Reinforcement of genetic coherence in a two-locus model
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Abstract
Background: In order to maintain populations as units of reproduction and thus enable anagenetic evolution, genetic factors must exist which prevent continuing reproductive separation or enhance reproductive contact. This evolutionary principle is called genetic coherence and it marks the often ignored counterpart of cladistic evolution. Possibilities of the evolution of genetic coherence are studied with the help of a two-locus model with two alleles at each locus. The locus at which viability selection takes place is also the one that controls the fusion of gametes. The second locus acts on the first by modifying the control of the fusion probabilities. It thus acts as a mating modifier whereas the first locus plays the role of the object of selection and mating. Genetic coherence is enhanced by modifications which confer higher probabilities of fusion to heterotypic gametic combinations (resulting in heterozygous zygotes) at the object locus.

Results: It is shown that mutants at the mating modifier locus, which increase heterotypic fusions but do not lower the homotypic fusions relative to the resident allele at the object locus, generally replace the resident allele. Since heterozygote advantage at the object locus is a necessary condition for this result to hold true, reinforcement of genetic coherence can be claimed for this case. If the homotypic fusions are lowered, complex situations may arise which may favor or disfavor the mutant depending on initial frequencies and recombination rates. To allow for a generalized analysis including alternative models of genetic coherence as well as the estimation of its degrees in real populations, an operational concept for the measurement of this degree is developed. The resulting index is applied to the interpretation of data from crossing experiments in Alnus species designed to detect incompatibility relations.

Introduction
Anagenetic (phyletic) and cladogenetic evolution can be basically distinguished by the fact that during the former genetic variation is transformed within a single population without losing the reproductive contact between the genetic variants, while in the latter genetic variation is distributed to reproductively separated populations. In other words, phyletic evolution has the capacity to maintain or strengthen "genetic coherence" among the genetic variants. This coherence is lost as a consequence of reproductive separation during cladistic processes. The necessity to consider these complementary processes as of equal significance in evolutionary reasoning was recognized, for example, by [1] and becomes already evident in the running title "Can speciation be prevented?" of this paper. Contrary to common concepts, the title suggests the existence of persistently acting forces of genetic
disjunction that have to be counteracted in order to maintain genetically variable reproductive communities.

In its probably most obvious form the separation-coherence dualism becomes relevant in hybrid zones, where genetic separation between the hybridizing populations is apparent for some traits but not for others. Hybrid zones may therefore be considered as a more or less stable balance between speciation and coherence. A concise review of the mechanisms that could be responsible for this situation is provided e.g. by [2]. As far as mating relations are considered as potential mechanisms they are confined to reinforcement of prezygotic isolation through hybrid disadvantage. The problems with experimental verification of reinforcement as well as with its consistent modeling are pointed out in a recent review by [3]. In view of these complications it might not be surprising that, according to these reviews, possibilities of reinforcing the internal reproductive coherence as mechanisms which enable populations to maintain their genetic integrity do not seem to have attracted any attention.

Yet, as the present authors demonstrated in a series of papers [4–7], the apparent evolutionary complementarity of reproductive separation and coherence in fact has fundamental genetic substance and can even be derived from Wallace’s early theory of speciation based on the evolutionary reinforcement of reproductive isolation in cases of hybrid disadvantage [8], p.175ff, called the Wallace effect in [9]. Replacing ”hybrid” by ”heterozygote”, inversion of Wallace’s idea allows to reformulate Felsenstein’s running title as ”does heterozygote advantage reinforce genetic coherence?” Herewith, reinforcement of genetic coherence is to be understood as the replacement of extant genetic types by mutants that increase mating preferences among different genetic types (increase heterotypic mating preferences; for the concept of mating preferences see [10]).

For a single-locus, three-allele model involving pleiotropic effects on survival and mating traits, the present authors demonstrated that Wallace’s extended concept of the reinforcement of mating preferences holds true. Thus, for pleiotropic gene action on viability and mating preferences, heterozygote disadvantage reinforces the evolution of homotypic mating preferences (avoidance of heterotypic matings), and heterozygote advantage reinforces heterotypic mating preferences.

When viewed in the framework of genetic load it turns out that Wallace’s theory can actually be extended to imply that reinforcement of the respective mating preferences simply reduces the genetic load without sacrificing adaptively relevant genetic variation by reducing the formation of unfit genotypes. In this way, adaptability is maintained at lower costs for adaptedness and population integrity and persistence are thus enhanced. Yet, this is so far confirmed only for pleiotropic gene action [7]. For non-pleiotropic gene action, which requires at least two gene loci, confirmation of this principle is limited to speciation [6]. Its counterpart, genetic coherence, still awaits modeling and analysis. The present paper is devoted to this topic. The model design will follow the two-locus principle argued by [4], where one locus modifies the mating relations realized at a second locus, and where this second locus is also subject to selection.

Since the above concept of genetic coherence embraces a continuum of mating (and gene flow) relations which extend from complete avoidance of heterotypic matings (completion of speciation) to exclusively heterotypic mating (complete reproductive coherence), the present paper will also be concerned with the development of an index which quantifies the different degrees of reproductive coherence. This index is intended to aid in recognizing evidence for genetic coherence in population genetic data. Its range of application will be demonstrated for an analysis of data from crossing experiments in *Alnus* species which were designed to detect incompatibility relations.

**The Model**

**Description of the model**

A model with two biallelic loci A and B is considered in which viability selection (in the diplophase) is restricted to the genotypes at the B-locus. The B-locus is also involved in the formation of zygotes in that the alleles present at this locus in the encountering gametes of different sex specificity determine their probabilities of fusion. The role of the A-locus consists solely in modifying these fusion probabilities according to the alleles carried by the encountering gametes at this locus. No selection occurs at the A-locus. As suggested by [4], the A- and B-locus will be referred to as the mating modifier and the object locus, respectively. Gametes of different sex specificity are assumed to encounter at random. The loci are linked with recombination rate r (the relevant notational details are compiled in Table 1 and illustrated in Figure 1). Generations are assumed to be separated and population size is effectively infinite.

**Mating modification via gamete fusion**

As detailed in Table 1, the probability that a pair of gametes $G^k_i$ and $G^l_j$ fuses to a zygote after an encounter is described by the probability $f^k_l$. In the case that a pair of gametes does not fuse after an encounter, both gametes are assumed to be incapable of further reproductive activity. This establishes a mating system described for
Figure 1
Schematic representation of the model determinants of reproduction and survival: (1) gametes encounter at random, (2) gamete fusion is determined by the B-locus (the object locus of mating), and fusion probabilities are modified by the A-locus (the mating modifier locus), (3) survival is determined by the B-locus (the object locus of survival) only; the B-locus thus is object of both gamete fusion and survival. The framed part refers to differential fusion modification with respect to homotypic and heterotypic encounters at the object locus B.

plants as "selective fertilization with pollen- and ovule-elimination" (see e.g. [11–13]). Such mating systems affect both the combination of gametes into zygotes and the mating success. Differential mating success is implied by fact that, even though all gametes of one sex may have the same chance to encounter a gamete of the other sex, they are differentially successful since they fail to fuse when encountering an “incompatible” gamete. The mating success of an individual thus depends on the frequencies of gametic types produced in the population which are "compatible" with the gametic types produced by this individual.

Since, basically, genetic coherence refers to mating relations among different in comparison to like genetic types, and since these relations are defined for the object locus B, fusion probabilities must reflect this fact. In particular, if the probabilities of fusion among gametes are the same for all allelic combinations at the B-locus, random fusion can be stated for this locus. This is in fact the situation of any genetic coherence, and it will be assumed to be realized for the wild type allele \(A_2\) at the mating modifier locus. Since recessivity is generally believed to be the most likely type of gene action for newly arising mutants, dominance of the wild type over the mutant \(A_1\) will be assumed in the effect on gamete fusion. Thus the probabilities of fusion are the same for all allelic combinations at the B-locus if at least one of the two encountering gametes carries \(A_2\). This probability will be denoted by \(f_2\), and it is characterized by

\[ f_2 := f_{2i}^{kl} \text{ for all } k, l. \]

In a homotypic encounter for the mutant mating modifier allele \(A_1\) it is assumed that the probability of fusion of the gametes is the same for the two homotypic associations at the object locus B, i.e.

\[ f_{11}^{11} = f_{12}^{22} =: f_1^{hom}. \]

This is a reasonable assumption in view of the fact that

\[ f_1^{hom} \]

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\[ f_{11}^{11} = f_{12}^{22} =: f_1^{hom}. \]

This is a reasonable assumption in view of the fact that
changes in genetic coherence show primarily in alterations of the fusion probabilities for heterotypic combinations at the object locus. These probabilities will be distinguished by the notation \( f_{11}^{het} := f_{11}^{12} = f_{11}^{21} \).

Figure 1 may again serve as an illustration of these details.

**Transition equations**

**Gamete formation**

Starting from a situation which is characterized by a frequency distribution of the 10 possible two-locus-genotypes \( G_{ij}^{kl} \), the gamete formation results after regular recombination at a rate \( r \) and for \( i \neq j, k \neq l \) as

\[
g_i^k = g_i^{kk} + \frac{1}{2} g_i^{kl} + \frac{1}{2} g_{ij}^{kk} + \frac{1}{2} (1 - r) g_{ij}^{kl} + \frac{1}{2} r g_{ij}^k
\]

**Zygote formation**

The assumption of random encounter of gametes of different sex yields pairs of (yet non-fused) gametes in the following relative frequencies (with \( i \neq j, k \neq l \)):

\[
G_i^k \times G_i^k : (g_i^k)^2
\]

\[
G_i^k \times G_i^l : 2g_i^k g_i^l
\]

\[
G_i^k \times G_j^k : 2g_i^k g_j^k
\]

\[
G_i^k \times G_j^l : 2g_i^k g_j^l
\]

The fusion probabilities decide about final zygote formation so that the new generation starts with zygotic frequencies

\[
g_{11}^{kk} = (g_1^k)^2 f_1^{hom} / \bar{f}
\]

\[
g_{11}^{kk} = (g_1^k)^2 f_2 / \bar{f}
\]

\[
g_{12}^{12} = 2g_1^1 g_2^2 f_1^{het} / \bar{f}
\]

\[
g_{12}^{12} = 2g_1^1 g_2^2 f_2 / \bar{f}
\]

\[
g_{12}^{12} = 2g_1^1 g_2^2 f_2 / \bar{f}
\]

\[
g_{12}^{12} = 2g_1^1 g_2^2 f_2 / \bar{f}
\]

\[
g_{12}^{12} = 2g_1^1 g_2^2 f_2 / \bar{f}
\]

with the average probability of fusion

\[
\bar{f} = \sum_k ((g_1^k)^2 f_1^{hom} + (g_2^k)^2 f_2 + 2g_1^k g_2^k f_2) + 2\sum_k g_1^k g_2^k f_1^{het} + g_1^2 g_2^2 f_2 + g_1^2 g_2^2 f_2 + g_1^2 g_2^2 f_2)
\]

The following analyses are organized along steps of increasing complexity of interaction between the two loci, starting with consistent effects of each locus and ending
with numerical analyses of complex effects suggested by the preceding analytical results.

**Analysis of the dynamics – analytical characterizations**

The focus is on the conditions under which the allele $A_1$ may become established and eventually fixed in the population. Since this allele is considered to increase the probability of fusion for gametes which carry different alleles at the $B$-locus (the object locus), its dynamics decides on the evolution of increased genetic coherence at the $B$-locus.

It is in fact possible to greatly simplify the analysis by considering that equations (4), when combined with equation (1), result in a representation of the transition equations which is mathematically equivalent to the classical two-locus model of viability selection and random mating (random fusion of gametes). In this representation, each encounter leads to fusion of the gametes. The resulting zygote has a probability of survival which is identical to the probability of fusion of its constituent gametes. This first viability selection phase affects both loci $A$ and $B$ jointly. A second phase is characterized by viability selection restricted to the $A$-locus, so that overall one obtains two-locus genotypic viabilities of the form

$$s_{ij}^{kl} = f_{ij}^{kl} \cdot v_{kl},$$

The $s$-values will be termed "combined selection value” in the following. This allows us to apply results known from analyses of the classical model.

Following the general concept suggested by [14] for the analysis of two-locus polymorphisms, we may start with observing for each genotype at one locus the ranking of the three genotypes at the other locus. For example, if

$$s_{ij}^{11} < s_{ij}^{12} < s_{ij}^{22},$$

for all $i,j$, then we have complete conditional overdominance in viability and thus a protected (stable) polymorphism at the $B$-locus irrespective of the recombination rate. Similarly, $s_{ij}^{kl} \leq s_{ij}^{kl} \leq s_{ij}^{kl}$ for all $k,l$ implies fixation of $A_1$ for all recombination rates if the sign of inequality is strict in at least one case. In terms of the restrictions of the present model, these cases can be more easily pictured by looking at the rows and columns in the arrangement of the two-locus viabilities presented in Table 2.

| Table 2: Combined selection values |
|------------------------------------|
| $s_{ij}^{kl}$ | $A_1 A_1$ | $A_1 A_2$ | $A_2 A_2$ |
| $B_1 B_1$ | $f_{1}^{hom}$ | $f_2 v_{11}$ | $f_2 v_{11}$ |
| $B_1 B_2$ | $f_{1}^{het}$ | $f_2 v_{12}$ | $f_2 v_{12}$ |
| $B_2 B_2$ | $3I$       | $f_2 v_{22}$ | $f_2 v_{22}$ |

Not destabilize the $B$-locus polymorphism provided

$$f_{1}^{het}/f_{1}^{hom} \geq \max\{v_{11}, v_{22}\}/v_{12},$$

Looking at the rows one notes that allele $A_1$ would become fixed if

$$\min\{f_{1}^{het}, f_{1}^{hom}\} \geq f_2$$

and if not both $f_i$-values are equal to $f_2$. The special case

$$f_{1}^{het} > f_{1}^{hom} = f_2$$

is included in this condition, and it is of direct relevance to the evolution of coherence, since it states that the mutant $A_1$ increases the fusion probabilities only among gametes differing at the $B$-locus. When realized together with $v_{12} \geq \max\{v_{11}, v_{22}\}$, this implies that the $B$-locus polymorphism is protected and, by fixation of $A_1$, increased genetic coherence becomes established. The expectation that overdominance reinforces genetic coherence is so far confirmed.

If one aims at more general results it must be taken into account, that increased coherence cannot evolve via substitution of $A_2$ by $A_1$ unless the $B$-locus polymorphism is maintained for fixation of $A_1$, i.e. unless

$$f_{1}^{het} \cdot v_{12} > f_{1}^{hom} \cdot \max\{v_{11}, v_{22}\},$$

which is equivalent to

$$f_{1}^{het}/f_{1}^{hom} > \max\{v_{11}, v_{22}\}/v_{12}.$$ In principle, this necessary condition includes situations other than overdominance at the $B$-locus ($v_{12} > \max\{v_{11}, v_{22}\}$). Such situations, however, allow only for transient $B$-locus polymorphisms prior to the advent of the $A_1$ mutant. Depending on the allele frequencies at the $B$-locus, it is conceivable that the $A_1$ mutant replaces the wild type and by this may stabilize the $B$-locus polymorphism. However, since this situation is only locally stable it is of limited interest for the evolution of increased genetic coherence.
Another case not ruled out by the necessary condition is the possibility that $f_2$ is located between $f_1^{het}$ and $f_1^{hom}$. If, in addition to the symmetry in homotypic fusion probabilities ($f_1^{11} = f_1^{22} = f_1^{hom}$) there exists symmetric overdominance in the viabilities at the $B$-locus ($v_{11} = v_{22} < v_{12}$), the polymorphism at this locus will be protected and the frequencies of the alleles $B_1$ and $B_2$ will ultimately become equal. The reason is to be seen in the fact that both $B$-homozygotes have equal average $s$ values which stay below the pertaining average $B_1B_2$-viability for each single $A$-genotype. As a consequence, initially present stochastic associations between the two loci will decay and the average viability of $A_1A_1$ will ultimately approach $\frac{1}{2}(f_1^{hom}v_{hom} + f_1^{het}v_{12})$, where $v_{hom} = v_{11} = v_{22}$. By the same reasoning the average viabilities of the other two $A$-genotypes both will approach $\frac{1}{2}f_2(v_{hom} + v_{12})$. On the basis of these average viabilities it can be stated that $A_1$ will or will not replace $A_2$ according to whether the difference $\frac{1}{2}(f_1^{hom}v_{hom} + f_1^{het}v_{12}) - \frac{1}{2}f_2(v_{hom} + v_{12})$ and thus $v_{12}(f_1^{het} - f_2) - v_{hom}(f_2 - f_1^{hom})$ is positive or negative.

It is straightforward to show that these analytical results still hold, if the mutant mating modifier $A_1$ is assumed to be dominant over the wild type $A_w$. All one has to do is replace $f_2$ in the $A_1A_2$-column of Table 2 by $f_1^{het}$ and $f_1^{hom}$, respectively, and then follow the above steps of analysis.

However, simple predictions of the dynamics for asymmetric overdominance in viability at the $B$-locus ($v_{11} \neq v_{22}$) are not possible. Since the analytical treatment of these cases is generally quite intricate, the following considerations will resort to numerical analyses of selected scenarios.

**Analysis of the dynamics — numerical studies**

According to the results of the above analytic considerations it remains to study situations of asymmetric overdominance in viabilities at the $B$-locus ($v_{11} \neq v_{22}$, $v_{kk} < v_{12}$) in combination with effects of $A_1$ that increase heterotypic fusions and decrease homotypic fusions ($f_1^{het} > f_2 > f_1^{hom}$). This will be done with the help of five scenarios concerning the specification of viability, fusion, and recombination parameters and initial conditions for genotypic frequencies. The scenarios $S1$ to $S5$ are compiled in Table 3. Since our major concern is the study of the conditions for establishment and ultimate fixation of increased coherence, all scenarios are characterized by initial conditions for genotypic frequencies, in which the mutant $A_1$ is represented at low frequency and frequencies at the $B$-locus are close to equilibrium.

Table 3: Scenarios Numerical scenarios for overdominance in viability at the B-locus

| Scenario | $f_1^{het}$ | $f_1^{hom}$ | $v_{11}$ | $v_{12}$ | $r$ | $r_1$ | $g_{11}$ | $g_{12}$ | $A_1$ |
|----------|-------------|-------------|---------|---------|-----|-------|---------|---------|-------|
| S1       | 0.8         | 0.3         | 0.5     | 0.4     | 0.3 | 0.003 | 0        | 0       | fix.   |
| S2       | 0.5         | 0.3         | 0.6     | 0.5     | 0.3 | 0.006 | 0        | 0       | elim.  |
| S3       | 0.4         | 0.2         | 0.6     | 0.5     | 0.3 | 0.001 | 0        | 0       | elim.  |
| S4       | 0.6         | 0.4         | 0.6     | 0.5     | 0.3 | 0.006 | 0        | 0.001   | fix.   |
| S5       | 0.7         | 0.5         | 0.6     | 0.5     | 0.3 | 0.01  | 0        | 0       | elim.  |

*Scenarios are identical to $S1$ except of the values given in the respective columns. elim.: elimination of $A_1$; fix.: fixation of $A_1$
very close to 0.6666 (the equilibrium frequency in the absence of different fitness values). The pronounced increase of \( A_1 \) between generations 2200 and 2400 towards fixation entails a decrease of \( b_1 \) to 0.5254.

(i) coherence by increasing \( f_{1 \text{het}} \) vs. decreasing \( f_{1 \text{hom}} \)

The coherence effect results from higher fusion probability for heterotypic encounters on the one hand and from reduced fusion probability for homotypic encounters on the other. While the first effect promotes increase of \( A_1 \) and a simultaneous increase of the population fitness, the second effect enables a rapid change of the frequency structure at locus \( B \) but at the same time reduces the population fitness especially the fitness of \( A_1 \) \( A_1 \) types, thus reducing the chances for establishment and fixation of coherence. If scenario \( S1 \) is modified by reducing \( f_{1 \text{hom}} \) to 0.1 (\( S2 \)), the overall disadvantage of \( A_1 \) results in a continuous decrease of \( A_1 \) with the exception of a small increase during the first 10 generations. Whether the combination of increased \( f_{1 \text{het}} > f_2 \) and decreased \( f_{1 \text{hom}} < f_2 \) results in higher or lower fitness of \( A_1 \) compared to \( A_2 \) depends on the two-locus genotypic structure. As allelic and genotypic frequencies change during the dynamics, the direction of the dynamics may change as is the case in scenarios \( S1 \) and \( S2 \), for example.

(ii) Degree of viability asymmetry

If \( S1 \) is modified by reducing \( v_{2 \omega} \) to 0.1 (other parameters, especially the \( f \)-values, remaining unchanged, see \( S3 \)), this increased disadvantage for homotypic encounters could be expected to favor the evolution of coherence. The numerical results, however, are in contrast to such intuitive expectation: After an initial increase during the first 12 generations, \( A_1 \) decreases and will be lost. The reason must be seen in the fact, that the asymmetric \( \nu \)-values lead to an equilibrium at \( B \) with a significantly higher frequency of \( B_1 \) and therefore to an increased frequency of homotypic encounters. In this situation, the fitness reducing \( f_{1 \text{hom}} \) cannot be compensated by the fitness increasing \( f_{1 \text{het}} \) as is the case in \( S1 \).

(iii) influence of recombination rate \( r \)

Starting with \( S3 \) as an example for failure of establishment of coherence, and reducing \( r \), it can be seen that for recombination rates of 0.05 or higher the increase of \( A_1 \) is prevented despite an initial increase (from 0.3% to 0.6% for \( r = 0.05 \), for example). For \( r = 0.04 \) or smaller, the initial increase is also followed by a phase of decrease, the dynamics’ direction, however, is reversed once more at about generation 110 (for \( r = 0.04 \)) or generation 160 (for \( r = 0.01 \), see \( S4 \)) leading to fixation of \( A_1 \) in about 2000 generations.

(iv) influence of starting frequencies

Using scenario \( S4 \) as a reference for successful establishment and fixation of coherence, a reduction of the starting frequency \( a_1 \) from 0.3% to 0.05% (\( S5 \)) results in the failure of establishment despite an initial increase until generation 22 (\( a_1 = 0.11% \)).

Measuring Genetic Coherence

To allow for a generalized analysis including alternative models of genetic coherence as well as the estimation of its degrees realized in actual populations, it is desirable to provide an operational concept for the measurement of this degree. For this purpose recall that genetic coherence and genetic separation are opposite evolutionary concepts which refer to the tendency for each allele to preferentially occur in association with other allelic types (heterozygosity) or with its own type (homozygosity) in diploid genotypes. Preferential association of an allele with its own type indicates isolation against and thus separation from other alleles. Such an allele thus contributes to the reproductive fragmentation of a population. Hence, an index \( C \) of genetic coherence should be specified for each allele, and it should attain its lowest value if it occurs only in association with its own type (complete isolation), while associations only with other types should determine its largest value. The borderline between coherence and separation is drawn by the situation where an allele is associated with its own type exactly in proportion to its occurrence in the population. For the \( B \)-locus with allele frequencies \( b_k \) and homozygote frequencies \( b_{kk} \) this implies that the index \( C \) reaches its lower bound for \( b_{kk} = b_k \) and its upper bound for \( b_{kk} = 0 \). The borderline, where the allele shows no preferential associations with its own nor with other types is reached at \( b_{kk} = b_k^2 \).

A conceptually consistent construction of such an index is achieved by making use of the above-mentioned concept of mating preferences in the form introduced by [10]. The mating preference \( U_{l \omega k} \) of type \( k \) for type \( l \) is there defined by the ratio \( P_{l \omega k} / R_{l \omega k} \) where \( P_{l \omega k} \) and \( R_{l \omega k} \) are the actual and potential frequencies, respectively, of type \( l \) mates among all mates of type \( k \). The preferences \( U_{l \omega k} \) are unbounded and are equal to 1 in the absence of any preferences of type \( k \) for type \( l \) (indifference, random mating). Yet, given the distribution of potential mates, \( U_{l \omega k} \) is bounded from above by \( 1/R_{l \omega k} \)
(since $P_{l< k} \leq 1$), and this bound characterizes the situa-
tion of complete preference of type $k$ for type $l$. Along
the same reasoning, $U_{l< k} = 0$ characterizes complete
rejection of $l$-type mates by $k$-types. To arrive at a mea-
sure of mating preference that varies symmetrically
around the situation of indifference and extends over the
range from complete rejection to complete preference, it is
desirable to normalize $U$ accordingly. The normalized
version $\bar{U}$ should ideally assume values of -1, 0, and +1
for complete rejection, indifference, and complete
preference, respectively. This is realized by

$$\bar{U}_{l< k} := \begin{cases} U_{l< k} - 1 & \text{if } U_{l< k} \leq 1 \\ \frac{U_{l< k} - 1}{R_{l< k}^{-1}} & \text{if } U_{l< k} > 1 \end{cases}$$

Substitution of "allele" for "type" and considering the
formation of a zygote as a mating event, the conditional
mating frequencies $P_{l< k}$ are given by $1/2b_{lk}/b_k$ for $l \neq k$
and by $b_{kk}/b_k$ for $l = k$. Since coherence is to be mea-
sured only among the gametes which entered the forma-
tion of zygotes, the "potential mates" are the same for all
alleles and equal their frequencies among the zygotes, i.e.
$R_{l< k} = b_l$. Hence, $U_{l< k} = \frac{1}{2}b_{lk}/(b_l \cdot b_k)$ for
$l \neq k$ and $U_{k< k} = b_{kk}/b_k^2$. By the above reason-
ing, coherence is characterized by heterotypic preferenc-
es and thus by preferential associations of one allele with
alleles other than its own type. If the subscript $l$ collec-
tively denotes all alleles other than $k$, one obtains for the
heterotypic

$$U_{l< k} = \frac{(b_k - b_{kk})}{((1 - b_k) \cdot b_k)}$$

with $R_{l< k} = 1 - b_k$. Taking account of the desired nor-
malization, this suggests to define an index $C_k$ of coher-
ence for the $k$-th allele by the heterotypic preference
$\bar{U}_{l< k}$ and thus by

$$C_k := \begin{cases} \frac{b_k^2 - b_{kk}}{b_k (1 - b_k)} & \text{if } b_k^2 \leq b_{kk} \ (\leq b_k) \\ \frac{b_k^2 - b_{kk}}{b_k^2} & \text{if } b_k^2 \geq b_{kk} \end{cases}$$

In closed form, $C_k$ can be written as

$$C_k = \frac{b_k^2 - b_{kk} + (1 - 2b_k) \cdot |b_k^2 - b_{kk}|}{2(1 - b_k)b_k^2}$$

If the $k$-th allele does not occur in heterozygotes, it is re-
productively completely isolated from other alleles as is
characteristic of a biological species. In this case $b_{kk} = 0$
and thus $C_k = -1$. At the other extreme, for gametophytic
incompatibility systems each allele occurs only in heter-
zygotes, so that $b_{kk} = 1$ and therefore $C_k = 1$. For each
such allele complete genetic coherence can be stated.

For two alleles the two $C_k$'s strongly depend on each oth-
er, since then $b_1^2 - b_{11} = b_2^2 - b_{22} = \frac{1}{2}b_{12} - b_1 b_2$.
Hence, $C_1$ and $C_2$ always have the same sign and, in
addition, for $b_k^2 - b_{kk} \leq 0$ (i.e. $C_k \leq 0$) (i.e. $C_k \leq 0$)
both $C$-values are even identical, i.e. $C_1 = C_2$. On the oth-
er hand, if $b_k^2 - b_{kk} > 0$, the relation between the two
allelic coherence indices is determined by the two allele
frequencies, since then $C_1/C_2 = (b_2/b_1)^2$. The less fre-
cquent allele shows in this case the larger coherence. In
other words, for homozygote excess (relative to Hardy-
Weinberg proportions) both alleles contribute equally to
the population’s genetic coherence, while for heterozy-
gote excess the less frequent allele contributes more to
genetic coherence than the predominant allele.

Taking the average over the $C_k$'s, i.e.
$\bar{C} = b_1 \cdot C_1 + b_2 \cdot C_2$, yields $\bar{C} = b_{12}/(2b_1 b_2) - 1$
irrespective of the sign of the $C_k$'s. This relates $\bar{C}$ to
Wright’s fixation index $F$ by $\bar{C}$. Hence, $F$ allows for an
interpretation that is usually not directly associated with
concepts of genetic coherence or separation/speciation.
The model-independence of the concept underlying the
$C_k$’s thus enlarges the scope of application of $F$ to the
interpretation of data on genotypic frequencies obtained
for stages close to the zygotic stage. The lower and upper
bounds of $\bar{C}$ for given allele frequencies at the B-locus
are realized for $b_{12} = 0$, which yields $\bar{C}$, and for $1/2b_{12} = \min(b_1, b_2)$, which yields $\bar{C} = \max\{b_1, b_2\}^{-1} - 1$
(for further details concerning boundaries of heterozy-
gosity and $F$ see e.g. the book of [15]).

In numerous computer runs of the present model it
turned out that $\bar{C}$ increases with the frequency of the al-
lele $A_1$ that enhances heterotypic fusions. This did not
generally hold for the dynamics of each of the individual
$C_k$-values. Since the $C_k$-values become positive as $A_1$ approaches fixation, this is possible according to the above analysis. If $A_1$ entails increased heterotypic fusions without lowering homotypic fusions, both $C$-values increase continuously with the establishment of $A_1$.

For the case of multiple alleles ($> 2$), $C$-based analyses of genotypic structures can be extended to more complex problems by forming groups of alleles which are considered equivalent in some defined sense. In the case of four alleles $B_1, \ldots, B_4$ for example, $B_1$ and $B_2$ can be considered as equivalent and to form a group $B_{12}$, say, with allele frequency $b_x = b_{11} + b_{12}$ and "homozygote" frequency $b_{xx} = b_{11} + b_{12} + b_{22}$. The coherence measure of this composite allele $B_x$ is then well defined by $C_x$, and degrees of reproductive isolation from or coherence with other alleles or groups of alleles can be analyzed. It should, however, be noted that the average $\bar{C} = \frac{1}{k} \sum_k C_k : b_k$ need no longer equal $-F$, since for multiple alleles $F = 1 - (1 - \sum_k b_{kk})/(1 - \sum_k b_{kk}^2)$ interpretation of $-F$ as average genetic coherence is thus limited to two alleles.

An application
The applicability of the coherence indices $C_k$ covers a range, which exceeds that of genotypic structures of populations. In the context of the present model involving selective fertilization, outcomes of controlled crosses are of particular interest, since they allow direct observation of fusion probabilities at the gametic level. Such crosses were performed by the present authors in a project concerned with the detection of mating incompatibility relations in *Alnus* species. Crosses between parents with the same heterozygote genotype at various isoenzyme gene loci yielded genotypic frequencies among their seed which differed significantly from the hypothesis of regular segregation and random fusion of the gametes. Two examples are provided by samples of $39 : 73 : 15$ for $A_1A_1 : A_1A_2 : A_2A_2$ at the SKDH-A locus in one cross, and $12 : 8 : 5$ for $B_2B_2 : B_2B_4 : B_4B_4$ at the 6PGDH-B locus in another cross.

The $C$-values for the SKDH locus are $C_1 = 0.131, C_2 = 0.282$ and $\bar{C} = 0.192$, while for the 6PGDH locus these values become $C_2 = C_4 = C = -0.306$. Note, that $C$-values are based on successful gametes only, so that they are not affected by segregation distortion but rather reflect solely effects of fusion preferences. Ignoring sampling effects, these observations suggest strongly opposing tendencies for the two loci, with homotypic fusion preferences at the SKDH locus and heterotypic preferences at the 6PGDH locus. This need, of course, not indicate the existence of opposing forces acting functionally at the two enzyme loci. Structural associations of the enzyme loci via chromosomal coupling with functionally effective loci in the genetic background may as well serve for an explanation. These functional loci, however, must in both crosses be assumed to be heterozygous in at least one crossing partner of each of the two crosses to explain the observations. It is also clear that in the case of the 6PGDH locus the two alleles must have been in coupling phase with the preferentially fusing alleles at the functional locus. In the same way, the two SKDH alleles must be assumed to be in repulsion phase with the preferentially fusing alleles at the functional locus.

In any case, this observation of strongly opposing effects at different loci can be expected to extend to the whole population only in the absence of noticeable stochastic associations between the loci. The reason is that an allele with a strongly positive degree of genetic coherence and a distinctly positive association with an allele at another locus prohibits strongly negative genetic coherence for this other allele. Consequently, (sympatric or parapatric) speciation can be initiated only at loci which show no associations with loci that exhibit high degrees of genetic coherence, and each of the speciating subpopulations inherits the genetic coherence relations of the base population.

Conclusions
Two factors are considered in the two-locus model presented in this paper: the mating system (with fusion probabilities at the $B$-locus depending on the allelic composition at the $A$-locus) and classical viability selection (at the $B$-locus). It turned out that the particular specification of the mating system allows for an evolutionarily equivalent interpretation of the model in terms of a two-locus viability selection model with random mating, the combined selection values $s_{ij}^{kl}$ resulting as the product of the fusion probability and the one-locus viability: $s_{ij}^{kl} = f_{ij}^{kl} \cdot v_{kl}$ (see Table 2). Coherence may be promoted in two ways, by increasing $f_{1}^{het}$ or by decreasing $f_{1}^{hom}$. In the first way the fitness of $A_i$ carriers is increased, and in the second way it is decreased.

A necessary prerequisite for the evolution of coherence is a stable polymorphism at the object locus $B$. Since the selection coefficients in our model are not frequency-dependent, overdominance is required to ensure the persistence of polymorphism. Prior to the appearance of any mating modifier, "simple" overdominance ($v_{11} < v_{12}$ and $v_{12} > v_{22}$) is sufficient for a stable $B$-polymorphism. With
mating modifiers present in the population, complete conditional overdominance at the B-locus 

\( (s_{21}^{kl} < s_{12}^{kl} > s_{11}^{kl}) \) is required for a stable polymorphism, and this is equivalent to

\[ f_1^{het} / f_1^{hom} \geq \max \{v_{11}, v_{22}\}/v_{12} < 1. \]

Given this condition, the mutant \( A_1 \) will replace the resident allele \( A_2 \) if \( \{ f_1^{het}, f_1^{hom} \} \geq f_2 \) and \( \max \{ f_1^{het}, f_1^{hom} \} > f_2 \). Since the latter inequalities include the case \( f_1^{het} > f_1^{hom} = f_2 \) thus increased coherence, the expectation that overdominance reinforces genetic coherence is confirmed so far. Conclusively, reversion of these inequalities, which characterizes decreased coherence for the mutant, prohibits its establishment.

The situation \( f_1^{het} \geq f_2 \geq f_1^{hom} \) is ambiguous with respect to its effect on genetic coherence. Yet, the analytical results obtained for symmetric viability \( (v_{11} = v_{22} < v_{12}) \) show that \( A_1 \) will become fixed or eliminated according to whether \( v_{12}(f_1^{het} - f_2) - v_1^{hom}(f_2 - f_1^{hom}) \) is positive or negative. Thus, if \( f_1^{het} \) exceeds \( f_2 \) by a sufficient amount, the evolution of increased coherence is again reinforced. For intermediate \( f_2 \) and non-symmetric \( v_{kk} \)'s, however, numerical studies demonstrated more complex dynamics. Examples are presented where a change only in the initial frequency of \( A_1 \) or in the recombination rate turns the dynamics from fixation to elimination of \( A_1 \) or vice versa.

Application of the conceptually generalized measures of coherence confirmed these results. Therefore, in essence the inverse of Wallace’s principle holds for the present model: heterozygote superiority not only prevents the evolution of reproductive separation of subpopulations but even reinforces the evolution of increased genetic coherence.

A single-locus model of reinforcement of genetic coherence previously suggested by the present authors ([7]) allowed for a complete analysis covering a much wider range of mating systems. For this model it was shown that overdominance in viability generally implies the replacement of a resident allele by a mutant conferring higher heterotypic mating preferences, while heterozygote disadvantage generally promotes the evolution of higher homotypic mating preferences. This clear dualism does not seem to exist in the present two-locus model despite its more detailed mating system. Fusion probabilities, viability parameters and recombination rates interact in more complex ways. Even if the selective effects of the mating system are separated from its purely combinational effects, as was possible in the one-locus model, recombination apparently introduces dynamical forces which become dominant for compensating forms of selection and combination.

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