Choosing the fittest as a speciation mechanism

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Abstract

When a population inhabits an inhomogeneous environment, the fitness value of traits can vary with the position in the environment. Gene flow caused by random mating can nevertheless prevent that a sexually reproducing population splits into different species under such circumstances. This is the problem of sympatric speciation. However, mating need not be entirely random. Here, we present a model where the individually advantageous preference for partners of high fitness can lead to genetic clustering as a precondition for speciation. In simulations, in appropriate parameter regimes, our model leads to the rapid fixation of the corresponding alleles.

Key words: Speciation, sympatric, sexual selection, mate preferences, fitness-based mating

1 Introduction

The question how new species arise is central for the theory of biological evolution. When there is no gene flow between subpopulations, different adaptations to the varying circumstances can cause divergent evolution and lead to new species. This is the mechanism of allopatric speciation. The question becomes more difficult for sexually reproducing populations without mating barriers. Here, the homogenizing effect of gene flow can counterbalance the divergent effects of differential selection in a non-homogeneous environment and can prevent the gradual accumulation of genetic and phenotypic differences that are a precondition for speciation. When the habitat is extended,
perhaps gene flow is too slow for counteracting the effects of differential selection at the boundaries. This is the mechanism of parapatric speciation. When the habitat is more contiguous, it can still offer different niches that could be utilized by more specialized individuals, but matings between genetically different individuals might always prevent the stabilization of different adaptive specializations within the population. This is the problem of sympatric speciation.

On one hand, it is an empirical question whether such sympatric speciation is possible. Careful case studies seem to have accumulated some evidence for sympatric speciation, both in field studies, e.g., described or surveyed in [1, 33, 34, 3], the most prominent example being the cichlid fish of West Africa, and in experiments, e.g., reviewed in [31, 22]. On the other hand, it is a theoretical question to identify mechanisms and to develop formal models that can account for sympatric speciation. It suggests itself to focus on the mating scheme. The simplest assumption is that individuals choose or accept their mating partners randomly within their population. Individuals, however, can potentially increase their reproductive success by being more discriminative and by selecting their mating partners more carefully. This, in turn, will lead to the evolution of traits that make individuals more attractive as mating partners. This is the mechanism of sexual selection identified by Darwin [5]. As long as the attractivity of traits is uniform across the population and its habitat, this will not be conducive to the speciation. On the contrary, it will rather produce an additional homogenizing effect because the selection pressure for these traits then is uniform.

When, however, different traits are attractive in different parts of the habitat, this may decrease gene flow and facilitate speciation. The question then is how such differential attractivity can come about. After all, it can only emerge and establish itself when it offers reproductive advantages to individuals.

In order to account for sympatric speciation, Dieckmann and Doebeli [8, 9] explored the mechanism of assortative mating which was originally proposed in [24]. This means that individuals prefer to mate with phenotypically similar individuals and avoid matings with dissimilar members of their population. Doebeli and Dieckmann have demonstrated [11] that in the presence of environmental gradients, this can lead to genetic clustering with two (or more) distinct phenotypes inside the population and it can sufficiently reduce the gene flow between these types so that speciation can set in. Two questions arise here. First, how can such a mechanism be implemented? In-
individuals need to recognize partners that are similar to themselves. In the absence of higher cognitive abilities, this seems to require a genetic linkage between specific phenotypic traits and mating preferences. Second, why is such assortative mating advantageous for individuals? A possible answer is that this might lead to better adapted offspring in a situation where intermediate phenotypes are less fit than more extreme ones. Under appropriate circumstances, assortative mating might be in that way superior to random mating. The question, however, is whether this is the best strategy. The contribution of the present paper then is to propose a simpler mating strategy with a more basic justification in terms of fitness, and to demonstrate that this can be a mechanism causing sympatric speciation. The proposed strategy is simply to try to mate with the fittest partner available. This offers the obvious prospect of securing good genes for the offspring. Again, a problem then is how to evaluate the fitness of other individuals and to recognize a fit potential mating partner. This, however, is well studied in the context of sexual selection, and the consequences of such mating schemes have been explored empirically and theoretically. In our context, the question then is how this can lead to phenotypic divergence as a precondition for speciation. In a non-homogeneous environment, phenotypes can have different fitness in different parts of the environment, and in particular, which phenotype is the fittest may vary across the environment. Thus, when in one part of the environment one particular phenotype is the fittest, and in another part another one, then in each part, the fittest phenotypes not only have the advantage of their own superior fitness, but also the additional advantage of access to particularly fit partners when their own fitness makes them preferred. We demonstrate that this double advantage can lead to genetic divergence even in the presence of strong migration between the different parts of the environment. Also, fitness-based mating preferences can lead to assortative mating, thereby providing a more basic evolutionary rationale for the latter. A somewhat related model has been proposed by [36] who propose a multilocus computational model of fitness-based mating in which the fitness superiority of males is displayed by a visual cue. Just after the levels of magnitude of male investment into this cue have evolved such that the cue can be used by females as a decision basis, females also evolve stronger preferences for the fittest males. The model of [36] differs to ours not only in the incorporation of a third trait, but also in its implementation as a stochastic computer model with larger genomes, quasi-continuous trait distributions, and complex competition schemes. Our approach presented here is an analytically
tractable model in the tradition of classic population-genetic models as those of [13, 35, 29, 23, 24, 7] or [28]. Our approach extends the understanding about divergence inducing mating schemes by proposing fitness-based mating as a simpler mechanism which is profitable for a larger set of fitness landscapes than assortative mating.

Fitness-based mating is an advantageous strategy under more general circumstances than assortative mating, however. For this discussion, it is useful to utilize Wright’s metaphor of the fitness landscape. Assortative mating is good in a fitness landscape with two peaks, that is, where extreme phenotypes have a higher fitness than intermediate ones, for instance, where both large and small individuals are fitter than those of intermediate size. In that situation, it is good for a small individual to seek a small mating partner, and analogously for large ones. Fitness-based mating then works when there is some inhomogeneity in the environment, that is, when in some part or niche or under some circumstances, smaller individuals are favored, and larger ones elsewhere. Then in that part, the small individuals are the most desired mating partners. When, however, there is only a single peak in the fitness landscape, that is, when medium size individuals are doing best, then a small one should rather seek a larger partner, and conversely. Thus, in that situation, disassortative mating would be best for those individuals that find themselves away from the fitness peak. This may be biologically unstable, however. Fitness-based mating in that situation would always go for the intermediate types, those that are closest to the fitness peak. In that way, fitness-based mating, in contrast to assortative mating, automatically adapts to the geometry of the fitness landscape.

For the purposes of this article, the term “fitness” is utilized in a simple and naive manner. We simply quantify fitness of an individual as the (expected) contribution to the number of offspring as the result of a mating. The contributions of the two mates are added to determine the expected number of offspring. In particular, the use of the term “fitness” is non-reflexive in the sense that it does not include the mating strategy. Obviously, since in our scheme, the number of offspring does not only depend on an individual, but on a mating pair, an individual can increase its number of offspring by selecting a good partner, and thereby become “fitter” in a deeper sense of the term. Hopefully, our naive use of the term “fitness” in the present contribution will not lead to misunderstanding. For a conceptual discussion of the fitness concept, we refer to [19].
Many other mechanisms of sympatric speciation have been proposed and explored, ranging from sexual conflict \cite{15} to chromosome rearrangements and other genetic mechanisms \cite{39}. As emphasized in \cite{26,10}, however, one should distinguish between evolutionary causes of speciation, like environmental gradients or sexual conflict, and mechanisms operating at the genetic level.

The starting point of the modern species discussion was Mayr’s \cite{25} biological species concept. According to this concept, species are groups of populations that show sexual reproduction and are reproductively isolated from other such groups. On this basis, \cite{2} developed the view of a species as a dynamical balance between the diverging forces of differential selection in a spatially or ecologically extended and therefore non-uniform habitat and the converging effects of gene flow through sexual recombination. (Sympatric) speciation then requires breaking this dynamical balance. The present contribution provides a simplified formal model that can be analyzed theoretically and tested in simulations.

In fact, there is a large body of literature on mating schemes and speciation, carefully described and reviewed in the book of Gavrilets \cite{14}. In order to organize the variety of schemes proposed in the literature, Gavrilets \cite{14} (pp. 280–287) developed a general framework in which non-random mating can be modelled. He proposed mating pools in which all individuals can potentially mate with each other. Individuals from different mating pools do not meet and hence do not mate. He then distinguished two cases. In the first case, individuals preferentially join a mating pool and randomly mate within this pool. In the second case, individuals randomly join the mating pool and preferentially mate. That means, encounters are random but matings depend on mate preferences. The fitness-based mating model falls into the second case where each niche’s population forms one mating pool in which individuals mate preferentially. He also distinguishes similarity-based and matching-based mate preference. If “mating is controlled by a single trait [...] expressed in both sexes” (e.g., as in assortative mating), he speaks of similarity-based mating. If “mating is controlled [...] by two different sex-linked traits”, it is matching-based. However, our scheme of fitness-based mating is neither similarity- nor matching-based. The model is developed and analyzed in detail in the first author’s thesis \cite{32} and in a forthcoming publication of her.
2 Fitness-based mating

2.1 Biological background

By Darwin’s principle of the survival of the fittest, the mate preference should be in favour of those mating candidates that best enhance the fitness prospects of the offspring. Logically, this involves two aspects. One is the fitness of the potential mate itself, and the other one is the compatibility with the own geno- and phenotype. We assume here that within the population that we model, compatibility is not an issue, in the sense that there is no hybrid inferiority for crossing between members of that population with different geno- or phenotypes. Hybrid inferiority cannot be the starting point of genetic differentiation within a population, but is rather a consequence of that. When we want to understand sympatric speciation, we should rather identify possible causes that trigger such a genetic divergence within a homogeneous population. Therefore, we concentrate on the first aspect, the selection of a mate on the basis of evidence for its fitness. In fact, many empirical examples of such fitness-based mating have been discovered and studied where individuals apparently include physical, behavioral, or mental properties of potential mates in their mating decisions. This can be seen at elaborated tests prior to mating whose outcome is correlated to the subsequent mating success. Such is found in fighting competitions in harem forming populations (red deer, sea lion, gorillas), lek-mating birds, territory defending animals like hummingbirds, as well as in the traditions of nuptial gifts, for example in balloon flies.

In addition, also the handicap hypothesis, which later developed to the theory of costly signalling, proposes that exaggerated ornaments or weapons can be seen as signals for outstanding health and good physical condition because exaggerated features are hindrances in daily life. For example, the brightness of coloration can on one hand indicate low parasite affection in fish or in birds, but on the other hand it leads to higher mortality risks. The darkness and condition of a male lion’s mane indicates his testosterone level and hitherto fighting success, but increases also body temperature and abnormal sperm.

In any case, the mechanism of sexual selection discovered by Darwin is based on the transformation of an indicator of fitness to a direct target of selection. That means, sexual selection as involved in mate choice no longer operates directly on survival abilities, but that rather on the indicators of
such abilities. When that happens, these indicators themselves undergo a
selection that need no longer be related to those underlying abilities, but
rather operates by triggering mating attractivity.

2.2 Preliminary considerations

In this section, we essentially argue verbally about the effects of different
mating schemes under various circumstances. The arguments presented,
however, are derived from a formal model to be introduced and discussed
below, and are supported by computer simulations of that model.

We consider a 2-locus haploid model. At each locus, there are two possible al-
leles. At the first locus, we can have $A$ or $a$. We assume that there are fitness
differences between the carriers of alleles $A$ and $a$, in the sense that matings
between $A$-carriers are expected to have more offspring than those between
$a$-carriers, with the number of offspring for mixed matings in-between. We
also assume that the fitness difference is visible, an issue to be discus-
se in more detail below. At the second locus, we can have $M$ or $m$. Carriers of
$M$ mate only with carriers of $A$, that is, with the fittest members of the
population, whereas $m$-carriers mate indiscriminately. We assume here that
the difference between $A$ and $a$ can be detected from the phenotype, but the
difference between $M$ and $m$ cannot be seen from the phenotype. (In fact,
this is slightly inconsistent, as $M$ vs. $m$ leads to a behavioral difference from
which, in principle, some inference can be made about a certain allele va-
ure at the second locus, but we do not grant our creatures sufficient cognitive
 sophistication for that.) The question then is under which circumstances
allele $M$ is advantageous in comparison to $m$, that is, when does it pay to
forgo mating opportunities in order to get the best mating partners. The
following observations can be readily supported by formal computations, but
those are omitted because they are straightforward.

When the probability of matings is proportional to the one of meetings be-
tween the types, except when an $M$-carrier refuses a mating with an $a$-carrier,
then $aM$-types will perform worst, because they not only carry the burden of
lower fitness, but also have the disadvantage of finding fewer mating partners.
In contrast, $Am$-types enjoy a higher fitness themselves, and in addition have
the best access to mating partners. Therefore, $aM$ will go extinct asymp-
totically, that is, the $M$-allele will only co-occur with the $A$-allele. Also,
either $AM$ or $am$ disappears because both have less mating opportunities
than $Am$, except possibly when $Am$ was initially absent. In addition, $Am$
and \( am \) cannot co-exist, as \( Am \) is fitter than \( am \), and since matings between the two are not prevented, \( Am \) will then eventually dominate the population. \( AM \) and \( Am \) can co-exist, however, because when only the fitter genotype \( A \) is present, the selection for \( M \) disappears. Finally, there exists an unstable equilibrium with only \( AM \) and \( am \) which do not interbreed, and where the equilibrium frequency of \( am \) needs to be correspondingly higher than the one of \( AM \) in order to compensate for the lower fitness.

The situation becomes more interesting when we have two niches in one of which \( A \) is fitter whereas in the other one \( a \) is more successful. The phenotypic effect that indicates fitness differences can arise in two different ways. Either the phenotypes produced by \( A \) and \( a \) are distinct, and one of them is better in the first, the other in the second environment. For instance, the camouflage provided by the coloration patterns can vary between the environments. Or, \( A \) leads to a good phenotype in one environment whereas in the other environment this phenotype is produced by \( a \). For example, different feeding habits in the different environments may be needed for a well nourished phenotypic appearance. Both these possibilities will succumb to the same type of analysis.

Thus, an \( M \)-carrier will attempt to meet with \( A \)-carriers in niche 1, and with \( a \)-carriers in niche 2. Without migration, we could then have an equilibrium population with \( AM \) and \( Am \)-types in niche 1, and with \( aM \) and \( am \)-types in niche 2. When migration occurs, however, then the \( AM \)-type in niche 1 will be less successful than \( Am \), and analogously the \( aM \)-type in niche 2 will be less successful than \( am \), because their mating success in the other niche is lower, and so there will be a higher back-migration of \( m \)-carriers than of \( M \)-carriers. Therefore, the effective reproduction of \( Am \) is higher than of \( AM \) in niche 1, and so, the latter type should become extinct. Analogously, \( aM \) should disappear in niche 2. For the remaining types, \( Am \) and \( am \), we then simply need to determine the selection-migration balance.

So far, the situation was polygamous, or more precisely, matings were not costly, and then, obviously, the best strategy is to mate as often as possible, regardless of the quality of the mates. Nevertheless, the preceding considerations will aid our thinking below. Also, analogous considerations apply to assortative mating, that is, when at the second locus we have allele \( B \) vs. \( b \), when \( AB \) mates only with \( A \), and \( aB \) with \( a \) only, while \( b \)-carriers are ready to accept any partner. Again, in each niche, the first-locus allele with lower fitness is at a disadvantage, but \( b \) profits from back-migration when competing with \( B \).
In any case, for monogamy the outcome changes (or more generally, when the number of matings is limited). Trivially, if every individual is assured of finding a mate, then each should mate only with the fittest. Of course, this is self-contradictory if mating decisions are reciprocal, because then the less fit individuals will find no partners willing to accept them. Thus, we should rather assume that an \(M\)-carrier mates with an individual of highest fitness if it meets one, but abstains from other matings, whereas an \(m\)-carrier mates with the first agreeing individual it meets (and will then not be permitted further matings). The outcome will now depend on both the fitness difference between \(A\) and \(a\) and on the original distribution of these two types. When the fitness difference is large or \(A\) is initially sufficiently frequent, \(M\) wins out, else \(m\). Again, however, the selection pressure for \(M\) decreases when \(A\) tends towards dominating the population.

The situation becomes more interesting and biologically more realistic if we introduce genders (female and male) with different mating strategies. Let us assume that the males mate indiscriminately and try to achieve as many matings as possible, the biological rationale being that their mating costs are very low, whereas the females try to mate only with the fittest available individuals as their mating costs are high (because of high reproductive investments) and consequently the number of times that they can possibly mate is strictly limited. (This will then in turn induce fierce competition between males.) We nevertheless assume autosomal inheritance of the mate preference allele. Then, it is preferable for a female to only accept fit mating partners, as long as this does not substantially decrease her mating opportunities, for more than one reason. Firstly, she can expect to derive more offspring from matings with fit partners. Secondly, that offspring can be expected to be fitter itself; in particular, her male progeny will then be more desired mating partners for females of subsequent generations. In turn, a male derives a double benefit from his fitness, as he is not only fitter himself, but also becomes a more desirable mating partner. That is, Darwin’s sexual selection sets in. And, as already argued by Darwin, the process can then acquire a dynamics of its own. It becomes advantageous for a male to produce the phenotype that is an indicator of genetic fitness, essentially regardless of whether this is a true indicator of fitness or not, as long as it serves the purpose of inducing females to accept him as a mate. In turn, for females, such a partner then becomes desirable, but no longer primarily because of his underlying fitness, but because it is advantageous for her to produce male offspring that inherits the trait for attractiveness. There are
many well documented or at least well argued examples where this process can go astray, that is, lead to certain exaggerated features as indicators of sexual attractiveness, but which are biologically useless, if not detrimental for their carriers. Therefore, as already mentioned in 2.1 the concept of costly signalling has been proposed as a solution to this dilemma. The idea is that while for a male it is best to cheaply fake an indicator of fitness, for females it is biologically advantageous to rely only on signals that are honest indicators of fitness because they are so costly to produce that they can only be afforded by the strongest, i.e., the fittest males. As this is well discussed in the literature, e.g., [18], we refrain from presenting examples.

We rather analyze the mate preference once more. Assuming that for a female a preference for fit (or fit looking, as discussed) males pays off, it then becomes beneficial for a male to also pass that mating preference on to his female offspring even though in the situation discussed here it plays no direct role in the male line. Therefore, the mating preference allele should be passed on autosomally and not become linked to a sex chromosome.

In any case, our purpose here is not to contribute to the theory of costly or honest signalling. We rather want to identify a simple mechanism that can trigger speciation in populations in varying environments. We shall therefore assume that genetic fitness is correctly signalled by the phenotypic expression of the underlying allele (A vs. a). As discussed, this is a simplifying assumption, but it will allow us to concentrate on a basic mechanism for sympatric speciation.

### 2.3 Model setup

Returning to population genetics, our basic model includes two niches between which individuals can migrate. The two niches are ecologically different in the sense that in each of them a different genotype has the highest fitness. Individuals have two genetic loci. One gene determines the fitness, the other one determines the probability or propensity for fitness-based mating. Mating fitness-based means choosing one of the fittest individuals. As an abbreviation, we call an individual that mates fitness-based a “fitmater” (a single word – to be distinguished from “fit mater”, that is, an individual that is itself fit).

Individuals are haploid. On one hand, the model could be readily extended to the diploid case, but on the other hand, that would not lead to new phenomena. Genetic loci are diallelic. The alleles of the first locus which
determines the fitness value are denoted by $A$ and $a$, and the alleles of the second locus which determine the mating behavior are denoted by $M$ and $m$. Inheritance follows Mendelian rules. The allele $A$ is advantageous in one niche, and $a$ is better in the other niche. While $m$-individuals mate randomly, carriers of $M$ are fitmaters with probability $\mu \in (0, 1]$. Pure fitness-based mating then corresponds to $\mu = 1$, and we shall mostly consider this case only. In principle, however, it is useful to have such a parameter available, because one can then differentiate suitable quantities like the expected number of offspring w.r.t. this parameter. In fact, some of our underlying analysis has been carried out in such a manner.

Let us first analyze the situation for a single niche where $A$ is fitter, in the sense that there is a parameter $f > 0$ which translates into fitness values for pairs according to the rules that a pair of two $a$-carriers has the value 1, a pair of two $A$-carriers the value $1 + f$, while a mixed pair gets $1 + \frac{f}{2}$. The expected number of offspring produced by such a pair then is proportional to that fitness value, where the proportionality factor may be chosen such that the total population size stays constant over time. As is typical for such models, we assume that the generations do not overlap, that is, the members of each generation are born at the same time, mate, produce offspring representing the next generation, and then die. Females mate once with a single male that the females can either choose randomly or select on the basis of his fitness value. Males can mate as often as they are accepted by a female, regardless of her fitness value.

It is now straightforward to analyze the effect of an increase of $\mu$. Let us assume that a female switches from random to fitmating and exchanges an $a$-partner against an $A$-carrier. We want to compute the effects $\delta p(A), \delta p(a)$ of the switch, i.e., the frequency change caused by the switch of her $A$ ($a$)-offspring. The female is an $A$ ($a$)-carrier herself with probability $p(A)$ ($p(a)$). If she has $a$, then she had produced 1 offspring of type $a$ with the $a$-male, but now she is expected to produce $\frac{1}{2}(1 + \frac{f}{2})$ offspring of each type $A$ and $a$ with the $A$-partner. Likewise, if she has $A$, then she had produced $\frac{1}{2}(1 + \frac{f}{2})$ offspring of each type $A$ and $a$ with the $a$-partner, but now she is expected to produce $1 + f$ $A$-offspring with her $A$-mate. Thus,

$$\delta p(a) = \frac{1}{2} \left( \frac{f}{2} - 1 \right) p(a) - \frac{1}{2} \left( \frac{f}{2} + 1 \right) p(A)$$

$$\delta p(A) = \frac{1}{2} \left( \frac{f}{2} + 1 \right) p(a) + \frac{1}{2} \left( \frac{3f}{2} + 1 \right) p(A).$$
From this, one readily checks that
\[
\frac{p(a) + \delta p(a)}{p(A) + \delta p(A)} = \frac{1 - 2p(A)}{1 + 2p(A)} < \frac{p(a)}{p(A)},
\]
that is, this leads to a decrease of the number of \(a\)-carriers. Actually, this may seem obvious, but it is not entirely trivial because the expected increase in reproductive success of \(a\)-females may be relatively stronger than that of \(A\)-females when they are in the minority, \(f\) is large, and fitmating is prevalent. Nevertheless, this does not lead to an increase of \(a\) in the population because after switching, the female \(a\)-carriers are no longer breeding true, and the male \(a\)-carriers loose their mates. Thus, fitmating will make the selective advantage of \(A\)-carriers even stronger.

It is also clear that fitmating is a superior strategy in terms of the expected number of offspring for less fit females than assortative mating whereas it does not make a difference for fit females. For less fit females, assortative mating is not a good option because that would require them to choose equally less fit mates. In particular, as long as a subpopulation of \(a\)-individuals persists, we do not expect an allele for assortative mating to become fixed in the population, in contrast to our fitmating allele \(M\).

When individuals can now migrate into the niche under consideration and mate there, coming from another niche where \(a\) is fitter than \(A\) and where therefore the \(a\)-carriers are in the majority, then this will induce a decrease of the frequency of \(A\) in our niche. When there are fewer \(A\)-carriers around, however, then fitmating becomes more advantageous, simply because then the chances are higher to randomly encounter an \(a\)-male and then to switch from that less fit \(a\)-carrier to a fitter \(A\)-male. (Or putting it the other way around, if most of the males are \(A\) anyway, then chances are that already a random choice will lead to an \(A\)-partner, and therefore, there is little expected gain from trying to be selective.) Thus, migration increases the selective pressure for fitmating. Consequently, since we have already shown that fitmating in turn increases the selective advantage of \(A\)-carriers, we overall see a stronger countereffect to the immigration of less fit \(a\)-carriers. In the other niche, in contrast, the same effect works in favor of \(a\), as it is assumed to be the fitter one there. This is our rationale for proposing fitmating as a possible mechanism for inducing speciation in populations occupying niches with different selective pressures.

We now come to the dynamics produced by our model. In order to state the recurrence equation for the change in time of the frequency of each
genotype combination in the subsequent generation, we need some notation: 
t \in \mathbb{N}_0 \) denotes the current generation. The parameter \( \alpha \in \{A,a\} \) stands for 
the allele at the first locus, \( \nu \in \{M,m\} \) for the one at the second locus. The 
frequency of individuals with genotype \((\alpha, \nu)\) in niche \( n \) at time \( t \) is denoted 
by \( p^n_t(\alpha, \nu) \). This frequency after individuals have had the opportunity to 
migrate is denoted by \( P^n_t(\alpha, \nu) \). The probability that offspring of type \((\gamma, \omega)\) 
is produced, given that the parents have the genotypes \((\beta, \rho)\) and \((\alpha, \nu)\), re-
spectively, is denoted by \( P_{\text{off}}(\gamma, \omega|\beta, \rho; \alpha, \nu) \); the Mendelian inheritance rules 
determine \( P_{\text{off}} \). The probability that \((\alpha, \nu)\) chooses \((\beta, \rho)\) for mating is de-
noted by \( P^n_{\text{mate}}(\beta, \rho|\alpha, \nu) \); it can be computed within our model, see [32]. The 
additive fitness value of two parents \( \alpha \) and \( \beta \) is denoted by \( F^n_{\alpha, \beta} \) and normalized 
by its mean value \( \bar{F}^n \). The recurrence equation then is (see [32] for the 
derivation)

\[
p^{n+1}_t(\gamma, \omega) = \sum_{\alpha, \nu} P^n_t(\alpha, \nu) \sum_{\beta, \rho} P_{\text{off}}(\gamma, \omega|\beta, \rho; \alpha, \nu) P^n_{\text{mate}}(\beta, \rho|\alpha, \nu) \frac{F^n_{\alpha, \beta}}{F^n}.
\] (4)

Equation (4) describes the genotype distribution of the subsequent 
generation \( p^{n+1}_t \), given the current distribution \( P^n_{t, \text{mig}} \) after migration in niche \( n \). 
The equilibrium distribution is then obtained by iterating equation (4), but 
also explicit equilibrium solutions have been derived in [32]. The next section 
will outline the main features of the model dynamics.

2.4 Model behavior

We now present some simulation results for two different mating schemes 
in one niche from the iteration of the recurrence equation (4) derived from 
the model. Figure 1 shows the population development for fitmating and 
assortative mating.

In the simulations the population dynamics reaches an equilibrium with 
the following properties.

1. The allele \( M \) for fitmating becomes fixed in a wide range of initial 
populations (Exceptions are when one of the alleles is already initially 
absent in both niches. Clearly, this allele would not reappear due to 
lacking mutation). In particular, the allele \( M \) establishes itself faster 
than an allele for assortative mating would under otherwise equal cir-
cumstances. At figure 1 for instance, we see that fitmating becomes
Figure 1: The initial gamete distribution has been set to a uniform distribution, which would be the result of a randomly mating population where each allele is present at the same frequency. The following parameters have been used: The fraction of individuals migrating from their niche of birth to the other niche is $p_m = 0.1$. The parameter $f$ is set to $f = 0.1$. The plots show the population development in the first niche, where the allele $A$ is fittest. These distributions are obtained from iterating equation (4). The situation in niche 2 leads to equivalent results, because the niche conditions are symmetric. (a) Fitness-based mating ($\mu = 0.5$) The $m$-carriers mate randomly, and $M$-carriers practise fit mating with a probability of $\mu$ and mate randomly with a probability of $1 - \mu$. (b) Assortative mating ($\mu = 0.5$) The $m$-carriers mate randomly, and $M$-carriers practise assortative mating with a probability of $\mu$ and mate randomly with a probability of $1 - \mu$. The axis ranges up to 20000 generations which compresses the graph at low generation values in a way that the population seems not to start from a uniform distribution, but in fact it does.
fixed within the first 500 generations, whereas assortative mating needs 20000 generations until fixation.

2. Fitness-based mating leads to a higher equilibrium frequency of the fitter allele in each subpopulation. Thus, fitmating leads to a stronger divergence between the subpopulations than random or even assortative mating, thereby possibly enhancing an incipient speciation process. At figure 2, for instance, we see that fitmating, i.e., the $M$-allele, goes to fixation for all migration rates $p_m \in (0, \frac{1}{2})$, whereas assortative mating cannot outcompete random mating if migration is high, i.e., $p_m > 0.3$.

3. A higher migration rate can speed up the approach to equilibrium as it increases the selective pressure in favor of the fitness-based mating allele $M$ which then in turn increases the selective advantage of the fitter allele in each subpopulation. At figure 3, for instance, we see that the point in time at which the equilibrium is attained under fitmating initially decreases, i.e., when $p_m \in (0, 0.2)$, whereas under assortative mating, the population needs increasingly a longer time when $p_m$ increases. Beyond $p_m = 0.2$, the time of approaching the equilibrium increases with $p_m$ in both models, but it is still considerable lower than in the assortative mating model.

4. The $M$-allele can become dominant quite rapidly, already after a few hundred generations, as seen again in figures 1 and 3.

In particular, at the final equilibrium when all individuals exhibit fitmating, the fitmating may not be distinguishable from assortative mating because then in each niche, only the fitter males are chosen. They are chosen by fit resident females as well as by a modicum of less fit females that have either immigrated or resulted from “mixed” matings. So the major part of matings take place between partners with the same first locus allele. When we restrict in our model the migration to males only, the equilibrium and the equivalence of fitness-based and assortative mating will be reached even faster. Our point, however, is that during the transient process, the two mechanisms of fitness-based and assortative mating are clearly distinct, and the former produces superior results.
Figure 2: The parameters and the initial gamete distribution have been set as in figure 1. The plots show the equilibrium population for various migration rates in the first niche, where the allele $A$ is fittest. These equilibria are obtained from iterating equation (3). (a) Fitness-based mating ($\mu = 0.5$) The $m$-carriers mate randomly, and $M$-carriers practise fit mating with a probability of $\mu$ and mate randomly with a probability of $1 - \mu$. (b) Assortative mating ($\mu = 0.5$) The $m$-carriers mate randomly, and $M$-carriers practise assortative mating with a probability of $\mu$ and mate randomly with a probability of $1 - \mu$. On the vertical axes in (a) and (b), we also display the equilibrium values in the absence of migration. The situation in niche 2 leads to equivalent results, because the niche conditions are symmetric.
Figure 3: The parameters and the initial gamete distribution have been set as in figure 1. The plots show the point in time at which the equilibrium population is reached for various migration rates. (a) Fitmating ($\mu = 0.5$). The $m$-carriers mate randomly, and $M$-carriers practise fitmating with a probability of $\mu$ and mate randomly with a probability of $1 - \mu$. We see in that there is an intermediate migration rate for which the population reaches fastest the equilibrium. (b) Assortative mating ($\mu = 0.5$). The $m$-carriers mate randomly, and $M$-carriers practise fitmating with a probability of $\mu$ and mate randomly with a probability of $1 - \mu$. 
3 Summary

Inspired by many biological observations of preferences for fit mating partners, in particular among females accepting only the fittest males, typically leading to fierce competitions among males, we have developed and implemented a model allowing for such a preference of fit mating partners, called fitness-based mating. We have shown that fitness-based mating is superior to random or even assortative mating in enhancing genetic differences between subpopulations in environments with different selective pressures. Fitness-based mating amplifies natural selection because fit males then heap the benefit of better access to females upon their own fitness advantage, and even less fit females profit from the opportunity of producing fitter offspring with fitter mates. When we then consider subpopulations occupying several niches with different selective pressures so that different alleles induce higher fitness in the different niches, fitness-based mating leads to a higher selection-migration equilibrium value in the niches, as quantified by the frequency of the fittest genotype. Thus, fitness-based mating can induce stronger polymorphism than random mating by maintaining a higher equilibrium frequency for well adapted genotypes in the different niches. Such a polymorphism could then trigger further divergence resulting in reproductive isolation, thus, speciation. It seems that fitness-based mating could easily induce runaway sexual selection as there will be a strong pressure for producing or even faking the phenotypic trait that indicates genetic fitness, but this issue is not explored in the present paper as it is already amply discussed in the literature and since it might distract from our main point which is at a more basic level.

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