Assortative mating driving spatial divergence of mating trait in diploid species: how dominance influences population differentiation?

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Abstract
Divergence between populations for a given trait can be driven by natural or sexual selection, interacting with migration behaviour. Mate preference for different phenotypes can lead to the emergence and persistence of differentiated populations, even without any local adaptation. However the genetic architecture underlying the trait targeted by mate preference may have a profound impact on population divergence. In particular, dominance between alleles encoding for divergent phenotypes can interfere in such differentiation processes. Using a diploid model of trait determining both mating success and migration rate, we explored differentiation between two connected populations, assuming either co-dominance or strict dominance between alleles. The model assumes that individuals prefer mating with partners displaying the same phenotype and therefore tend to move to the other population when their phenotype is rare. We showed that the emergence of differentiated populations in this diploid model is limited as compared to results obtained with the same model assuming haplody. When assuming co-dominance, differentiation arises only when migration is limited as compared to preference. Such differentiation is less dependent on migration when assuming strict dominance between haplotypes. Dominant alleles frequently invade populations because their phenotype is more frequently expressed, resulting in higher mating success and rapid decrease in migration. However, depending on the initial distribution of alleles, this advantage associated with dominance (i.e. Haldane’s sieve) may lead to fixation of the dominant allele throughout both populations. Depending on the initial distribution of heterozygotes in the two populations, persistence of polymorphisms within populations can also occur because heterozygotes displaying the predominant phenotype benefit from mating preferences. Altogether, our results highlight that heterozygotes’ behaviour has a strong impact on population differentiation and stress out the need of diploid models of differentiation and speciation driven by natural and sexual selection.

Keywords: Mate preference, Heterozygote, Spatial segregation, Migration, Uneven population size

1. Introduction
Understanding processes leading to biological diversification is a central question in evolutionary biology. Traits may diverge neutrally because of geographic barriers limiting gene flow, or simple isolation by distance due to limited dispersal, resulting in genetic and phenotypic differentiation (Lande 1980; Slatkin 1987). Local selective pressures may also trigger disruptive selection and spatial segregation of differentiated traits (Nosil 2012). Trait differentiation can then be reinforced by mate preference on the ecological trait under disruptive selection (Gavrilets 2006; Servedio et al. 2011)). However, disentangling the effect of mate preference and adaptive value of a trait on its spatial differentiation is still challenging. Furthermore, the genetic architecture of the trait under selection may also influence the evolution of differentiation. Linkage disequilibrium between loci controlling the adaptive trait and preference trait is known to favour the divergence in a Fisherian runaway process (Fisher 1930). Dominance relationships among differentiated alleles may also greatly influence the spatial distribution of different phenotypes (Pannell et al. 2005). The effective migration of advantageous alleles is indeed favoured when they are dominant; immigrant alleles entering a new population will mostly occur at heterozygous state so that they will be picked up by positive selection only if they are expressed. Recessive adaptive alleles, scarcely expressed, are more likely to be lost by genetic drift because of their neutrality at heterozygous state. This Haldane’s sieve effect (Haldane 1927) predicts a greater effective migration of dominant adaptive alleles as compared to recessive ones. For example, in the polymorphic locus of sporophytic self-incompatibility where rare alleles benefit from increased reproductive success, migration of dominant alleles has been shown to be more effective than migration of recessive ones (Schierup et al. 1997). On the contrary, when the direction of selection differs across populations, recessive alleles can be advantaged because their rarer expression protects them from local purifying selection. In the case of mimicry, where phenotypes matching local communities are advantaged, recessive mimetic alleles have a greater effective

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migration across populations with different phenotypic optima, because they are frequently hidden at heterozygous state, preventing selection by locally-trained predators (Laurans et al. (2013)). Dominance among alleles thus plays an important role on the dynamics of spatial differentiation of traits under sexual or natural selection. Here we investigate the influence of dominance on spatial differentiation of a trait determining both mating and migration between populations. Our model is an extension of a previously described model assuming haploid individuals (Coron et al. (2016)). Two populations, linked by migration, are assumed. A mating trait, encoded by one locus has two consequences: (1) encountering pairs mate more often when both individuals display the same phenotype for this trait and (2) the migration rate of an individual is proportional to the frequency of the other phenotype in its patch: individuals are more prone to move if they do not find a suitable mate in their patch. This hypothesis is relevant for all organisms with active mate searching (e.g., patrolling behaviours in butterflies (Jugovic et al. (2017)) or mate sampling in Bowerbirds (Uy et al. (2001)), but also in organisms where gametes are involved in dispersal (e.g., sea urchins (Crimaldi (2012)) or plants (Millar et al. (2014)), and may travel large distance before encountering a suitable mate. This original hypothesis linking preference and migration contrasts with assumptions found in classical models of speciation (see (Gavrilets (2014)) for a review) where the preference traits are generally not directly linked to migration behaviour. In the haploid model studied in (Coron et al. (2016)), this preference behaviour can lead to spatial differentiation of the trait between the two populations with fixation of different phenotypes in the two populations despite migration, without any local adaptation. More precisely, if at initial state one phenotype is predominant in one patch and the other phenotype predominant in the other patch, then there is a spatial differentiation regardless of the strength of the migration. Given the importance of dominance on migration of alleles, here we extend the model to a diploid case with dominance relationships between alleles, and explore how dominance may modulate the dynamics of spatial differentiation on this mating trait.

2. Materials and methods

In this section we present the model that governs the population dynamics. We also describe the mathematical methods used to derive analytical results and how we performed numerical simulations. More formal details are given in the Supplementary Materials.

We consider a population of hermaphroditic diploid individuals characterized by their genotype at one bi-allelic locus (A and a), and by their position on a space divided in two patches (1 and 2). The number of individuals AA, Aa and aa in the two patches follow a dynamical system, which can be obtained as a limit of a stochastic multi-type birth and death process with competition in continuous time (Coron et al. (2016)). In particular, populations sizes in the patches are varying and generations are overlapping. The model is ecologically neutral in the sense that individuals with different genotypes are not characterized by different adaptations to environment or by different resource preferences. However, individuals reproduce sexually according to mating preferences that depend on their phenotype: two individuals having the same phenotype have a higher probability to mate (see (Jiang et al. (2013)) for a recent review of the mechanisms of assortative matings in animals). In addition to this sexual preference, individuals can migrate from one patch to another, at a rate depending on the frequency of individuals carrying the other phenotype and living in the same patch. Examples of animals migrating to find suitable mates are well documented (Schwagmeyer (1988); Honer et al. (2007)). A migration mechanism similar to the one presented here has been studied in (Coron et al. (2016)) and in (Payne and Krakauer (1997)) in a continuous space model.

Five parameters are needed to describe the population dynamics:

- $b$ is the minimal individual birth rate. It corresponds to the rate at which an individual gives birth if there is no individual with the same phenotype in its patch.
- $\beta \geq 1$ is the sexual preference. Individuals encounter randomly, and two individuals with similar phenotypes have a higher probability to mate (see Section 2.1 for details).
- $p$ describes the individuals’ ability to migrate. The effective migration rate of an individual is the product of $p$ and of the proportion of ‘not preferred’ individuals (see Appendix A for details).
- $d$ is the individual natural death rate.
- $c$ represents the competition for food or space exerted by an individual on another one of the same patch. An additional individual death rate results from the total competition exerted on this individual.

The model is ecologically neutral in the sense that the parameters $b$, $p$, $d$, and $c$ do not depend on the individuals’ phenotypes or on its patch. The only way individuals differ is their behaviour in terms of reproduction and migration.

2.1. Dominance

We assume Mendelian reproduction. That is to say, a parent transmits every allele with probability 1/2. To study the effect of dominance on population differentiation, we contrast two opposite scenarios: complete co-dominance and complete dominance. In the complete dominance scenario, individuals with genotypes AA and Aa have the same phenotype, A, whereas individuals with genotype aa have the phenotype a. In the co-dominance scenario we consider two possibilities. Either the preference expressed by an individual is an ‘average preference’ of its alleles ($\beta$ for pairs (AA, AA), (aa, aa) and (Aa, Aa), ($\beta + 1$)/2 for pairs (AA, Aa) and (aa, Aa), and 1 for pairs (AA, aa)) and the migration rate follows the same rule, or heterozygotes express no preference and thus do not migrate (in this case only the homozygotes express a preference towards individuals of the same genotype). The preference parameter is thus $\beta$ for pairs (AA, AA) and (aa, aa), and 1 for the other pairs.
2.2. Mathematical analysis

In the Supplementary Materials we carry out a mathematical analysis of the dynamical systems governing the population evolution. We describe some fixed points of the systems, their stability, and obtain some convergence results in the case without migration. In order to get these results we use the theory of dynamical systems (in particular Lyapunov functions and the Local Center Manifold Theorem) as well as the theory of polynomial functions.

2.3. Simulations

To illustrate some dynamics of the dynamical systems governing the evolution of the population sizes, we used the software Mathematica.

We also performed numerical simulations of the dynamical systems presented in Appendix A. We investigated the solution of the dynamical systems for different values of migration rate $p$ and of preference coefficient $\beta$. For each value of $\beta$ and $p$, we solved the dynamical systems for 10000 different initial conditions. First, we set the size of the population in patch 1: we considered 100 values of sizes regularly distributed between 1 and $2 * (2 * b - d)/c$. Then, we set the size of the population in patch 2 such that the difference between the two sizes was 0.01. This allowed us to reduce the number of parameters explored without changing the results. Finally, for each couple of sizes, we examined 100 initial situations which we fixed randomly. For each patch $i$, we set uniformly at random the proportion $p_{Ai}$ of allele $A$ using a uniform random variable between 0.5 and 1 in the case where the majority allele was $A$ or between 0 and 0.5 in the other case. The proportion of $AA$-individuals in patch $i$ was fixed randomly using a uniform random variable between 0 and $2 * \min(p_{Ai}, 1 - p_{Ai})$. The proportion of $AA$-individuals and $aa$-individuals in each patch can be easily deduced.

For each initial condition, we numerically solved the three dynamical systems using a finite difference method. The value of the discretization time step $h$ used in this paper was 0.005. We were interested in the stationary state and we assumed that a stationary state was reached as soon as the norm of the difference between the two time steps was lower than $\varepsilon = 10^{-6}$. Different values of $h$ and $\varepsilon$ were tested. We selected the couple of values with the best trade-off between the rapidity of the algorithm and the accuracy of the solution: more precision did not give significantly best results in the set of parameters tested. Once the stationary state was found, we considered that the final population in a patch was monomorphic if the proportion of one of the alleles was larger than 99%. Otherwise, it was said to reach a polymorphic equilibrium.

3. Results

3.1. Diploid models with co-dominance

First, we explored the diploid model assuming co-dominance between alleles, where both alleles have the same level of expression. This assumption exhibits high similarity with the haploid case, although the behaviour of heterozygous individuals displaying intermediate phenotypes might influence model outputs. We contrasted two hypotheses: (1) preferences between homozygotes and heterozygotes were half less than between the same genotypes, (2) heterozygotes had no preferences and were not preferred by homozygotes (preference parameter 1 for any encountering pair with an $Aa$ individual). We then investigated the equilibrium reached in both populations using a mathematical analysis and simulations assuming different preference coefficients ($\beta$) and migration rates ($p$).

3.1.1. System without migration

When there is no migration ($p = 0$) we are able to give necessary and sufficient conditions on the initial numbers of individuals with genotypes $AA$, $Aa$ and $aa$ in both patches for the system to converge to the different fixed points, in both codominant models. Equilibria can be expressed using $\xi$, the equilibrium population size in a patch when there is only one type of individuals ($AA$ or $aa$):

$$\xi := \frac{\beta b - d}{c}.$$  

Let us denote by $n_{AA,i}(t)$ the number of individuals with genotype $aa^{\prime}$ ($AA$, $Aa$ or $aa$) in the patch $i$ (1 or 2) at time $t$. As there is no migration, it is enough to consider the patch 1. Under hypothesis (1) the system admits two stable fixed points, $(z_{AA,1} = \xi, z_{Aa,1} = 0, z_{aa,1} = 0)$ (fixation of allele $A$) and $(z_{AA,1} = 0, z_{Aa,1} = 0, z_{aa,1} = \xi)$ (fixation of allele $a$), and one unstable fixed point with persistence of all three genotypes (see Appendix B.1). If $z_{AA,1}(0) > z_{aa,1}(0)$, allele $A$ gets fixed, and the numbers of individuals converge to the stable equilibrium $(\xi, 0, 0)$, if $z_{AA,1}(0) < z_{aa,1}(0)$. The exact same conclusion holds with $a$ replacing $A$. Finally, if $z_{AA,1}(0) = z_{aa,1}(0)$, the system converges to the unstable equilibrium. Under hypothesis (2) we get the same result, except that the unstable fixed point is different (see Appendix B.2 for details).

3.1.2. Fixed points of the system with migration

When there is a migration between the two patches ($p > 0$), the dynamics is much more complex (see Figures 3 and 4 for examples of dynamics) and we were unable to obtain convergence results analytically. However we were able to describe some of the fixed points and determine their stability. There are exactly four fixed points with monomorphic populations in both patches: fixation of $A$ in both patches ($z_{AA,1} = \xi, z_{Aa,1} = 0, z_{aa,1} = 0, z_{AA,2} = \xi, z_{Aa,2} = 0, z_{aa,2} = 0$), fixation of $a$ in both patches ($0, 0, 0, 0, 0, 0$), or fixation of different alleles in the two patches, $(\xi, 0, 0, 0, 0, 0)$ or $(0, 0, \xi, \xi, 0, 0)$. For the two codominant models, the first two fixed points are stable for all parameters values, and the two last fixed points are stable if $p < b\beta(\beta - 1)/2$ and unstable if $p > b\beta(\beta - 1)/2$. This result contrasts with the haploid case, where the fixed points with a genotype in each patch were stable for all the values of the migration parameter $p$ (see [Coron et al., 2016]). This may be explained by the fact that the migration of heterozygotes has a major impact on the population behaviour, as explicit below.
using numerical simulations. In the figure displaying the behaviour of the model in the codominant case, we have indicated the curve $p = b\beta(\beta - 1)/2$ (see Figure 1).

3.1.3. Conditions for differentiated populations

![Figure 1: Conditions for the emergence of differentiated populations with fixation of allele $A$ in population 1 and $a$ in population 2, assuming hypothesis (1) regarding codominance (outcomes are very similar under the alternative hypothesis of codominance). Color indicates the percentage of simulations where $A$ get fixed in population 1 and $a$ in population 2. Black line shows the limit of the stability of the equilibrium with differentiated populations, $p = b\beta(\beta - 1)/2$ (see previous section).](image)

Under both assumptions regarding co-dominance, differentiated populations with fixation of different phenotypes in the two populations can emerge only when the frequencies of allele $a$ are asymmetrical at initial state, with frequency of allele $a$ smaller than $1/2$ in one population and larger than $1/2$ in the other population (Fig. 1). As shown in Appendix C.1 and Appendix C.2, this equilibrium cannot be reached when $p > b\beta(\beta - 1)/2$. However, an initial asymmetry and the condition $p < b\beta(\beta - 1)/2$ are not enough to ensure differentiated populations.

This equilibrium does not arise when one of the alleles is initially predominant in both populations (see Appendix D.2). The number of simulations exhibiting differentiation increases when the preference coefficient $\beta$ increases as expected, and decreases when the migration rate $p$ increases. Indeed when migration increases or preference decreases, this equilibrium becomes unstable (see black curve in Fig. 1) and is no longer reached. This contrasts with the dynamics of the model when individuals are haploid. Assuming haploid genotypes, Coron et al. (2016) proved that differentiated populations emerge as soon as the frequencies of allele $a$ are asymmetrical at initial state, regardless of the value of the migration strength, $p$, and preference $\beta > 1$. However, the negative effect of migration on population differentiation is observed under both assumptions regarding co-dominance, including hypothesis (2) where heterozygotes never migrate. This indicates that their presence may be enough to maintain the migration of both $A$ and $a$ homozygotes across populations when $p$ is large, even if they do not move themselves.

![Figure 2: Conditions of fixation of allele $a$ in both populations. Columns represent simulations assuming hypotheses (1) and (2) regarding heterozygote behaviour. Rows differ in initial conditions. First row: Asymmetrical frequency of allele $a$ (more frequent in population 2); Second row: Frequency of allele $a$ greater than 0.5 in both populations. The colors indicate the percentage of simulations where $a$ get fixed in both populations.](image)

3.1.4. Fixation of a single phenotype throughout both populations

Under hypothesis (1), when migration increases, the two populations tend to be more homogeneous, leading to the fixation of a single allele throughout both populations, whatever the initial frequencies. The identity of the fixed allele depends on the initial frequency because of positive frequency-dependent selection triggered by homogamy. In cases where initial frequencies of allele $a$ are asymmetrical in the two populations, we indeed observed fixation of allele $a$ in 50% of simulations when migration increases (Fig 2a-b). As the system is symmetrical in $a$ and $A$, in the other half of simulations, the fixation of allele $A$ was observed (data not shown). When allele $a$ initially predominates in both patches, the fixation of allele $a$ is observed in all simulations for hypothesis (1) regarding heterozygote behaviour (Fig. 2c). When heterozygotes express a preference for themselves and migrate, their migration leads to a fast equalization of the numbers of individuals with the same genotype in the two populations (see Figure 2d) (i.e. $n_{A,A,1}$ (resp. $n_{A,a,1}$) very close to $n_{A,A,2}$ (resp. $n_{A,a,2}$)). Once this equalization is reached, the migration does not influence the dynamics since the numbers of emigrants and immigrants of each population are the same. Both patches evolve as if they were isolated. From the study of the system without migration in Section 3.1.1, we know that there is no polymorphic stable equilibrium in one isolated patch. As a consequence, the same allele gets fixed in both patches.

Assuming no preference and no migration of heterozygotes
(hypothesis (2)) leads to the overall fixation of one of the two alleles only when migration is limited or preference is high (Fig. 2d). Otherwise in many simulations, polymorphism persists in both populations.

### 3.1.5. Polymorphic equilibria

The dynamics leading to these equilibria are highly non-monotonic and migration persists at equilibrium, which explains the difficulty to study the model analytically. The presence of individuals of type $Aa$ maintains the migration of $AA$ and $aa$ individuals at equilibrium (see Figures 4 and 5).

According to numerical simulations, stable monomorphic equilibria are of the following form:

- one 'large' population (with a size larger than $(\beta b - d)/c$) with one of the homozygote type in large majority, $AA$ or $aa$ respectively,
- one 'small' population (with a size smaller than $(b - d)/c$) with a large proportion of individuals of type $aa$ (resp. $AA$) and $Aa$.

This result is rather unexpected since $(\beta b - d)/c$ is the maximal equilibrium population size of an isolated population whereas $(b - d)/c$ is smaller than the minimal one. Indeed, the maximal birth rate of any individual is $\beta b$, which is its birth rate when surrounded by individuals with the same phenotype, whereas its minimal birth rate is $b$ if surrounded by individuals with different phenotypes. In all cases, its death rate is the sum of its natural death rate, $d$, and of the competition death rate which is equal to the product of $c$ and of the total population size in its patch. As a consequence, in an isolated patch without any migration, this leads to a maximal (resp. minimal) equilibrium.

### 3.2. Dominance between alleles

We now assume a total dominance of the allele $A$, so that $Aa$ heterozygotes display the same phenotype and behaviour as $AA$ homozygotes.

#### 3.2.1. System without migration

When there is no migration ($p = 0$), the system admits two stable fixed points, $(z_{AA,1} = \zeta, z_{AA,1} = 0, z_{aa,1} = 0)$ (fixation of allele $A$) and $(z_{AA,1} = 0, z_{AA,1} = 0, z_{aa,1} = \zeta)$ (fixation of allele $a$), and one unstable fixed point with persistence of all three genotypes (see Appendix B.3). In this case we were only able to give a sufficient condition on the initial number of individuals of different types for the system to converge to the stable fixed point characterizing the fixation of allele $A$: if $z_{AA,1}(0) \geq z_{aa,1}(0)$, the solution converges to the stable equilibrium $(\zeta, 0, 0)$.  

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Figure 3: Number of individuals in both patches under hypothesis (1). $\beta = 1.1$ and $p = 5$. Colors: the dynamics of the number of individuals in the patch 1 (resp. 2) are represented in red (resp. black), the dynamics of the number of individuals with genotype $AA$ (resp. $Aa$, $aa$) are represented using a full line (resp. dashed line, dotted line) The initial conditions are $z_{AA,1}(0) = z_{AA,2}(0) = z_{AA,2}(0) = 0.1$, $z_{AA,1}(0) = 2$, $z_{aa,1}(0) = 1$ and $z_{aa,2}(0) = 2$.

Figure 4: Number of individuals carrying each genotypes and their migration rates under hypothesis (2). $\beta = 1.1$ and $p = 5$. The initial conditions are $z_{AA,1}(0) = z_{AA,2}(0) = z_{AA,2}(0) = 0.1$, $z_{AA,1}(0) = 2$, $z_{aa,1}(0) = 1$ and $z_{aa,2}(0) = 2$. Colors: (a) the dynamics in the patch 1 (resp. 2) are represented in red (resp. black), the dynamics of the number of individuals with genotype $AA$ (resp. $Aa$, $aa$) are represented using full (resp. dashed, dotted) lines; (b) the migration from patch 1 to patch 2 (resp. 2 to 1) is drawn in red (resp. black), the migration of $aa$-individuals (resp. $AA$) is represented using dotted (resp. full) lines.
3.2.2. Fixed points of the system with migration

When there is a migration between the two patches \((p > 0)\), once again the dynamics is much more complex and we were unable to obtain convergence results. However we were able to describe some of the fixed points and determine their stability (see Appendix C.3). There are exactly four fixed points with monomorphic populations in both patches, which are the same as in the case of codominance: fixation of \(A\) in both patches \((\zeta_{AA,1} = 0, \zeta_{AA,2} = 0, \zeta_{aa,1} = 0, \zeta_{aa,2} = 0)\), fixation of \(a\) in both patches \((0, 0, 0, 0)\), or fixation of different alleles in the two patches. \((\zeta, 0, 0, 0, 0, 0)\) and \((0, 0, 0, 0, 0, 0)\).

The first two fixed points are stable for all the parameters values. The two last fixed points admit five negative eigenvalues and one null eigenvalue but we were not able to conclude on their stability. Since the recessive allele \(a\) has no influence on the phenotypes of \(Aa\) heterozygotes, it behaves neutrally with respect to mating and migration behaviour when occurring in heterozygotes. This neutral behaviour may substantially complexify the two-populations dynamics observed here.

Numerical simulations were then performed to study the influence of preference and migration parameters on the equilibria reached.

3.2.3. Fixation of the dominant allele \(A\)

In many simulations assuming an asymmetrical initial state (more \(a\) alleles in one patch and more \(A\) alleles in the other patch), the fixation of the dominant allele \(A\) was observed, when preference was strictly larger than 1 (Fig. [a]). Dominance of allele \(A\) makes the phenotype \(A\) (displayed by both \(AA\) and \(Aa\) genotypes) more frequent therefore provoking its fixation through assortative mating advantage. When allele \(A\) was in minority at initial state however, its fixation happened in much less simulations, because the large initial frequency of genotypes \(aa\) displaying phenotype \(a\) overrides the dominance effect (Fig. [b]).

Interestingly, although increasing migration promotes the fixation of the dominant allele \(A\) through its homogenizing effect, increasing preference tends to weaken this fixation. This non-trivial effect may stem from the limitation of migration when homogeneous population emerges: individuals matching the predominant phenotype within a patch migrates less. Therefore, when preference is strong and populations are initially differentiated, equilibria with fixation of different alleles in the two populations might be frequent, despite the frequency-dependent advantage of the phenotype carried by the dominant allele.

3.2.4. Conditions for differentiated populations

As observed in Fig. [7], simulations with initial differentiation mainly result in the fixation of different alleles in populations 1 and 2 when the preference coefficient \(\beta\) increases and migration strength is not too high. However, it is worth noting that differentiated populations subsist for values of the migration parameter \(p\) much higher than in both codominant cases (see Figure [1]). When allele \(a\) is predominant at initial state in both patches, simulations mostly lead to the fixation of the recessive allele \(a\) (data not shown). Note that around 25\% of simulations lead to differentiated populations whereas in the haploid version of the model studied in (Coron et al. 2016) differentiated populations could emerge only when the initial
state was asymmetrical. Note also that in some parameters regions (small preference parameter $\beta$ or high migration strength $p$) no simulation leads to differentiated populations. This may indicate that equilibria ($\xi, 0, 0, 0, 0, \xi$ and $0, 0, \xi, \xi, 0, 0$) (see Section 3.2.2) are unstable for such parameters.

### 3.2.5. Polymorphic equilibria

![Figure 8: Population sizes and migrations under dominance hypothesis.](image)

Figure 8: Population sizes and migrations under dominance hypothesis. $\beta = 1.5$ and $p = 5$. The initial conditions are $\omega_{0,1}(0) = 0.5$ and $0.1$ for the initial number of individuals with the other genotypes. Colors: (a) the dynamics in the patch 1 (resp. 2) are represented in red (resp. black), the dynamics of the number of individuals with genotype $AA$ (resp $Aa$, $aa$) are represented using full (resp. dashed, dotted) lines; (b) the migration from patch 1 to patch 2 (resp. 2 to 1) is drawn in red (resp. black), the migration of $aa$-individuals (resp. $AA$) is represented using dotted (resp. full) lines.

In some cases, even if initial conditions are asymmetrical (more $a$ alleles in one patch and more $A$ alleles in the other patch), genetic polymorphism can persist in one or both populations. However, the populations are almost phenotypically monomorphic in both patches: almost only $aa$ individuals in one patch, and almost only $AA$ and $Aa$ individuals in the other one (see Figure 8 and 9). As a consequence, individuals reproduce at their maximal birth rate $b\beta$ and do not migrate, and the population sizes in both patches are close to their carrying capacity $(b\beta - d)/c$.

![Figure 9: Proportions of different genotypes in the two patches at equilibrium.](image)

Figure 9: Proportions of different genotypes in the two patches at equilibrium. $\xi_{4,1} = 0.01$, $\omega_{1,1} = 0.009$, $\omega_{0,1} = 3.96$, $\omega_{3,2} = 3.45$, $\omega_{0,2} = 0.51$, $\omega_{1,2} = 0.02$. Total population sizes in patch 1 and 2 very close to $(b\beta - d)/c = 4$. Same parameters, initial conditions and colors than in Figure 8.

### 4. Discussion

#### 4.1. Effect of ploidy on population differentiation

Altogether, these results show that simulations of diploid organisms assuming codominance between alleles depart from equilibria observed in the haploid model. Notably, migration limits the probability of population differentiation in the diploid model which was not observed in haploids. Populations differentiation tightly depends on initial conditions, because alleles with high frequencies are strongly advantaged by homogamy, with a positive frequency-dependent selection regime, favouring fixation of the predominant phenotype within populations. Because migration depends on the number of individuals with different phenotypes, population differentiation is quickly achieved in the haploid model because of a rapid decrease of migration as soon as differentiation starts, until a complete isolation of the two populations, which fixed different alleles. In the diploid model however, when the two alleles are codominant, the presence of heterozygotes with intermediate phenotypes promotes migration even when populations are initially differentiated, and frequently leads to the fixation of a single allele throughout both connected populations. The discrepancy observed here between haploid and diploid assumptions highlights the need to consider the effect of ploidy in spatially-structured models of trait evolution, because the presence of intermediate phenotype can interfere in the differentiation process.

#### 4.2. Effect of intermediate phenotypes’ behaviour on polymorphism

Evolution of traits under disruptive selection are known to strongly depend on heterozygotes fitness (Rueffler et al. 2006), with for instance reinforcement of the differentiation process when heterozygotes suffer from a reduced fitness. Depending on the assumption regarding codominance, the resulting equilibrium slightly differed. The absence of preference of heterozygotes for their own phenotypes (hypothesis (2)) can promote polymorphism of the trait under sexual selection, notably when population are initially uneven. These heterozygotes do not migrate and reproduce equally with any genotypes. When they initially occur in significant proportion within population, it promotes migration of homozygous genotypes and limits fixation of the initially predominant allele. This contrasts with the co-dominance drawn from hypothesis (1), where heterozygotes can migrate and are half less preferred by homozygotes. In this case, fixation of a single allele throughout both populations is always achieved when the same allele is predominant in both populations at initial state.

Empirical data on mating behaviour of heterozygotes with intermediate phenotypes are scare. In *Heliconius* butterflies, wing colour pattern is known to be an important visual cue for choosing mate: in a recent review on mating preference of F1 hybrids between different pairs of Heliconius species, (Merot et al. (2017)) show that hybrids can either display a preference for one out the two parental colours or no preference. In the specific case of *Heliconius heurippa*, which displays a red and white colour pattern, which can be obtained by
crossing its red sister species \textit{H. melpomene} to the white sister species \textit{H. cydno}, assortative mate preferences have been demonstrated (Mavarez et al. (2006)). This assortative mating has been hypothesized to favour the emergence of the species \textit{H. heurippa}, putatively created by hybridization events between \textit{H. melpomene} and \textit{H. cydno} (Jiggins et al. (2009)).

Migration behaviour of intermediate phenotypes is also rarely characterized in natural populations. In the stick insect \textit{Timema christina}, two ecotypes specialized on different host-plant coexist and display different body colour, camouflaged on their respective host-plant leaves: intermediates display brown morph, camouflaged on both host-plant trunks and can thus move between host-plants without suffering an increased predation. These intermediate phenotypes are thus suspected to promote gene flow between the two main ecotypes, and to limit ecological speciation in this species (Comeault et al. (2015)).

We therefore hope that our predictions on the important impact of co-dominant heterozygotes behaviour on the evolution of mating trait differentiation will motivate further empirical research on mating and migration behaviour of intermediate phenotypes.

4.3. Evolutionary consequences of dominance for population differentiation and speciation

The fixation of the recessive allele \( a \) when initially predominant in both populations is rarer when the alternative allele is dominant as compared to codominant. Dominant allele spreads among populations more easily than codominant one because of Haldane’s sieve effect (Haldane (1927)). Assuming strict dominance, fixation of the dominant allele throughout both population is thus frequent, and favoured when predominant in both populations (data not shown). This is in accordance with other models of population differentiation with local adaptation, where dominant phenotypes tend to spread throughout populations (e.g. ‘dominance drive’ interacting with local selection on mimetic coloration (Mallet (1986))).

However, the invasion of the dominant haplotype throughout both populations is limited when initial populations display uneven proportions of the two alleles, leading to either (1) population differentiation or (2) persistent polymorphism within populations.

(1) Dominance may reinforce population differentiation, because heterozygotes display the dominant phenotype and therefore rapidly increase the number of individuals carrying this phenotype within one population, therefore causing a decrease in migration between populations. Consequently, population differentiation is more frequently observed when one allele is dominant as compared to co-dominant, even when assuming a high migration rate.

(2) Depending on the initial distribution of heterozygotes among populations, polymorphism can also be maintained within a population where the dominant phenotype is frequent: heterozygotes then display the preferred phenotype and therefore do not suffer from mate rejection and scarcely migrates. This last result is in accordance with a recent paper (Schneider et al. (2016)), where the authors explore the consequences of dominance at loci involved in genetic incompatibilities on the dynamics of speciation in a spatially-explicit individually centered model. They observed that the distance between mates necessary for a spatial mosaic of species to emerge needed to be more restricted in model assuming diplodity with strict dominance as compared to haploid model. This highlights how dominance may modulate spatial differentiation and emergence of well-separated species. Altogether this stresses out the need for diploid models of speciation, and should stimulate empirical comparisons of speciation dynamics driven by adaptive or sexually-selected traits displaying contrasted dominance relationships.

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Appendix A. Definition of the models

In these Supplementary Materials, we will study some properties of the dynamical systems governing the evolution of the population. In what follows, we denote the number of individuals of type \( \alpha \) in the patch \( i \) at time \( t \) for any \( \alpha \in \{AA, Aa, aa\} \), \( i \in \{1, 2\} \) and \( t \geq 0 \) by \( z_{\alpha i}(t) \). Moreover we denote the total number of individuals in the patch \( i \) at time \( t \) by

\[ N_i(t) := z_{AAi}(t) + z_{Aai}(t) + z_{aai}(t). \]

Finally, we recall that the parameter

\[ \zeta := \frac{h\beta - d}{c} \]

is the equilibrium size of a monomorphic AA or aa population. It will be a characteristic quantity in many equilibria for the three dynamical systems.

In the codominant case, we consider two different models, depending on the heterozygotes behaviour:

(1) Either the preference expressed by an individual is an ‘average preference’ of its alleles (\( \beta \) for pairs (\( AA, AA \)), (\( aa, aa \)) and (\( Aa, Aa \)), \( (\beta + 1)/2 \) for pairs (\( AA, Aa \)) and (\( aa, Aa \)), and 1 for couples (\( AA, aa \))) and the migration rate follows the same rule.

(2) Or heterozygotes express no preference and thus do not migrate (in this case only the homozygotes express a preference towards individuals of the same genotype). The preference parameter is thus \( \beta \) for pairs (\( AA, AA \)) and (\( aa, aa \)), and 1 for the other pairs.

The parameters \( b, d \), and \( c \) are ecological parameters, describing the minimal birth rate, death rate, and competition pressure of individuals. They are shared by all the population. The parameter \( \beta \) measures the strength of the sexual preference: \( \beta = 1 \) means no preference, and a large \( \beta \) indicates a strong
preference. We are only interested in homogamy in this work, and \(\beta\) will always be larger than one. Finally, the parameter \(p\) describes the maximum migration rate of an individual. The migration rate of an individual is the product of this parameter \(p\) and of the proportion of 'non-suitable' mates in its patch.

Let us now explain how we obtain the dynamical systems governing the evolution of the population. We will go into details for the first codominant model. The other models follow the same ideas.

Individuals are hermaphroditic and diploid. At a rate \(B > \beta B\), they play a 'female' role by looking for a mate to reproduce. They encounter uniformly an individual, the 'father', in the population. If this individual has the same phenotype, the probability that they mate and produce an offspring is \(\beta B\). If this is a pair formed by a homozygote and a heterozygote (that is of the form \((AA, Aa)\) or \((aa, Aa)\)), then the probability that they mate and produce an offspring is \(b(\beta + 1)/2B\). Finally if it is a pair of homozygotes with different phenotypes, the probability of successful mating is \(b/B\).

Let us first consider the births when an AA individual reproduces as a female. In the patch 1, they will generate:

- an offspring of type AA in the patch 1 at a rate
  \[
  \frac{Bz_{AA,1}}{z_{AA,1} + z_{AA,1} + z_{AA,1}} = \frac{B(\beta B + \beta + 1)z_{AA,1}}{Bz_{AA,1} + (\beta B + 2)z_{AA,1}}.
  \]

  Indeed, as we consider a Mendelian reproduction, parents of genotypes \(AA\) and \(Aa\) generate an offspring of type \(AA\) with a probability 1/2 and an offspring of type \(Aa\) with a probability 1/2.

- an offspring of type \(Aa\) in the patch 1 at a rate
  \[
  \frac{Bz_{AA,1}}{z_{AA,1} + z_{AA,1} + z_{AA,1}} = \frac{B(\beta B + \beta + 1)z_{AA,1}}{Bz_{AA,1} + (\beta B + 2)z_{AA,1}}.
  \]

We can perform the same type of calculation when an individual of genotype \(Aa\) or \(aa\) reproduce as a female. We refer to Section Model in the main text for the rates at which individuals die and migrate. We finally get for the first model (COD1):

\[
\begin{align*}
\dot{z}_{AA,j} &= \frac{b}{N_j} \left( \beta z_{AA,j} + \frac{\beta + 1}{2} z_{AA,1} z_{AA,j} + \frac{\beta z_{AA,j}}{4} \right) - (d + cN_j)z_{AA,j} \\
&\quad - p \frac{z_{AA,1} + z_{AA,1} + z_{AA,1}}{N_j} z_{AA,j} + p \frac{z_{AA,1} + z_{AA,1}}{N_j} z_{AA,j}.
\end{align*}
\]

The second codominant model writes

\[
\begin{align*}
\dot{z}_{AA,j} &= \frac{b}{N_j} \left( \beta z_{AA,j} + \frac{\beta + 1}{2} z_{AA,1} z_{AA,j} + \frac{\beta z_{AA,j}}{4} \right) - (d + cN_j)z_{AA,j} \\
&\quad - p \frac{z_{AA,1} + z_{AA,1} + z_{AA,1}}{N_j} z_{AA,j} + p \frac{z_{AA,1} + z_{AA,1}}{N_j} z_{AA,j}.
\end{align*}
\]

In the dominant case, only individuals \(aa\) express the phenotype \(a\). Other individuals are of phenotype \(A\). The population dynamics in this case writes:

\[
\begin{align*}
\dot{z}_{Aa,1} &= \frac{b}{N} \left( \beta z_{Aa,1} + \frac{\beta + 1}{2} z_{Aa,1} z_{Aa,1} + \frac{\beta z_{Aa,1}}{4} \right) - (d + cN)z_{Aa,1} \\
&\quad - p \frac{z_{Aa,1} + z_{Aa,1} + z_{Aa,1}}{N} z_{Aa,1} + p \frac{z_{Aa,1} + z_{Aa,1}}{N} z_{Aa,1}.
\end{align*}
\]

Notice that the dynamical systems governing the population dynamics in the co-dominant and the dominant cases can be obtained as large population limits of stochastic individual based models (see Coron et al. [2016]). The mechanism of mating preference presented in this model is similar to the ones classically used in ecology literature (see for instance Gavrilets and Boake [1998], Matessi et al. [2002], Bürger and Schneider [2006], Servedio [2010] and references therein). The non usual form of the equations comes from the fact that we model a varying size population evolving in continuous time and with overlapping generations, whereas classical models consider discrete non overlapping generations models with an infinite population size (see Section 'Discussion of the model’ in Coron et al. [2016]) for a detailed comparison.

To ensure the survival of the population and that the total population size remains bounded, we make the following assumptions:

\[ b > d > 0 \quad \text{and} \quad c > 0. \]

We recall that we are interested in the case of assortative mating, which means that

\[ \beta \geq 1. \]
Appendix B. Behaviour of the system without migration

Let us first study the behaviour of the system when there is no migration. In this case the two patches have independent dynamics, and it is enough to study one patch.

Appendix B.1. First codominant case

We will prove the following result:

Lemma 1. If \( p = 0 \), there are two stable and one unstable fixed points in the patch \( i \) for \( i \in \{1, 2\} \):

\[
(\zeta, 0, 0), \quad (0, 0, \zeta) \quad \text{and} \quad (\delta \xi, \xi, \delta \xi),
\]

where \( \delta \) is the unique positive root of the polynomial functional

\[
P(X) := X^3 + \frac{1}{2} X^2 - \frac{1}{4} X - \frac{\beta}{8},
\]

and

\[
\xi := \frac{b(\delta + \beta/2) - d}{2(\delta + 1)c}.
\]

Moreover, we have the following asymptotic behaviours for the dynamical system \( (A.1) \):

- If \( z_{AA}(0) > z_{aa}(0) \), then the solution converges to the stable fixed point \( (\zeta, 0, 0) \).
- If \( z_{AA}(0) = z_{aa}(0) \), then the solution converges to the unstable fixed point \( (\delta \xi, \xi, \delta \xi) \).
- If \( z_{AA}(0) < z_{aa}(0) \), then the solution converges to the stable fixed point \( (0, 0, \zeta) \).

Proof. To begin with, we describe the different stable fixed points in the codominant case. We recall that the dynamics of the system in one patch is given by the system of equations:

\[
\begin{align*}
\dot{z}_{AA}(t) &= \frac{b}{N} \left( \beta \zeta_{AA}^2 + \frac{\beta + 1}{2} z_{AA} z_{aa} + \frac{\beta^2}{4} z_{aa}^2 \right) - (d + cN) z_{AA} \\
\dot{z}_{aa}(t) &= \frac{b}{N} \left( \beta \zeta_{aa}^2 + \frac{\beta + 1}{2} z_{aa} (z_{AA} + z_{aa}) + 2 \zeta_{AA}z_{aa} \right) - (d + cN) z_{aa} \\
\dot{z}_{aa}(t) &= \frac{b}{N} \left( \beta z_{aa}^2 + \frac{\beta + 1}{2} z_{aa} (z_{aa} + 2 \zeta_{AA} z_{aa}) + 2 \zeta_{AA} z_{aa} \right) - (d + cN) z_{aa},
\end{align*}
\]

where \( N = z_{AA} + z_{aa} + z_{aa} \).

The fixed points \( (z_{AA}, z_{aa}, z_{aa}) \) are solutions to the following system of equations:

\[
\begin{align*}
\frac{b}{N} \left( \beta z_{AA}^2 + \frac{\beta + 1}{2} z_{AA} z_{aa} + \frac{\beta^2}{4} z_{aa}^2 \right) &= (d + cN) z_{AA} \\
\frac{b}{N} \left( \beta z_{aa}^2 + \frac{\beta + 1}{2} z_{aa} (z_{AA} + z_{aa}) + 2 \zeta_{AA}z_{aa} \right) &= (d + cN) z_{aa} \\
\frac{b}{N} \left( \beta z_{aa}^2 + \frac{\beta + 1}{2} z_{aa} (z_{aa} + 2 \zeta_{AA} z_{aa}) + 2 \zeta_{AA} z_{aa} \right) &= (d + cN) z_{aa}.
\end{align*}
\]

Monomorphic equilibria

We first check that if \( z_{aa} = 0 \) for \( \alpha \in \{A, a\} \), then \( z_{aa} \) is necessarily equal to 0. Hence we obtain the two following monomorphic fixed points:

\[
(\zeta, 0, 0) \quad \text{and} \quad (0, 0, \zeta).
\]

The eigenvalues for these fixed points are

\[
\begin{pmatrix}
-\beta \delta, \beta \delta - \beta + d
\end{pmatrix}.
\]

They are all negative under our assumptions.

If \( z_{aa} > 0 \) then from the first and the last equations in \( (B.2) \) we see that necessarily \( z_{AA} > 0 \) and \( z_{aa} > 0 \). Hence we look for a fixed point with the three coordinates positive. From the first and the last equations in \( (B.2) \) we get that

\[
(d + cN) z_{AA} z_{aa} = z_{aa} \left( \beta z_{AA}^2 + \frac{\beta + 1}{2} z_{AA} z_{aa} + \frac{\beta^2}{4} z_{aa}^2 \right) = z_{AA} \left( \beta z_{aa}^2 + \frac{\beta + 1}{2} z_{aa}^2 + \frac{\beta^2}{4} z_{aa}^2 \right),
\]

which yields

\[
(z_{AA} - z_{aa}) (z_{AA} - z_{aa}) = 0.
\]

Hence, either \( 4 z_{AA} z_{aa} = \frac{z^2_{AA}}{4} \) or \( z_{aa} = z_{AA} \).

Case \( 4 z_{AA} z_{aa} = \frac{z^2_{AA}}{4} \)

By expressing in two different ways \( (d + cN) N \) thanks to the second and last equations in \( (B.2) \) and replacing \( z_{AA} \) by \( z_{aa} \), we get

\[
\frac{1}{z_{aa}} \left( \beta z_{aa}^2 + \frac{\beta + 1}{2} z_{aa} z_{aa} + \frac{\beta^2}{4} z_{aa}^2 \right) = \frac{1}{z_{aa}} \left( \beta^2 z_{aa} + \frac{\beta + 1}{2} z_{aa} \left( \frac{z^2_{aa}}{4} + z_{aa} \right) + \frac{\beta^2}{2} \right).
\]

This implies

\[
\beta - \frac{1}{2} \left( z_{aa} + \frac{z^2_{aa}}{4} \right) = 0,
\]

and contradicts the fact that all the fixed point coordinates are positive.

Case \( z_{aa} = z_{AA} \)

The fixed point is thus of the form \( (x, y, x) \), with \( x > 0 \) and \( y > 0 \). Equalizing the first equation of \( (B.2) \) divided by \( y \) and the second one divided by \( y \), we find

\[
\begin{pmatrix}
\beta x + \frac{\beta + 1}{2} \frac{y^2}{x} + \frac{\beta^2}{4}
\end{pmatrix} = \begin{pmatrix}
\beta \frac{y}{y} + (\beta + 1) \frac{x^2}{y} + \frac{\beta^2}{4}
\end{pmatrix}
\Rightarrow \begin{pmatrix}
\frac{x}{y}^3 + \frac{1}{2} \frac{x}{y} - \frac{1}{4} \frac{y}{x} - \frac{\beta}{8} = 0.
\end{pmatrix}
\]
Let us set \( \delta := \frac{x}{y} > 0 \). The polynomial function \( P(X) = X^3 + \frac{1}{4}X^2 - \frac{1}{4}X - \frac{\beta}{2} \), has only one positive root and this latter belongs to \([1/2, +\infty[\). Indeed by taking the first derivative of \( P \) we can check that \( P(X) \) is increasing until \( x = -1/2 \), then decreasing until \( X = 1/6 \) and then increasing again. As \( P(-1/2) = (1 - \beta)/8 < 0 \), we conclude that there is only one positive root. Finally we can check that \( P(1/2) < 0 \). Then using the fact that \( x = \delta y \) and the second equation of \((B.2)\), we conclude that there exists only one equilibrium with positive coordinates which is
\[
(\delta \xi, \xi, \delta \xi) \quad \text{where} \quad \xi := \frac{b(\delta + \beta/2) - d}{(2\delta + 1)c},
\]
and \( \delta \) is the unique positive solution of \( P(X) = 0 \).

Using again that \( P(\delta) = 0 \), we can write the eigenvalues of the Jacobian Matrix at \( (\delta \xi, \xi, \delta \xi) \) as
\[
\left( \frac{bh}{4\delta}(2\delta - 1), \lambda_2, \lambda_3 \right),
\]
where \( \lambda_2 \) and \( \lambda_3 \) are complex numbers. As \( \delta \in ]1/2, +\infty[\), this ensures that the fixed point \((\delta \xi, \xi, \delta \xi)\) is unstable.

We now prove that its stable manifold is of dimension 2 and is exactly the set
\[
\mathcal{A}^* = \{z \in (\mathbb{R}^+)^3, z_{AA} = z_{aa}\}.
\]

By subtracting the third equation of \((B.1)\) to the first one, we get
\[
\dot{z}_{AA} - \dot{z}_{aa} = (z_{AA} - z_{aa}) \left( \frac{bh - d - cN - b\beta - 1}{2} - \frac{1}{N} z_{aa} \right),
\]
and we deduce that the set \( \mathcal{A}^* \) is invariant under the flow defined by \((B.1)\). Thus, let us assume that the initial condition \( z_{AA}(t) = z_{aa}(t) \). Moreover,
\[
\frac{d}{dt} \left( \frac{\dot{z}_{AA}(t) - 1}{\dot{z}_{AA}(t)} \right) = -\frac{2b}{\delta z_{AA}(t)N} \left[ z_{AA} + \frac{\beta + \delta}{2} z_{AA} - \frac{1}{2} z_{aa} \right].
\]

Since \( \dot{P}(\delta) = 0 \), \( \delta \dot{z}_{AA} \) is a root of the polynomial function with respect to the variable \( z_{AA} \) of the right hand side. Thus
\[
\frac{d}{dt} \left( \frac{\dot{z}_{AA}(t) - 1}{\dot{z}_{AA}(t)} \right) = -\frac{2b}{\delta z_{AA}(t)N} \left( z_{AA} + \frac{\beta + \delta}{2} z_{AA} - \frac{1}{2} z_{aa} \right).
\]

The polynomial function of degree two of the r.h.s in \((B.5)\) is non-negative. This ensures that the function
\[
W_1(z) = \ln \left( \frac{z_{AA}}{\dot{z}_{AA}} - 1 \right)
\]
is a Lyapunov function for the dynamical system \((B.1)\) restricted on \( \mathcal{A}^* \). Theorem 1 in \cite{Lasalle1960} implies that the flow \( z(t) \) converges to \( \{(\delta \xi, \xi, \delta \xi)\} \), the largest invariant set included in \( \{z_{AA} = \delta z_{aa}\} \cap \mathcal{A}^* \). This implies that \( \mathcal{A}^* \) is included in the stable manifold of \((\delta \xi, \xi, \delta \xi)\).

Let us now deal with the solution outside \( \mathcal{A}^* \). First note that by \((B.3)\), the two sets
\[
\mathcal{A}^* = \{z \in (\mathbb{R}^+)^3, z_{AA} > z_{aa}\} \quad \text{and} \quad \mathcal{A}^e = \{z \in (\mathbb{R}^+)^3, z_{AA} < z_{aa}\}
\]
are two invariant sets under the dynamical system \((B.1)\). Since the system \((B.1)\) is symmetric with respect to \( z_{AA} \) and \( z_{aa} \), we only have to deal with one of the previous sets, the dynamics in the other one being symmetric. In what follows, we study the dynamics in the set \( \mathcal{A}^* \).

On the set \( \mathcal{A}^* \), the Lyapunov function
\[
W_2(z) = \ln \left( \frac{z_{AA} + z_{aa} + \beta z_{aa}}{z_{AA} - z_{aa}} \right)
\]
is well defined and is clearly non-negative. Moreover, its derivative is
\[
\frac{d}{dt} W_2(z) = -\frac{b(\beta - 1)}{2N(z_{AA} + z_{aa} + \beta z_{aa})} \leq 0,
\]
and this derivative is equal to 0 on the set \( \mathcal{O}^* = \{z \in \mathcal{A}^*, z_{aa} = 0\} \). The largest invariant set with respect to \((B.1)\) including in \( \mathcal{O}^* \) is \( \{z \in \mathcal{A}^*, z_{aa} = 0\} \) and it is obvious that any trajectory starting from this invariant set converges to \( (\zeta, 0, 0) \). Using Theorem 1 in \cite{Lasalle1960}, it is sufficient to conclude that any trajectory starting from \( \mathcal{A}^* \) converges to \( (\zeta, 0, 0) \).

Appendix B.2. Second codominant case

Using the same ideas and the same proofs as in the previous section \cite{Appendix B.1}, we prove the following lemma for the codominant model when heterozygotes are not preferred and do not migrate:

**Lemma 2.** If \( p = 0 \), there are two stable and one unstable fixed points in the patch \( i \) for \( i \in \{1, 2\} \):
\[
(\zeta, 0, 0), \quad (0, 0, \zeta) \quad \text{and} \quad (\delta \xi', \xi', \delta \xi'),
\]
where \( \delta' \) is the unique positive root of the polynomial functional
\[
Q(X) := X^3 + \frac{2 - \beta}{2} X^2 - \frac{1}{4} X - \frac{1}{8},
\]
and
\[
\xi' := \frac{b(\delta' + 1/2) - d}{(2\delta' + 1)c}.
\]

Moreover, we have the following asymptotic behaviours for the dynamical system \((A.1)\):

- If \( z_{AA}(0) > z_{aa}(0) \), then the solution converges to the stable fixed point \( (\zeta, 0, 0) \).
- If \( z_{AA}(0) = z_{aa}(0) \), then the solution converges to the unstable fixed point \( (\delta \xi', \xi', \delta \xi') \).
- If \( z_{AA}(0) < z_{aa}(0) \), then the solution converges to the stable fixed point \( (0, 0, \zeta) \).

The proof is really similar except that we use the Lyapunov function
\[
W_3(z) = \ln \left( \frac{z_{AA} + z_{aa} + z_{aa}}{z_{AA} - z_{aa}} \right)
\]
to end it.
Appendix B.3. Dominant case

We recall that the dynamics of the system in one patch is given by the system of equations:

\[
\begin{align*}
\dot{z}_{AA}(t) &= \frac{b\beta}{N} \left( z_{AA} + \frac{1}{2} z_{AA} \right)^2 - (d + cN) z_{AA} \\
\dot{z}_{Au}(t) &= \frac{b}{N} \left( \beta z_{Au} + 2 z_{au} \right) \left( z_{AA} + \frac{1}{2} z_{AA} \right) - (d + cN) z_{Au} \\
\dot{z}_{au}(t) &= \frac{b}{N} \left( \beta^2 z_{au} + z_{aa} z_{Au} + \beta^2 \frac{1}{4} z_{Au} \right) - (d + cN) z_{au},
\end{align*}
\]

where \( N = z_{AA} + z_{Au} + z_{au} \).

In this section, we will prove the following result:

**Lemma 3.** The dynamical system (B.6) admits exactly three fixed points:

- Two stable fixed points
  \[(\zeta, 0, 0) \text{ and } (0, 0, \zeta).\]

- One unstable fixed point
  \[\frac{b(\beta + 1) - 2d}{4c} \left( \frac{1}{\beta + 1}, \frac{2}{\beta + 1 + 1}, \frac{1}{\beta + 1 + 1} \right).\]

**Proof.** The fixed points \((z_{AA}, z_{Au}, z_{au})\) are solutions to the following system of equations:

\[
\begin{align*}
\frac{b\beta}{N} \left( z_{AA} + \frac{1}{2} z_{AA} \right)^2 &= (d + cN) z_{AA} \\
\frac{b}{N} \left( \beta z_{Au} + 2 z_{au} \right) \left( z_{AA} + \frac{1}{2} z_{AA} \right) &= (d + cN) z_{Au} \\
\frac{b}{N} \left( \beta^2 z_{au} + z_{aa} z_{Au} + \beta^2 \frac{1}{4} z_{Au} \right) &= (d + cN) z_{au}
\end{align*}
\]

Again we can show that if \(z_{au} = 0\) for \(\alpha \in \{A,a\}\), then necessarily \(z_{Au} = 0\), and we find the two following monomorphic equilibria

\[(\zeta, 0, 0) \text{ and } (0, 0, \zeta)\]

with respective eigenvalues

\[0, -b\beta, d - b\beta\] and \(-b\beta, b - b\beta, d - b\beta)\).

Hence the equilibrium \((0, 0, \zeta)\) is stable. To find the stability of the equilibrium \((\zeta, 0, 0)\), we will use a Lyapunov function. First notice that the derivative of the total population size satisfies:

\[\frac{d}{dt} N = (b\beta - d - cN)N - 2b(\beta + 1) \frac{(z_{AA} + z_{Au})z_{au}}{N},\]

and the derivative of the difference \(z_{AA} - z_{au}\) satisfies:

\[\frac{d}{dt} (z_{AA} - z_{au}) = (z_{AA} - z_{au})(\beta\beta - d - cN) + b(\beta + 1) \frac{z_{Au}z_{au}}{N}.
\]

In particular, the set \(\mathcal{A} := \{z_{AA} \geq z_{au}\}\) is stable. Indeed, if we consider a point where \(z_{AA} = z_{au}\) then the previous derivative is positive and we stay in the set \(\mathcal{A}\). Moreover in this set

\[\frac{d}{dt} \ln \left( \frac{z_{AA} - z_{au}}{N} \right) = \frac{b(\beta - 1)}{N} \left( \zeta_{Au} + 2 \frac{(z_{AA} + z_{Au})z_{au}}{N} \right) \geq 0.
\]

We deduce that \(-\ln((z_{AA} - z_{au})/N)\) is a Lyapunov function which cancels out of the set \(\{z_{au} = 0\} \cup \{z_{AA} = z_{Au} = 0\}\). Beside the only fixed point in this set is \((\zeta, 0, 0)\). Applying Theorem 1 in [LaSalle (1959)], we deduce that any solution to (B.6) starting from \(\mathcal{A}\) converges to the fixed point \((\zeta, 0, 0)\).

Let us now find and study the positive equilibrium. By subtracting the second equality to the first one in (B.7), we get

\[\frac{\beta}{z_{Au}} \left( z_{AA} + \frac{1}{2} z_{Au} \right) = \frac{1}{z_{Au}} (\beta z_{Au} + 2 z_{au}),
\]

which gives the equality

\[\beta z_{Au}^2 = 4 z_{AA} z_{au}.
\]

Besides,

\[\frac{b}{z_{au}} \left( \beta^2 z_{au} + z_{Au} z_{Au} + \beta^2 \frac{1}{4} z_{Au} \right) = \frac{b\beta}{z_{Au}} \left( z_{Au} + \frac{1}{2} z_{Au} \right)^2 - b(\beta - 1) z_{au}.
\]

Hence, by subtracting the third to the first inequality in (B.7), we find

\[\frac{\beta}{z_{Au} z_{au}} \left[ z_{Au} \left( z_{AA} + \frac{1}{2} z_{Au} \right)^2 - z_{AA} \left( z_{Au} + \frac{1}{2} z_{Au} \right)^2 \right] + (\beta - 1) z_{au} = 0
\]

\[\iff \beta (z_{au} - z_{AA}) \left( \frac{1}{4} z_{Au} - z_{aa} z_{AA} \right) + (\beta - 1) z_{Au} z_{Au} z_{au} = 0.
\]

Finally, by using (B.8), we deduce

\[\frac{\beta - 1}{4} \left( z_{AA} - z_{Au} + z_{au} \right) = 0,
\]

which leads to

\[z_{AA} + z_{Au} = z_{au}.
\]

From (B.8) and (B.9), we get

\[z_{AA} = \frac{z_{Au}}{2} \left( \sqrt{\beta + 1} - 1 \right) \text{ and } z_{au} = \frac{z_{Au}}{2} \left( \sqrt{\beta + 1} + 1 \right).
\]

If we inject these inequalities in the derivative of \(z_{Au}\), we obtain

\[0 = \left( b \frac{\beta + 1}{2} - d - c z_{Au} \left( \sqrt{\beta + 1} + 1 \right) \right) z_{Au}.
\]

Hence

\[z_{Au} = \frac{b(\beta + 1) - 2d}{c(\sqrt{\beta + 1} + 1)}.
\]

We deduce that the positive equilibrium we are looking for, if it exists, has necessarily the following coordinates

\[\frac{b(\beta + 1) - 2d}{4c} \left( \frac{\sqrt{\beta + 1} - 1}{\sqrt{\beta + 1} + 1}, \frac{\sqrt{\beta + 1} + 1}{\sqrt{\beta + 1} + 1}, 1 \right).
\]
Conversely, we can check that this point is indeed an equilibrium. The eigenvalues of the Jacobian matrix at this point are \((2\beta(\sqrt{\beta + 1} + 1)^2)^{-1}\) times the roots of the polynomial

\[ x^3 + ax^2 + ex + f, \]

with

\[
0 > f = -2b\beta^3 (\beta^2 - 1)(b\beta + b - 2d) \\
\left( (\sqrt{\beta + 1} + 5)\beta^2 + 4(3\sqrt{\beta + 1}+ 1)\beta + 16\left( \sqrt{\beta + 1} + 1 \right) \right)
\]

and

\[
0 < a = 6b\beta + 6b\beta^2 \sqrt{1 + \beta} + 2b\beta^2 \sqrt{1 + \beta} - 4b\beta d \\
- 2b^2 d - 4\beta \sqrt{1 + \beta} d.
\]

We deduce that there are two negative and one positive eigenvalues. This equilibrium is thus unstable.

As a conclusion, in the dominant case, the only stable fixed points are \((\zeta, 0, 0)\) and \((0, 0, \zeta)\).

\[ \Box \]

Appendix C. Stability of the monomorphic fixed points in the system with migration

As the systems (A.1) and (A.3) are complex, we are not able to derive an analytical form for all the fixed points. As a consequence in the next two subsections we focus on the fixed points which are monomorphic in one patch, \((\zeta, 0, 0, 0, 0, 0)\), \((0, 0, 0, 0, 0, 0)\), \((\zeta, 0, 0, 0, 0, 0)\), \((0, 0, \zeta, 0, 0, 0)\), \((0, 0, 0, 0, \zeta, 0)\),

Appendix C.1. First codominant case

We will prove that for the first codominant model the monomorphic fixed points have the following properties:

**Lemma 4.** There are four fixed points which are monomorphic in every patch:

- \((\zeta, 0, 0, \zeta, 0, 0)\) and \((0, 0, \zeta, 0, 0, \zeta)\) are stable.
- \((\zeta, 0, 0, 0, 0, 0)\) and \((0, 0, \zeta, 0, 0, \zeta)\) are stable if \(2p < b\beta(\beta - 1)\) and unstable if \(2p > b\beta(\beta - 1)\).

Since the alleles \(a\) and \(A\) are codominant, the two fixed points \((\zeta, 0, 0, \zeta, 0, 0)\) and \((0, 0, \zeta, 0, 0, \zeta)\) have the same characteristics. The eigenvalues of the Jacobian Matrix at these fixed points are

\[
\left( -b\beta, -\frac{1}{2}(b\beta - 1), d - b\beta, d - b\beta, -b\beta - 2p, -\frac{1}{2}(b\beta - 1) + 2p \right).
\]

They are all negative, and we conclude that \((\zeta, 0, 0, \zeta, 0, 0)\) and \((0, 0, \zeta, 0, 0, \zeta)\) are two stable fixed points.

In the codominant case, the two fixed points \((\zeta, 0, 0, 0, 0, 0)\) and \((0, 0, \zeta, 0, 0, 0)\) have the same properties since the alleles \(a\)

and \(A\) are codominant. The eigenvalues of the Jacobian Matrix at these fixed points are

\[
\left( d - b\beta, d - b\beta, \frac{1}{4} \left( -\sqrt{b}\beta^2 + 2b\beta + 16p - 3b\beta + b \right), \right. \\
\left. \frac{1}{4} \left( -\sqrt{b}\beta^2 + 2b\beta + b + 16p - 3b\beta + b \right) \right),
\]

\[
\frac{1}{4} \left( -\sqrt{b}\beta^2 + 2b\beta + b + 2p - 12b\beta + 4p^2 - 3b\beta + b - 6p \right),
\]

\[
\frac{1}{4} \left( \sqrt{b}\beta^2 + 2b\beta + b + 2p - 12b\beta + 4p^2 - 3b\beta + b - 6p \right).
\]

All the eigenvalues, except the fourth one, are negative. The fourth eigenvalue is negative only if the migration parameter \(p\) is small enough:

\[
\frac{1}{4} \left( \sqrt{b}\beta^2 + 2b\beta + b + 16p - 3b\beta + b \right) < 0 \Rightarrow 2p < b\beta(\beta - 1)
\]

Hence the eigenvalues \((\zeta, 0, 0, 0, 0, 0)\) and \((0, 0, \zeta, 0, 0, 0)\) are stable only if \(2p < b\beta(\beta - 1)\).

Appendix C.2. Second codominant case

Lemma 4 is still valid for the second codominant case, although the eigenvalues of the fixed points are not the same:

\[
(-b\beta, b - b\beta, b - b\beta, -b\beta + d, -b\beta + d, -b\beta - 2p)
\]

for the fixed points \((\zeta, 0, 0, \zeta, 0, 0)\) and \((0, 0, \zeta, 0, 0, \zeta)\), and

\[
(-b\beta, d - b\beta, d - b\beta, -b\beta + b - 2p, \frac{1}{2}(-2b\beta - \sqrt{b}\beta + 8p + b),
\]

\[
\frac{1}{2}(-2b\beta + \sqrt{b}\beta + 8p + b))
\]

for the fixed points \((\zeta, 0, 0, 0, 0, \zeta)\) and \((0, 0, \zeta, 0, 0, \zeta)\).

Appendix C.3. Dominant case

In the dominant case, the two fixed points \((\zeta, 0, 0, \zeta, 0, 0)\) and \((0, 0, \zeta, 0, 0, \zeta)\) are not symmetrical, as the two alleles \(A\) and \(a\) do not have the same role. We prove the following Lemma.

**Lemma 5.** There are four fixed points which are monomorphic in every patch:

- \((0, 0, \zeta, 0, 0, \zeta)\) (equilibrium with genotype aa in both patches) is stable and there exists a neighborhood \(V^{aa}\) of \((0, 0, \zeta, 0, 0, \zeta)\) such that any solution starting from \(V^{aa}\) converges exponentially fast to the equilibrium,

- \((\zeta, 0, 0, \zeta, 0, 0)\) (equilibrium with genotype AA in both patches) is stable and there exists a neighborhood \(V^{AA}\) of \((\zeta, 0, 0, \zeta, 0, 0)\) such that any solution starting from \(V^{AA}\) converges to the equilibrium with a rate \(t \mapsto \frac{1}{t}\),

- \((\zeta, 0, 0, 0, 0, \zeta)\) and \((0, 0, \zeta, 0, 0, \zeta)\) are two equilibria whose Jacobian Matrices admit five negative eigenvalues and a null eigenvalue.
In the case of the two last equilibria, we were not able to prove theoretically their stability. Simulations of the solution seem to show that the stability depends on the values of the parameters.

**Proof.** **Equilibrium** $(0, 0, \zeta, 0, 0, \zeta)$: The fixed point $(0, 0, \zeta, 0, 0, \zeta)$ is the easiest to study, as all the eigenvalues of the Jacobian Matrix at this point are negative:

$$(-h\beta, b - h\beta, -h\beta + d, -h\beta + d, -h\beta + d - 2p, b - h\beta - 2p).$$

Hence, the equilibrium $(0, 0, \zeta, 0, 0, \zeta)$ is stable.

**Equilibrium** $(\zeta, 0, \zeta, 0, 0, 0)$: The second fixed point, $(\zeta, 0, \zeta, 0, 0, 0)$, is more involved to study, since the Jacobian Matrix at this point admits four negative eigenvalues, and 0 as an eigenvalue with multiplicity two:

$$(0, 0, -h\beta, -h\beta + d, -h\beta + d, -h\beta - 2p).$$

As a consequence, we have to go further to get the stability of this fixed point. The Jacobian Matrix at this fixed point is

$$
\begin{pmatrix}
-h\beta + d & -h\beta + d & -2h\beta + d - p & 0 & 0 & p \\
0 & 0 & 2b & 0 & 0 & 0 \\
0 & 0 & -h\beta - p & -h\beta + d & -h\beta + d & -2h\beta + d - p \\
0 & 0 & 0 & 0 & 0 & 2b \\
0 & 0 & 0 & 0 & 0 & -h\beta - p
\end{pmatrix}
$$

and its eigensystem is

$$(0, 0, 0, 0, -1, 1, 0, 0)$$

$$(0, -1, 1, 0, 0, 0, 0)$$

where the parameters $(h_{ij}, i \in \{1, 2, 3\}, j \in \{1, 2, 3, 4\})$ have to be computed. To compute these latter, we inject the expression of $h$ into (C.4) and compute the second order of the Taylor series which is the first non null order of the series. First we notice that the second order on the left hand side of (C.4) is null. As a consequence, we only have to develop the right hand side and identify the coefficients $h_{ij}$. We get

$$h : \begin{pmatrix} x_1 \\ x_2 \end{pmatrix} \mapsto \begin{pmatrix} h_{11} \\ h_{12} \\ h_{13} \\ h_{14} \\ h_{21} \\ h_{22} \\ h_{23} \\ h_{24} \end{pmatrix} x_1 x_2 + \begin{pmatrix} h_{31} \\ h_{32} \\ h_{33} \end{pmatrix} x_2^2 + O \left( \left\| \begin{pmatrix} x_1 \\ x_2 \end{pmatrix} \right\| \right)^3, \quad (C.5)
$$

Here for every $r \in \mathbb{N}$, $X \in C^r(\mathbb{R}, \mathbb{R}^3)$, $Y \in C^r(\mathbb{R}, \mathbb{R}^4)$, $G_1 \in C^r(\mathbb{R}^6, \mathbb{R}^2)$, $G_1(0, 0) = 0$, $DG_1(0, 0) = 0$, $G_2 \in C^r(\mathbb{R}^6, \mathbb{R}^4)$, $G_2(0, 0) = 0$, $DG_2(0, 0) = 0$, and $D$ is a diagonal matrix whose main diagonal is $(-h\beta, -h\beta + d, -h\beta + d, -h\beta + d - 2p)$. According to Theorem 2.12.1 in [Perko 2013], there exists a real function $h$ defined in a neighbourhood of $(0, 0)$ and with values in $\mathbb{R}^3$ such that $h(0) = 0$ and $Dh(0) = 0$, which defines the center manifold. That is to say: close to the null fixed point, $Y = h(X)$. The function $h$ satisfies

$$Dh(X) \cdot G_1(X, h(X)) = D \cdot h(X) + G_2(X, h(X)). \quad (C.4)$$

We only need the first non null order of the function $h$ in a neighbourhood of $(0, 0)$. Hence we are looking for a function which satisfies

$$h : \begin{pmatrix} x_1 \\ x_2 \end{pmatrix} \mapsto \begin{pmatrix} h_{11} \\ h_{12} \\ h_{13} \\ h_{14} \\ h_{21} \\ h_{22} \\ h_{23} \\ h_{24} \end{pmatrix} x_1 x_2 + \begin{pmatrix} h_{31} \\ h_{32} \\ h_{33} \end{pmatrix} x_2^2 + O \left( \left\| \begin{pmatrix} x_1 \\ x_2 \end{pmatrix} \right\| \right)^3, \quad (C.5)
$$

where the parameters $(h_{ij}, i \in \{1, 2, 3\}, j \in \{1, 2, 3, 4\})$ have to be computed. To compute these latter, we inject the expression of $h$ into (C.4) and compute the second order of the Taylor series which is the first non null order of the series. First we notice that the second order on the left hand side of (C.4) is null. As a consequence, we only have to develop the right hand side and identify the coefficients $h_{ij}$. We get

$$h = \begin{pmatrix} h_{11} \\ h_{12} \\ h_{13} \\ h_{14} \\ h_{21} \\ h_{22} \\ h_{23} \\ h_{24} \end{pmatrix} x_1 x_2 + \begin{pmatrix} h_{31} \\ h_{32} \\ h_{33} \end{pmatrix} x_2^2 + O \left( \left\| \begin{pmatrix} x_1 \\ x_2 \end{pmatrix} \right\| \right)^3, \quad (C.5)
$$

From the first equation in (C.3) we know that in a neighbourhood of $(0, 0)$, $X = G_1(X, h(X))$. Hence

$$\begin{pmatrix} \dot{x}_1 \\ \dot{x}_2 \end{pmatrix} = \begin{pmatrix} \frac{bc \beta}{(b\beta - d)(b\beta + 2p)} [-\beta(b\beta - 1) + 2p] x_1^2 + p(x_1^2 + x_2^2) \\ \frac{bc}{2(b\beta - d)(b\beta + 2p)} [p(x_1^2 + x_2^2) - \beta(b\beta - 1) + 2p] x_2^2 \end{pmatrix} + O \left( \left\| \begin{pmatrix} x_1 \\ x_2 \end{pmatrix} \right\| \right)^3.
$$

But we notice that the solutions $(\tilde{x}_1, \tilde{x}_2)$ of

$$\begin{pmatrix} \dot{\tilde{x}}_1 \\ \dot{\tilde{x}}_2 \end{pmatrix} = \begin{pmatrix} \frac{bc \beta}{(b\beta - d)(b\beta + 2p)} [-\beta(b\beta - 1) + 2p] \tilde{x}_1^2 + p(\tilde{x}_1^2 + \tilde{x}_2^2) \\ \frac{bc}{2(b\beta - d)(b\beta + 2p)} [p(\tilde{x}_1^2 + \tilde{x}_2^2) - \beta(b\beta - 1) + 2p] \tilde{x}_2^2 \end{pmatrix}, \quad (C.6)
$$

satisfy

$$\dot{\tilde{x}}_1 + \dot{\tilde{x}}_2 = -\frac{b^2 \beta \beta - 1}{2(b\beta - d)(b\beta + 2p)} (\tilde{x}_1^2 + \tilde{x}_2^2).$$

Moreover, using that $\tilde{x}_1^2 + \tilde{x}_2^2 \leq (z_1 + z_2)^2 \leq 2(z_1^2 + z_2^2)$ for any
\((z_1, z_2) \in \mathbb{R}^2\), we get

\[
- \frac{b^2 \beta (\beta - 1) c}{2 (b \beta - d) (b \beta + 2 p)} (\tilde{x}_1 + \tilde{x}_2)^2 \\
\leq \frac{b^2 \beta (\beta - 1) c}{4 (b \beta - d) (b \beta + 2 p)} (\tilde{x}_1 + \tilde{x}_2)^2.
\]

Hence, \(x_1 + x_2\) has a constant sign and converges to 0 with a rate \(t \mapsto \frac{1}{t}\) in a neighbourhood of the fixed point \((0, 0, 0, 0, 0)\). But by inversion of the matrix \(C\), we see that

\[
x_1 + x_2 = \frac{2}{\beta} (z_{a1} + z_{a2}) + z_{a1} + z_{a2}.
\]

This ends the proof of the stability of the fixed point \((\zeta, 0, 0, \zeta, 0, 0)\).

Notice that this method has been used recently in a similar system in Bovier and Neukirch (2017). In this paper the authors were interested in a system of diploid individuals, with dominance but without sexual preference and migration. Their center manifold was of dimension one.

**Equilibria**\((\zeta, 0, 0, 0, 0, \zeta)\) and \((0, 0, \zeta, 0, 0, 0)\): Those two equilibria with different monomorphic populations in the two patches are symmetrical. We only prove the results on \((0, 0, \zeta, \zeta, 0, 0)\). The eigenvalues of the Jacobian Matrix at this fixed point are

\[(0, -b \beta + d, -b \beta + d),\]

as well as the roots of the polynomial:

\[
P(X) = X^3 + (b (3 \beta - 1) + 3 p) X^2 + b^2 \beta (\beta - 1) + b^2 \beta p (3 \beta - 2) + 2 b p (\beta - 1) + (b^2 \beta (3 \beta - 2) + 2 b p (3 \beta - 1) + 2 p^2) X
\]

\[= X^3 + AX^2 + EX + F.
\]

We notice that the coefficients of \(P\) are positive. Hence any real root is negative. This proves that all the roots are negative in the case where the three roots are real numbers. The second possibility is that \(P\) admits one negative real root (denoted by \(-r\)) and two complex conjugate roots (denoted by \(\phi e^{i \theta}\) and \(\phi e^{-i \theta}\), \(\phi \in \mathbb{R}, \theta \in [0, 2 \pi]\)). We aim at showing that \(\cos \theta < 0\), which will ensure that all the roots of \(P\) have negative real parts.

With these notations, \(P\) can be rewritten as follows

\[
P(X) = X^3 + (\rho - 2 \phi \cos \theta) X^2 + \phi (\phi - 2 \rho \cos \theta) X + \rho \phi^2.
\]

As the coefficients of \(P\) are positive, we get

\[
\rho > 2 \phi \cos \theta \quad \text{and} \quad \phi > 2 \rho \cos \theta,
\]

which yields

\[
2 \cos \theta < \frac{\rho}{\phi} < \frac{1}{2 \cos \theta},
\]

and thus

\[
4 \cos^2 \theta < 1.
\]

But we also have the following series of inequalities:

\[
0 < b^2 \beta (2 + 7 \beta - 1) / 2 (b \beta - d) (b \beta + 2 p) (\beta - 1) p + 4 b (5 \beta - 1) p + 6 b^3
\]

\[
= AE - 2 F = (\rho - 2 \phi \cos \theta) \phi (\phi - 2 \rho \cos \theta) - 2 \rho \phi^2
\]

\[
= \phi^2 (4 \cos^2 \theta - 1) - 2 \phi \cos \theta (\phi^2 + \rho^2) \leq -2 \phi \cos \theta (\phi^2 + \rho^2).
\]

This implies that \(\cos \theta < 0\), as expected. Unfortunately, as we do not know explicitly the roots of \(P\), we cannot apply Theorem 2.12.1 in Ferko (2013) to get the behaviour of the solutions of \((B.15)\) in the center manifold and deduce the stability of the fixed point \((0, 0, \zeta, \zeta, 0, 0)\).

**Appendix D. Some properties of the system with migration**

**Appendix D.1. Polymorphic equilibria**

We were not able to determine all the polymorphic equilibria of the three dynamical systems governing the population dynamics in the two codominant and the dominant cases. Of course, thanks to our analysis of the cases without migration, we are able to give one unstable polymorphic equilibrium for each dynamical system:

- \((\delta \xi, \xi, \delta \xi, \xi, \delta \xi, \xi)\) for the first codominant model
- \((\delta \xi', \xi', \delta \xi', \xi', \delta \xi', \xi')\) for the second codominant model
- \((b \beta + d - \frac{d}{\sqrt{p+1}}) \left(\frac{\sqrt{p+1} - 1}{\sqrt{p+1} + 1}, \frac{2}{\sqrt{p+1} + 1}, \frac{2}{\sqrt{p+1} + 1} \right)\) for the model with dominance

To give an idea of the complexity of the dynamical systems under study, for the parameters \(b = 2, d = 1, c = 0.5, \beta = 1.1\) and \(p = 5\), Mathematica gives the numerical approximation of 9 polymorphic equilibria for the second codominant model.

**Appendix D.2. A majority allele**

Let us denote by \(\alpha\) the complement of \(\sigma \in [A, a]\). In both codominant models, if \(z_{a1}(0) \geq z_{a2}(0)\) for \(i = 1, 2\), then \(z_{a1}(t) \geq z_{a2}(t)\) for \(i = 1, 2\) and for every positive \(t\). Indeed if \((z_{a1}, \ldots, \alpha \in [A, A, A, a, i \in \{1, 2\}\) evolve according to the dynamical system \((A.1)\), we have

\[
z_{a1} - z_{a1} = (z_{a1} - z_{a1}) \left(\beta b - d - c N_i - \frac{b (\beta - 1) + p z_{a1}}{2 N_i}\right)
\]

\[
+ p \frac{z_{a2}}{N_2} (z_{a2} - z_{a2}),
\]

and if the evolve according to the dynamical system \((A.2)\), we have

\[
z_{a1} - z_{a1} = (z_{a1} - z_{a1}) \left(\beta b - d - c N_i - (b \beta - 1) + p \frac{z_{a1}}{N_i}\right)
\]

\[
+ p \frac{z_{a2}}{N_2} (z_{a2} - z_{a2}).
\]

From these two equalities we get that the sets

\[
\mathcal{B}^a := \{z_{a1} \geq z_{a1}\} \cap \{z_{a2} = z_{a2}\}
\]

and

\[
\mathcal{B}^p := \{z_{a1} > z_{a1}\} \cap \{z_{a2} > z_{a2}\}
\]

are invariant under the dynamical systems \((A.1)\) and \((A.2)\).
