many additional EEMs may come into play and more knowledge will be required to improve our understanding of hybridization. Nevertheless, one thing is certain, some EEMs must have played a structuring role in the evolution of diversity in our various case studies, considering that the neutral scenario is not sufficient to predict the patterns observed in reality.

6.1 Do eco-evolutionary mechanisms really matter for management?

Finally, the outcome of management practices varied based on the eco-evolutionary scenario implemented, suggesting that both interplay to influence the evolution of diversity. More precisely, it is the consideration, or not, of GxE interactions that lead to these differences. For instance, patterns of evolutionary rescue follow the implementation of management practices such as translocation of native individuals. Furthermore, in Chapter 5, I demonstrated that the efficiency of management practices could highly vary based on variations in important ecological factors – in our case temperature – when such GxE interactions are implemented.

Altogether, the results of the present thesis point to the importance of EEMs involved in natural selection, and the underlying selective pressure, for the management of intraspecific diversity. Indeed, genotype-by-environment interactions, which lead to various fitness differences in different environments, appear to be structuring diversity dynamics. It is a good avenue to explain the spatial variation observed in introgression dynamics in various case studies. It also interacts with management practices to influence their outcome and efficiency. Therefore, such mechanisms can no longer be discarded in the fields of wildlife management and conservation science.

6.1.3 General importance of such EEMs for management

Since reproduction and survival of genotypes – parental gene pool or hybrids – drive hybridization dynamics, the consideration of any EEMs potentially influencing these two aspects of fitness should be compulsory to the management of intraspecific diversity. On the one hand, reproduction will create the diversity available for selection to act on. While Nathan et al. (2019), and the present study have evidenced that mating preference in Salmonids appears to barely influence hybridization dynamics, other studies in mammals and plants indicate that mating system plays a structuring role in the evolution of

diversity (Fredrickson & Hedrick, 2006; Godineau et al., 2021; Santostasi, Bauduin, et al., 2020; Santostasi, Ciucci, et al., 2020; Soularue & Kremer, 2014). Therefore, exploring the evolution of traits considering the dynamic aspects of mating systems, especially when sexual preference and competition over mating partners occur remains essential in any case. For instance, sexual selection can determine the reproductive success of immigrants in a population (Labonne & Hendry, 2010). This can influence the strength and direction of demo-genetic consequences of dispersal, potentially resulting in various outcomes, from demographic and evolutionary rescue (Carlson et al., 2014; Fitzpatrick et al., 2020) to gene swamping (Allendorf et al., 2001; Haldane & Ford, 1956; Rutherford et al., 2019); and therefore have large consequences for management practices.

On the other hand, many studies corroborate our findings and demonstrate the importance of survival differences in driving hybridization dynamics (Castellani et al., 2015; Nathan et al., 2019; Santostasi, Bauduin, et al., 2020). Indeed, the survival of each genotype will condition the genotypic and phenotypic composition of the population, thereby influencing the evolution of diversity. Knowledge of the ecological factors that may cause such survival differences – or more generally fitness differences – through GxE interactions, could represent a leverage for managers. Given the importance of such mechanisms, more research should focus on survival differences between parental and hybrid individuals in various environments to understand to what extent and in which environmental conditions these mechanisms are influencing hybridization dynamics.

Indeed, in other *taxa*, genotype-by-environment interactions may also lead to fitness variations among individuals and dictate the evolutionary outcome of hybridization. This has been observed at intra and interspecific levels (Campbell & Waser, 2001; Fraser et al., 2008; Genovart, 2009; Janes & Hamilton, 2017) with studies pointing toward the effects of environmental factors, such as temperature (Drury & Lirman,

2021; Krehenwinkel & Tautz, 2013; Nathan et al., 2019), pH (Fraser et al., 2008), or eutrophication (Vonlanthen et al., 2012) on the fitness of hybrid complexes. A growing number of studies are highlighting the need to identify environmental and ecological factors involved in hybridization dynamics (Genovart, 2009; Lindtke et al., 2014; M. K. Schwartz et al., 2004), specifically when a combination of environmental factors will influence the maintenance of reproductive barriers between and within species (Janes & Hamilton, 2017). As in our case study, spatial—or even temporal—variations of such factors could be the key to building future management strategies of intraspecific diversity for admixed gene pools. Indeed, they will be able to address simultaneously several objectives, such as conserving native diversity in some areas (Bohling, 2016; Janes & Hamilton, 2017) and maximizing evolutionary potential as a whole in others, in order to cope with future environmental variation (Nuismer & Gandon, 2008).

Overall, knowledge about the ecological and demographic factors influencing the outcome of hybridization is essential to develop meaningful management and conservation measures, especially when hybridization poses a threat to diversity (Bohling, 2016).

6.2 DG-ABM: A VALUABLE TOOL IN THE CONTEXT OF HYBRIDIZATION

6.2.1 A framework to understand hybridization dynamics

Our modelling framework, MEDITERRANEA, was a valuable tool to investigate and understand the evolution of diversity and demography under various eco-evolutionary and management scenarios. Such DG-ABMs have already been used in similar ways in other studies of hybridization (Castellani et al., 2015; Nathan et al., 2019; Santostasi, Bauduin, et al., 2020) and have proved to be useful for both scientists and managers. While the interest of such models is not to give quantitative predictions, their main purpose is to provide some qualitative insight into the expected outcomes of alternative eco-evolutionary and

management scenarios. Such models can integrate various sources of knowledge, either at the mechanism level or by using pattern-oriented modelling. Both of these can be provided by various parties (scientists, managers or users...).

DG-ABMs provide a complete modelling framework to study hybridization dynamics, as they combine properties of ecological and genetic models. By realistically simulating interactions between individuals, such models give rise to unique demographic and genetic processes. It allows the implementation of different sub-models based on the genetic or phenotypic characteristics of individuals. Therefore, many fitness and behavioural differences between parental gene pools, but also hybrid individuals can be implemented. Demographic parameters can also be linked to environmental variables, allowing one to predict hybridization dynamics under fluctuating environmental conditions. Overall, DG-ABM allowed us to simulate complex ecological and evolutionary processes, which are not easily empirically measured (Nathan et al., 2019).

6.2.2 A tool to assess management strategies in an adaptive management loop

A key feature of DG-ABMs, described in *section 1.6.3*, is their capacity to model the impacts of management practices, or more generally human-induced changes on ecological dynamics – *i.e.* individuals, the environment and their interactions. In a growing context of uncertainties, DG-ABMs could be used to inform decision-making and contribute to management and conservation policies. Indeed, our results and others (Ayllón, Nicola, et al., 2019; Ayllón, Railsback, et al., 2018; Piou et al., 2015; Santostasi, Bauduin, et al., 2020; H.-Y. Wang et al., 2017; H.-Y. Wang & Höök, 2009) demonstrate that they are efficient prospective tools to assess the impact of human induced-changes on ecological and evolutionary dynamics.

However, these types of models rely on a large number of assumptions and parameters, which can be difficult to estimate and provide. For instance, in our MED/ATL case study, only a few short-term monitoring, like in the Borne River and the Chevenne Creek are available. Therefore, I suggest that scientists and managers work together, in an adaptive management loop in order to (i) gather adequate data to inform the model; (ii) use the model to guide managers' decisions on the “best” management strategy to implement; (iii) implement that strategy and continue the monitoring; (iv) use these data to validate (or not) the model (*Figure 6 – 1*). Going through this adaptive management loop in detail:

- ☞ First, scientists and managers should decide on the hydrographic network to implement in MEDITERRANEA based on the data available – demographic and genetic parameters but also water temperature. Indeed, the more the model will be calibrated with parameters specific to the population, the more reliable the management recommendation will be. Regular monitoring should then be implemented to gather additional data and draw a proper timeline. The same type of data should always be collected to ease their implementation in the model.
- ☞ The second step is to use the model to inform and guide managers' decisions. To do so the available data has to be integrated into the model, *via* the initial data file and the initial parameters settings (*Section 3.5.1 & 3.5.2*). Then after defining the management goal and the various strategies to evaluate using the model, the simulations can be run. The predictions obtained will then help managers to decide which management strategy is the best one regarding the predefined management goal.
- ☞ The third step is to implement the chosen management strategy and keep on monitoring the population during and after, in order to gather data that can be used to verify the model predictions.

∞ Finally, these data can be used to (i) validate (or not) the model and/or (ii) calibrate some processes in order to further improve the model.

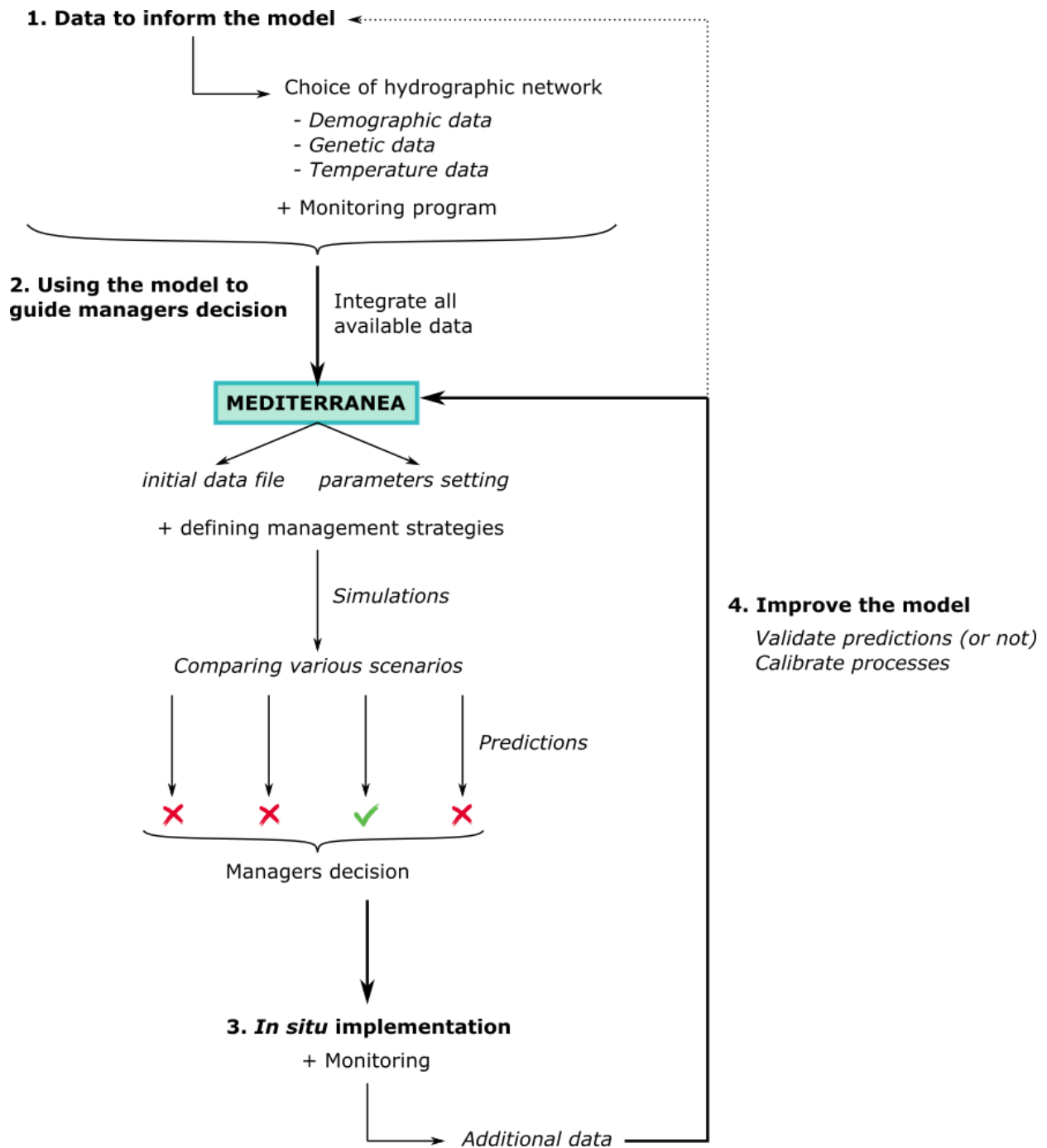


Figure 6—1: MEDERRANEA as a decision-making tool for managers: representation of the adaptive management loop to inform management strategies.

Since scientific studies are not often considered by resource managers (Hart & Calhoun, 2010; Sutherland et al., 2004); the development of such collaborative research is important to bring together management and scientific methods (Caudron, Vigier, et al., 2012).

6.2.3 A tool to guide future empirical studies

DG-ABMs can also be used to identify the EEMs that need to be empirically investigated further to more accurately predict hybridization dynamics (Nathan et al., 2019), and consequently the outcomes of management strategies (Santostasi, Bauduin, et al., 2020). Defining and assessing these EEM will further help to improve the model, as the empirical data may be used to validate and calibrate the model (*Figure 6 – 1, step 1*), exactly as suggested in the adaptive management loop.

As mentioned in Chapter 1 (*Section 2.4.3*), other factors have been hypothesised to contribute to the evolution of diversity in the MED/ATL hybridization complex. MEDITERRANEA could be used to explore whether these factors actually play a role in diversity dynamics and to what extent. Indeed, as done here for the two demonstrated mechanisms, we could project how each mechanism will interact with all the other ecological, genetic, and demographic drivers to influence the evolution of diversity and demography.

☞ For instance, the model could be easily improved to test more **differences in survival** implemented at various life stages up to adulthood (as indicated in Gil, 2015). Indeed, as done for embryonic survival, an additional mortality process could be implemented at a given age – for example, 2 years old when individuals become mature. The user will then be able to test out different curves of survival based on individual introgression and evaluate whether such differences in fitness on a given life stage play a role in structuring diversity dynamics. Considering

that survival differences applied at the embryonic stage only had a large impact on diversity dynamics and demography, we can imagine that such differences throughout life could massively matter to evolution.

- ☞ Regarding the differences in sensitivity to fishing hypothesised, the model allows for the implementation of selective fishing based on individual introgression (*Section 3.4.2*). This intervention could be used to test whether different sensitivity to fishing could affect diversity dynamics significantly. The user could consider different catchability of individuals based on their origin - ATL, HYB or MED to evaluate how this may affect diversity dynamics.
- ☞ Finally, the model could also be used to evaluate whether differential female choices for spawning habitat do have an impact on diversity dynamics in case of a flood event. With some modifications, we could use the viability analyses intervention – which simulates extreme mortality events (*Section 3.4.3*) – to simulate the impact of a flood on female nests, considering that those of MED females might be less impacted due to habitat choice diversification compared to those of ATL females (Champigneulle et al., 2003). The user could here simply implement different mortality rates for offspring based on maternal introgression. Trying to test this, *in natura*, would be time-consuming and complicated, as flood events are unpredictable. Therefore, the model could provide valuable information on whether experimental work is really needed here or not.

6.3 POINTING AT THE IMPORTANCE OF MATERNAL EFFECTS

The present results combined with empirical knowledge on the MED/ATL hybridization complex point to the importance of maternal effects on the evolution of diversity. For instance, the maternal genotype-by-

temperature interaction on survival plays a structuring role in diversity dynamics. In addition, other studies on brown trout in the Atlantic zone have also highlighted the importance of maternal effects, especially during the earlier phases of development (Gauthey et al., 2017; Lelong, 2006; Lelong et al., 2008; Régnier, Bolliet, et al., 2012; Régnier, Labonne, et al., 2012). Therefore, more research on the impact of maternal lineages should be conducted in the MED/ATL hybridization complex, as it may have the potential to explain many of the variations in diversity observed in the Mediterranean area.

6.3.1 Maternal ascendance in hybrid zone

The present results combined with empirical findings (*Appendix F*; Folio et al., 2021) may explain the predominance of the native MED maternal ascendance in hybrid zones. In the Chevenne creek for instance – one of the rivers studied here – mitochondrial lineage exclusively points to the MED lineage (Gil et al., 2016). Such a predominance of the native maternal ascendance is also found in other areas (Poteaux, Bonhomme, et al., 1998) and in other hybrid zones in *Salmo trutta* for a different lineage (Pujolar, Lucarda, et al., 2011; Pujolar, Vincenzi, et al., 2011) or in other species (Bonnet et al., 2017; M. K. Schwartz et al., 2004; Taillebois et al., 2020). Combined with the results on GxE interactions (Folio et al., 2021), this indicates that maternal effects (genetic and non-genetic) may have a preponderant role in hybridization dynamics, notably because they are especially present during the first stages of life (R. S. Burton et al., 2006; T. Burton et al., 2020; Giesing et al., 2011; Régnier, Bolliet, et al., 2012; Régnier, Labonne, et al., 2012; Shu et al., 2016). In particular, cold adaptation – suggested by Folio et al. (2021) – is partly mediated through physiological mechanisms, which often involve mitochondrial functions that are hence linked to maternal ascendancy (White et al., 2012) and can differ between lineages (Kavanagh et al., 2010).

6.3.2 *Insight from researches on the ATL trout*

Science on ATL trout – performed in the Atlantic zone – has provided considerable knowledge on brown trout ecology and evidenced the important role of maternal effects. Among other things, it has uncovered many parts of the life cycle where ample phenotypic and genetic variation occur in relation to maternal effects. This led us to think that the same sorts of variations could be found for MED trout. In addition, there is also reason to believe that the mean and variance for each lineage might be different due to their divergent evolutionary history – allopatric evolution for 0.5 to 2 million years (Bernatchez, 2001). There are therefore a lot of opportunities to build some new research directions on MED trout to improve our understanding of hybridization dynamics and fitness differences in hybridized areas.

Emergence timing and competition. Research on ATL brown trout has evidenced a large amount of individual variability in energetic status among emerging fry (Lelong et al., 2008); which might influence emergence behaviour and timing (Lelong et al., 2008; Régnier, Labonne, et al., 2012). Indeed, a large variance in emergence dates of ATL trout fry was observed among, but also within female nests (Régnier, Labonne, et al., 2012). Furthermore, Régnier, Bolliet, et al. (2012) indicate that within clutch variance of metabolic and yolk consumption rates differ between females, which can lead to developmental variations. For instance, offspring from larger eggs have lower metabolic costs and higher yolk conversion efficiencies; and are therefore at an advantage.

It was hypothesised that emergence could result from a trade-off between energy stores and developmental stage (Lelong et al., 2008) and that within nest variation was related to increased within clutch variability in metabolic rate (Régnier, Labonne, et al., 2012). In addition, variable investment in egg size can influence the emergence duration of female nests (Régnier, Labonne, et al., 2012), and therefore modulate the level of sibling competition. Indeed, in salmonids, the synchronization of emergence timing can result in intense competition for resources among emerging fry (Ojanguren et al., 1996).

In the MED/ATL hybridization complex, lineage-related differences in such maternal effects could have large consequences on diversity dynamics, through offspring competition for territories and resources during the critical post-emergence period. For instance, if the mean and variance of emergence timing among but also within clutches vary between lineages – for any of the reasons mentioned above – then offspring from the lineage that can adjust emergence timing might be at an advantage. Indeed, such competition will result in soft selection (*sensu* Wallace, 1975 in Bell et al., 2021) when territories are limited. Therefore, reduced competition at emergence within one lineage should favour the recruitment of that genotype to the next generation.

Morphology and dispersal. Dispersal and larvae morphology can also be influenced by maternal life history traits (Lelong, 2006). During her PhD, Amandine Lelong showed that populations living in different environments developed different strategies of emergence, but also differed with regard to post-emergence dispersal. Some individuals were more likely to perform downstream migration compared to others, and this strategy was often related to the emergence strategy, in order to reduce competition and increase survival. In our case study, lineage-related differences in post-emergence dispersal could play an important role in hybridization given that movement appears to highly influence diversity dynamics in the model.

Reproductive investment. In different ATL populations, differences in reproductive investment conditional on environmental stochasticity have been observed (Gauthey et al., 2015). For instance, only individuals from one population – usually experiencing a more stochastic environment – adapted their reproductive investment based on water flow variations. This study highlighted that mechanisms to cope with environmental stochasticity might differ between populations of the same species. In our context, this suggests that such differences might exist between the MED and the ATL

lineages. Indeed, while the MED lineage evolved in highly stochastic environmental conditions, the ATL lineage came from domesticated strains experiencing buffered conditions.

Egg size differences. Data from Folio et al. (2021) show different mean egg sizes based on maternal genotype. In their sample, a majority of MED females produced bigger eggs - but not the biggest, while ATL females produced either the biggest or the smallest eggs (*Appendix G*). Such a difference could modulate lineage contribution to population growth. Indeed, since egg size is positively correlated to female body size in salmonids, as is fecundity (Lobon-Cervia et al., 1997): Large females lay large and numerous eggs. However, for the ATL lineage, studies have indicated that “bigger is not always better” (Régnier et al., 2013) since larger eggs show lower survival (Folio et al., 2021; Régnier et al., 2013). In addition, given the survival difference between the MED and the ATL lineages at cold temperatures (Folio et al., 2021), MED females may massively contribute to population growth in some environments compared to ATL females.

Habitat spawning choice. Various individual strategies have been evidenced for habitat spawning choice and nest building in the ATL trout based on female body size (Gauthey et al., 2017). This study also indicated that these different strategies could have large consequences on scouring risks, which was the main driver of egg mortality (75%). Nest burial depth and shear stress force above the nest were the main drivers of scouring. Deeper nests and higher shear force stress reduced scouring risks. Considering the extremely high mortality rate related to scouring, strategies to reduce scouring risk could be highly beneficial for females to increase their reproductive success (Gauthey et al., 2017; Montgomery et al., 1996). Indeed, spawning habitats are known to further improve offspring fitness (Armstrong et al., 2003; DeVries, 1997; Gauthey et al., 2017; Riedl & Peter, 2013). Therefore, Gauthey et al. (2017) suggested that traits and tactics that reduce nest scouring should be under strong selection. If that is also the case in the

Mediterranean area, such differences, in addition to the potential impact of spawning habitat diversification (*Section 2.4.3*), could result in strong selection in favour of the MED maternal lineage.

If such differences exist between lineages in the MED/ATL hybridization complex, one may expect the MED maternal lineage to be at a reproductive advantage given that mitochondrial DNA mainly points to the MED lineage in hybrid zones (Expertise Scimabio Interface). Such an advantage for the MED lineage may alter the genetic structure of the population by strongly favouring MED maternal ascendancy, as more offspring from MED females might be recruited; and even more so, in cold environments considering the GxE interactions uncovered in Folio et al. (2021).

6.4 NATIVE CONSERVATION VS HYBRIDS

6.4.1 Native conservation

In the recent past, the terms “hybrid”, “invasive” and “non-native” have mainly been used negatively and regarded with suspicion by wildlife conservationists and managers. For instance, the process of species interbreeding with each other, although not new, is often regarded as a problem rather than a normal evolutionary process. In Europe, hybridization between native and domesticated individuals (often from different lineages) is considered one of the most serious threats to native diversity conservation in brown trout (Ferguson, 2007; Laikre et al., 1999). Therefore, in the MED/ATL hybridization complex, managers have expressed the will to conserve the native MED lineage. Management practices implemented so far are aimed at the conservation, restoration and introduction of MED populations in areas where an ATL population threatened a nearby MED population and/or where some hybridization has occurred. There are multiple reasons to explain this choice:

- ☞ First, the native diversity of this species has a considerable socio-economic value (Laikre et al., 1999). For instance, the native MED lineage has a patrimonial value to anglers and fisheries managers, since MED trout are phenotypically different from ATL and HYB trout. Experienced anglers can often differentiate between the two lineages and their hybrids.

- ☞ Second, the MED lineage appears to show more diversity compared to the ATL lineage, specifically considering that domesticated individuals were introduced. Indeed, some microsatellites markers – used on the Borne River for instance – indicate that allelic diversity is higher for the MED lineage (in total on two markers: 11 alleles for the MED lineage *versus* 5 alleles for the ATL lineage, Caudron et al., 2009). Also, more generally, the MED lineage appears to show a higher genetic diversity compared to the other lineages (Suárez et al., 2001).

- ☞ Finally, it has been hypothesised that MED diversity might be associated with local adaptation since the MED lineage has evolved in the Mediterranean area. In other contexts, there has been evidence that local adaptation is associated with brown trout intraspecific diversity (Pakkasmaa & Piironen, 2001; Ryman, 1991). In addition, in the Northern French Alps, many native MED populations are found in typical high-altitude rivers and streams characterised by harsh environments for the brown trout species. In brown trout, populations from different environments – more or less stochastic – show different abilities to adapt to an increase in stochastic conditions (Gauthey et al., 2015). Therefore, these native populations may have a good ability to adapt to various conditions and are therefore important to conserve, especially in the context of climate change. Indeed, these harsh conditions (high stochasticity, frequent floods, high human disturbances: fragmentation, pollution, exploitation...) might become more and more frequent with climate change, and not just in high-altitude rivers.

It seems therefore important to maintain the genetic integrity of MED populations and more generally that of the various lineages of brown trout (Laikre et al., 1999; Ryman et al., 1995; Taylor et al., 2015; Utter, 2004) to ensure the long term-evolutionary potential of the species. Indeed, high gene flow may reduce the genetic diversity between populations and consequently hinder potential adaptive differentiation, which can result in extinction by hybridization (Rhymer & Simberloff, 1996). However, in the MED/ATL hybridization complex, there is no evidence of adaptive divergence between the lineages.

6.4.2 Hybrids in the Mediterranean area

While it is certain that the ATL lineage has been (domestication, Caudron & Champigneulle, 2002) and still is (in cold environments at least, Folio et al., 2021) at a disadvantage compared to the MED lineage. There is little evidence to assert that HYB individuals found in wild populations fare less well compared to native MED individuals. On the contrary, data suggest that HYB individuals might have equal or even better fitness compared to MED individuals.

- ☞ First, many populations are fully hybridized in the Mediterranean area (*Section 2.2.3, Figure 2 – 6*) and no negative impact on population dynamics has been reported. In such contexts, adaptive introgression may have occurred (De La Torre et al., 2014; Fitzpatrick et al., 2019; Whitney et al., 2015) and adaptive variation may be more resistant to introgression (Fitzpatrick et al., 2020), leading to highly fit hybrids. Indeed, introgression along the genome has been shown to be variable but non-random, suggesting that some *loci* might be more or less sensitive to gene flow (Ozerov et al., 2016).
- ☞ Second, considering the importance of maternal effects discussed above (*Section 6.3.1*), and the maternal genotype-by-temperature interaction uncovered (Folio et al., 2021); HYB individuals

from the MED maternal ascendance might be equally fit compared to pure MED individuals. Indeed, data points toward the MED mitochondrial lineage in hybridized populations (Scimabio Interface Expertise).

☞ Furthermore, one has to keep in mind that most knowledge and lineage-based relationship were measured on wild populations present in this environment for possibly multiple generations. Therefore, HYB individuals – but also MED and ATL – do not represent what could have been observed following the first secondary contact, which happened in some cases more than a century ago. These individuals have actually undergone decades of selection and are hence the result of post-invasion evolution (The “after” hypothesis, (Reznick, Losos, et al., 2019)). In invasion research, the after hypothesis was introduced to oppose the precedent idea that invasion success was determined by the initial characteristics of organisms (invaders and natives) and/or environments (the “before” hypothesis, (Reznick, Losos, et al., 2019)).

In the Mediterranean area, hybrid individuals might actually be associated with ample genetic variation and potentially be adapted to various environmental conditions. Therefore, in addition to the conservation of the MED lineage in certain environments, managers should also account for this variation as it could represent a resilience mechanism against environmental change (C. N. Cook & Sgrò, 2018; Jump et al., 2009; López-Pujol et al., 2012; Violle et al., 2012). Indeed, reliance on the idea that native or local individuals are more adapted to local environments can be detrimental to management practices, especially when it reduces genetic diversity (Broadhurst et al., 2008; Kronenberg et al., 2018). This has already been the case in the Mediterranean area where local genetic diversity was reduced following stocking with the local strain (Leitwein et al., 2016).

6.5 WHAT IS A HYBRID?

The definition associated with the term “hybrid” remains obscure in our context. For instance, multiple metrics have been used to differentiate between individuals and categorise them. On the one hand, hybrids can be defined based on their degree of admixture using some genetic markers. However, genetic monitoring remains expensive and the number of genetic markers used usually varies from one study to another. On the other hand, as pigmentation can reflect admixture in salmonids (Aparicio et al., 2005; Kocabaş et al., 2018; Mezzera et al., 1997), robe *criteria* can be used as a proxy for admixture. It has been the case in our context for many management purposes, as anglers often use body patterns to identify native trout.

6.5.1 *Managers’ perception of pure native and hybrid individuals*

For management purposes, managers often categorise pure *versus* hybrid individuals based on trout phenotype. By doing so, they assume that the robe *criteria* used are a relevant proxy to infer genome-wide admixture, which may not always be the case. For instance, in other Mediterranean populations, Valette et al. (2020) indicated that some pigmentation patterns used by managers were not reliable proxies of genome-wide admixture between ATL and MED individuals. Therefore, by only relying on robe *criteria*, many mistakes are likely to happen in hybridized areas where ATL, HYB and MED individuals are found in sympatry. For example, considering management practices such as MED translocation, managers might actually select admixed individuals exhibiting local robe *criteria*.

6.5.2 Genotype-phenotype relationship

The complex relationship between genotype and phenotype is still unclear in the Mediterranean area. On the one hand, the correlation between a given set of robe *criteria* and a given set of genetic markers appears to vary depending on the study and the sampling site (35%: Aparicio et al., 2005; Gil et al., 2015; 50%: data from Scimabio Interface and 70%: Folio et al., 2021), but also on the statistical analyses used (not presented in the manuscript). A recent study indicates that such an approach may still miss a large part of the recent genetic admixture (Saint-Pé et al., 2019). In addition, information is also missing regarding the links between *loci* coding for robe *criteria* and the genetic markers used, and whether these are actually relevant proxies of genome-wide admixture (Valette et al., 2020). Improving our knowledge of the links between genotype and phenotype is essential to appropriately support management decisions if they are to be based on phenotype.

6.5.3 The genetic system used

In the Mediterranean area, many diagnostic markers – including microsatellites and SNPs – can be used to differentiate between the ATL and the MED lineages. While these markers were initially established on the two separate lineages, results from Folio et al. (2021) indicate that despite several generations in sympatry, there is still a link between the markers used and genes under potential selection. These markers might therefore be good proxies of alleles enhancing local fitness, meaning that management practices using these markers might help promote locally adapted genetic variation.

In the model, the use of these markers is simplified in the sense that they are directly linked to fitness following the results found in Gil et al. (2015) and Folio et al. (2021). In reality, we do not know whether these markers are directly under selection or whether they are linked to functional loci, and especially

which ones of them are. Indeed, the use of markers that are not linked, or even mismatched with alleles enhancing fitness might put management practices at risk of failure. It will therefore be important to determine the ecological relevance of the genetic markers used for conservation purposes.

6.5.4 Defining an appropriate individual admixture threshold

As already discussed before (*Section 4.6.4*), the number of markers used will highly influence the categorisation of individuals, especially considering that they are all unlinked: an individual is more likely to be categorised as a hybrid when a higher number of markers are used. Managers should therefore pay good attention to this aspect, especially when (i) using a very low number of markers or (ii) comparing data using a different number of markers. Evaluating the relevance of our measure of introgression is important to define ecologically appropriate admixture thresholds to distinguish between parental and hybrid individuals. However, the definition of such a threshold is often challenging and context-specific (Allendorf et al., 2001). Therefore, as a first step to facilitate the comparison of data, we advise managers to define individual admixture thresholds based on the number of markers used. Indeed, when a high number of markers is used, very lowly introgressed individuals might be considered pure individuals from a management perspective – especially if their *robo criteria* match the local phenotype.

6.6 CLIMATE CHANGE

For the last decades, climate change and global warming have been negatively affecting freshwater fish, as well as many other *taxa* (Comte et al., 2013). Trout species have experienced changes in their distribution and population declines (Almodóvar et al., 2012; Ayllón et al., 2013; Eby et al., 2014). Studies investigating the impact of climate change on resident trout focused on thermal regimes (Filipe et al.,

2013; Kovach et al., 2016) and stream flow (Wade et al., 2016; Wenger et al., 2011). The rise of global temperature and the unpredictability of river flow are exceptional challenges to freshwater conservationists. For instance, more extreme events, such as floods and droughts are to be expected with strong consequences for habitat quality and availability (eventually habitat loss: Wenger et al., 2011). For salmonids populations, this will likely result in changes in carrying capacity (Ayllón et al., 2012; L. E. Sundt-Hansen et al., 2018) and hence affect demography. In addition, freshwater fish are faced with more localised anthropogenic pressures and/or modifications, including management practices (Comte & Grenouillet, 2013). In particular, the consequences of climate change on hybridization may pose a threat to native conservation (Muhlfeld et al., 2014, 2017).

6.6.1 Potential consequences of climate change on the MED/ATL hybridization complex

In our context, an increase in water temperature may lead to full hybridization in environments where cold temperatures were allowing the MED lineage to persist. This poses a problem for managers interested in the conservation of the native MED lineage. Pressing conservation actions might have to be undertaken now, while the environment still favours the MED lineage. However, there is no certainty that the positive effects of certain management strategies – reduction of ATL alleles – will last in the long term, if temperatures were to increase. Attempting any management strategy in this context might be a waste of resources.

On the other hand, under such global changes, managers might have to cycle between “managing for resilience” and “managing for change” (West et al., 2009) to ensure the long-term persistence of wild populations. In fact, evolutionary change is the norm whereas a static view of biodiversity is a biased perception of reality. In our context, managers may want to favour diversity given that adaptation to new

environments is mainly incited by standing genetic variation compared to new mutations (Barrett & Schluter, 2008). For instance, hybridization may help maintain high levels of diversity to help populations cope with ongoing changes. Managers attempting to only conserve the native lineage take the risk of decreasing genetic diversity, especially when management strategies result in negative consequences (Fernández-Cebrián et al., 2014; Leitwein et al., 2016; Lusardi et al., 2015).

6.6.2 DG-ABMs to predict the impact of climate change

MEDITERRANEA could be used to investigate the evolution of diversity considering various scenarios of climate change combined with different management strategies aiming at either native conservation or resilience. Indeed, DG-ABMs are becoming essential tools to explore alternative management scenarios and support decision-making (Ayllón, Nicola, et al., 2019; Schmolke et al., 2010; Stillman et al., 2015). Particularly, because of their dendritic shape, rivers are likely to experience heterogeneous responses to global changes. Such a framework will therefore help managers understand the potential consequences of one or the other avenue based on the local changes experienced. Nevertheless, this work remains beyond the scope of the present study because it still requires to further develop models to predict water temperature and hydrologic trends. Indeed, a good quantification of future climatic exposure is required to understand the role of climate change on demo-genetic processes. In addition, this will require the improvement of the actual framework to include a hydrological aspect to model stream flow, as is the case in (Ayllón, Railsback, et al., 2019). For instance, their simulations suggest that hydrological variation is a critical dimension for the persistence of trout populations. Finally, one will also have to consider the capacity of individuals to adapt to changing conditions (Wade et al., 2016). Many studies show that species have already started to adapt to new conditions (Muñoz & Moritz, 2016).

6.6.3 *Forecasting temperature and hydrology*

It is a challenge to forecast and predict trends for water temperature and stream flow regimes at a small spatial scale. Very complex models are required to represent realistically the ecological system (Ayllón, Grimm, et al., 2018; Evans et al., 2013). In the Mediterranean area, no model is yet available to forecast the state of ecological systems; but scientists are presently working on it. For instance, we had the opportunity to meet Guillaume Thirel who is currently working on hydrological models in french rivers to predict trends in water temperatures and stream flow regimes. However, the case of mountain rivers and streams represents an additional challenge to them. Such models, when available, could then be implemented in MEDITERRANEA. For example, Ayllón, Railsback, et al. (2019) have already implemented climatic projections in a DG-ABM to predict the thermal and hydrological effects of climate change on Mediterranean trout in Spanish rivers.

6.7 IMPLICATIONS FOR MANAGEMENT PRACTICES

6.7.1 *Advices for the management of MED/ATL hybridization*

In the present thesis, I demonstrated that genotype-by-environment interactions on embryonic survival play a structuring role in the evolution of diversity dynamics in the MED/ATL hybridization complex. The strength of the resulting selection appeared to be dependent upon various environmental factors, among which water temperature, a factor that can show contrast at small scales (Brown & Hannah, 2008; Daigle et al., 2016). In addition, the results of Chapter 5 (*Section 5.3.1 vs 5.3.3*) demonstrated that temperature variations can highly influence the efficiency of management practices. Therefore, I suggest that management practices should always be context-dependent and adapted to the local conditions

considering temperature variations at small spatial scales. I advise allocating management efforts where they can bring a higher overall benefit.

For managers interested in protecting “native” MED genetic variation, some environments should be particularly targeted for conservation actions: For instance, cold environments may naturally and very efficiently select for native MED alleles, as demonstrated in our simulations. While it may not always allow for the conservation of pure MED genotype, it will at least help to preserve the native MED female lineage and potential adaptation related to maternal effects. This opens a path for managers to target sanctuaries based on thermal monitoring. It suggests that baseline information on climatic parameters and spatial projection related to the local effects of climate change should be performed by managers. Using such spatial mapping of the factor of interest (here, water temperature) at small scales and considering the spatial distribution of available genetic variation (Razgour et al., 2019) may considerably help to forecast the evolution of intraspecific dynamics. Targeted to the right environment, management strategies aimed at conserving native diversity could become much more efficient. In short, knowledge of such GxE interactions opens a path for a cost-effective approach to native diversity conservation.

On the other hand, in environments where hybrids already occur, with intermediate-to-high temperatures, it might be counter-productive to attempt to eradicate them, since they might have there an equal or even better fitness compared to native MED individuals. Especially considering that hybridization might be very frequent – as indicated by the model but also managers' data – and does not necessarily lead to negative impacts on population dynamics. For instance, in Haute-Savoie, many naturally persistent hybrids populations are found (*Section 2.2.3, Figure 2 – 8*). In such hybrid zones, ample genetic variation might be found. Managers interested in the general resilience of the whole species (Chan et al., 2019; López-Pujol et al., 2012) should also account for such variation. In fact, with specific attention

devoted to connectivity and dispersal rate (Labonne et al., 2008; Razgour et al., 2019), it should be possible to elaborate eco-evolutionary management plans accounting for small-scale contrasts in environments. For instance, hybridization could be used as a management tool to perform assisted and controlled gene flow in order to increase the evolutionary responsiveness of endangered species facing global changes (Drury & Lirman, 2021; Stelkens et al., 2014).

6.7.2 Management as part of the eco-evolutionary feedback loop

Traditional management has focused on, and used ecological solutions to conservation issues and species endangerment (Reznick, Losos, et al., 2019). This conception was based on the idea that, as management practices are happening on short time scales, they will only affect ecological processes. Consequently, fisheries, as well as wildlife science, have been little influenced by evolutionary biology (Reznick, Losos, et al., 2019). However, the current assessment is that ecology and evolution can happen on commensurate timescales (Carroll et al., 2007; N. G. J. Hairston et al., 2005; M. T. Kinnison & Hairston Jr, 2007; Pelletier et al., 2009; Reznick, Bassar, et al., 2019; Reznick, Losos, et al., 2019).

Consequently, by interfering with population dynamics, management practices might actually have consequences for evolution. Indeed, by (1) altering the composition of the population (harvesting, introduction...), modifying the environment (habitat fragmentation, pollution, climate change...) and potentially modifying or acting as additional selective pressures, (2) they may interfere with eco-evolutionary processes – direction or intensity – and (3) eventually trigger evolutionary changes (*Figure 6 – 2*). For instance, contemporary evolution is actually often triggered by anthropogenic disturbances (Carroll et al., 2005, 2007; Hendry et al., 2006, 2008, 2017; Strauss et al., 2006) and it has been demonstrated in many contexts that management practices and more generally human interference can

have large consequences on diversity. A common example is that of selective harvesting – in the case of exploitation (Allendorf et al., 2008; Heino et al., 2015) or demographic control (Lefèvre et al., 2014) – which often causes changes in traits distribution and has been acknowledged to cause evolution (Allendorf & Hard, 2009). In the context of hybridization, the effects of human-induced environmental perturbation on eco-evolutionary processes often result in the erosion of reproductive isolation between previously separated lineages (Grabenstein & Taylor, 2018). Elucidating the evolutionary mechanisms controlling this erosion could help to formulate sound management decisions.

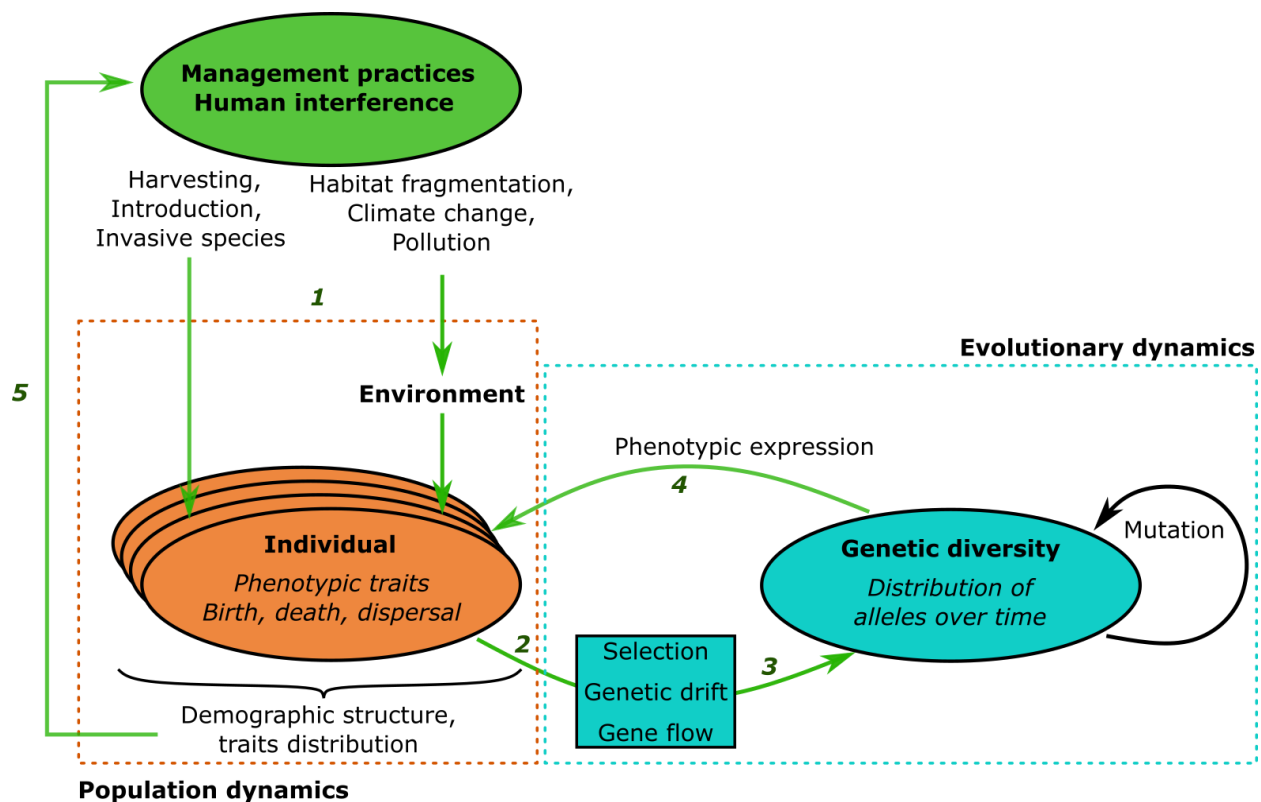


Figure 6—2: Representation of how management practices may influence the entire eco-evolutionary feedback loop through their effects on population dynamics.

Furthermore, (5) evolution might also in turn influence management practices as it can (4) feedback on population dynamics, by potentially triggering further changes in traits distribution and changing the

demographic structure (*Figure 6–2*). For example, this happened in the context of fish exploitation, where the overexploitation of large individuals caused the evolution of smaller body size, at the disadvantage of exploitation practices. In the context of the MED/ATL hybridization, it is initially management practices that led to the creation of hybrids – changes in the population composition –, which in turn resulted in changes in management practices – conservation of the MED lineage, having further and further effects on evolutionary and ecological processes. These constant changes in population dynamics make conservation more complex (Carroll et al., 2007).

6.7.3 *The rise of evolutionary management*

This shift in the perception of management and eco-evolutionary dynamics has led to the development of new ideas, such as genetic or evolutionary rescue, to help management strategies. Indeed, in many fields of conservation, there is now a growing interest in evolutionary management (Carlson et al., 2014; Chan et al., 2019; Fitzpatrick et al., 2019; Gauzere et al., 2020; Postolache et al., 2021; Walsworth et al., 2019; Whiteley et al., 2015). The idea is to use evolution to help management strategies. In the context of climate change, for instance, evolutionary management aims at preserving the evolutionary potential of populations in order to ease their adaptation to changing environments (Aitken & Whitlock, 2013; Carroll et al., 2007; Lefèvre et al., 2014; Reznick, Bassar, et al., 2019; Reznick, Losos, et al., 2019). To do so, scientists promote the conservation of high genetic diversity, as it represents a resilience mechanism (C. N. Cook & Sgrò, 2018; Jump et al., 2009; López-Pujol et al., 2012; Violle et al., 2012). In addition, they focus on the environment maximizing the chances of individuals to adapt to new conditions to provide managers with conservation guidelines (Carlson et al., 2014; Whiteley et al., 2015). Nowadays, with the increasing impact of climate change on populations, the concept of evolutionary management is growing

fast. Indeed, scientists are becoming more aware that conservation goals may only be met by “harnessing the power of evolution” (Carroll et al., 2007).

Entre Ce que je pense, Ce que je veux dire, Ce que je crois dire, Ce que je dis, Ce que vous avez envie d'entendre, Ce que vous entendez, Ce que vous comprenez... il y a dix possibilités qu'on ait des difficultés à communiquer. Mais essayons quand même...

Bernard Werber

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8 ABBREVIATIONS

ABM: Agent-Based Model

ATL: Atlantic

BR: Barrier Removal

BSR: Body-Size Ratio

DG-ABM: Demo-Genetic Agent-Based Model

DNA: Deoxyribonucleic acid

DT: Direct translocation

EEM: Eco-Evolutionary Mechanism

GCP: Genetic Contribution to Preference

GR: Genetic Refuge

GxE: Genotype-by-Environment

HYB: Hybrid

MED: Mediterranean

OSR: Operational Sex Ratio

SNF: Stocking with Native Fry

9 APPENDICES

APPENDIX A – STATE VARIABLES ASSOCIATED WITH REACH, WEIR, HATCH AND FISH OBJECTS.

For each object, the name and definition of each state variable are provided. In addition, I indicate whether that variable remains fixed throughout the simulation or whether it changes at each time step.

Table 1: Description of state variables associated with the reach object.

<i>Name</i>	<i>Definition</i>	<i>Fixed or Changing?</i>
<i>ID</i>	Object reference number	Fixed
<i>Father ID</i>	Father reference number	Fixed
<i>Coordinates</i>	Origin, vertices and endpoints	Fixed
<i>Order</i>	Reach Strahler Order	Fixed
<i>Length</i>	In metre	Fixed
<i>Mean width</i>	In metre	Fixed
<i>Slope</i>	Reach mean slope in percentage	Fixed
<i>Altitude</i>	In metre	Fixed
<i>Reproduction factor</i>	Represent habitat quality for reproduction (impact fecundity and reproductive movement) $\rightarrow [0, 1]$	Fixed
<i>Carrying factor</i>	Represent habitat quality for resources (impact carrying capacity and growth movement) $\rightarrow [0, 1]$	Fixed
<i>Regulation status</i>	Type of regulation in place for fishing	Fixed
<i>Minimum catch size</i>	Fishing can be allowed below or above In centimetres	Fixed
<i>Maximum catch size</i>	Fishing can be allowed below or above In centimetres	Fixed
<i>Specificities</i>	Particular characteristics of the reach	Fixed
<i>Mean temperature</i>	Vector of 12 monthly mean temperature	Changing

<i>Cumulated temperature</i>	Vector of 12 monthly cumulated temperature In degree-days	Changing
<i>Adults</i>	Number of adults in the Reach	Changing
<i>Sub-adults</i>	Number of sub-adults in the Reach	Changing
<i>Juveniles</i>	Number of juveniles in the Reach	Changing
<i>Fishes</i>	Fishes object belonging to that Reach	Changing
<i>Hatches</i>	Hatches object belonging to that Reach	Changing

Table 2: Description of state variables associated with the weir object.

Name	Definition	Fixed or Changing?
<i>ID</i>	Object reference number	Fixed
<i>Father ID</i>	Father reference number	Fixed
<i>Origin</i>	Coordinates of the point	Fixed
<i>Fish pass</i>	Is it a fish pass?	Fixed
<i>Up Pass</i>	Weir Passability, 0 means fully passable, highest value informed means impassable (usually 100)	Fixed
<i>Down Pass</i>	Weir Passability, 0 means fully passable, highest value informed means impassable (usually 100)	Fixed

Table 3: Description of state variables associated with the hatch object.

Name	Definition	Fixed or Changing?
<i>Creation date</i>	The month where the hatch was created (~ birthdate) Used as an ID reference (1 hatch/reach/time step)	Fixed
<i>Egg number</i>	Number of eggs in the Hatch	Changing
<i>Age</i>	Age of all individuals in the hatch, in months	Changing
<i>Fork length</i>	Size of all individuals in the hatch, in months	Changing
<i>Has Hatched</i>	Have eggs hatched yet? [yes, no], change once	Changing
<i>Has Emerged</i>	Have larvae emerged yet? [yes, no], change once	Changing
<i>mpContribution</i>	Table with the parental contribution to the Hatch Key = "maternal ID - paternal ID"	Changing

	Value = “number of eggs”	
<i>Reach</i>	For access to the birth reach	Fixed

Table 4: Description of state variables associated with the fish object.

<i>Name</i>	<i>Definition</i>	<i>Fixed or Changing?</i>
<i>ID</i>	Object reference number	Fixed
<i>Creation date</i>	Object creation date ≠ individual birthdate as fish objects are created later on (hatches first)	Fixed
<i>Maternal ID</i>	Reference number of maternal fish object	Fixed
<i>Paternal ID</i>	Reference number of paternal fish object	Fixed
<i>Nuclear DNA</i>	Individual genome	Fixed
<i>Forklength</i>	Fish size in centimetres	Changing
<i>Male</i>	Fish sex: yes is for males and no for females	Fixed
<i>Age</i>	In months	Changing
<i>Spawning age</i>	Represent maturation age in months	Fixed
<i>Just moved</i>	Yes indicates a Fish has already moved for survival	Changing
<i>Just migrated</i>	Yes indicate a Fish has already moved for reproduction	Changing
<i>Just spawned</i>	Yes indicates a Fish has already spawned	Changing
<i>Spawn count</i>	Number of spawning acts, reset to 0 every year	Changing
<i>Last spawned</i>	Indicate the last spawning date of a Fish	Changing
<i>Birth reach ID</i>	Reach where the individual was born	Fixed
<i>Growth reach ID</i>	Last known reach for growth, <i>i.e.</i> before reproductive movement	Changing
<i>Current Reach ID</i>	Reach where the fish is located during a given time step	Changing
<i>Individual</i>	Fish trait value calculated based on his genotype	Fixed
<i>Introgression</i>		
<i>Has hatched</i>	Has egg hatched yet? [yes, no], change once	Changing
<i>Has Emerged</i>	Has egg emerged yet? [yes, no], change once	Changing

**APPENDIX B – MODEL PARAMETERS (TO BE INFORMED BY THE USER) FOR EACH OF THE SUB-MODELS IN
MEDITERRANEA**

For each sub-model, default values are given for parameter settings. These values are the ones pertinent in the MED/ATL hybridization context. Parameters state provides information on whether its value will remain fixed between scenarios tested in the present manuscript or variable.

Table 1: Initial parameter settings for survival processes.

Survival process parameters		
Parameter name	Default value	State
General parameters		
Overall eggs survival rate (< 380 degree-days)	0.66	Set
Overall larvae survival rate (< 700 degree-days)	0.64	Set
Overall juvenile survival rate	0.59	Set
Annual sub-adults survival rate (< 12 months)	0.54	Set
Annual adults survival rate (< 24 months)	0.54	Set
KmaxE: survival parameter to manage maximum carrying capacity	2	Variable
Post-zygotic survival		
β: Slop intercept	2.197	Variable
α: Temperature effect	0	Variable
δ: Maternal genotype effect	0	Variable
γ: Maternal genotype x temperature interaction	0	Variable
% Genetic contribution to survival	100	Variable

Table 2: Initial parameter settings for the growth process.

Growth process parameters		
Parameter name	Default value	
General parameters		
Base growth effect	0.23	Set
Maximum body size	50	Set
<i>ME</i> : Maturation effect	0.7	Set
Temperature related parameters		
<i>optimalTemp</i> : Optimal temperature for growth	15	Set
<i>tempAmpE</i> : Amplitude around optimal temperature	4	Set
Density related parameters		
α : density effect for juveniles	0.45	Set
α : density effect for sub-adults	0.45	Set
α : density effect for adults	0.45	Set

Table 3: Initial parameter settings for movement processes.

Movement process parameters		
Parameter name	Default value	
Growth movement parameters		
Maximum growth movement probability	0.2	Set
Probability to move downstream	0.5	Set
Maximum density in the river (ind.m ⁻²)	0.5	Variable
Reproductive movement parameters		
Probability to move during spawning season	0.5	Set
Probability for homing (returning to birthreach)	0.8	Set
Non-homing movement parameters		

Maximum distance for movement (<i>i.e.</i> reach number)	2	Set
Upstream movement	True	Set
Upstream movement with habitat selection	False	Set
Habitat quality threshold	0.5	Set

Table 4: Initial parameter settings for reproductive processes.

Reproductive process parameters			
Parameter name		Default value	
General parameters			
Maximum spawning count per female per year		2	Set
Maximum spawning count per male per year		10	Set
Maximum number of mating events per month		2	Set
Maximum cannibalism pressure on eggs		5	Set
Mean OSR (number of males sampled per female)		4	Set
Fecundity coefficient		0.0011236	Set
Fecundity exponent		2.36	Set
Individualisation age (for individuals in hatches)		8	Set
Male competition			
Mediterranean dominance		False	Set
Atlantic dominance		False	Set
Stalemate (equality)		True	Set
Female preference			
Absolute preference		True	Set
Non-genetic preference		True	Variable
Genetic dependent preference	MED females	False	Set
	ATL females	False	
Homo/heterogamous preference		False	Variable
Intercept value		0	Variable
Preference strength (slope)		0	Variable
% Contribution to mating system		100	Variable

Table 5: Initial parameter settings for the fishing process.

Fishing process parameters		
Parameter name	Default value	
Fishing periods		
October, November, December, January, February, March	False	Set
April, May, June, July, August, September	True	Set
Legal-size options		
Fishing below the minimum size	False	Set
Fishing between legal sizes	True	Set
Fishing above the maximum size	True	Set
Fishing mortality rate per regulation		
Standard reach	0.01	Set
Active reserve reach	0.005	Set
No-kill reach	0.002	Set
Full reserve reach	0	Set

APPENDIX C – MONTHLY RELATIONSHIP BETWEEN WATER TEMPERATURE AND ALTITUDE.

The relationship between water temperature and altitude was plotted using many rivers in Haute-Savoie, including those studied in this manuscript – the Borne River and the Dranse d’Abondance System with the Chevenne Creek.

Figure 1 illustrates this relationship in spring and summer – from April to September – and shows that water temperature is negatively correlated with altitude. Figure 2 illustrates this relationship in autumn and winter – from October to March – and shows that the negative correlation observed between water temperature and altitude is progressively less pronounced from autumn to winter, as temperatures are getting very low. Usually, observed temperatures in this area rarely exceed 5°C in winter, notably during the embryonic phase – starting from December in the model.

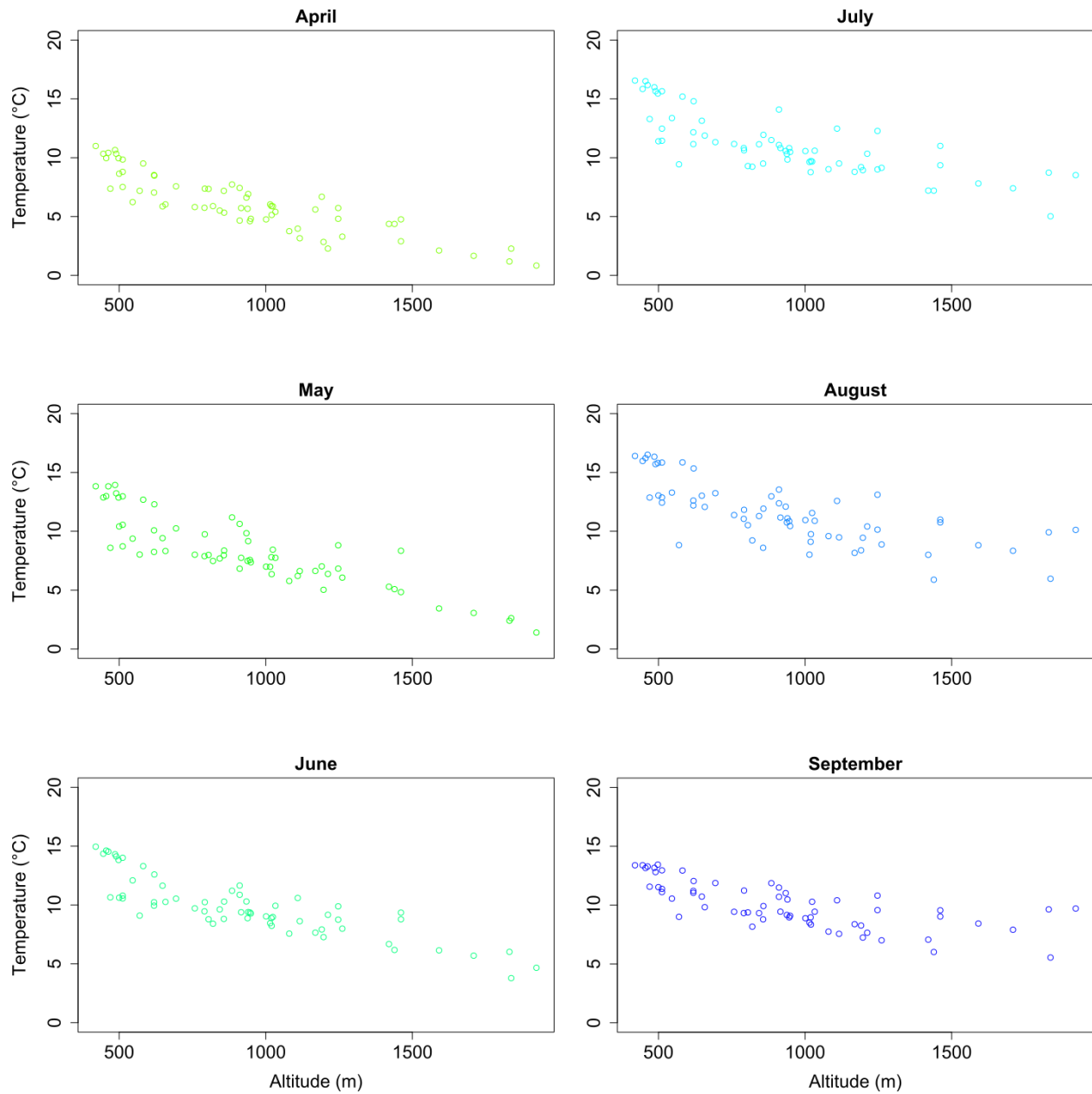


Figure 1: Water temperature (°C) as a function of altitude (meter) from April to September. Each circle represent one value: i.e. temperature measured in one section of a river at a given altitude.

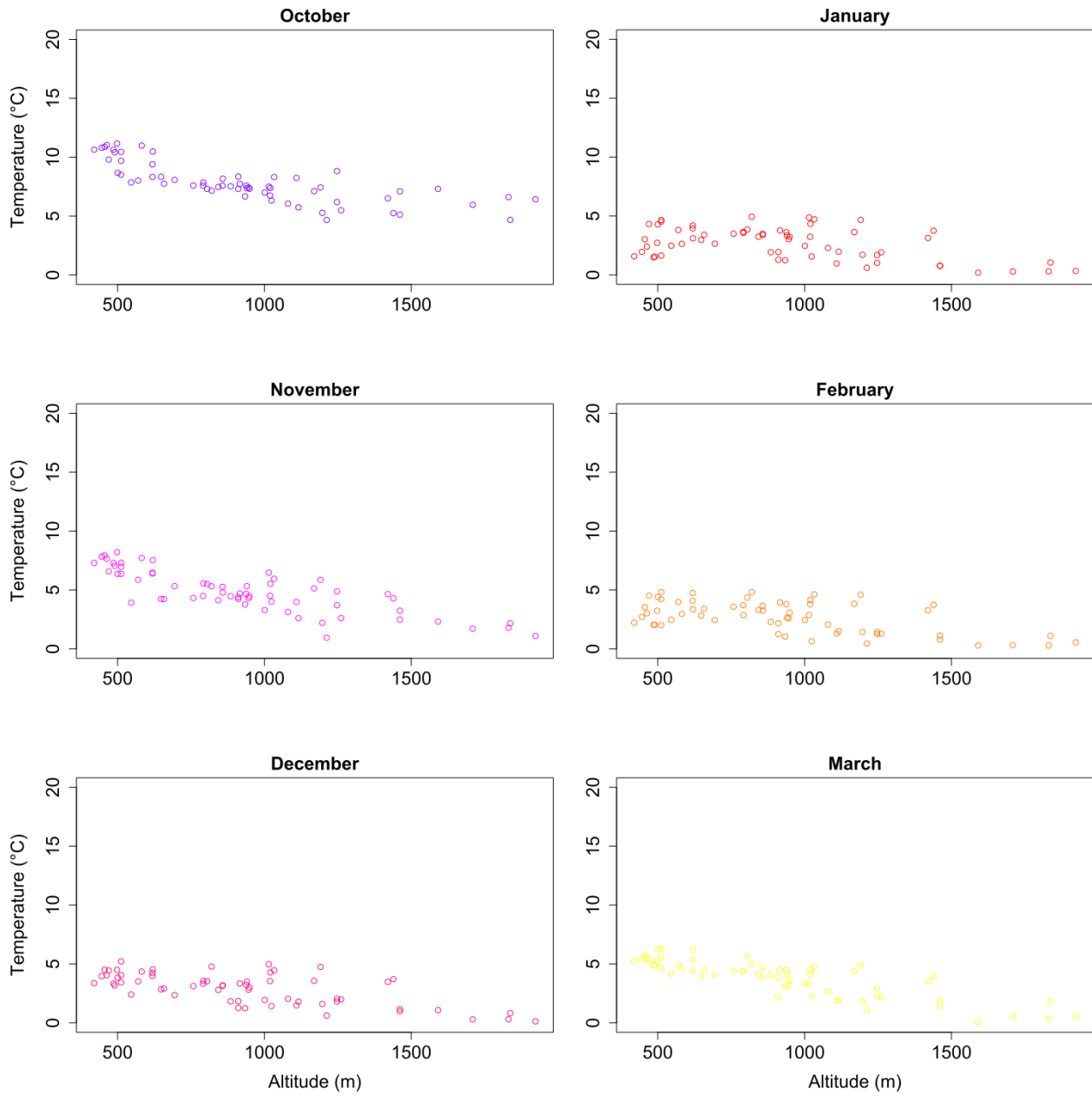


Figure 2: Water temperature (°C) as a function of altitude (meter) from October to March. Each circle represent one value: i.e. temperature measured in one section of a river at a given altitude.

APPENDIX D – RIVERS PHYSICAL CHARACTERISTICS AND TOPOLOGY.

This appendix presents the physical characteristics of the Borne River and the Chevenne Creek, as well as the topology implemented in MEDITERRANEA (information on fathers ID).

Table 1: Reaches physical characteristics of the Chevenne Creek.*

Reach ID	Father ID	Stalher	Order	Length	Mean	width	Slope	Altitude	Repro-	duction	Capacity	Status	CSL min	CSL max
1	1	1		825	3.5		10	1050	1		1	4	25	40
2	2	1		558	3		10	1100	1		1	4	25	40
3	3	1		702	3		12	1200	1		1	4	25	40
4	4	1		806	2.5		17	1300	1		1	4	25	40
5	5	1		650	2.5		16	1350	0		0	4	25	40

*Table 2: Weirs physical characteristics of the Chevenne Creek**.*

Weir ID	Father ID	Fish Pass	Up Pass	Down Pass
1	0	0	20	60
2	1	0	80	60
3	2	0	60	60
4	3	0	99	99
5	4	0	100	60

Table 3: Reaches physical characteristics of the Borne River*.

<i>Reach ID</i>	<i>Father ID</i>	<i>Stalher Order</i>	<i>Length</i>	<i>Mean width</i>	<i>Slope</i>	<i>Altitude</i>	<i>Repro-duction</i>	<i>Capacity</i>	<i>Fishing status</i>	<i>CSL min</i>	<i>CSL max</i>
1	1	3	4266	14	1	466	1	0.5	1	25	40
2	2	3	1241	7	4	516	1	1	1	25	40
3	3	3	2817	7	3	578	1	1	1	25	40
4	4	3	2486	10	2	634	1	1	1	25	40
5	5	3	3751	11	2	698	1	1	1	25	40
6	6	3	2025	11	2	757	1	1	1	25	40
7	7	3	1194	11	2	784	1	1	1	25	40
8	8	3	724	11	2	803	1	1	1	25	40
9	9	3	1812	11	3	838	1	0.8	1	25	40
10	10	3	1170	8	2	874	1	1	1	25	40
11	11	3	1925	7	2	903	1	1	1	25	40
12	12	2	1819	4	4	956	1	0.8	1	25	40
13	13	2	4109	5	2	1039	1	0.8	1	25	40
14	14	1	1111	2	3	1106	1	0.6	1	25	40
15	15	1	3086	1	26	1518	1	0	1	25	40
16	5	1	469	2	13	685	1	0.6	1	25	40
17	16	1	2736	2	19	973	1	0.6	1	25	40
18	6	1	43	2	22	741	1	0.6	1	25	40
19	17	1	2385	2	22	999	1	0.6	1	25	40
20	7	1	973	3	8	810	1	0.8	1	25	40
21	18	1	3752	2	17	1170	1	0.8	1	25	40
22	12	2	258	6	9	953	1	0.6	1	25	40
23	19	2	2646	4	10	1075	1	0.6	1	25	40
24	20	2	1833	4	4	1240	1	0.6	1	25	40
25	21	1	1178	1	12	1345	1	0.6	1	25	40
26	22	1	924	1	13	1476	1	0	1	25	40
27	21	1	3612	3	11	1472	1	0.6	1	25	40

28	14	1	427	5	8	1104	1	0	1	25	40
29	23	1	1597	3	19	1275	1	0	1	25	40
30	24	1	1266	2	6	1470	1	0.6	1	25	40
31	25	1	1316	1	16	1614	1	0	1	25	40

Table 4: Weirs physical characteristics of the Borne River**.

Weir ID	Father ID	Fish Pass	Up Pass	Down Pass
1	0	0	0	0
2	1	0	100	100
3	2	0	0	0
4	3	0	100	100
5	4	0	0	0
6	5	0	0	0
7	6	0	0	0
8	7	0	100	100
9	8	0	0	0
10	9	0	0	0
11	10	0	0	0
12	11	0	0	0
13	12	0	0	0
14	13	0	0	0
15	14	0	0	0
16	16	0	0	0
17	18	0	0	0
18	20	0	100	100
19	22	0	100	100
20	23	0	0	0
21	24	0	0	0
22	25	0	0	0

23	28	0	100	100
24	29	0	0	0
25	30	0	0	0

* Father ID corresponds to the weir located just downstream. Length, mean width and altitude are given in metres. Reproduction and capacity are habitat quality variables ranging between [0, 1]. Reproduction determines the reproductive capacity of the reach by influencing female egg number and, possibly, the upstream movement for reproduction. Capacity influences the maximum carrying capacity of each reach. Fishing status determines the fishing regulation in place and CSL represents catch size limits (minimum and maximum value).

** Father ID corresponds to the reach located just downstream. Fish Pass indicates whether an actual fish pass is present at the weir: 0 means “no” and 1 means “yes”. Up and Down Pass inform on the passability of the weir for fish movement. It is measured on a scale [0, 100]. 0 indicates that there is no obstacle and the weir is entirely passable. 1 indicates that a barrier makes the weir fully unpassable. Any intermediate values are for passable weirs (more or less easy to pass depending on the value).

APPENDIX E – THE ROLE OF HOMOGAMOUS VS HETEROGAMOUS PREFERENCE.

Results from a poster presentation for the EEEF international conference (Berkeley, 2021).

How does intraspecific diversity evolve under different mating preferences (random vs heterogamous vs homogamous), when considering GxE interactions?

The model was used to simulate a first contact between lineages in a simple hydrographic network (similar to *section 4.3*). The initial population was composed of an equal number of MED and ATL individuals. These simulations aimed at evaluating and comparing the role of different types of female preference on the evolution of diversity dynamics. Three female preference scenarios were defined: homogamous, random and heterogamous preference (*Figure 1*). For each scenario, the value of GCP was set at 50% to test for an intermediate value. A medium modality of GxE interactions was implemented.

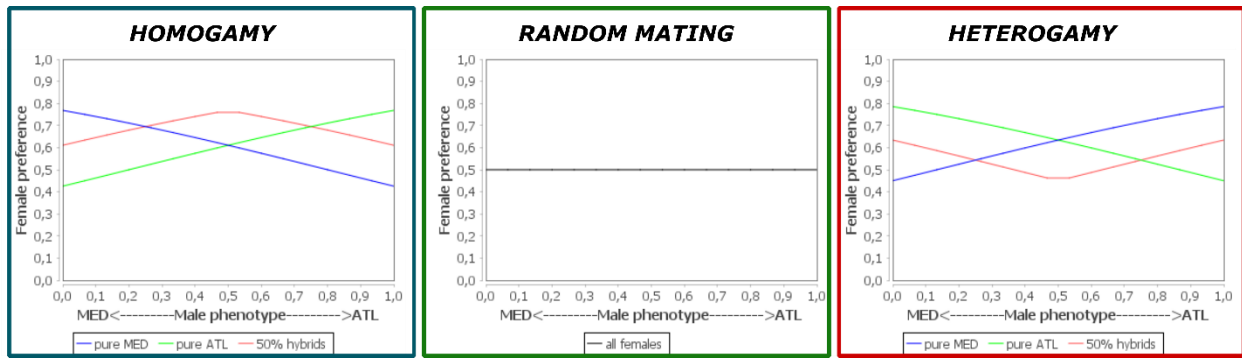


Figure 1: Female preference curves implemented in the model for each scenario: homogamous, random and heterogamous preference.

Evolution of introgression. Due to the selection mediated by GxE interactions, a progressive decrease in introgression rate can be observed for all scenarios (Figure 2). The implementation of different female preferences only appears to either slow down (heterogamous preference) or accelerate (homogamous preference) that decrease compared to random preference. However, the differences observed remain small, as observed in the simulations from the main manuscript.

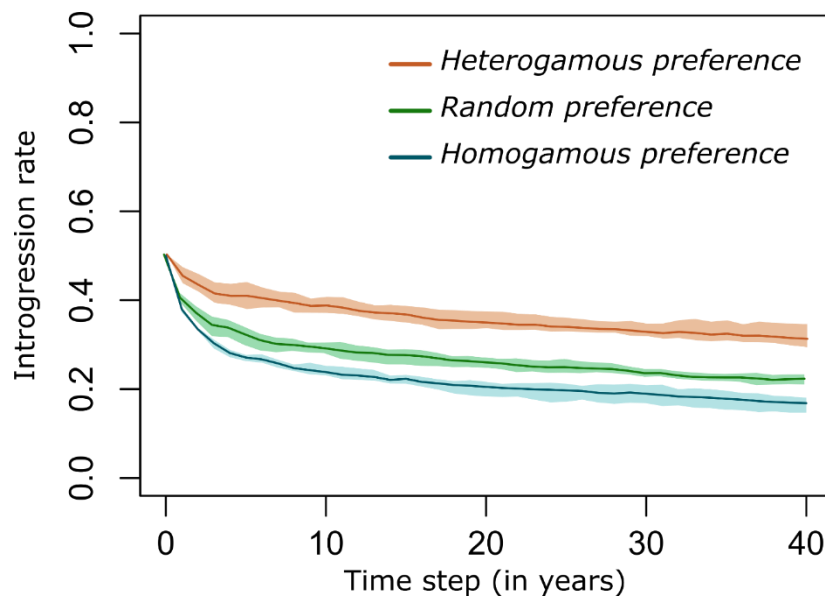


Figure 2: Evolution of introgression under random (green), heterogamous (orange) and homogamous (blue) preference following first contact and when considering GxE interactions.

Distribution of individual introgression. The distribution of individual introgression through time shows that no matter the mating preference implemented the main pattern is the same (Figure 3). Following a first secondary contact, there is a large creation of F1 HYB individuals. A bell-shaped distribution is progressively formed throughout time and is biased toward low introgression values, as selection progressively acts to remove ATL alleles. The only slight difference is the value on which the distribution is centred. For heterogamous preference, at $t = 40$, the distribution is centred around 0.3, while it is lower for random preference and homogamous preference (both around 0.2).

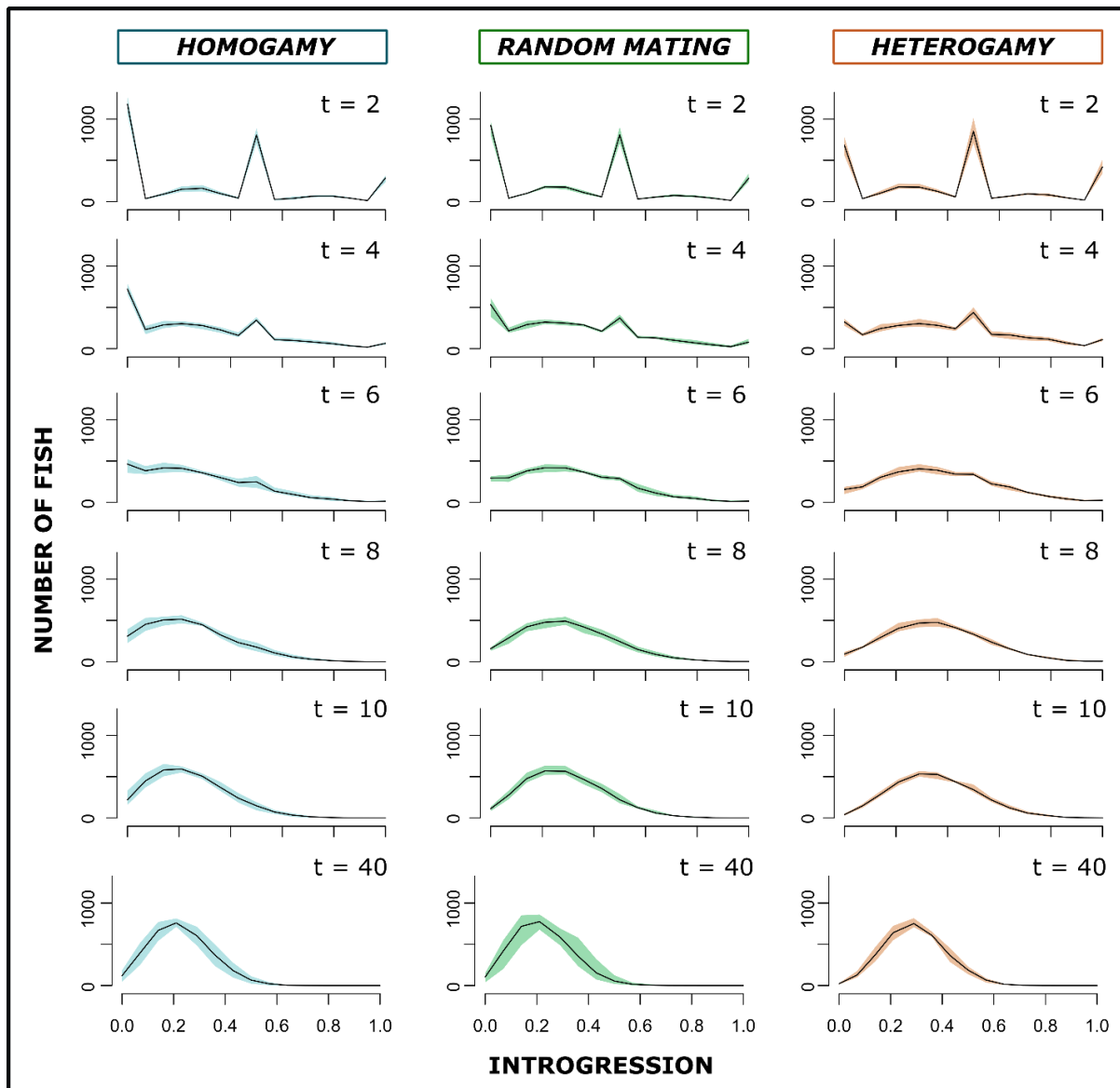


Figure 3: Distribution of individual introgression throughout time, from $t = 2$ to $t = 40$ for random (green), heterogamous (orange) and homogamous (blue) preference and when considering GxE interactions.

APPENDIX F – MED MATERNAL ASCENDANCE IN HYBRID POPULATIONS.

Focusing on hybrid individuals, I followed the proportion of MED *versus* ATL alleles transmitted maternally and paternally to (i) investigate whether introgression mainly happened through one sex (paternally) and (ii) verify if simulated data also pointed at the MED maternal ascendance in hybrid populations. Results are presented for the eco-evolutionary scenario considering both eco-evolutionary mechanisms: heterogamous female preference and GxE interactions on survival.

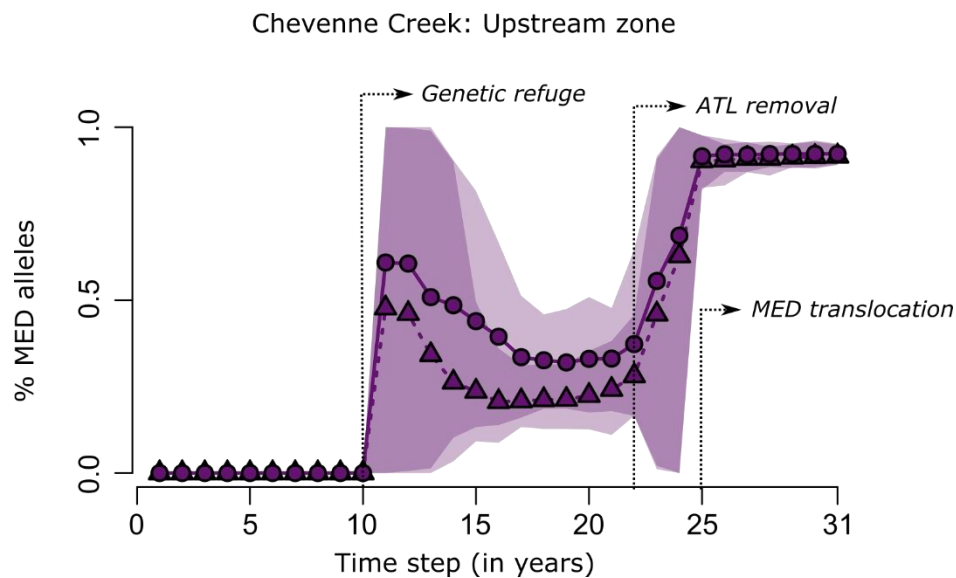


Figure 1: Proportion of MED alleles (p) inherited maternally (circle) versus paternally (triangle) throughout time for HYB individuals, in the upstream zone of the Chevenne Creek. For each parent, $1 - p$ corresponds to the proportion of ATL alleles inherited.

In the Chevenne Creek (Figure 1), following the implementation of the genetic refuge strategy, mean values indicated that a higher proportion of MED alleles was transmitted to HYB individuals maternally compared to paternally. However, following ATL removal and MED translocation, proportions became almost equal (> 90% of MED alleles) as the population was mainly composed of pure MED individuals.

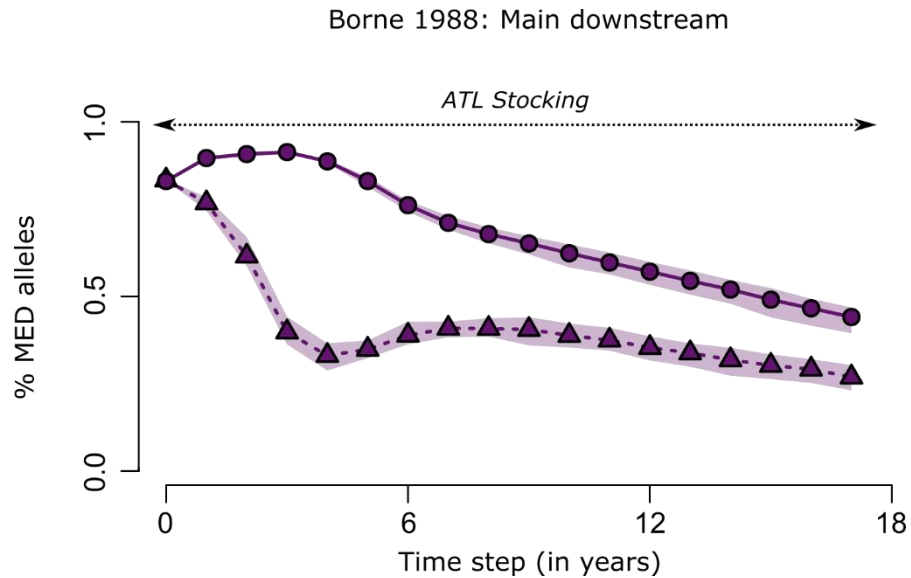


Figure 2: Proportion of MED alleles inherited maternally (circle) versus paternally (triangle) throughout time for HYB individuals, in the main downstream section of the Borne River (case study: “Borne 1988”). For each parent, $1 - p$ corresponds to the proportion of ATL alleles inherited.

In the Borne, following the first years of ATL stocking (Figure 2, up to $t = 4$), MED alleles represented up to 90% of the alleles transmitted through the maternal way, whereas it was lower through the paternal way. Indeed the proportion of MED alleles transmitted paternally decreased from 80% ($t = 0$) to 35% ($t = 4$) within four years of stocking. Throughout time, the proportion of MED alleles transmitted to HYB individuals', maternally and paternally, decreased as more and more ATL alleles were brought into the population through continuous ATL stocking. Nevertheless, the proportion of MED alleles inherited maternally always remained higher than that inherited paternally.

In the Borne, following MED translocation (Figure 3), HYB individuals inherited a majority of MED alleles maternally ($\sim 90\%$) against a majority of ATL alleles paternally ($< 10\%$ of MED alleles). Throughout time, the proportion of MED alleles inherited maternally then decreased while that inherited paternally increased until both proportions equalised, as more and more HYB individuals were created.

Borne 2004: Upstream zone

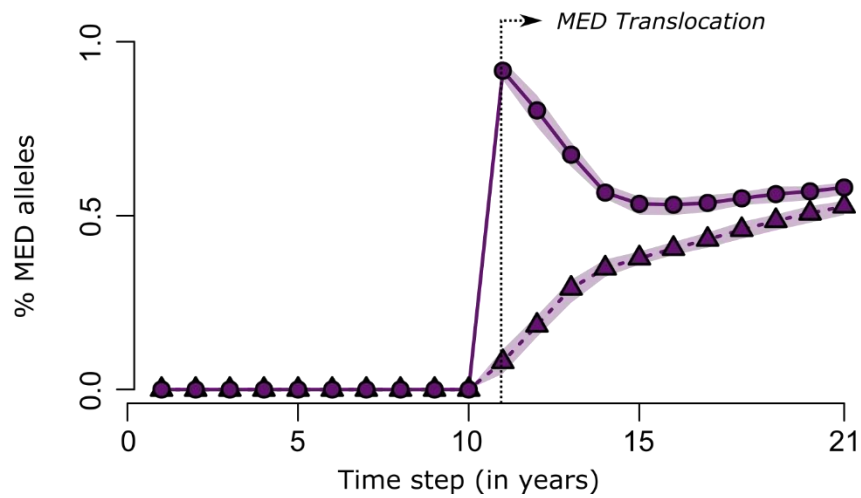


Figure 3: Proportion of MED alleles inherited maternally (circle) versus paternally (triangle) throughout time for HYB individuals, in the upstream zone of the Borne River (case study: “Borne 2004”). For each parent, $1 - p$ corresponds to the proportion of ATL alleles inherited.

Take home message. Following allelic transmission (maternal vs paternal) in hybrid individuals, data indicate that more MED alleles are transmitted to hybrids maternally compared to paternally. In addition, a very high initial proportion of MED alleles (vs ATL alleles) is transmitted maternally following the first secondary contact. On the contrary, more ATL alleles (vs MED alleles) are generally transmitted paternally. Therefore, results indicate that introgression initially happens through paternal inheritance and hence point to the MED maternal ascendance in hybridized populations.

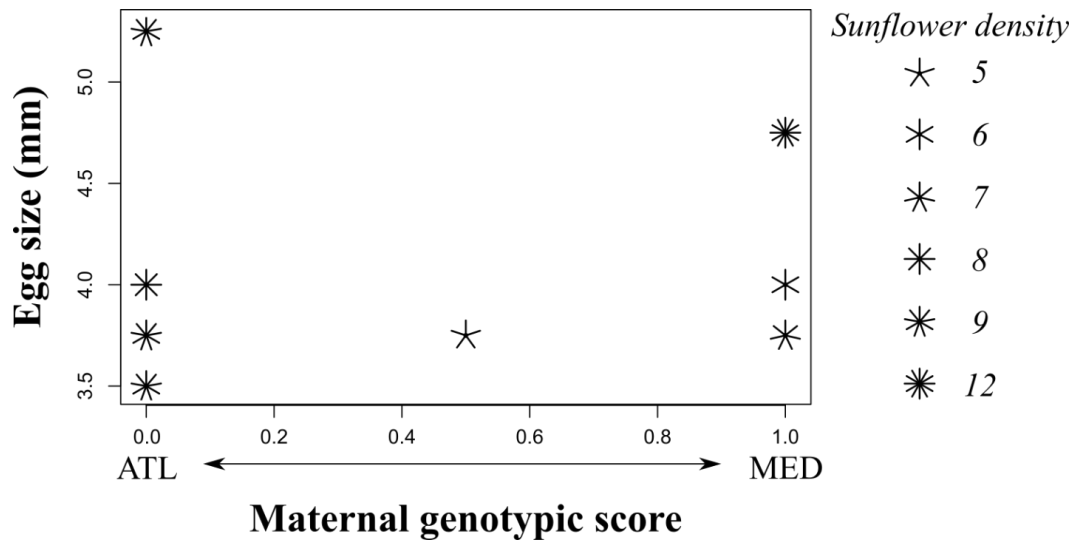
APPENDIX G – RELATIONSHIP BETWEEN MATERNAL GENOTYPIC SCORE AND MEAN EGG SIZE.

Figure 1: Sunflower plot representing mean egg diameter (mm) within a sub-batch as a function of maternal genotypic score for the 65 recovered incubation boxes. The sunflower density indicates the number of incubation boxes for a given combination of maternal genotypic score and mean egg diameter.