1 **Title**

2 Linkage disequilibrium under polysomic inheritance

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28 Linkage disequilibrium under polysomic inheritance

29 **Abstract:** The influence of genetic drift on linkage disequilibrium in finite
 30 populations has been extensively studied in diploids. However, to date the
 31 effects of ploidy on LD has not been extensively studied. We here extend the
 32 linkage disequilibrium measure D and Burrow's Δ statistic to include
 33 polysomic inheritance, as well as their corresponding squared correlation
 34 coefficients r^2 and r_{Δ}^2 , where the former is for phased genotypes and the
 35 latter for unphased genotypes. Weir & Hill's double non-identity framework is
 36 also extended to include polysomic inheritance, and the expressions of double
 37 non-identity coefficients are derived under five mating systems. On this basis,
 38 the approximated expectations of estimated r^2 and r_{Δ}^2 at equilibrium state,
 39 d^2 and δ^2 , are derived under five mating systems. We assess the behaviors of
 40 the estimated r^2 and r_{Δ}^2 and the influence of the recombination rate on d^2
 41 or δ^2 , simulate the application of estimating effective population size, and
 42 evaluate the statistical performance of the method of estimating.

43 **Keywords:** Linkage disequilibrium, recombination rate, effective population
 44 size, mating system.

45 Introduction

46 Linkage disequilibrium (LD) is the non-random association of alleles at

different loci in a given population (SLATKIN 2008), and can be influenced by many factors, such as selection, mutation, recombination, genetic drift, and the mating system (NEI 1987). Linkage disequilibrium can be measured by several parameters, such as the correlation coefficient r , Lewontin's (1964) D' , Hill's (1975) Q , Maruyama's (1982) D^* , Ohta's (1980) F^* , and Brown *et al.*'s (1980) χ . The most frequently used measure of LD is the squared correlation coefficient r^2 (HILL AND WEIR 1994), which is the weighted sum of the squared correlation coefficient between alleles at two loci.

The influence of genetic drift on linkage disequilibrium in finite populations has been extensively studied in diploids (HILL AND ROBERTSON 1968; OHTA AND KIMURA 1969; SVED AND FELDMAN 1973; HILL 1974; WEIR 1979; WEIR AND COCKERHAM 1979; WEIR AND HILL 1980). In general, this previous work has shown that the squared correlation coefficient r^2 (or r_{Δ}^2 for unphased genotypes) will converge to a constant after several generations of random mating. This constant is determined by the recombination rate, effective population size and the mating system. Based on these factors, LD has been incorporated into two major applications: (i) gene mapping (HÄSTBACKA *et al.* 1992; HILL AND WEIR 1994; DEVLIN AND RISCH 1995; JORDE 1995; HOSKING *et al.* 2002) and (ii) the estimation of effective population size (HILL 1981; HAYES *et al.* 2003; ENGLAND *et al.* 2006; SVED *et al.* 2013; WAPLES *et al.* 2014).

Many plant species are polyploid, with anywhere between 30-80% of

angiosperm species being at least partially polyploid (BUROW *et al.* 2001), with evidence for paleo-polyploidy in most plant lineages (OTTO 2007). Polyploidy is also a major factor in the evolution of both wild and cultivated plants, and plays a key role in plant breeding (UDALL AND WENDEL 2006; SATTLER *et al.* 2016). However, to date the effects of ploidy on LD has not been extensively studied.

There are at least three typical features in polysomic inheritances: (i) the chromosomes are randomly paired and exchange their chromatid segments during meiosis, in which the recombination rate c is $1 - 1/v$ if the corresponding loci are located on different chromosomes (v is the ploidy level), or ≤ 0.5 if the corresponding loci are located on the same chromosome; (ii) the decay coefficient of heterozygosity (i.e. the ratio of single non-identity coefficients in the next and the current generations) is $1 - \frac{1}{vN_e}$ in polyploids (N_e is the effective population size); (iii) the multivalents may be formed during meiosis (RIEGER *et al.* 1968), resulting in a particular phenomenon in polysomic inheritance, termed the double-reduction (BUTRUILLE AND BOITEUX 2000), in which a gamete may inherit a single gene copy twice.

In this paper, we extend both the linkage disequilibrium measure D and Burrow's Δ statistic to account for polysomic inheritance, and calculate their corresponding squared correlation coefficients r^2 and r_{Δ}^2 . We also extend

Weir & Hill's (1980) double non-identity framework to account for polysomic inheritance, and derive the expressions of these double non-identity coefficients under five mating systems. On this basis, we are able to derive $E(\hat{r}^2)$ and $E(\hat{r}_\Delta^2)$ at equilibrium state, and these two expectations are approximated by d^2 and δ^2 , respectively. Both approximates are closely related to the mating system together with the effective population size N_e and the recombination rate c . We study the behavior of the squared correlation coefficient estimators $\hat{r}^2$ and $\hat{r}_\Delta^2$ during genetic drift, investigate the influence of recombination rate c on d^2 or δ^2 , simulate the application for estimating effective population size N_e , and evaluate the statistical performance of estimating $\hat{N}_e$. We discuss the relationship between r^2 and c (or between r_Δ^2 and c), and that between r^2 and v (or between r_Δ^2 and v). We enable the estimation of Burrow's Δ , the testing of linkage disequilibrium based on Burrow's Δ , and the estimation of effective population size in our software package POLYGENE V1.3 (HUANG *et al.* 2020), which is freely available via <http://github.com/huangkang1987/polygene>.

Theory and modelling

LD measurements

We denote A and B for two alleles each from a unique locus. The generalized LD measurement D between A and B is defined as the

difference between the observed and the expected frequencies of the haplotype AB . We model five specific variants of D : (i) D_s^{AB} (for the same haplotype), (ii) D_d^{AB} (for two different haplotypes within the same individual), (iii) D_w^{AB} (for the within-individual component), (iv) D_b^{AB} (for the between-individual component) and (v) D_{AB} (for the usual LD measurement). These measurements can be defined by symbols as follows:

$$D_s^{AB} \stackrel{\text{def}}{=} P_s^{AB} - p_A q_B,$$

$$D_d^{AB} \stackrel{\text{def}}{=} P_d^{AB} - p_A q_B,$$

$$D_w^{AB} \stackrel{\text{def}}{=} P_s^{AB} - P_d^{AB},$$

$$D_b^{AB} \stackrel{\text{def}}{=} P_d^{AB} - p_A q_B,$$

$$D_{AB} \stackrel{\text{def}}{=} D_w^{AB} + D_b^{AB},$$

where P_s^{AB} is the probability that the alleles in the same haplotype are A and B , P_d^{AB} is the probability that alleles in different haplotypes within the same individual are A and B , and p_A and q_B are respectively the frequencies of A and B , respectively.

According to these definitions, the following expressions hold:

$$D_w^{AB} = D_s^{AB} - D_d^{AB}, \quad D_b^{AB} = D_d^{AB} \quad \text{and} \quad D_{AB} = D_s^{AB}.$$

The usual LD measurement D_{AB} is the covariance between A and B in the same haplotype, i.e. $D_{AB} = \text{Cov}(\mathcal{B}_A, \mathcal{B}_B)$, where $\mathcal{B}_A = 1$ if the first allele copy

in the target allele pair is A , otherwise $\mathcal{B}_A = 0$, and the meaning of $\mathcal{B}_B$ is analogous.

The values of D_{AB} may be negative, and its range is influenced by the frequencies of A and B . It is therefore more intuitive to use Pearson's correlation coefficient r_{AB} to measure LD, which is the quotient of D_{AB} divided by its theoretical maximum $\sqrt{Q_{AB}}$. In other words, $r_{AB} \stackrel{\text{def}}{=} \frac{D_{AB}}{\sqrt{Q_{AB}}}$, whose range is $[-1, 1]$, where $Q_{AB} = p_A p_X q_B q_X$ (X represents any allele distinct from both A and B , and thus $p_X = 1 - p_A$ and $q_X = 1 - q_B$). Note that $Q_{AB} = \text{Var}(\mathcal{B}_A)\text{Var}(\mathcal{B}_B)$. We obtain

$$r_{AB} = \frac{\text{Cov}(\mathcal{B}_A, \mathcal{B}_B)}{\sqrt{\text{Var}(\mathcal{B}_A)\text{Var}(\mathcal{B}_B)}}.$$

The values of r_{AB} may also be negative. However, the squared correlation coefficient r_{AB}^2 ensures that its values are non-negative, ranging from 0 to 1. We will adopt the average value of r_{AB}^2 across all allele pairs to evaluate the LD between two loci for the situation of phased genotypes.

The above LD measurements are applicable for phased genotypes although unphased genotypes are more common. For unphased genotypes, Burrows's Δ statistic (COCKERHAM AND WEIR 1977) can be used, and we will extend this to account for polysomic inheritance. By using D_s^{AB} and D_d^{AB} , Burrows's Δ statistic between A and B can be defined as $\Delta_{AB} \stackrel{\text{def}}{=} D_s^{AB} + (v - 1)D_d^{AB}$. Moreover, for two-locus unphased genotypes, Burrow's Δ

147 statistic can be expanded to:

$$148 \quad \Delta_{AB} = \left(\sum_{i=1}^v \sum_{j=1}^v \frac{ij}{v} G_{B^j X^{v-j}}^{A^i X^{v-i}} \right) - vp_A q_B, \quad (1)$$

149 where X is an arbitrary allele distinct from both A and B , with each $G_{B^j X^{v-j}}^{A^i X^{v-i}}$
 150 denoting a two-locus unphased genotypic frequency whose superscript (or
 151 subscript) is an unphased genotype containing exactly i copies of A (or j
 152 copies of B). In Appendix A, we use triploids to illustrate how Δ_{AB} is
 153 expanded. Substituting the observed values of p_A , p_X , q_B , q_X and $G_{B^j X^{v-j}}^{A^i X^{v-i}}$
 154 into Equation (1), Δ_{AB} can be estimated.

155 Similarly, the Pearson's correlation coefficient $r_{\Delta AB}$ is the standardization
 156 of Δ_{AB} . Where $r_{\Delta AB} \stackrel{\text{def}}{=} \frac{\Delta_{AB}}{\sqrt{R_{AB}}}$, and $\sqrt{R_{AB}}$ is the theoretical maximum of Δ_{AB} .
 157 Because D_d^{AB} is determined by both LD and inbreeding, $\sqrt{R_{AB}}$ is defined as
 158 the value of Δ_{AB} under both complete LD and the current degree of inbreeding,
 159 denoted by $\Delta_{AB, \text{complete}}$. In this case, if $p_A = q_B$, the corresponding p_s^{AB} , p_d^{AB} ,
 160 D_s^{AB} and D_d^{AB} can be calculated by the following formulas:

$$161 \quad p_{s, \text{complete}}^{AB} = p_A,$$

$$162 \quad p_{d, \text{complete}}^{AB} = \mathcal{F}p_A + (1 - \mathcal{F})p_A^2,$$

$$163 \quad D_{s, \text{complete}}^{AB} = p_{s, \text{complete}}^{AB} - p_A^2 = p_A(1 - p_A),$$

$$164 \quad D_{d, \text{complete}}^{AB} = p_{d, \text{complete}}^{AB} - p_A^2 = \mathcal{F}p_A(1 - p_A),$$

165 where $\mathcal{F}$ is the inbreeding coefficient. Therefore

$$166 \quad \sqrt{R_{AB}} = \Delta_{AB, \text{complete}} = D_{s, \text{complete}}^{AB} + (v - 1)D_{d, \text{complete}}^{AB}$$

$$167 \quad = p_A(1 - p_A) + (v - 1)\mathcal{F}p_A(1 - p_A).$$

168 Let P_{AA} be the probability of sampling two copies of A within the same
169 individual without replacement. Then $P_{AA} = \mathcal{F}p_A + (1 - \mathcal{F})p_A^2$, and so $\mathcal{F}$ can
170 be calculated by

$$171 \quad \mathcal{F} = \frac{P_{AA} - p_A^2}{p_A(1 - p_A)} = \frac{P_{AA} - p_A^2}{p_A p_X} \quad (X \neq A).$$

172 Substituting the expression of $\mathcal{F}$ into that of $\sqrt{R_{AB}}$, a simplified expression of
173 $\sqrt{R_{AB}}$ for the case of $p_A = q_B$ is obtained, which is

$$174 \quad \sqrt{R_{AB}} = p_A p_X + (v - 1)(P_{AA} - p_A^2).$$

175 Next, if $p_A \neq q_B$, we let $\sqrt{R_{AB}}$ be the following geometric mean:

$$176 \quad \sqrt{R_{AB}} = \sqrt{[p_A p_X + (v - 1)(P_{AA} - p_A^2)][q_B q_X + (v - 1)(P_{BB} - q_B^2)]}. \quad (2)$$

177 Likewise, $r_{\Delta AB}$ may be negative, but the squared correlation coefficient $r_{\Delta AB}^2$
178 ranges from 0 to 1, which can also be used to evaluate the LD between two loci
179 for unphased genotypes.

180 In the following text, for simplicity, we will use D_w , D_b , D , Δ , Q , R , r
181 and r_{Δ} to replace D_w^{AB} , D_b^{AB} , D_{AB} , Δ_{AB} , Q_{AB} , R_{AB} , r_{AB} and $r_{\Delta AB}$ in turn. Due
182 to genetic drift, D^2 and Q (or Δ^2 and R) converge to zero after an infinite

number of generations. However, the ratio r^2 of D^2 to Q (or the ratio r_{Δ}^2 of Δ^2 to R) converges to a constant, whose value is determined by the mating system together with the recombination rate c and the effective population size N_e (WEIR AND HILL 1980). In the following sections, we extend Weir and Hill's (1980) double non-identity framework, to obtain the expectations of r^2 and r_{Δ}^2 .

Double non-identity coefficients

The double non-identity coefficients can be used to derive the moments of various LD measurements and to approximate $E(\hat{r}^2)$ and $E(\hat{r}_{\Delta}^2)$ at equilibrium state. The term *identity* means identical-by-descent (IBD).

The single non-identity coefficient is defined as the probability that the two alleles of an allele pair are not IBD. There are two configurations for two such alleles: (i) they originate from the same individual, or (ii) they originate from different individuals. We denote the single non-identity coefficient by P for (i), or by Π for (ii). Then, P and Π can be described by symbols as follows:

$$P \stackrel{\text{def}}{=} 1 - \mathcal{F} \quad \text{and} \quad \Pi \stackrel{\text{def}}{=} 1 - \bar{\theta},$$

where $\bar{\theta}$ is the average kinship coefficient between all individuals in a population, i.e. the probability that two alleles (each randomly sampled from a separate individual) are IBD.

The double non-identity coefficient is defined as the probability that

neither of two allele pairs are IBD. There are multiple configurations for these two allele pairs. Based on Weir & Hill (1980), we establish 3 digenic, 6 trigenic and 13 quadgenic two-locus allele configurations for different polysomic inheritances, including the following four novel allele configurations (9th, 15th, 21st and 22nd) that have more than two haplotypes within individuals. These allele configurations along with the notations of the corresponding frequencies, double non-identity coefficients, and expectations are presented in Table 1, where the first nine allele configurations do not have corresponding double non-identity coefficients because they share the same alleles.

For example, the 10th allele configuration $Z_{BB...}^{AA...}$ in Table 1 means that these two allele pairs are from two haplotypes within the same individual, the first A and first B are in one haplotype, and the second A and second B are in another haplotype. Moreover, the corresponding frequency, double non-identity coefficient and the expectation of frequency are denoted by P_{10} , Θ_1 and E_{10} , respectively.

The expectation E_i of each frequency P_i in Table 1 is derived by assuming no initial LD, which is a linear combination of $p_A q_B$, $p_A q_B (p_X + q_X)$ and $p_A p_X q_B q_X$, whose combination coefficients are listed in the three cells before E_i in Table 1. For example, the combination coefficients of E_{18} are 1, $-\Pi$ and Δ_3 . The allele pair AA or BB in the 18th allele configuration $Z_{\cdot B...|\cdot...|B...}^{A\cdot...|A...|\cdot...}$ consists of the alleles from different individuals, then the single

non-identity coefficient of each allele pair is Π and the double non-identity coefficient is Δ_3 . Hence the identity states of these two allele pairs can be described by the following three aspects: (i) both pairs are non-IBD at the probability Δ_3 , (ii) only one pair is IBD at the probability $\Pi - \Delta_3$ or (iii) both pairs are IBD at the probability $1 - 2\Pi + \Delta_3$. Therefore, the expectation E_{18} is the following linear combination with 1, $-\Pi$ and Δ_3 as the combination coefficients:

$$\begin{aligned} E_{18} &= \Delta_3 p_A^2 q_B^2 + (\Pi - \Delta_3)(p_A q_B^2 + p_A^2 q_B) + (1 - 2\Pi + \Delta_3)p_A q_B \\ &= p_A q_B - \Pi p_A q_B (p_X + q_X) + \Delta_3 p_A p_X q_B q_X. \end{aligned}$$

Various moments of LD measurements can be derived by using the expectations E_1 to E_{22} , with the derivations presented in Appendix B. Because these expectations are functions of both the single and the double non-identity coefficients, by using Table 1, each moment in Appendix B can be converted to a function of double non-identity coefficients (two single non-identity coefficients P and Π are accommodated into double non-identity coefficients), whose essential factors are listed in Table 2.

The expressions of various moments can now be expressed uniformly by matrices. Let $\mathbf{M}$ be the row vector consisting of the 7 moments in the header row of Table 2, and let Φ be the column vector consisting of the 13 double non-identity coefficients in the header column of Table 2. Denote $\mathbf{A}$ as a

244 13×7 matrix, whose i^{th} column consists of the i^{th} column divided by the
245 last column of Table 2. Then

$$246 \quad \mathbf{M} = \mathbf{\Phi}^T \mathbf{A}. \quad (3)$$

247 We call $\mathbf{M}$ the *moment vector*, and $\mathbf{\Phi}$ the *double non-identity vector*. Moreover,
248 $\mathbf{A}$ can be decomposed as the following combination:

$$249 \quad \mathbf{A} = Q\mathbf{A}_1 + Qn^{-1}\mathbf{A}_2 + \mathcal{O}(n^{-2}), \quad (4)$$

250 if we let

$$251 \quad \mathbf{A}_1 = \lim_{n \rightarrow \infty} \mathbf{A}/Q \quad \text{and} \quad \mathbf{A}_2 = \lim_{n \rightarrow \infty} n(\mathbf{A}/Q - \mathbf{A}_1),$$

252 where the elements in the combination matrices $\mathbf{A}_1$ and $\mathbf{A}_2$ in the principal
253 part of $\mathbf{A}$ are listed in Tables S1 and S2, respectively.

254 Finally, if the correlation between $E(\hat{D}^2)$ and $E(\hat{Q})$ is not considered, the
255 ratio d^2 of $E(\hat{D}^2)$ to $E(\hat{Q})$ can be used as an approximation of the moment
256 $E(\hat{r}^2)$. Similarly, the ratio δ^2 of $E(\hat{\Delta}^2)$ to $E(\hat{R})$ can also be used as that of
257 $E(\hat{r}_\Delta^2)$ if the correlation between $E(\hat{\Delta}^2)$ and $E(\hat{R})$ is not considered. These
258 facts can be denoted by symbols as follows:

$$259 \quad E(\hat{r}^2) \approx \frac{E(\hat{D}^2)}{E(\hat{Q})} = d^2 \quad \text{and} \quad E(\hat{r}_\Delta^2) \approx \frac{E(\hat{\Delta}^2)}{E(\hat{R})} = \delta^2. \quad (5)$$

260 **Transition matrix of double non-identity coefficients**

261 The transition matrix of double non-identity coefficients can be used to

describe the behavior of double non-identity coefficients due to genetic drift.

Let Φ be the double non-identity vector in the current generation, and let Φ' be that in the next generation. If Φ is given, then Φ' can be calculated from Φ . We use a diploid Wright-Fisher population with N individuals to demonstrate how to calculate Φ' . For this population, we have $\theta_1 = \theta_2$, $\Gamma_1 = \Gamma_2 = \Gamma_3$ and $\Delta_1 = \Delta_2 = \Delta_3 = \Delta_4 = \Delta_5$, but Γ_4 , Δ_6 and Δ_7 are undefined. Therefore, both Φ and Φ' contain 10 elements, and there are only three distinct elements in Φ or Φ' . Because the individuals are formed by the random union of gametes, θ_1 in Φ can be updated to θ'_1 in Φ' , in the sense that

$$\begin{aligned}\theta'_1 &= \frac{1}{2N} [(1-c)^2 \cdot 0 + 2c(1-c) \cdot 0 + c^2 \cdot 0] \\ &\quad + \frac{1}{2N} [(1-c)^2 \cdot \theta_1 + 2c(1-c) \cdot 0 + c^2 \cdot \theta_1] \\ &\quad + \frac{N-1}{N} [(1-c)^2 \cdot \theta_2 + 2c(1-c) \cdot \Gamma_1 + c^2 \cdot \Delta_1],\end{aligned}$$

where c is the recombination rate between the two given loci. Similarly, the other two elements Γ'_1 and Δ'_1 in Φ' can also be calculated. It can be shown that each element in Φ' can be expressed as a linear combination in the form of $a\theta_1 + b\Gamma_1 + c\Delta_1$.

In general, each updated double non-identity coefficient can also be expressed as a linear combination of the current double non-identity

coefficients. If Ω denotes the matrix consisting of those combination coefficients, then Φ' can be expressed as $\Phi' = \Omega\Phi$. We call Ω the *transition matrix* from Φ to Φ' .

Let Φ_0 be the double non-identity vector in the founder generation and let Φ_t be that in the t^{th} generation. This gives $\Phi_t = \Omega^t\Phi_0$. If a population is allowed to reproduce for several generations, the vector sequence is:

$$\Phi_0, \Phi_1, \Phi_2, \dots, \Phi_t, \dots$$

and will reach a steady state as t increases. In other words, this sequence will converge to a constant vector, denoted by Φ_∞ . This limit vector Φ_∞ is independent to the initial vector Φ_0 if $\Phi_0 \neq \mathbf{0}$.

To simplify the model for polysomic inheritance, we established a virtual mating system, named the *haplotype sampling (HS) mating system*. In this mating system, it is assumed that each individual is reproduced by randomly sampling v haplotypes with replacement from the previous generation. The genes in an offspring therefore come from a maximum of v parents. Because the haplotypes within (or among) individuals are randomly sampled, there is no difference among dihaplotypic, trihaplotypic and quadhaplotypic double non-identity coefficients, symbolically $\Theta_1 = \Theta_2$, $\Gamma_1 = \Gamma_2 = \Gamma_3 = \Gamma_4$ and $\Delta_1 = \Delta_2 = \dots = \Delta_7$. Therefore, for this mating system, the transition matrix Ω can be simplified as a 3×3 matrix, whose transposition Ω^T is listed in Table S3 and

derivation is given in Appendix C. The transposition of a simplified transition matrix (still denoted by Ω) is presented in Table 3, and its element expressions can be easily exported from this table. In the following discussion, we will also use Table 3 to investigate the behavior of LD in polyploids.

It is noteworthy that the sum of the combination coefficients of 1 in each column in Table 3 is exactly one, but the sum of the elements in each column of Ω^T is less than one. This indicates that the transition (i.e. a generation of random mating) will gradually reduce the double-nonidentity coefficients, and their values will be eventually converge to zero, i.e. $\Omega^\infty = \mathbf{0}$. This illustrates the loss of heterozygosity and the fixation of alleles.

Although Φ_∞ will eventually converge to zero, the ratio of the moments $E(\hat{D}^2)$ to $E(\hat{Q})$, and of the moments $E(\hat{\Delta}^2)$ to $E(\hat{R})$ will converge to some constants. This can be considered as the double non-identity vector Φ reaches a relatively stable state so the direction of Φ is constant during reproduction, symbolically $\Phi' = \nu\Phi$. The direction of Φ (say ω) and the scale factor ν can be solved by performing eigen-value decomposition for Ω , i.e. solving $\Omega\omega = \nu\omega$, which means ν is an eigenvalue of Ω , and ω is an eigenvector of Ω belonging to ν . It is also noteworthy that there are multiple eigenvalues, with the highest eigenvalue be of our interest. Therefore, d^2 and δ^2 can be calculated from the *moment vector* calculated from Equation (3) by substituting Ω with ω , i.e. $\mathbf{M}_\omega = \omega^T \mathbf{A}$. We denote the elements in $\mathbf{M}_\omega$ as $E_\omega(\cdot)$, e.g.

322 $E_{\omega}(\widehat{D}^2)$, then the exact d^2 and δ^2 are as follows:

$$323 \quad d^2 = \frac{E_{\omega}(\widehat{D}^2)}{E_{\omega}(\widehat{Q})} + \frac{1}{vn}, \quad (6a)$$

$$324 \quad \delta^2 = \frac{E_{\omega}(\widehat{\Delta}^2)}{E_{\omega}(\widehat{R})} + \frac{1}{n}. \quad (6b)$$

325 The additional terms $1/vn$ and $1/n$ are used to include any error resulting
326 from finite sample size (see Appendix D for details)

327

328 **Approximations of d^2 and δ^2**

329 To simplify the calculation and to facilitate the discussion of the properties
330 of d^2 and δ^2 , Weir & Hill (1980) adopted a matrix decomposition technique
331 to approximate v and ω for disomic inheritance and also to approximate d^2
332 and δ^2 . Here, we will follow this approach to derive the approximate
333 expressions of d^2 and δ^2 for the HS mating system and four additional
334 mating systems.

335 Let Ω be the simplified transition matrix for the HS mating system, as
336 detailed in Table 3. If N is large enough, the values of the terms with N^{-2} and
337 N^{-3} in Table 3 will be small, then Ω can be decomposed to:

$$338 \quad \Omega = \mathbf{T} + N^{-1}\mathbf{S} + \mathcal{O}(N^{-2}).$$

339 For the matrices $\mathbf{T}$ and $\mathbf{S}$ in the principal part of Ω , if we denote $c_i = c - i$ and
340 $v_i = v - i$ ($i = 1, 2$), we will obtain from Table 3:

$$\mathbf{T} = \begin{bmatrix} c_1^2 & -2c_1c & c^2 \\ 0 & -c_1 & c \\ 0 & 0 & 1 \end{bmatrix} \quad \text{and} \quad \mathbf{S} = \begin{bmatrix} \frac{c^2}{v_1} - \frac{1+2c_1c}{v} & \frac{4c(2c-1)}{v} - \frac{2c^2}{v_1} & \frac{2c^2(3-2v)}{v_1v} \\ -\frac{c_1}{v} & \frac{6c-3}{v} & -\frac{5c}{v} \\ 0 & \frac{4}{v} & -\frac{6}{v} \end{bmatrix}.$$

Similarly, v and ω can be decomposed to

$$v = 1 + N^{-1}r + \mathcal{O}(N^{-2}),$$

$$\omega = \mathbf{1} + N^{-1}\mathbf{x} + \mathcal{O}(N^{-2}),$$

where $\mathbf{1} = [1, 1, 1]^T$ and $\mathbf{x} = [x_1, x_2, x_3]^T$. According to $\Omega\omega = v\omega$, we obtain a matrix equation as follows:

$$\mathbf{T}\mathbf{1} + N^{-1}\mathbf{T}\mathbf{x} + N^{-1}\mathbf{S}\mathbf{1} = \mathbf{1} + N^{-1}\mathbf{x} + N^{-1}r\mathbf{1} + \mathcal{O}(N^{-2}).$$

Because $\mathbf{T}\mathbf{1} = \mathbf{1}$, if the term $\mathcal{O}(N^{-2})$ is omitted, we obtain

$$(\mathbf{S} - r\mathbf{I})\mathbf{1} = (\mathbf{I} - \mathbf{T})\mathbf{x}.$$

This matrix equation is an approximation of the previous equation, which is a linear equation set with 3 equations and 4 unknowns, the solutions of which are as follows:

$$r = -2/v, \quad x_1 = \frac{2cv_1 - v_1 - c^2v}{c_2cvv_1} + \zeta, \quad x_2 = \zeta, \quad x_3 = \zeta \quad (\zeta \text{ is any number}).$$

If we let $\zeta = 0$, we obtain a special solution: $r = -2/v$ and $\mathbf{x} =$

$$\left[\frac{2cv_1 - v_1 - c^2v}{c_2cvv_1}, 0, 0 \right]^T.$$

Replacing this solution into the expressions of v and ω , it follows that:

$$v \approx \frac{Nv-2}{Nv} \quad \text{and} \quad \omega \approx \left[1 + \frac{2cv_1 - v_1 - c^2v}{c_2cNvv_1}, 1, 1 \right]^T.$$

Now, by substituting ω in Equation (3) with the approximation of ω , it can be calculated that

$$E_\omega(\hat{D}^2) = E_\omega(\hat{\Delta}^2) \approx 2cv_1 - v_1 - c^2v \quad \text{and} \quad E_\omega(\hat{Q}) = E_\omega(\hat{R}) \approx c_2cNv_1v.$$

Therefore, the approximated d^2 and δ^2 are as follows:

$$d_{\text{HS}}^2 \approx \frac{2cv_1 - v_1 - c^2v}{c_2cN_e v_1 v} + \frac{1}{vn}, \quad (7a)$$

$$\delta_{\text{HS}}^2 \approx \frac{2cv_1 - v_1 - c^2v}{c_2cN_e v_1 v} + \frac{1}{n}, \quad (7b)$$

where N_e and N are equivalent under the HS mating system. The results from Equations (7a) and (7b) accord with those of Ohta and Kimura (1969) and Weir & Hill (1980) for the monoecious selfing mating system in diploids.

The transition of single non-identity coefficients satisfies the relations:

$$P' = \frac{Nv-1}{Nv}P \quad \text{and} \quad \Pi' = \frac{Nv-1}{Nv}\Pi. \quad \text{Moreover, if two loci are located at two extreme}$$

far locations on the same chromosome, and the thirteen double non-identity

coefficients are all equal to P^2 and $\Phi' = \left(\frac{Nv-1}{Nv}\right)^2 \Phi$, and thus also the

corresponding eigenvalue $v = \left(\frac{Nv-1}{Nv}\right)^2 \approx \frac{Nv-2}{Nv}$. By comparing with the

previous conclusion of $v \approx \frac{Nv-2}{Nv}$ by substituting $\zeta = 0$, we see that $r = -2/v$

is a good approximation to the rate of loss of heterozygosity at the pairs of

374 independent loci.

375 We now follow the approach of Weir & Hill (1980) to establish four
376 additional mating systems. Two are monocious mating systems: (i) selfing
377 being allowed (termed MS), and (ii) selfing being excluded (termed ME). In
378 both of these mating systems, the effective population size N_e is the same as
379 the population size N . The other two mating systems we use are both
380 dioecious systems: (i) dioecious with random pairing (termed DR), and
381 dioecious with lifetime pairing (termed DH). In DR, each offspring is produced
382 from a new pairing. In DH, each individual remains in a single reproductive
383 unit for its entire lifetime. Moreover, in both DR and the DH, there are M
384 males and F females in the population for each generation and $F = fM$, the
385 effective population size is calculated by $N_e = \frac{4MF}{M+F}$.

386 The transition matrix $\mathbf{\Omega}$ for each of the four additional mating systems is
387 a 13×13 matrix, whose element expressions are derived in Appendices E to
388 G. The results are not shown, but the matrices $\mathbf{T}$ and $\mathbf{S}$ in the principal part
389 of $\mathbf{\Omega}$ for all five mating systems (HS, MS, ME/DR and DH) are listed in
390 Appendix H.

391 The equality $\mathbf{T}\mathbf{1} = \mathbf{1}$ still holds for all five mating systems. Therefore, the
392 same approximations of d^2 and δ^2 can be used to derive the next matrix
393 equation if N_e is large enough:

$$(S - rI)\mathbf{1} = (I - T)\mathbf{x},$$

where $\mathbf{x} = [x_1, x_2, \dots, x_{13}]^T$. From Appendix H, we show that the elements in the 11th row of $I - T$ are all zero, and the 11th element in the vector $(S - rI)\mathbf{1}$ is $-\frac{v}{2} - r$ for all five mating systems. Therefore, the 11th equation in this matrix equation is $-\frac{v}{2} - r = 0$, and thus $r = -2/v$. For the other 13 unknowns $x_1, x_2, \dots, x_{13}$, the 13 differences

$$x_1 - x_{11}, x_2 - x_{11}, \dots, x_{13} - x_{11}$$

can be solved for each mating system. The appropriate expressions are listed in Table 4.

Let $a_i = x_i - x_{11}$, then $x_i = a_i + x_{11}$, $i = 1, 2, \dots, 13$. The solutions of the matrix equation for each mating system can be expressed as

$$r = -2/v, \quad x_1 = a_1 + \zeta, \quad x_2 = a_2 + \zeta, \dots, \quad x_{13} = a_{13} + \zeta,$$

where ζ is any number. Now, if we let ζ be 0, we obtain a special solution as follows:

$$r = -2/v \quad \text{and} \quad \mathbf{x} = [a_1, a_2, \dots, a_{13}]^T.$$

In addition, $v = 1 + N_e^{-1}r + \mathcal{O}(N^{-2})$ and $\boldsymbol{\omega} = \mathbf{1} + N_e^{-1}\mathbf{x} + \mathcal{O}(N^{-2})$, it follows

$$v \approx \frac{N_e v - 2}{N_e v} \quad \text{and} \quad \boldsymbol{\omega} \approx \left[\frac{N_e + a_1}{N_e}, \frac{N_e + a_2}{N_e}, \dots, \frac{N_e + a_{13}}{N_e} \right]^T. \quad (8)$$

Similarly, by substituting the approximation of $\boldsymbol{\omega}$ into Equation (3), we can

calculate the approximations of various moments, and then annotate the approximate expressions of d^2 and δ^2 for four mating systems (MS, ME, DR and DH) as follows:

$$\begin{aligned}
 d_{\text{MS}}^2 &\approx \frac{8c_2c^2 - 4c_2cv(5c - 1) + 2v^2(7c_2c^2 + c + 2) - 3c_1^2v^3(c + 1)}{c_2cN_e v^2(cv_2 + v)(3v - 4)} + \frac{1}{vn}, \\
 \delta_{\text{MS}}^2 &\approx \frac{v^2[4 - 3v + 8c^2 - 14c - cv(2c^2 + 4c - 13) + c_2cv^2(c + 1)]}{c_2c(cv_2 + v)(3v - 4)(N_e v^2 - 2v^2 + 6v - 4)} + \frac{1}{n}; \\
 d_{\text{ME/DR}}^2 &\approx \frac{8c_2c^2 - 4c_2cv(5c - 1) + 2v^2(7c_2c^2 + c + 2) - 3c_1^2v^3(c + 1)}{c_2cN_e v^2(cv_2 + v)(3v - 4)} + \frac{1}{vn}, \\
 \delta_{\text{ME/DR}}^2 &\approx \frac{v^2[4 - 3v + 8c^2 - 14c - cv(2c^2 + 4c - 13) + c_2cv^2(c + 1)]}{c_2c(cv_2 + v)(3v - 4)(N_e v^2 - 4v^2 + 8v - 4)} + \frac{1}{n}; \\
 d_{\text{DH}}^2 &\approx \{(1 + f)[cv(3v^2 + 2v - 8) - v^2(3v - 4)] \\
 &\quad + c^2(3v - 4)[v^2 - 10v + 4 + f(v^2 - 8v + 4)] \\
 &\quad - c^3v_2[3v^2 - 10v + 4 + f(3v^2 - 8v + 4)]\} \\
 &\quad / [c_2c(1 + f)N_e v^2(cv_2 + v)(3v - 4)] + \frac{1}{vn}, \\
 \delta_{\text{DH}}^2 &\approx v^2\{c^3(3 + f)v_2v - (1 + f)(3v - 4) - c^2[3v^2 - 8 + f(v^2 + 4v - 8)] \\
 &\quad - c[f(2v^2 - 13v + 14) + 3(2v^2 - 7v + 6)]\} \\
 &\quad / [c_2c(1 + f)(cv_2 + v)(3v - 4)(N_e v^2 - 4v^2 + 8v - 4)] + \frac{1}{n}.
 \end{aligned}$$

The approximate expressions of d^2 and δ^2 for each of the five mating systems for inheritances ranging from disomic to decasomic (with even ploidy levels) are presented in Tables S4 and S5. The corresponding values between unlinked loci located on either the same chromosome ($c = 0.5$) or different chromosomes ($c = 1 - 1/v$) are presented in Table 5.

Simulations and evaluations

Behaviors of $\hat{r}^2$ and $\hat{r}_\Delta^2$

In this section, we discuss the behaviors of the squared correlation coefficient estimators $\hat{r}^2$ and $\hat{r}_\Delta^2$ during reproduction and provide the exact and the approximate values of d^2 or δ^2 for reference.

Because the approximations of $E(\hat{r}^2)$ and $E(\hat{r}_\Delta^2)$ in Equation (5) are affected by the correlation between $\hat{D}^2$ and $\hat{Q}$ (or between $\hat{\Delta}^2$ and $\hat{R}$), to eliminate such effects, we consider all values of $\hat{D}^2$, $\hat{Q}$, $\hat{\Delta}^2$ and $\hat{R}$, and let $\hat{r}^2$ and $\hat{r}_\Delta^2$ be the following ratios:

$$\hat{r}^2 = \frac{\sum_{(l_1, l_2)} \sum_{A \in l_1, B \in l_2} \hat{D}_{AB}^2}{\sum_{(l_1, l_2)} \sum_{A \in l_1, B \in l_2} \hat{Q}_{AB}} \quad \text{and} \quad \hat{r}_\Delta^2 = \frac{\sum_{(l_1, l_2)} \sum_{A \in l_1, B \in l_2} \hat{\Delta}_{AB}^2}{\sum_{(l_1, l_2)} \sum_{A \in l_1, B \in l_2} \hat{R}_{AB}}, \quad (9)$$

where (l_1, l_2) is taken from all diallelic locus pairs, the symbol $A \in l_1$ (or $B \in l_2$) represents A (or B) is taken from all alleles at the first (or the second) locus in (l_1, l_2) .

We adopt a Monte-Carlo method to simulate the behavior of $\hat{r}^2$ and $\hat{r}_\Delta^2$. During simulation, a population with the MS mating system is generated, which contains 40 or 80 individuals with a ploidy level of either 2 or 4. Next, the individuals generated are genotyped at 200 linked diallelic locus pairs, with a recombination rate 0.1 for each locus pair. The population is then allowed to reproduce for 250 generations. For each generation, by using the

data of genotypes of all individuals under various situations, $\hat{r}^2$ and $\hat{r}_\Delta^2$ are calculated by Equation (9), and the exact and the approximate d^2 and δ^2 are also calculated by Equations (6) and (7), respectively. This process is performed 300,000 times in total. The results are shown in Figure 1.

Figure 1 shows that the approximate d^2 or δ^2 are both slightly higher than their exact value, and both the exact and the approximate d^2 or δ^2 decrease as N_e or v increases. The values of $\hat{r}^2$ and $\hat{r}_\Delta^2$ are both initially 1, and reduce respectively to exact d^2 and δ^2 after about 40 generations. Henceforth, $\hat{r}^2$ and $\hat{r}_\Delta^2$ achieve a relatively stable state, and remain around the exact values of d^2 and δ^2 for several generations. In particular, if the ploidy level is four, these values will both converge to the exact d^2 and δ^2 as the number of generations increases.

Due to genetic drift, some loci become fixed and are excluded from the simulation, causing that the number L of locus pairs used for genotyping to decline. The correlation between the numerator and the denominator in each of both formulas in Equation (9) therefore increases, such that $\hat{r}^2$ and $\hat{r}_\Delta^2$ correspondingly decrease. The duration of a stable state depends on three factors: (i) ploidy level v , (ii) effective population size N_e and (iii) the number L of locus pairs. As the value of each of these factors increases, the longer the duration of the stable state of both $\hat{r}^2$ and $\hat{r}_\Delta^2$.

We also simulate the behaviors of $\hat{r}^2$ and $\hat{r}_{\Delta}^2$ during reproduction for five mating systems (including cases with f being set to either 2 or 5 for the DR and the DH mating systems). The simulation process is as follows. First, a population for each of the five mating systems is generated, which contains 40 individuals with a ploidy level of either 2, 4, 6 or 8. Next, these 40 individuals are genotyped as described for the previous simulation. Then, the population is allowed to reproduce for 50 generations. For each generation, by using data of the genotypes of all individuals under various situations, $\hat{r}^2$ and $\hat{r}_{\Delta}^2$ are calculated. The exact and approximate d^2 and δ^2 values are also calculated. The process is repeated 30,000 times. The results are shown in Figure S1, and are similar to those shown in Figure 1. However, the approximate values d^2 and δ^2 deviate more from their exact values for some mating systems.

Finally, we also simulate the behaviors of $\hat{r}^2$ and $\hat{r}_{\Delta}^2$ for the MS mating system under different recombination rates (set $N_e = 80$, $v = 2$ or 4, $L = 200$ and $c = 0.001, 0.002, 0.004, 0.01, 0.02, 0.04, 1$ or 2). The simulation process is similar to the previous method and is performed 20,000 times. The population is allowed to reproduce for 100 generations. For each generation, $\hat{r}^2$ and $\hat{r}_{\Delta}^2$ are calculated, with the results shown in Figure S2. This shows that the convergent rates for $\hat{r}^2$ or $\hat{r}_{\Delta}^2$ among different ploidy levels differ little as the number of generations increases, but are strongly affected by the recombination rate: the higher the recombination rate, the faster the rate of

convergence.

Recombination rate

To investigate the influence of the recombination rate c on d^2 and δ^2 , the exact and the approximate d^2 and δ^2 are calculated for each mating system under different recombination rates (set $N_e = 100$, $n = 100$, $v = 2, 4, 6$ or 8 , $f = 1$ for DR and $f = 2$ or 5 for DH). The recombination rate c ranges from 0 to 1. The results for the MS mating system are shown in Figure 2, and the results for all mating systems (including MS) are uniformly shown in Figure S3.

Figure 2 shows that d^2 or δ^2 are high at a low recombination rate, and decrease gradually to a relatively low value as c increases. The rate of decrease steepens as the ploidy level increases. However, after c reaches ~ 0.5 , d^2 (at $v = 2$) or δ^2 (at all ploidy levels) both begin to increase. The approximate values of d^2 are close to their exact values, whilst the difference between the approximate and the exact values of δ^2 are more obvious, especially when $c > 0.5$.

The exact values for d^2 and δ^2 for the unlinked loci located on the same or different chromosomes are calculated for all five mating systems (set $N_e = 100$, $n = 100$, $v = 2, 4, 6, 8$ or 10 , $c = 0.5$ or $1 - 1/v$ and $f = 1, 2$ or 5 for DR /DH). Moreover, the error rates for d^2 or δ^2 under different conditions are also calculated. The results are presented in Table S6. It is clear that the

difference between $\delta_{c=0.5}^2$ and $\delta_{c=1-1/v}^2$ is low under all conditions, but the difference between $d_{c=0.5}^2$ and $d_{c=1-1/v}^2$ is ~50 to 100 times higher. For example, for tetraploids, the error rate is about 13% for d^2 but it is 0.13% for δ^2 .

Estimation of effective population size

In this section, we estimate the effective population size N_e from unphased genotypes. Previous methods for this assume that loci are all unlinked, and the recombination rate is 0.5 (e.g. ENGLAND *et al.* 2006). However, in polysomic inheritances, the recombination rate is $1 - 1/v$ between two loci located on different chromosomes. Because $\delta_{c=0.5}^2$ and $\delta_{c=1-1/v}^2$ are close, with the error rate at most 1.5% (Table S6), we assume the recombination rate $c = 0.5$ between any two loci.

We preliminarily solve N_e using the approximated δ^2 , e.g. Equation (7b), by

$$\hat{N}_{e,\text{initial}} = \frac{1}{3(\hat{r}_{\Delta}^2 - 1/n)} + \eta \text{ for the HS/MS/ME/DR mating systems,} \quad (10a)$$

$$\hat{N}_{e,\text{initial}} = \frac{3+f}{3(1+f)(\hat{r}_{\Delta}^2 - 1/n)} + \eta \text{ for the DH mating system,} \quad (10b)$$

where $\hat{r}_{\Delta}^2$ is calculated by Equation (9), and the expression of η is either 0 for the HS mating system, $\frac{2(v-2)(v-1)}{v^2}$ for the MS mating system, or $\frac{4(v-1)^2}{v^2}$ for the ME/DR/DH mating systems.

We further optimize the solution of N_e using the exact δ^2 , i.e. Equation

(6b). The exact δ^2 is related to the double non-identity coefficients and the effective population size N_e . Therefore, the exact δ^2 can be regarded as a function of N_e , denoted by $\delta^2(N_e)$ such that N_e is the root of the equation:

$$\delta^2(N_e) - \hat{r}_\Delta^2 = 0,$$

and we solve N_e with Newton's method using $\hat{N}_{e,\text{initial}}$ as the initial solution.

This approach is denoted as NEWTON'S approach.

Equation (10a) or (10b) demonstrates that N_e is approximately proportional to $\frac{1}{\hat{r}_\Delta^2 - 1/n}$. If $\hat{r}_\Delta^2$ is close to $1/n$, then $\hat{N}_e$ becomes very large, indicating that the estimation of N_e is biased. However, because $1/N_e$ is approximately proportional to $\hat{r}_\Delta^2 - 1/n$, the estimation of $1/N_e$ is almost unbiased. Therefore, it is more convenient to evaluate the statistical performance of NEWTON'S approach by using the estimator $1/\hat{N}_e$.

We use a Monte-Carlo method to simulate the estimation of effective population size N_e from unphased genotypes, and then evaluate the statistical performance of NEWTON'S approach under different ploidy levels, numbers of loci, numbers of alleles and sample sizes. Two types of markers are used during simulation: (i) SNP (diallelic) and (ii) SSR (hexa-allelic). For simulation, first a founder population with 200 individuals all with a ploidy level of either 2, 4, 6 or 8 is created. To avoid the fixation of alleles, each allele in the founder generation is set as being unique. Second, the 200 individuals are genotyped at

100 or 200 diallelic SNPs, or at 20 or 40 hexa-allelic SSRs. These loci are assumed to be isometrically distributed on 10 chromosomes, and the length of each chromosome is 100 cM. Third, the founder population is allowed to reproduce for a fixed number of generations to reach the linkage equilibrium; the number of generations is 44 or 86 for SNP, and 11 or 19 for SSR. Fourth, after the final generation has been attained, to reduce the number of alleles k , we repeat collapsing two randomly selected alleles until the value of k is less than 2 (for SNP) or 6 (for SSR). Fifth, for the final generation, 400 individuals are created in total, and n individuals are randomly sampled from this generation, where $n = 40, 80, \dots, 400$ (interval 40). Finally, using the data of unphased genotypes of the n individuals sampled ($n = 40, 80, \dots, 400$), $\hat{N}_e$ can be estimated by using NEWTON'S approach. This process is performed 2000 times. If we subsequently let $\hat{V} = 1/\hat{N}_e$, the RMSE and the bias of $\hat{V}$ can be calculated, the results being shown in Figures 3 and S4.

Figure S4 shows that the results for SNP are more biased than those for SSR, with $\hat{V}$ slightly increasing as the number of loci L also increases. The bias of $\hat{V}$ is small, and is generally less than 2×10^{-3} , especially less than 3×10^{-4} for the hexasomic and the octosomic inheritances, thus $\hat{V}$ is nearly unbiased, as expected. Therefore, each RMSE of $\hat{V}$ is approximately equal to its standard deviation. Figure 3 shows that the RMSEs of $\hat{V}$ decrease as n

increases, the values of which among different ploidy levels are similar.

Moreover, the RMSEs for polyploids are slightly smaller than that for diploids.

In general, the performances of SNPs and SSRs are similar.

Data Accessibility

POLYGENE is a user-friendly software and can be run on 64bit Windows/Linux/Mac OS X platform. The binary executable files, user manual and source code of POLYGENE V1.3 are available on GitHub (<https://github.com/huangkang1987/polygene>). POLYGENE was developed using C++ and C# and requires .net framework V4.0 runtime library.

The simulation program, the source code (developed with C#), the readme file and the script to generate figures (developed with MATLAB) are provided as supplementary materials and can be downloaded via a link on the online version of this manuscript.

Discussion

LD test

We here follow the method proposed by WEIR AND COCKERHAM (1979) to extend two LD measures, D and the Burrow's Δ , to account for different levels of polysomic inheritance. These two measures can be used to perform

the LD test. The null hypothesis of a LD test is that a pair of loci is under linkage equilibrium, which is equivalent to all D_{AB} (or all Δ_{AB}) values being equal to zero.

For a sample with n individuals, there are nv haplotypes. The observed and the expected occurrences of a haplotype AB are, respectively, nP_s^{AB} and np_Aq_B . Because $D_{AB} = P_s^{AB} - p_Aq_B$, the χ^2 statistic for the LD measure D can be established as follows:

$$\chi_D^2 = n \sum_{AB} \frac{\hat{D}_{AB}^2}{p_Aq_B} \text{ with d.f. } (k_1 - 1) \times (k_2 - 1),$$

where d.f. is the number of degrees of freedom, k_i is the number of alleles among the allele copies in those haplotypes at the i^{th} locus ($i = 1, 2$), A is taken from all k_1 alleles at the first locus, and B is taken from all k_2 alleles at the second locus.

Next, for a sample with n individuals, there are nv^2 allele pairs, the observed and the expected occurrences of an allele pair AB are respectively $nvP_s^{AB} + nv(v-1)P_d^{AB}$ and $nv^2p_Aq_B$. Because $\Delta_{AB} = D_s^{AB} + (v-1)D_d^{AB}$ and $D_s^{AB} = P_s^{AB} - p_Aq_B$, the χ^2 statistic for Burrow's Δ statistic can be established as follows:

$$\chi_\Delta^2 = n \sum_{AB} \frac{\hat{\Delta}_{AB}^2}{p_Aq_B} \text{ with d.f. } (k_1 - 1) \times (k_2 - 1).$$

d^2 and δ^2

In this study, various moments of LD measures are derived by extending

Weir & Hill's (1980) double non-identity coefficients, and thus the exact d^2 can be obtained by using the moments $E(\hat{D}^2)$ and $E(\hat{Q})$ under various mating systems. The exact δ^2 can also be obtained by using the moments $E(\hat{\Delta}^2)$ and $E(\hat{R})$. Hence the value of $\hat{r}^2$ (or $\hat{r}_A^2$) can be approximately replaced by that of d^2 (or δ^2) under each mating system at the equilibrium state. Moreover, the approximate expressions of d^2 and δ^2 under various mating systems are derived by using the transitional matrix, and several relations are discussed, such as the relation between $\hat{r}^2$ (or $\hat{r}_A^2$) and the number of generations during reproduction, the relation between d^2 (or δ^2) and the recombination rate c , and so on.

Figure 1 shows that after the population has been allowed to reproduce for about 40 generations, $\hat{r}^2$ (or $\hat{r}_A^2$) reaches a relatively steady state remains close to the exact d^2 (or δ^2) for several generations. After that, $\hat{r}^2$ (or $\hat{r}_A^2$) begins to decrease again, due to both the fixation of alleles and the positive correlation between $\hat{D}^2$ and $\hat{Q}$ (or between $\hat{\Delta}^2$ and $\hat{R}$). As the number L of diallelic locus pairs decreases, the number of terms in the numerator or the denominator in Equation (9) is reduced, due to the weighted scheme in Equation (9) being unable to effectively eliminate the correlation. The number of generations at which $\hat{r}^2$ (or $\hat{r}_A^2$) begins to decrease again depends on v , N_e , L and the initial heterozygosity.

Figure S2 shows that regardless of $\hat{r}^2$ or $\hat{r}_A^2$, the smaller the recombination

rate, the slower the rate of convergence. Generally, $\hat{r}^2$ and $\hat{r}_\Delta^2$ decrease to a relatively steady state after about $-4.21/\ln 1 - c$ generations. Moreover, under the same recombination rate, the convergent rates of $\hat{r}^2$ (or $\hat{r}_\Delta^2$) are similar for all levels of ploidy but differ markedly under different recombination rates.

Figure 2 (and S3) show that the relationship between d^2 (or δ^2) and the recombination rate c has two main features: (i) if c is small (e.g. < 0.25), both d^2 and δ^2 for polysomic inheritance decreases more rapidly than those for disomic inheritance and (ii), the difference between $d_{c=0.5}^2$ and $d_{c=1-1/v}^2$ under polysomic inheritance is considerable (the error rate ranges from 10% to 23%), whereas the difference between $\delta_{c=0.5}^2$ and $\delta_{c=1-1/v}^2$ is negligible (the error rate is less than 1.5% for non-HS mating systems).

For (i), this infers that a higher density genetic map is required to detect any linkage in polyploids. A rough estimate would be the locus density in tetraploids (hexaploids or octoploids) to be 1.58 (2.16 or 2.67) times of that for diploids (estimated by the threshold $\delta^2 = 0.2$, see Figure 2). However, if the locus density is sufficient, the gene mapping in polyploids may be more accurate than that in diploids due to the steep slope of the curve at a low c .

For (ii) this indicates that it is unnecessary to distinguish whether two loci are located on the same chromosome or not if the effective population size N_e is estimated by $\hat{r}_\Delta^2$. From this reason, we can simply let the recombination rate

between any two loci be equal to 0.5, as is assumed in other methods (e.g. ENGLAND *et al.* 2006). However, it is necessary to model the case that two loci are located on different chromosomes if N_e is estimated by $\hat{r}^2$ using phased genotypes.

Effective population size

Among the parameters v , n , r^2 , r_{Δ}^2 , N_e , c and f , the first two v and n are known, the next two r^2 and r_{Δ}^2 can be estimated from the genotype data, and the mating system and the ratio f can be obtained from either *a priori* information, field observations or experiments. The remaining two parameters N_e and c are the parameters we usually need to estimate, and one can be estimated if the other is known.

After simulation, we evaluate the RMSE and the bias of $\hat{V}$ (i.e. $1/\hat{N}_e$). However, in practice, we are interested in N_e . To ensure that the estimation of N_e is applicable, the estimator $1/\hat{V}$ (i.e. $\hat{N}_e$) should be within $\pm 20\%$ of the true N_e . Therefore, the RMSE of $\hat{V}$ should be smaller than $1/10N_e$. For example, if $N_e = 1000$, the RMSE of $\hat{V}$ should be below 0.0001. It is hard to achieve such a small value if N_e is large. This is because the influence of sampling error $1/n$ on δ^2 is relatively high, which covers the effect of N_e on δ^2 (e.g. see Equation (6b)), and thus more samples are required to reduce the sampling variance.

From Figure 3 it is clear that the curves of RMSE among different ploidy

levels are similar, indicating that the estimations of the effective population sizes N_e in polyploids is almost the same as for diploids. Such estimation therefore requires similar numbers of samples and loci regardless of ploidy level. Figure S4 also shows that the results for polyploids may be better than for diploids due to smaller biases. The performance of 100/200 diallelic SNPs is as good as that of 20/40 hexa-allelic SSRs, indicating that the RMSE is mainly determined by the number $\sum_l^L (k_l - 1)$ of independent alleles.

From Figure S4, the estimation of $1/N_e$ is biased. Some possible sources of this bias are enumerated as follows. (i) According to Equation (10a) or (10b), $\hat{r}_\Delta^2 - 1/n$ is actually proportional to $1/(N_e - \eta)$, not $1/N_e$, indicating that the estimation of $1/(N_e - \eta)$ may be unbiased, but the estimation of $1/N_e$ is biased. (ii) The recombination rate between two loci located on the same chromosome is less than 0.5, but it is assumed to be 0.5. (iii) The recombination rate between two loci located on different chromosomes is $1 - 1/v$, but it is also assumed to be 0.5.

We suggest that (ii) is the main source of this bias. This is because the bias is largely influenced by both the number L of loci used and the ploidy level v (Figure S4). Because the length of each chromosome is a constant in each simulation, the loci become denser at higher levels of L . The value of δ^2 between two close loci (implying smaller c) therefore increases in the deviation from $\delta_{c=0.5}^2$ (Figure 2). In addition, the simulation results for

polyploids are less biased. This is because the curve of δ^2 at a higher ploidy level is flat for the majority of situations (e.g. $c > 0.2$). To validate our prediction, we simulated the scenario that the loci on the same chromosome are all unlinked (i.e. $c = 0.5$ for all locus pairs) and found that bias is reduced to $\sim 10^{-4}$ in diploids and in tetraploids (data not shown).

The bias sources (ii) and (iii) can be reduced if the *a priori* information about the length of chromosomes is considered. For this case, it is possible to calculate δ^2 by

$$\delta^2 = (1 - \rho) \delta_{c=1-1/v}^2 + \rho \int_0^\infty \psi(\mathcal{D}) \delta_{c=c_D}^2 d\mathcal{D},$$

where ρ is the probability that two loci are on the same chromosome, $\delta_{c=1-1/v}^2$ and $\delta_{c=c_D}^2$ are the exact δ^2 at the recombination rates $1 - 1/v$ and c_D , respectively, $\mathcal{D}$ is the genetic distance between two loci in the same chromosome, and $\psi(\mathcal{D})$ is the probability density function of $\mathcal{D}$, which is the following weighted average:

$$\psi(\mathcal{D}) = \frac{1}{\sum_i \mathcal{L}_i} \sum_i \mathcal{L}_i \psi(\mathcal{D} | \mathcal{L}_i),$$

in which $\mathcal{L}_i$ is the length of i^{th} chromosome, and $\psi(\mathcal{D} | \mathcal{L}_i)$ is the probability density function of $\mathcal{D}$ given $\mathcal{L}_i$, whose expression is

$$\psi(\mathcal{D} | \mathcal{L}_i) = \begin{cases} \frac{2}{\mathcal{L}_i} - \frac{2\mathcal{D}}{\mathcal{L}_i^2} & \text{if } 0 \leq \mathcal{D} \leq \mathcal{L}_i, \\ 0 & \text{otherwise.} \end{cases}$$

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799 **Conflicts of Interest**

800 The authors declare no conflict of interest.

801 **Author Contributions**

802 KH and BGL designed the project, KH constructed the model and wrote
803 the draft, WKL and DW performed simulations and drawn the figures, and
804 DWD checked the model and helped to write the manuscript.

Figure legends

Figure 1. The behaviors of $\hat{r}^2$ and $\hat{r}_\Delta^2$ during reproduction for the MS mating system (set $N_e = 40$ or 80 , $v = 2$ or 4 , $L = 200$ and $c = 0.1$). Each of the two columns shows the results of a different ploidy level, and each of the two rows shows the results of a different effective population size. Solid gray lines denote approximate d^2 or δ^2 , dotted gray lines denote exact d^2 or δ^2 , and solid lines denote $\hat{r}^2$ or $\hat{r}_\Delta^2$, where the lines representing δ^2 (or $\hat{r}_\Delta^2$) are above those representing d^2 (or $\hat{r}^2$) for each situation.

Figure 2. The relationship between d^2 (or δ^2) and the recombination rate c for the MS mating system (set $N_e = 100$, $n = 100$ and $v = 2, 4, 6$ or 8). The solid, dashed, dash-dotted and dotted lines denote the values for diploids, tetraploids, hexaploids and octoploids in turn, and the black and the red lines denote the exact and the approximate values, respectively.

Figure 3. The relationship between the RMSE of $\hat{V}$ and the sample size n (set $N_e = 200$, $v = 2, 4, 6$ or 8 , $L = 100$ or 200 for SNP and $L = 20$ or 40 for SSR). The results are obtained from the unphased genotypes of 40 to 400 individuals (interval 40). The solid, dashed, dash-dotted and dotted lines denote results for disomic, tetrasomic, hexasomic and octosomic inheritances in turn.

Figures

Figure 1.

Figure 2.

Figure 3.

835 Tables

836 **Table 1. Allele configurations and their expected frequencies**

Allele configuration	Freq. notation	Double non-identity	Expectation			Expectation notation
			p_Aq_B	$p_Aq_B(p_X + q_X)$	$p_Ap_Xq_Bq_X$	
Digenic						
$Z_{B\dots}^{A\dots}$	P_1		1			E_1
$Z_{\cdot B\dots}^{A\cdot\dots}$	P_2		1			E_2
$Z_{\cdot\dots \cdot\dots}^{A\dots \cdot\dots}$ $Z_{\cdot\dots B\dots}$	P_3		1			E_3
Trigenic						
$Z_{B\cdot\dots, Z_{BB\dots}}^{AA\dots, Z_{BB\dots}^{A\cdot\dots}}$	P_4		2	$-P$		E_4
$Z_{\cdot\cdot\dots B\dots, Z_{BB\dots \cdot\dots}}^{AA\dots \cdot\dots, Z_{BB\dots \cdot\dots}^{A\cdot\dots}}$	P_5		2	$-P$		E_5
$Z_{B\dots \cdot\dots, Z_{B\dots B\dots}}^{A\dots A\dots, Z_{B\dots B\dots}^{A\cdot\dots \cdot\dots}}$	P_6		2	$-\Pi$		E_6
$Z_{\cdot B\dots \cdot\dots, Z_{\cdot B\dots B\dots}}^{A\cdot\dots A\dots, Z_{\cdot B\dots B\dots}^{A\cdot\dots \cdot\dots}}$	P_7		2	$-\Pi$		E_7
$Z_{\cdot\dots A\dots \cdot\dots, Z_{\cdot\dots \cdot\dots \cdot\dots}}^{A\dots A\dots \cdot\dots, Z_{\cdot\dots \cdot\dots \cdot\dots}^{A\cdot\dots \cdot\dots}}$ $Z_{\cdot\dots \cdot\dots B\dots, Z_{\cdot\dots \cdot\dots B\dots B\dots}}^{A\dots \cdot\dots \cdot\dots, Z_{\cdot\dots \cdot\dots B\dots B\dots}^{A\cdot\dots \cdot\dots \cdot\dots}}$	P_8		2	$-\Pi$		E_8
$Z_{\cdot\cdot\cdot B\dots, Z_{\cdot\cdot\cdot BB\dots}}^{AA\cdot\dots, Z_{\cdot\cdot\cdot BB\dots}^{A\cdot\cdot\dots}}$	P_9		2	$-P$		E_9
Quadgenic						
Dihaplotypic						
$Z_{BB\dots}^{AA\dots}$	P_{10}	Θ_1	1	$-P$	Θ_1	E_{10}
$Z_{B\dots B\dots}^{A\dots A\dots}$	P_{11}	Θ_2	1	$-\Pi$	Θ_2	E_{11}
Trihaplotypic						
$Z_{B\dots A\cdot\dots}^{A\dots A\cdot\dots}$ $Z_{B\dots \cdot B\dots}$	P_{12}	Γ_1	1	$-\Pi$	Γ_1	E_{12}
$Z_{B\cdot\dots B\dots, Z_{BB\dots \cdot\dots}}^{AA\dots \cdot\dots, Z_{BB\dots \cdot\dots}^{A\cdot\dots A\dots}}$	P_{13}	Γ_2	2	$-P - \Pi$	$2\Gamma_2$	E_{13}
$Z_{B\dots A\dots \cdot\dots}$ $Z_{B\dots \cdot\dots B\dots}$	P_{14}	Γ_3	1	$-\Pi$	Γ_3	E_{14}
$Z_{B\cdot\cdot B\dots}^{AA\cdot\dots}$	P_{15}	Γ_4	1	$-P$	Γ_4	E_{15}
Quadhaplotypic						
$Z_{\cdot B\dots A\cdot\dots}^{A\cdot\dots A\cdot\dots}$ $Z_{\cdot\cdot\dots \cdot\cdot\dots}^{AA\dots \cdot\cdot\dots}$ $Z_{\cdot\cdot\dots BB\dots}$	P_{16}	Δ_1	1	$-\Pi$	Δ_1	E_{16}
$Z_{\cdot B\dots \cdot\dots B\dots}$	P_{17}	Δ_2	1	$-P$	Δ_2	E_{17}
$Z_{\cdot B\dots A\dots \cdot\dots}$ $Z_{\cdot B\dots \cdot\dots B\dots}$	P_{18}	Δ_3	1	$-\Pi$	Δ_3	E_{18}
$Z_{\cdot\dots \cdot\dots \cdot\dots \cdot\dots, Z_{\cdot\dots \cdot\dots \cdot\dots \cdot\dots}}^{AA\dots \cdot\dots \cdot\dots \cdot\dots, Z_{\cdot\dots \cdot\dots \cdot\dots \cdot\dots}^{A\cdot\dots \cdot\dots \cdot\dots \cdot\dots}}$ $Z_{\cdot\dots \cdot\dots B\dots B\dots, Z_{BB\dots \cdot\dots \cdot\dots \cdot\dots}}$	P_{19}	Δ_4	2	$-P - \Pi$	$2\Delta_4$	E_{19}
$Z_{\cdot\dots A\dots \cdot\dots \cdot\dots}$ $Z_{\cdot\dots \cdot\dots B\dots B\dots}$	P_{20}	Δ_5	1	$-\Pi$	Δ_5	E_{20}
$Z_{\cdot\cdot\cdot BB\dots}^{AA\cdot\dots}$	P_{21}	Δ_6	1	$-P$	Δ_6	E_{21}
$Z_{\cdot\dots \cdot\dots \cdot\dots, Z_{\cdot\cdot\cdot A\dots A\dots}}$ $Z_{\cdot\cdot\cdot B\dots B\dots, Z_{BB\cdot\dots \cdot\dots \cdot\dots}}$	P_{22}	Δ_7	2	$-P - \Pi$	$2\Delta_7$	E_{22}

837 The vertical bars in superscripts and subscripts are used to separate the phased

838 genotypes of different individuals, $\cdot$ denotes an allele copy in any form.

839

840 **Table 2. Essential factors of moment expressions**

	$E(\hat{D}_w^2)$	$E(\hat{D}_b^2)$	$E(\hat{D}_w \hat{D}_b)$	$E(\hat{D}^2)$	$E(\hat{\Delta}^2)$	$E(\hat{Q})$	$E(\hat{R})$	Divisor
Θ_1	$n^2 v^2 \times$ $(2 + vv_2)$	λ_7	$-nv \times$ $(vv_1 + \lambda_1)$	$v_1^2 \lambda_5$	$2v^2 n_1^2 v_1^2$	$2v_1^2$	$2v^2 n_1^2 v_1^2$	$n^3 v^3 v_1 / Q$
Θ_2	$n^2 v^2$	2	$-nv$	λ_5	$v^2 \lambda_2$	2	$2v^2$	$n^3 v^2 / n_1 Q$
Γ_1	$-2n^2 v^2$	$-2\lambda_1$	$nv(1 + \lambda_4)$	$-2v_1 \lambda_3$	$2v^2 v_1 \lambda_2$	$4v_1$	$4v^2 v_1$	$n^3 v^2 / n_1 Q$
Γ_2	0	$-2\lambda_1$	$-nv v_2$	$-2v_1 \lambda_3$	$-4v^2 n_1 v_1$	$4v_1$	$-4v^2 n_1 v_1$	$n^3 v^2 / 2n_1 Q$
Γ_3	0	4	$-nv$	$-2\lambda_3$	$-2v^2 n_2$	4	$4v^2$	$n^3 v / n_1 n_2 Q$
Γ_4	$-2n^2 v^2 v_2$	$2\lambda_1 \lambda_4$	λ_6	$-2v_1^2 \lambda_3$	$4v^2 n_1^2 v_1^2$	$4v_1^2$	$4v^2 n_1^2 v_1^2$	$n^3 v^3 v_1 / v_2 Q$
Δ_1	$n^2 v^2$	λ_7	$-nv \lambda_4$	$2v_1^2$	$v^2 v_1^2 \lambda_2$	$2v_1^2$	$2v^2 v_1^2$	$n^3 v^2 / n_1 Q$
Δ_2	0	1	0	1	v^2	1	$v^2 n_1^2$	$n^3 v^2 / n_1 v_1^2 Q$
Δ_3	0	$-2\lambda_1$	nv	$4v_1$	$-2v^2 n_2 v_1$	$4v_1$	$4v^2 v_1$	$n^3 v / n_1 n_2 Q$
Δ_4	0	v_1	0	v_1	$v^2 v_1$	v_1	$-v^2 n_1 v_1$	$n^3 v / 2n_1 n_2 Q$
Δ_5	0	1	0	1	v^2	1	v^2	$n^3 / n_1 n_2 n_3 Q$
Δ_6	$n^2 v^2$	λ_4^2	$-nv \lambda_4$	v_1^2	$v^2 n_1^2 v_1^2$	v_1^2	$v^2 n_1^2 v_1^2$	$n^3 v^3 v_1 / v_2 v_3 Q$
Δ_7	0	$-2\lambda_4$	nv	$2v_1$	$-2v^2 n_1 v_1$	$2v_1$	$-2v^2 n_1 v_1$	$n^3 v^2 / 2n_1 v_2 Q$

841 For brevity, we denote $n - i$ by n_i and $v - i$ by v_i , and let $\lambda_1 = n_2 v + 2$, $\lambda_2 =$
842 $nn_2 + 2$, $\lambda_3 = nv - 2$, $\lambda_4 = vn_1 + 1$, $\lambda_5 = 2 + nv\lambda_3$, $\lambda_6 = nv[2 + (\lambda_3 - \lambda_4)(1 + \lambda_4)]$,
843 $\lambda_7 = 2 + 2n_2 v + \lambda_2 v^2$.

844

845 **Table 3. Simplified Ω^T for HS mating system**

1	N^{-1}	1	N^{-1}	N^{-2}	1	N^{-1}	N^{-2}	N^{-3}
$(c - 1)^2$	$\frac{c^2}{v - 1} - \frac{1 + 2c(c - 1)}{v}$	0	$\frac{1 - c}{v}$	$\frac{2c - 1}{v^2}$	0	0	$\frac{2}{v^2}$	$-\frac{2}{v^3}$
$2c(1 - c)$	$\frac{4c(2c - 1)}{v} - \frac{2c^2}{v - 1}$	$1 - c$	$\frac{6c - 3}{v}$	$\frac{2 - 8c}{v^2}$	0	$\frac{4}{v}$	$-\frac{12}{v^2}$	$\frac{8}{v^3}$
c^2	$\frac{2c^2(3 - 2v)}{v(v - 1)}$	c	$-\frac{5c}{v}$	$\frac{6c}{v^2}$	1	$-\frac{6}{v}$	$\frac{11}{v^2}$	$-\frac{6}{v^3}$

846 Each element of Ω^T is a combination of 1, N^{-1} , N^{-2} and N^{-3} with the combination
847 coefficients in the corresponding cell. The combination coefficients are zero for
848 unrepresented terms.

849

Table 4. Expressions of $x_1 - x_{11}, x_2 - x_{11}, \dots, x_{13} - x_{11}$

	HS	MS	ME/ DR	DH
$x_1 - x_{11}$	$\frac{2c + c_1^2 v - 1}{c_2 c v_1 v}$	*	*	*
$x_2 - x_{11}$	$\frac{2c + c_1^2 v - 1}{c_2 c v_1 v}$	*	*	*
$x_3 - x_{11}$	0	$\frac{4c v_1 v_2}{v^2(c v_2 + v)(3v - 4)}$	$\frac{4c v_1 v_2}{v^2(c v_2 + v)(3v - 4)}$	$\frac{2c v_2(2f v_1 + 3v - 2)}{(1 + f)v^2(c v_2 + v)(3v - 4)}$
$x_4 - x_{11}$	0	$\frac{v_2}{v^2}$	$\frac{2v_1}{v^2}$	$\frac{2v_1}{v^2}$
$x_5 - x_{11}$	0	0	0	0
$x_6 - x_{11}$	0	*	*	*
$x_7 - x_{11}$	0	$\frac{v_2^2}{v_1 v^2(3v - 4)}$	$\frac{v_2^2}{v_1 v^2(3v - 4)}$	$\frac{f v_2^2 + 3v^2 - 6v + 4}{(1 + f)v_1 v^2(3v - 4)}$
$x_8 - x_{11}$	0	$\frac{2v_2}{v^2}$	$\frac{4v_1}{v^2}$	$\frac{4v_1}{v^2}$
$x_9 - x_{11}$	0	0	0	0
$x_{10} - x_{11}$	0	$\frac{v_2}{v^2}$	$\frac{2v_1}{v^2}$	$\frac{2v_1}{v^2}$
$x_{11} - x_{11}$	0	0	0	0
$x_{12} - x_{11}$	0	*	*	*
$x_{13} - x_{11}$	0	$\frac{v_2}{v^2}$	$\frac{2v_1}{v^2}$	$\frac{2v_1}{v^2}$

The expressions represented by * are too long and are placed in the supplementary files.

854 **Table 5. Approximations of d^2 and δ^2**

	v	HS	MS/ ME/DR		DH	
		d^2 & δ^2	d^2	δ^2	d^2	δ^2
Same chromosome ($c = 1$)	2	$\frac{1}{3}$	$\frac{1}{3}$	$\frac{1}{3}$	$\frac{3+2f}{6(1+f)}$	$\frac{3+f}{3(1+f)}$
	4	$\frac{1}{9}$	$\frac{61}{480}$	$\frac{1}{3}$	$\frac{75+61f}{480(1+f)}$	$\frac{3+f}{3(1+f)}$
	6	$\frac{1}{15}$	$\frac{19}{252}$	$\frac{1}{3}$	$\frac{22+19f}{252(1+f)}$	$\frac{3+f}{3(1+f)}$
	8	$\frac{1}{21}$	$\frac{559}{10560}$	$\frac{1}{3}$	$\frac{627+559f}{10560(1+f)}$	$\frac{3+f}{3(1+f)}$
	10	$\frac{1}{27}$	$\frac{277}{6825}$	$\frac{1}{3}$	$\frac{609+554f}{13650(1+f)}$	$\frac{3+f}{3(1+f)}$
	2	$\frac{1}{3}$	$\frac{1}{3}$	$\frac{1}{3}$	$\frac{3+2f}{6(1+f)}$	$\frac{3+f}{3(1+f)}$
	4	$\frac{1}{15}$	$\frac{439}{5280}$	$\frac{109}{330}$	$\frac{673+439f}{5280(1+f)}$	$\frac{343+109f}{330(1+f)}$
	6	$\frac{1}{35}$	$\frac{1147}{30870}$	$\frac{579}{1715}$	$\frac{1747+1147f}{30870(1+f)}$	$\frac{1779+579f}{1715(1+f)}$
	8	$\frac{1}{63}$	$\frac{22357}{1068480}$	$\frac{5662}{16695}$	$\frac{33921+22357f}{1068480(1+f)}$	$\frac{17226+5662f}{16695(1+f)}$
	10	$\frac{1}{99}$	$\frac{18529}{1383525}$	$\frac{18775}{55341}$	$\frac{56093+37058f}{2767050(1+f)}$	$\frac{56845+18775f}{55341(1+f)}$
Divisor		N_e	N_e	$N_e - \eta$	N_e	$N_e - \eta$

855 * $\eta = \frac{2(v-2)(v-1)}{v^2}$ for the MS mating system or $\eta = \frac{4(v-1)^2}{v^2}$ for the ME/DR/DH
856 mating systems. Therefore, each value should be divided by the last expression
857 (i.e. N_e or $N_e - \eta$) in the column juxtaposed to this value. Then, either $1/(vn)$
858 for d^2 or $1/n$ for δ^2 should be added in order to account for the sampling
859 error.

Supplementary Materials For “Linkage disequilibrium under polysomic inheritance”

Appendix A. Expansion of Δ_{AB} in triploids

In triploids, the value of Δ_{AB} is given by $\Delta_{AB} = D_s^{AB} + 2D_d^{AB}$, where D_s^{AB} and $2D_d^{AB}$ can be respectively expanded as

$$D_s^{AB} = \frac{1}{3}(D_{B^{\cdot\cdot}}^{A\cdot\cdot} + D_{B^{\cdot}}^{A\cdot} + D_{B^{\cdot\cdot}}^{\cdot A}),$$

$$2D_d^{AB} = \frac{1}{3}(D_{B^{\cdot}}^{A\cdot\cdot} + D_{B^{\cdot\cdot}}^{A\cdot} + D_{B^{\cdot}}^{\cdot A} + D_{B^{\cdot\cdot}}^{\cdot A} + D_{B^{\cdot}}^{\cdot A} + D_{B^{\cdot\cdot}}^{\cdot A}),$$

in which the superscripts (or the subscripts) of D in the right side of equal sign denote the phased genotype at the first (or the second) locus, and the dot $\cdot$ denotes any allele.

Each term in the right side can be further expanded as follows (the terms with the same two-locus unphased genotypes in the expansion are put together):

$$\begin{aligned} \frac{1}{3}D_{B^{\cdot\cdot}}^{A\cdot\cdot} &= \frac{1}{3}(D_{BBB}^{AAA} + D_{BBB}^{AAX} + D_{BBB}^{AXA} + D_{BBB}^{AAA} + D_{BBB}^{AAX} + D_{BBB}^{AAX} + D_{BBB}^{AAX} + D_{BBB}^{AXA} + D_{BBB}^{AXA} + D_{BBB}^{AXX} \\ &\quad + D_{BBB}^{AXX} + D_{BBB}^{AXX} + D_{BBB}^{AXX} + D_{BBB}^{AXA} + D_{BBB}^{AXX}), \\ \frac{1}{3}D_{B^{\cdot}}^{A\cdot\cdot} &= \frac{1}{3}(D_{BBB}^{AAA} + D_{BBB}^{AAX} + D_{BBB}^{XAA} + D_{BBB}^{AAA} + D_{BBB}^{AAX} + D_{BBB}^{AAX} + D_{BBB}^{XAA} + D_{BBB}^{XAA} + D_{BBB}^{XAX} \\ &\quad + D_{BBB}^{XAX} + D_{BBB}^{XAX} + D_{BBB}^{XAX} + D_{BBB}^{XAA} + D_{BBB}^{XAX}), \\ \frac{1}{3}D_{B^{\cdot\cdot}}^{\cdot A} &= \frac{1}{3}(D_{BBB}^{AAA} + D_{BBB}^{XAA} + D_{BBB}^{AXA} + D_{BBB}^{AAA} + D_{BBB}^{AAX} + D_{BBB}^{AAX} + D_{BBB}^{AAX} + D_{BBB}^{AXA} + D_{BBB}^{AXA} + D_{BBB}^{XXA} \\ &\quad + D_{BBB}^{XXA} + D_{BBB}^{XXA} + D_{BBB}^{XXA} + D_{BBB}^{XXA} + D_{BBB}^{XXA}), \\ \frac{1}{3}D_{B^{\cdot}}^{A\cdot\cdot} &= \frac{1}{3}(D_{BBB}^{AAA} + D_{BBB}^{AAX} + D_{BBB}^{AXA} + D_{BBB}^{AAA} + D_{BBB}^{AAX} + D_{BBB}^{AAX} + D_{BBB}^{AAX} + D_{BBB}^{AXA} + D_{BBB}^{AXA} + D_{BBB}^{AXX} \\ &\quad + D_{BBB}^{AXX} + D_{BBB}^{AXX} + D_{BBB}^{AXX} + D_{BBB}^{AXA} + D_{BBB}^{AXX}), \\ \frac{1}{3}D_{B^{\cdot\cdot}}^{A\cdot} &= \frac{1}{3}(D_{BBB}^{AAA} + D_{BBB}^{AAX} + D_{BBB}^{AXA} + D_{BBB}^{AAA} + D_{BBB}^{AAX} + D_{BBB}^{AAX} + D_{BBB}^{AAX} + D_{BBB}^{AXA} + D_{BBB}^{AXA} + D_{BBB}^{AXX} \\ &\quad + D_{BBB}^{AXX} + D_{BBB}^{AXX} + D_{BBB}^{AXX} + D_{BBB}^{AXA} + D_{BBB}^{AXX}), \\ \frac{1}{3}D_{B^{\cdot}}^{\cdot A} &= \frac{1}{3}(D_{BBB}^{AAA} + D_{BBB}^{AAX} + D_{BBB}^{XAA} + D_{BBB}^{AAA} + D_{BBB}^{AAX} + D_{BBB}^{AAX} + D_{BBB}^{XAA} + D_{BBB}^{XAA} + D_{BBB}^{XAX} \\ &\quad + D_{BBB}^{XAX} + D_{BBB}^{XAX} + D_{BBB}^{XAX} + D_{BBB}^{XAA} + D_{BBB}^{XAX}), \\ \frac{1}{3}D_{B^{\cdot\cdot}}^{\cdot A} &= \frac{1}{3}(D_{BBB}^{AAA} + D_{BBB}^{XAA} + D_{BBB}^{AXA} + D_{BBB}^{AAA} + D_{BBB}^{AAX} + D_{BBB}^{AAX} + D_{BBB}^{AAX} + D_{BBB}^{AXA} + D_{BBB}^{AXA} + D_{BBB}^{XXA} \\ &\quad + D_{BBB}^{XXA} + D_{BBB}^{XXA} + D_{BBB}^{XXA} + D_{BBB}^{XXA} + D_{BBB}^{XXA}), \end{aligned}$$

$$\frac{1}{3}D_B^{::A} = \frac{1}{3}(D_{BBB}^{AAA} + D_{BBB}^{XAA} + D_{BBB}^{AXA} + D_{BBB}^{AAA} + D_{BBB}^{AAA} + D_{BBB}^{XAA} + D_{BBB}^{XAA} + D_{BBB}^{AXA} + D_{BBB}^{AXA} + D_{BBB}^{XXX} + D_{BBB}^{XXX} + D_{BBB}^{XXX} + D_{BBB}^{XAA} + D_{BBB}^{XAA} + D_{BBB}^{XAA}),$$

By summing all terms of the same two-locus unphased genotypes in the right sides of equal signs, we obtain the following equalities:

$$\begin{aligned} 3D_{BBB}^{AAA} &= 3G_{BBB}^{AAA} - 3p_A^3q_B^3, \\ 2(D_{BBB}^{AXX} + D_{BBB}^{AXX} + D_{BBB}^{AXX}) &= 2G_{BBB}^{AXX} - 6p_A^2p_Xq_B^3, \\ 2(D_{BBB}^{AXX} + D_{BBB}^{AXX} + D_{BBB}^{AXX}) &= 2G_{BBB}^{AXX} - 6p_A^3q_B^2q_X, \\ \frac{4}{3}(D_{BBB}^{AXX} + D_{BBB}^{AXX} + D_{BBB}^{AXX} + D_{BBB}^{AXX} + D_{BBB}^{AXX} + D_{BBB}^{AXX} + D_{BBB}^{AXX} + D_{BBB}^{AXX} + D_{BBB}^{AXX}) &= \frac{4}{3}G_{BBB}^{AXX} - 12p_A^2p_Xq_B^2q_X, \\ D_{BBB}^{AXX} + D_{BBB}^{AXX} + D_{BBB}^{AXX} &= G_{BBB}^{AXX} - 3p_Ap_X^2q_B^3, \\ D_{BBB}^{AXX} + D_{BBB}^{AXX} + D_{BBB}^{AXX} &= G_{BBB}^{AXX} - 3p_A^3q_Bq_X^2, \\ \frac{2}{3}(D_{BBB}^{AXX} + D_{BBB}^{AXX} + D_{BBB}^{AXX} + D_{BBB}^{AXX} + D_{BBB}^{AXX} + D_{BBB}^{AXX} + D_{BBB}^{AXX} + D_{BBB}^{AXX} + D_{BBB}^{AXX}) &= \frac{2}{3}G_{BBB}^{AXX} - 6p_Ap_X^2q_B^2q_X, \\ \frac{2}{3}(D_{BBB}^{AXX} + D_{BBB}^{AXX} + D_{BBB}^{AXX} + D_{BBB}^{AXX} + D_{BBB}^{AXX} + D_{BBB}^{AXX} + D_{BBB}^{AXX} + D_{BBB}^{AXX} + D_{BBB}^{AXX}) &= \frac{2}{3}G_{BBB}^{AXX} - 6p_Ap_X^2q_B^2q_X, \\ \frac{1}{3}(D_{BBB}^{AXX} + D_{BBB}^{AXX} + D_{BBB}^{AXX} + D_{BBB}^{AXX} + D_{BBB}^{AXX} + D_{BBB}^{AXX} + D_{BBB}^{AXX} + D_{BBB}^{AXX} + D_{BBB}^{AXX}) &= \frac{1}{3}G_{BBB}^{AXX} - 3p_Ap_X^2q_Bq_X^2, \end{aligned}$$

where each $G_{::}$ denotes a two-locus unphased genotypic frequency, whose superscript and subscript represent two unphased genotypes. It can be seen that each expression on the right sides of above equalities is one of the following:

$$\frac{ij}{v}G_{B^jX^{v-j}}^{A^iX^{v-i}} - v\binom{v-1}{v-i}\binom{v-1}{v-j}p_A^ip_X^{v-i}q_B^jq_X^{v-j}, \quad i, j = 1, 2, 3 \text{ and } v = 3,$$

in which A^iX^{v-i} denotes an unphased genotype containing exactly i copies of A , and the meaning of B^jX^{v-j} is similar. Because Δ_{AB} is the sum of these expressions, it follows

$$\Delta_{AB} = \sum_{i=1}^v \sum_{j=1}^v \left[\frac{ij}{v}G_{B^jX^{v-j}}^{A^iX^{v-i}} - v\binom{v-1}{v-i}\binom{v-1}{v-j}p_A^ip_X^{v-i}q_B^jq_X^{v-j} \right],$$

where $v = 3$. This formula can be extended to a higher ploidy level v by similar discussion. Note that

$$\begin{aligned} \sum_{i=1}^v \sum_{j=1}^v \binom{v-1}{v-i}\binom{v-1}{v-j}p_A^ip_X^{v-i}q_B^jq_X^{v-j} &= \left[\sum_{i=1}^v \binom{v-1}{v-i}p_A^ip_X^{v-i} \right] \left[\sum_{j=1}^v \binom{v-1}{v-j}q_B^jq_X^{v-j} \right] \\ &= \left[p_A \sum_{k=0}^{v-1} p_A^k p_A^{(v-1)-k} \right] \left[q_B \sum_{l=0}^{v-1} q_B^l q_B^{(v-1)-l} \right] \\ &= p_A q_B (p_A + p_X)^{v-1} (q_B + q_X)^{v-1} = p_A q_B. \end{aligned}$$

The next formula is valid for any ploidy level v :

$$\Delta_{AB} = \left(\sum_{i=1}^v \sum_{j=1}^v \frac{ij}{v} G_{Bj}^A x_{jv-i} \right) - vp_A q_B.$$

Appendix B. Derivation of moments of LD measurements

In the process of deriving the moments of LD measurements, we need to use the estimates of frequencies $P_1, P_2, \dots, P_{22}$ listed in Table 1, and so we first discuss $\hat{P}_1$ to $\hat{P}_{22}$, and then derive various moments.

$\hat{P}_1$ to $\hat{P}_{22}$

Denote x_{ij} for the state indicator of allele A related to the j^{th} haplotype within the i^{th} individual at the first locus, and y_{ij} for that of B at the second locus, where $x_{ij} = 1$ if the allele copy at the first locus is A , otherwise $x_{ij} = 0$; the meaning of y_{ij} is similar. Moreover, we let the number of the sampled individuals be n (the sample size), and let the number of haplotypes within each individual be v (the ploidy level). Then $\hat{P}_1$ to $\hat{P}_{22}$ can be expressed as follows.

Digenic:

$$\hat{P}_1 = \hat{P}_{B \dots}^A = \frac{1}{nv} \sum_i \sum_j x_{ij} y_{ij}$$

$$\hat{P}_2 = \hat{P}_{B \dots}^{A \cdot \dots} = \frac{1}{nv(v-1)} \sum_i \sum_{j \neq j'} x_{ij} y_{ij'}$$

$$\hat{P}_3 = \hat{P}_{\cdot \dots | B \dots}^{A \dots | \cdot \dots} = \frac{1}{n(n-1)v^2} \sum_{i \neq i'} \sum_{j, j'} x_{ij} y_{i'j'}$$

Trigenic:

$$\hat{P}_4 = \hat{P}_{B \dots}^{AA \dots} + \hat{P}_{BB \dots}^{A \cdot \dots} = \frac{1}{nv(v-1)} \sum_i \sum_{j \neq j'} (x_{ij} y_{ij} x_{ij'} + x_{ij} y_{ij} y_{ij'})$$

$$\hat{P}_5 = \hat{P}_{\cdot \cdot \cdot | B \dots}^{AA \dots | \cdot \dots} + \hat{P}_{BB \dots | \cdot \dots}^{A \cdot \cdot \dots | A \dots} = \frac{1}{n(n-1)v^2(v-1)} \sum_{i \neq i'} \sum_{j \neq j'} \sum_{j''} (x_{ij} x_{ij'} y_{i'j''} + y_{ij} y_{ij'} x_{i'j''})$$

$$\hat{P}_6 = \hat{P}_{B \dots | \cdot \dots}^{A \dots | A \dots} + \hat{P}_{B \dots | B \dots}^{A \dots | \cdot \dots} = \frac{1}{n(n-1)v^2} \sum_{i \neq i'} \sum_{j, j'} (x_{ij} y_{ij} x_{i'j'} + x_{ij} y_{ij} y_{i'j'})$$

$$\hat{P}_7 = \hat{P}_{\cdot B \dots | \cdot \dots}^{A \cdot \cdot \dots | A \dots} + \hat{P}_{\cdot B \dots | B \dots}^{A \cdot \cdot \dots | \cdot \dots} = \frac{1}{n(n-1)v^2(v-1)} \sum_{i \neq i'} \sum_{j \neq j'} \sum_{j''} (x_{ij} y_{ij'} x_{i'j''} + x_{ij} y_{ij'} y_{i'j''})$$

$$\hat{P}_8 = \hat{P}_{\cdot \dots | \cdot \dots | B \dots}^{A \dots | A \dots | \cdot \dots} + \hat{P}_{\cdot \dots | \cdot \dots | B \dots}^{A \dots | \cdot \dots | \cdot \dots} = \frac{1}{n(n-1)(n-2)v^3} \sum_{\substack{i \neq i' \neq i'' \\ i \neq i''}} \sum_{j, j', j''} (x_{ij} x_{i'j'} y_{i''j''} + x_{ij} y_{i'j'} y_{i''j''})$$

$$81 \quad \hat{P}_9 = \hat{P}_{\cdot\cdot\cdot B\cdot\cdot\cdot}^{AA\cdot\cdot\cdot} + \hat{P}_{\cdot\cdot\cdot BB\cdot\cdot\cdot}^{A\cdot\cdot\cdot} = \frac{1}{nv(v-1)(v-2)} \sum_i \sum_{\substack{j \neq j' \neq j'' \\ j \neq j''}} (x_{ij}x_{ij'}y_{ij''} + x_{ij}y_{ij'}y_{ij''})$$

82 **Quadrigenic:**

83 Dihaplotypic:

$$84 \quad \hat{P}_{10} = \hat{P}_{BB\cdot\cdot\cdot}^{AA\cdot\cdot\cdot} = \frac{1}{nv(v-1)} \sum_i \sum_{j \neq j'} x_{ij}x_{ij'}y_{ij}y_{ij'}$$

$$85 \quad \hat{P}_{11} = \hat{P}_{B\cdot\cdot\cdot|B\cdot\cdot\cdot}^{A\cdot\cdot\cdot|A\cdot\cdot\cdot} = \frac{1}{n(n-1)v^2} \sum_{i \neq i'} \sum_{j, j'} x_{ij}y_{ij}x_{i'j'}y_{i'j'}$$

86 Trihaplotypic:

$$87 \quad \hat{P}_{12} = \hat{P}_{B\cdot\cdot\cdot|B\cdot\cdot\cdot}^{A\cdot\cdot\cdot|A\cdot\cdot\cdot} = \frac{1}{n(n-1)v^2(v-1)} \sum_{i \neq i'} \sum_{j, j' \neq j''} x_{ij}y_{ij}x_{i'j'}y_{i'j''}$$

$$88 \quad \hat{P}_{13} = \hat{P}_{B\cdot\cdot\cdot|B\cdot\cdot\cdot}^{AA\cdot\cdot\cdot|A\cdot\cdot\cdot} + \hat{P}_{BB\cdot\cdot\cdot|A\cdot\cdot\cdot}^{A\cdot\cdot\cdot|A\cdot\cdot\cdot} = \frac{1}{n(n-1)v^2(v-1)} \sum_{i \neq i'} \sum_{j \neq j'} \sum_{j''} (x_{ij}y_{ij}x_{ij'}y_{i'j''} + x_{ij}y_{ij}y_{ij'}x_{i'j''})$$

$$89 \quad \hat{P}_{14} = \hat{P}_{B\cdot\cdot\cdot|B\cdot\cdot\cdot}^{A\cdot\cdot\cdot|A\cdot\cdot\cdot} = \frac{1}{n(n-1)(n-2)v^3} \sum_{\substack{i \neq i' \neq i'' \\ i \neq i''}} \sum_{j, j', j''} x_{ij}y_{ij}x_{i'j'}y_{i''j''}$$

$$90 \quad \hat{P}_{15} = \hat{P}_{B\cdot\cdot\cdot}^{AA\cdot\cdot\cdot} = \frac{1}{nv(v-1)(v-2)} \sum_i \sum_{\substack{j \neq j' \neq j'' \\ j \neq j''}} x_{ij}y_{ij}x_{ij'}y_{ij''}$$

91 Quadhaplotypic:

$$92 \quad \hat{P}_{16} = \hat{P}_{\cdot\cdot\cdot|B\cdot\cdot\cdot}^{A\cdot\cdot\cdot|A\cdot\cdot\cdot} = \frac{1}{n(n-1)v^2(v-1)^2} \sum_{i \neq i'} \sum_{\substack{j \neq j' \\ j'' \neq j'''}} x_{ij}y_{ij'}x_{i'j''}y_{i'j'''}$$

$$93 \quad \hat{P}_{17} = \hat{P}_{\cdot\cdot\cdot|BB\cdot\cdot\cdot}^{AA\cdot\cdot\cdot|A\cdot\cdot\cdot} = \frac{1}{n(n-1)v^2(v-1)^2} \sum_{i \neq i'} \sum_{\substack{j \neq j' \\ j'' \neq j'''}} x_{ij}x_{ij'}y_{i'j''}y_{i'j'''}$$

$$94 \quad \hat{P}_{18} = \hat{P}_{\cdot\cdot\cdot|B\cdot\cdot\cdot}^{A\cdot\cdot\cdot|A\cdot\cdot\cdot} = \frac{1}{n(n-1)(n-2)v^3(v-1)} \sum_{\substack{i \neq i' \neq i'' \\ i \neq i''}} \sum_{j \neq j'} \sum_{j'', j'''} x_{ij}y_{ij'}x_{i'j''}y_{i''j'''}$$

$$95 \quad \hat{P}_{19} = \hat{P}_{\cdot\cdot\cdot|B\cdot\cdot\cdot}^{AA\cdot\cdot\cdot|A\cdot\cdot\cdot} + \hat{P}_{BB\cdot\cdot\cdot|A\cdot\cdot\cdot}^{A\cdot\cdot\cdot|A\cdot\cdot\cdot} = \frac{1}{n(n-1)(n-2)v^3(v-1)} \sum_{\substack{i \neq i' \neq i'' \\ i \neq i''}} \sum_{j \neq j'} \sum_{j'', j'''} (x_{ij}x_{ij'}y_{i'j''}y_{i''j'''} + y_{ij}y_{ij'}x_{i'j''}x_{i''j'''})$$

$$96 \quad \hat{P}_{20} = \hat{P}_{\cdot\cdot\cdot|B\cdot\cdot\cdot}^{A\cdot\cdot\cdot|A\cdot\cdot\cdot} = \frac{1}{n(n-1)(n-2)(n-3)v^4} \sum_{\substack{i, i', i'', i''' \\ \text{are distinct}}} \sum_{j, j', j'', j'''} x_{ij}x_{i'j'}y_{i''j''}y_{i'''j'''}$$

$$97 \quad \hat{P}_{21} = \hat{P}_{\cdot\cdot\cdot}^{AA\cdot\cdot\cdot} = \frac{1}{nv(v-1)(v-2)(v-3)} \sum_i \sum_{\substack{j, j', j'', j''' \\ \text{are distinct}}} x_{ij}x_{ij'}y_{ij''}y_{ij'''}$$

$$\hat{P}_{22} = \hat{P}_{B \dots B \dots B \dots B \dots}^{AA \dots A \dots A \dots A \dots} + \hat{P}_{BB \dots B \dots B \dots B \dots}^{\dots \dots A \dots A \dots} = \frac{1}{n(n-1)v^2(v-1)(v-2)}$$

$$\sum_{i \neq i'} \sum_{j \neq j'} \sum_{j''} (x_{ij} x_{ij'} y_{ij''} y_{i'j''} + y_{ij} y_{ij'} x_{ij''} x_{i'j''})$$

101 $\mathbf{E}(\hat{D}_w)$ and $\mathbf{E}(\hat{D}_w^2)$

$$102 \quad \hat{D}_w = \hat{P}_{B \dots B \dots B \dots B \dots}^{A \dots A \dots A \dots A \dots} - \hat{P}_{B \dots B \dots B \dots B \dots}^{\dots \dots A \dots A \dots} = \hat{P}_1 - \hat{P}_2 \text{ by the definition of } D_w, \text{ in which}$$

$$103 \quad \hat{P}_1 = \frac{1}{nv} \sum_i \sum_j x_{ij} y_{ij} \quad \text{and} \quad \hat{P}_2 = \frac{1}{nv(v-1)} \sum_i \sum_{j \neq j'} x_{ij} y_{ij'}.$$

$$104 \quad \mathbf{E}(\hat{D}_w) = \mathbf{E}(\hat{P}_1) - \mathbf{E}(\hat{P}_2) = E_1 - E_2$$

$$105 \quad \hat{D}_w^2 = (\hat{P}_1 - \hat{P}_2)^2$$

$$106 \quad = \frac{1}{n^2 v^2} \sum_{i,i'} \sum_{j,j'} x_{ij} y_{ij} x_{i'j'} y_{i'j'} - \frac{2}{n^2 v^2 (v-1)} \sum_{i,i'} \sum_{j,j' \neq j''} x_{ij} y_{ij} x_{i'j'} y_{i'j''}$$

$$107 \quad + \frac{1}{n^2 v^2 (v-1)^2} \sum_{i,i'} \sum_{j \neq j', j'' \neq j'''} x_{ij} y_{ij'} x_{i'j''} y_{i'j'''}$$

$$108 \quad = \frac{1}{n^2 v^2} [C_1 \hat{P}_1 + C_{10} \hat{P}_{10} + C_{11} \hat{P}_{11}] - \frac{2}{n^2 v^2 (v-1)} [C_4 \hat{P}_4 + C_{12} \hat{P}_{12} + C_{15} \hat{P}_{15}]$$

$$109 \quad + \frac{1}{n^2 v^2 (v-1)^2} [C_2 \hat{P} + C_9 \hat{P} + C_{10} \hat{P}_{10} + 2C_{15} \hat{P}_{15} + C_{16} \hat{P}_{16} + C_{21} \hat{P}_{21}]$$

$$110 \quad \mathbf{E}(\hat{D}_w^2) = \frac{1}{n^2 v^2} [C_1 E_1 + C_{10} E_{10} + C_{11} E_{11}] - \frac{2}{n^2 v^2 (v-1)} [C_4 E_4 + C_{12} E_{12} + C_{15} E_{15}]$$

$$111 \quad + \frac{1}{n^2 v^2 (v-1)^2} [C_2 E_2 + C_9 E_9 + C_{10} E_{10} + 2C_{15} E_{15} + C_{16} E_{16} + C_{21} E_{21}]$$

112 where the coefficient C_i is the reciprocal of coefficient before the summation sign in the
113 expression of $\hat{P}_i$, e.g. the final coefficient C_{21} is $nv(v-1)(v-2)(v-3)$.

114 $\mathbf{E}(\hat{D}_b)$ and $\mathbf{E}(\hat{D}_b^2)$

$$115 \quad \hat{D}_b = \hat{P}_{B \dots B \dots B \dots B \dots}^{A \dots A \dots A \dots A \dots} - \hat{p} \hat{q} = \hat{P}_2 - \hat{p} \hat{q} \text{ by the definition of } D_b, \text{ in which}$$

$$116 \quad \hat{P}_2 = \frac{1}{nv(v-1)} \sum_i \sum_{j \neq j'} x_{ij} y_{ij'} \quad \hat{p}_A = \frac{1}{nv} \sum_i \sum_j x_{ij} \quad \text{and} \quad \hat{q}_B = \frac{1}{nv} \sum_i \sum_j y_{ij}.$$

$$117 \quad \hat{D}_b = \frac{1}{nv(v-1)} \sum_i \sum_{j \neq j'} x_{ij} y_{ij'} - \frac{1}{n^2 v^2} \sum_{i,i'} \sum_{j,j'} x_{ij} y_{i'j'}$$

$$118 \quad = \hat{P}_2 - \frac{1}{n^2 v^2} [nv \hat{P}_1 + nv(v-1) \hat{P}_2 + n(n-1)v^2 \hat{P}_3]$$

$$119 \quad \mathbf{E}(\hat{D}_b) = E_2 - \frac{1}{n^2 v^2} [C_1 E_1 + C_2 E_2 + C_3 E_3]$$

$$\begin{aligned}
 120 \quad \widehat{D}_b^2 &= \frac{1}{n^2 v^2 (v-1)^2} \sum_{i,i'} \sum_{\substack{j \neq j' \\ j'' \neq j'''}} x_{ij} y_{ij'} x_{i'j''} y_{i'j'''} \\
 121 \quad &- \frac{2}{n^3 v^3 (v-1)} \sum_{i,i',i''} \sum_{j \neq j'} \sum_{j'',j'''} x_{ij} y_{ij'} x_{i'j''} y_{i''j'''} \\
 122 \quad &+ \frac{1}{n^4 v^4} \sum_{i,i',i'',i'''} \sum_{j,j',j'',j'''} x_{ij} y_{i'j'} x_{i''j''} y_{i'''j'''} \\
 123 \quad E(\widehat{D}_b^2) &= \frac{1}{n^2 v^2 (v-1)^2} [C_2 E_2 + C_9 E_9 + C_{10} E_{10} + 2C_{15} E_{15} + C_{16} E_{16} + C_{21} E_{21}] \\
 124 \quad &- \frac{2}{n^3 v^3 (v-1)} [C_2 E_2 + C_4 E_4 + C_7 E_7 + C_9 E_9 + C_{10} E_{10} + C_{12} E_{12} + C_{13} E_{13} \\
 125 \quad &+ 3C_{15} E_{15} + C_{16} E_{16} + C_{18} E_{18} + C_{21} E_{21} + C_{22} E_{22}] \\
 126 \quad &+ \frac{1}{n^4 v^4} [C_1 E_1 + C_2 E_2 + C_3 E_3 + 2C_4 E_4 + C_5 E_5 + 2C_6 E_6 + 2C_7 E_7 + C_8 E_8 \\
 127 \quad &+ C_9 E_9 + 2C_{10} E_{10} + 2C_{11} E_{11} + 4C_{12} E_{12} + 4C_{13} E_{13} + 4C_{14} E_{14} + 4C_{15} E_{15} \\
 128 \quad &+ 2C_{16} E_{16} + C_{17} E_{17} + 4C_{18} E_{18} + C_{19} E_{19} + C_{20} E_{20} + C_{21} E_{21} + 2C_{22} E_{22}]
 \end{aligned}$$

$$129 \quad E(\widehat{D}_w \widehat{D}_b)$$

$$\begin{aligned}
 130 \quad \widehat{D}_w \widehat{D}_b &= \left(\frac{1}{nv} \sum_i \sum_j x_{ij} y_{ij} - \frac{1}{nv(v-1)} \sum_i \sum_{j \neq j'} x_{ij} y_{ij'} \right) \left(\frac{1}{nv(v-1)} \sum_i \sum_{j \neq j'} x_{ij} y_{ij'} - \frac{1}{n^2 v^2} \sum_{i,i'} \sum_{j,j'} x_{ij} y_{i'j'} \right) \\
 131 \quad &= \frac{1}{n^2 v^2 (v-1)} \sum_{i,i'} \sum_j \sum_{j' \neq j''} x_{ij} y_{ij'} x_{i'j''} y_{i'j'''} - \frac{1}{n^3 v^3} \sum_{i,i',i''} \sum_{j,j',j''} x_{ij} y_{ij'} x_{i'j''} y_{i''j'''} \\
 132 \quad &- \frac{1}{n^2 v^2 (v-1)^2} \sum_{i,i'} \sum_{\substack{j \neq j' \\ j'' \neq j'''}} x_{ij} y_{ij'} x_{i'j''} y_{i'j'''} + \frac{1}{n^3 v^3 (v-1)} \sum_{i,i',i''} \sum_{j \neq j'} \sum_{j'',j'''} x_{ij} y_{ij'} x_{i'j''} y_{i''j'''} \\
 133 \quad E(\widehat{D}_w \widehat{D}_b) &= \frac{1}{n^2 v^2 (v-1)} [C_4 E_4 + C_{12} E_{12} + C_{15} E_{15}] \\
 134 \quad &- \frac{1}{n^3 v^3} [C_1 E_1 + C_4 E_4 + C_6 E_6 + C_{10} E_{10} + C_{11} E_{11} + C_{12} E_{12} + C_{13} E_{13} + C_{14} E_{14} \\
 135 \quad &+ C_{15} E_{15}] \\
 136 \quad &- \frac{1}{n^2 v^2 (v-1)^2} [C_2 E_2 + C_9 E_9 + C_{10} E_{10} + 2C_{15} E_{15} + C_{16} E_{16} + C_{21} E_{21}] \\
 137 \quad &+ \frac{1}{n^3 v^3 (v-1)} [C_2 E_2 + C_4 E_4 + C_7 E_7 + C_9 E_9 + C_{10} E_{10} + C_{12} E_{12} + C_{13} E_{13} \\
 138 \quad &+ 3C_{15} E_{15} + C_{16} E_{16} + C_{18} E_{18} + C_{21} E_{21} + C_{22} E_{22}]
 \end{aligned}$$

$$139 \quad E(\widehat{D}) \text{ and } E(\widehat{D}^2)$$

$$140 \quad \widehat{D} = \widehat{D}_w + \widehat{D}_b \text{ by the definition of } D, \text{ then}$$

$$141 \quad E(\widehat{D}) = E(\widehat{D}_w) + E(\widehat{D}_b) = E_1 - \frac{1}{n^2 v^2} [C_1 E_1 + C_2 E_2 + C_3 E_3]$$

$$142 \quad \widehat{D}^2 = (\widehat{D}_w + \widehat{D}_b)^2 = \widehat{D}_w^2 + 2\widehat{D}_w \widehat{D}_b + \widehat{D}_b^2$$

$$143 \quad E(\widehat{D}^2) = E(\widehat{D}_w^2) + 2E(\widehat{D}_w \widehat{D}_b) + E(\widehat{D}_b^2)$$

144 $\mathbf{E}(\hat{\Delta})$ and $\mathbf{E}(\hat{\Delta}^2)$

145 $\hat{\Delta} = \hat{D}_w + v\hat{D}_b$ by the definition of Δ , then

$$146 \quad \mathbf{E}(\hat{\Delta}) = \mathbf{E}(\hat{D}_w) + v\mathbf{E}(\hat{D}_b) = E_1 - \frac{1}{n^2v} [C_1E_1 + C_2E_2 + C_3E_3]$$

$$147 \quad \hat{\Delta}^2 = (\hat{D}_w + v\hat{D}_b)^2 = \hat{D}_w^2 + 2v\hat{D}_w\hat{D}_b + v^2\hat{D}_b^2$$

$$148 \quad \mathbf{E}(\hat{\Delta}^2) = \mathbf{E}(\hat{D}_w^2) + 2v\mathbf{E}(\hat{D}_w\hat{D}_b) + v^2\mathbf{E}(\hat{D}_b^2)$$

149 $\mathbf{E}(\hat{Q})$

150 $\hat{Q} = \hat{p}_A\hat{p}_X\hat{q}_B\hat{q}_X = (\hat{p}_A - \hat{p}_A^2)(\hat{q}_B - \hat{q}_B^2)$ by $Q = p_Ap_Xq_Bq_X$, in which

$$151 \quad \hat{p}_A = \frac{1}{nv} \sum_i \sum_j x_{ij} \quad \text{and} \quad \hat{q}_B = \frac{1}{nv} \sum_i \sum_j y_{ij}.$$

$$152 \quad \hat{Q} = \left(\frac{1}{nv} \sum_i \sum_j x_{ij} - \frac{1}{n^2v^2} \sum_{i,i'} \sum_{j,j'} x_{ij} x_{i'j'} \right) \left(\frac{1}{nv} \sum_i \sum_j y_{ij} - \frac{1}{n^2v^2} \sum_{i,i'} \sum_{j,j'} y_{ij} y_{i'j'} \right)$$

$$153 \quad = \frac{1}{n^2v^2} \sum_{i,i'} \sum_{j,j'} x_{ij} y_{i'j'} - \frac{1}{n^3v^3} \sum_{i,i',i''} \sum_{j,j',j''} (x_{ij} y_{i'j'} y_{i''j''} + x_{ij} x_{i'j'} y_{i''j''})$$

$$154 \quad + \frac{1}{n^4v^4} \sum_{i,i',i'',i'''} \sum_{j,j',j'',j'''} x_{ij} x_{i'j'} y_{i''j''} y_{i'''j'''}$$

$$155 \quad \mathbf{E}(\hat{Q}) = \frac{1}{n^2v^2} [C_1E_1 + C_2E_2 + C_3E_3]$$

$$156 \quad - \frac{1}{n^3v^3} [2C_1E_1 + 2C_2E_2 + 2C_3E_3 + 2C_4E_4 + C_5E_5 + 2C_6E_6 + 2C_7E_7 + C_8E_8$$

$$157 \quad + C_9E_9]$$

$$158 \quad + \frac{1}{n^4v^4} [C_1E_1 + C_2E_2 + C_3E_3 + 2C_4E_4 + C_5E_5 + 2C_6E_6 + 2C_7E_7 + C_8E_8$$

$$159 \quad + C_9E_9 + 2C_{10}E_{10} + 2C_{11}E_{11} + 4C_{12}E_{12} + 4C_{13}E_{13} + 4C_{14}E_{14} + 4C_{15}E_{15}$$

$$160 \quad + 2C_{16}E_{16} + C_{17}E_{17} + 4C_{18}E_{18} + C_{19}E_{19} + C_{20}E_{20} + C_{21}E_{21} + 2C_{22}E_{22}]$$

161 $\mathbf{E}(\hat{R})$

162 $\hat{P}_{AA} = \frac{1}{nv(v-1)} \sum_i \sum_{j \neq j'} x_{ij} x_{ij'}$ and $\hat{P}_{BB} = \frac{1}{nv(v-1)} \sum_i \sum_{j \neq j'} y_{ij} y_{ij'}$ by the definition of P_{AA} .

163 $\hat{R} = [\hat{p}_A - v\hat{p}_A^2 + (v-1)\hat{P}_{AA}][\hat{q}_B - v\hat{q}_B^2 + (v-1)\hat{P}_{BB}]$ by Equation (2).

$$164 \quad \hat{R} = \left(\frac{1}{nv} \sum_i \sum_j x_{ij} - \frac{1}{n^2v} \sum_{i,i'} \sum_{j,j'} x_{ij} x_{i'j'} + \frac{1}{nv} \sum_i \sum_{j \neq j'} x_{ij} x_{ij'} \right) \left(\frac{1}{nv} \sum_i \sum_j y_{ij} \right.$$

$$165 \quad \left. - \frac{1}{n^2v} \sum_{i,i'} \sum_{j,j'} y_{ij} y_{i'j'} + \frac{1}{nv} \sum_i \sum_{j \neq j'} y_{ij} y_{ij'} \right)$$

$$\begin{aligned}
 &= \frac{1}{n^2 v^2} \sum_{i,i'} \sum_{j,j'} x_{ij} y_{i'j'} - \frac{1}{n^3 v^2} \sum_{i,i',i''} \sum_{j,j',j''} (x_{ij} y_{i'j'} y_{i''j''} + x_{ij} x_{i'j'} y_{i''j''}) \\
 &\quad + \frac{1}{n^4 v^2} \sum_{i,i',i'',i'''} \sum_{j,j',j'',j'''} x_{ij} x_{i'j'} y_{i''j''} y_{i'''j'''} \\
 &\quad + \frac{1}{n^2 v^2} \sum_{i,i'} \sum_j \sum_{j' \neq j''} (x_{ij} y_{i'j'} y_{i''j''} + y_{ij} x_{i'j'} x_{i''j''}) \\
 &\quad - \frac{1}{n^3 v^2} \sum_{i,i',i''} \sum_{j,j'} \sum_{j'' \neq j'''} (x_{ij} x_{i'j'} y_{i''j''} y_{i'''j'''} + y_{ij} y_{i'j'} x_{i''j''} x_{i'''j'''}) \\
 &\quad + \frac{1}{n^2 v^2} \sum_{i,i'} \sum_{\substack{j \neq j' \\ j'' \neq j'''}} x_{ij} x_{i'j'} y_{i''j''} y_{i'''j'''} \\
 E(\hat{R}) &= \frac{1}{n^2 v^2} [C_1 E_1 + C_2 E_2 + C_3 E_3] \\
 &\quad - \frac{1}{n^3 v^2} [2C_1 E_1 + 2C_2 E_2 + 2C_3 E_3 + 2C_4 E_4 + C_5 E_5 + 2C_6 E_6 + 2C_7 E_7 + C_8 E_8 \\
 &\quad + C_9 E_9] \\
 &\quad + \frac{1}{n^4 v^2} [C_1 E_1 + C_2 E_2 + C_3 E_3 + 2C_4 E_4 + C_5 E_5 + 2C_6 E_6 + 2C_7 E_7 + C_8 E_8 \\
 &\quad + C_9 E_9 + 2C_{10} E_{10} + 2C_{11} E_{11} + 4C_{12} E_{12} + 4C_{13} E_{13} + 4C_{14} E_{14} + 4C_{15} E_{15} \\
 &\quad + 2C_{16} E_{16} + C_{17} E_{17} + 4C_{18} E_{18} + C_{19} E_{19} + C_{20} E_{20} + C_{21} E_{21} + 2C_{22} E_{22}] \\
 &\quad + \frac{1}{n^2 v^2} [2C_4 E_4 + C_5 E_5 + C_9 E_9] - \frac{1}{n^3 v^2} [2C_4 E_4 + C_5 E_5 + C_9 E_9 + 4C_{10} E_{10} \\
 &\quad + 4C_{13} E_{13} + 8C_{15} E_{15} + 2C_{17} E_{17} + C_{19} E_{19} + 2C_{21} E_{21} + 2C_{22} E_{22}] \\
 &\quad + \frac{1}{n^2 v^2} [2C_{10} E_{10} + 4C_{15} E_{15} + C_{17} E_{17} + C_{21} E_{21}]
 \end{aligned}$$

Appendix C. HS mating system

The double non-identity coefficients are closely related to the haplotypes that are used to detect the specific alleles. In this appendix, we consider such relationships in the haplotype sampling (HS) mating system. The effective population size N_e in this system is assumed to be the same as the population size N . We will adopt N_e instead of N in our discussion in order to accommodate other mating systems, and we will also write the double non-identity coefficient as the dni-coefficient for brevity.

For the case of dni-coefficients θ_1 and θ_2 , it can be seen from Table 1 that only two haplotypes (say H_1 and H_2) are sampled, and both alleles in each haplotype need to be detected. These two haplotypes can be copied from either the same haplotype (written as $H_1 \equiv H_2$), or different haplotypes in the same individual (written as $H_1 \asymp H_2$), or different haplotypes in different individuals (written as $H_1 \sim H_2$). For this case, we will divide into three situations (named HS01, HS02 and HS03) to carry out our discussion.

HS01 $H_1 \equiv H_2$, weight 1, dni-coefficient 0;

HS02 $H_1 \asymp H_2$, weight $v - 1$,

(a) none recombined, probability $(1 - c)^2$, dni-coefficient θ_1 ;

(b) one recombined, probability $2c(1 - c)$, dni-coefficient $\frac{v-2}{v-1} \Gamma_4$;

(c) both recombined, prob. c^2 , dni-coefficient $\frac{1}{(v-1)^2} \theta_1 + \frac{2(v-2)}{(v-1)^2} \Gamma_4 + \frac{(v-2)(v-3)}{(v-1)^2} \Delta_6$;

HS03 $H_1 \sim H_2$, weight $(N_e - 1)v$,

(a) none recombined, probability $(1 - c)^2$, dni-coefficient θ_2 ;

- (b) one recombined, probability $2c(1-c)$, dni-coefficient Γ_1 ;
(c) both recombined, probability c^2 , dni-coefficient Δ_1 .

Now, the expression of dni-coefficients θ'_1 or θ'_2 in the next generation can be written out. In fact, let $\mathbf{W}_\theta = [w_{1\theta}, w_{2\theta}, w_{3\theta}]$ be the vector consisting of those weights, i.e. $\mathbf{W}_\theta = [1, v-1, (N_e-1)v]$, and let $\boldsymbol{\theta} = [\theta_1, \theta_2, \theta_3]$, where each θ_i is the weighted sum of dni-coefficients in $\text{HS}\theta_i$, with the corresponding recombination probabilities as their weights (if the recombination probability does not occur, θ_i is set as the dni-coefficient in $\text{HS}\theta_i$), $i = 1, 2, 3$, that is

$$\begin{aligned}\theta_1 &= 0, \\ \theta_2 &= (1-c)^2\theta_1 + 2c(1-c)\frac{v-2}{v-1}\Gamma_4 + c^2\left[\frac{1}{(v-1)^2}\theta_1 + \frac{2(v-2)}{(v-1)^2}\Gamma_4 + \frac{(v-2)(v-3)}{(v-1)^2}\Delta_6\right], \\ \theta_3 &= (1-c)^2\theta_2 + 2c(1-c)\Gamma_1 + c^2\Delta_1.\end{aligned}$$

Then $\theta'_1 = \theta'_2 = \mathbf{W}_\theta \boldsymbol{\theta}^T / \mathbf{W}_\theta \mathbf{1} = \frac{w_{1\theta}\theta_1 + w_{2\theta}\theta_2 + w_{3\theta}\theta_3}{w_{1\theta} + w_{2\theta} + w_{3\theta}}$, where $\mathbf{1}$ is the column vector $[1, 1, 1]^T$.

This is a linear combination of dni-coefficients in the current generation, and the products of combination coefficients times $N_e v(v-1)$ are listed in the second column of Table S3.

For the case of Γ_1 to Γ_4 , it can be seen from Table 1 that three haplotypes are sampled, in which one is the haplotype that both alleles need to be detected, denoted by H_1 , another is that only the allele at the first locus needs to be detected, denoted by H_2 , and the third is that only the allele at the second locus needs to be detected, denoted by H_3 . Because H_2 and H_3 are only detected the allele at a single locus, it is unnecessary to model their recombination. For this case, the combinations among three relations $\equiv$, $\asymp$ and $\sim$ can be divided into nine situations (named HSG1 to HSG9).

- HSG1 $H_1 \equiv H_2 \equiv H_3$, weight 1, dni-coefficient 0;
HSG2 $H_1 \equiv H_2 \asymp H_3$ or $H_1 \equiv H_3 \asymp H_2$, weight $2(v-1)$,
(a) not recombined, probability $1-c$, dni-coefficient 0;
(b) recombined, probability c , dni-coefficient $\frac{1}{2(v-1)}\theta_1 + \frac{v-2}{2(v-1)}\Gamma_4$;
HSG3 $H_1 \asymp H_2 \equiv H_3$, weight $v-1$,
(a) not recombined, probability $1-c$, dni-coefficient θ_1 ;
(b) recombined, probability c , dni-coefficient $\frac{v-2}{v-1}\Gamma_4$;
HSG4 $H_1 \asymp H_2 \asymp H_3$, weight $(v-1)(v-2)$,
(a) not recombined, probability $1-c$, dni-coefficient Γ_4 ;
(b) recombined, probability c , dni-coefficient $\frac{1}{v-1}\Gamma_4 + \frac{v-3}{v-1}\Delta_6$;
HSG5 $H_1 \equiv H_2 \sim H_3$ or $H_1 \equiv H_3 \sim H_2$, weight $2(N_e-1)v$,
(a) not recombined, probability $1-c$, dni-coefficient 0;
(b) recombined, probability c , dni-coefficient $\Gamma_2/2$;
HSG6 $H_2 \equiv H_3 \sim H_1$, weight $(N_e-1)v$,
(a) not recombined, probability $1-c$, dni-coefficient θ_2 ;
(b) recombined, probability c , dni-coefficient Γ_1 ;
HSG7 $H_1 \asymp H_2 \sim H_3$ or $H_1 \asymp H_3 \sim H_2$, weight $2(N_e-1)v(v-1)$,
(a) not recombined, probability $1-c$, dni-coefficient Γ_2 ;
(b) recombined, probability c , dni-coefficient $\frac{1}{2(v-1)}\Gamma_2 + \frac{v-2}{v-1}\Delta_7$;
HSG8 $H_1 \sim H_2 \asymp H_3$, weight $(N_e-1)v(v-1)$,
(a) not recombined, probability $1-c$, dni-coefficient Γ_1 ;
(b) recombined, probability c , dni-coefficient Δ_1 ;
HSG9 $H_1 \sim H_2 \sim H_3$, weight $(N_e-1)(N_e-2)v^2$,
(a) not recombined, probability $1-c$, dni-coefficient Γ_3 ;

(b) recombined, probability c , dni-coefficient Δ_3 .

Now, let $\mathbf{W}_\gamma = [w_{1\gamma}, w_{2\gamma}, \dots, w_{9\gamma}]$ and $\mathbf{\Gamma} = [\gamma_1, \gamma_2, \dots, \gamma_9]$, where the definitions of $\mathbf{W}_\gamma$ and $\mathbf{\Gamma}$ are similar to those of $\mathbf{W}_\theta$ and $\mathbf{\Theta}$. Then

$$\Gamma'_1 = \Gamma'_2 = \Gamma'_3 = \Gamma'_4 = \frac{\mathbf{W}_\gamma \mathbf{\Gamma}^T}{\mathbf{W}_\gamma \mathbf{1}} = \frac{w_{1\gamma}\gamma_1 + w_{2\gamma}\gamma_2 + \dots + w_{9\gamma}\gamma_9}{w_{1\gamma} + w_{2\gamma} + \dots + w_{9\gamma}}.$$

This is also a linear combination, and the products of combination coefficients times $N_e^2 v^2$ are listed in the third column of Table S3.

For the case of Δ_1 to Δ_7 , we see from Table 1 that four haplotypes are sampled, in which two are the haplotypes that the allele at the first locus is detected, denoted by H_1 and H_2 , and the other two are that the allele at the second locus is detected, denoted by H_3 and H_4 . Because there is only the allele at a single locus to be detected, the recombination of these four haplotypes need not be modelled. For this case, the combinations of three relations can be divided into 22 situations (named HSA1 to HSA22).

- HSA1 $H_1 \equiv H_2 \equiv H_3 \equiv H_4$, weight 1, dni-coefficient 0;
- HSA2 $H_1 \equiv H_2 \asymp H_3 \equiv H_4$, weight $v - 1$, dni-coefficient 0;
- HSA3 $H_1 \equiv H_2 \sim H_3 \equiv H_4$, weight $(N_e - 1)v$, dni-coefficient 0;
- HSA4 $H_1 \equiv H_2 \equiv H_3 \asymp H_4$ or $H_1 \equiv H_2 \equiv H_4 \asymp H_3$ or $H_1 \asymp H_2 \equiv H_3 \equiv H_4$ or $H_2 \asymp H_1 \equiv H_3 \equiv H_4$, weight $4(v - 1)$, dni-coefficient 0;
- HSA5 $H_1 \equiv H_2 \sim H_3 \asymp H_4$ or $H_1 \asymp H_2 \sim H_3 \equiv H_4$, weight $2(N_e - 1)v(v - 1)$, dni-coefficient 0;
- HSA6 $H_1 \equiv H_3 \equiv H_4 \sim H_2$ or $H_2 \equiv H_3 \equiv H_4 \sim H_1$ or $H_1 \equiv H_2 \equiv H_3 \sim H_4$ or $H_1 \equiv H_2 \equiv H_4 \sim H_3$, weight $4(N_e - 1)v$, dni-coefficient 0;
- HSA7 $H_1 \sim H_2 \asymp H_3 \equiv H_4$ or $H_2 \sim H_1 \asymp H_3 \equiv H_4$ or $H_1 \equiv H_2 \asymp H_3 \sim H_4$ or $H_1 \equiv H_2 \asymp H_4 \sim H_3$, weight $4(N_e - 1)v(v - 1)$, dni-coefficient 0;
- HSA8 $H_1 \sim H_2 \sim H_3 \equiv H_4$ or $H_1 \equiv H_2 \sim H_3 \sim H_4$, weight $2(N_e - 1)(N_e - 2)v^2$, dni-coefficient 0;
- HSA9 $H_1 \asymp H_2 \asymp H_3 \equiv H_4$ or $H_1 \equiv H_2 \asymp H_3 \asymp H_4$, weight $2(v - 1)(v - 2)$, dni-coefficient 0;
- HSA10 $H_1 \equiv H_3 \asymp H_2 \equiv H_4$ or $H_1 \equiv H_4 \asymp H_2 \equiv H_3$, weight $2(v - 1)$, dni-coefficient Θ_1 ;
- HSA11 $H_1 \equiv H_3 \sim H_2 \equiv H_4$ or $H_1 \equiv H_4 \sim H_2 \equiv H_3$, weight $2(N_e - 1)v$, dni-coefficient Θ_2 ;
- HSA12 $H_1 \equiv H_3 \sim H_2 \asymp H_4$ or $H_1 \equiv H_4 \sim H_2 \asymp H_3$ or $H_2 \equiv H_3 \sim H_1 \asymp H_4$ or $H_2 \equiv H_4 \sim H_1 \asymp H_3$, weight $4(N_e - 1)v(v - 1)$, dni-coefficient Γ_1 ;
- HSA13 $H_1 \equiv H_3 \asymp H_2 \sim H_4$ or $H_1 \equiv H_4 \asymp H_2 \sim H_3$ or $H_2 \equiv H_3 \asymp H_1 \sim H_4$ or $H_2 \equiv H_4 \asymp H_1 \sim H_3$ or $H_1 \equiv H_3 \asymp H_4 \sim H_2$ or $H_1 \equiv H_4 \asymp H_3 \sim H_2$ or $H_2 \equiv H_3 \asymp H_4 \sim H_1$ or $H_2 \equiv H_4 \asymp H_3 \sim H_1$, weight $8(N_e - 1)v(v - 1)$, dni-coefficient Γ_2 ;
- HSA14 $H_1 \equiv H_3 \sim H_2 \sim H_4$ or $H_1 \equiv H_4 \sim H_2 \sim H_3$ or $H_2 \equiv H_3 \sim H_1 \sim H_4$ or $H_2 \equiv H_4 \sim H_1 \sim H_3$, weight $4(N_e - 1)(N_e - 2)v^2$, dni-coefficient Γ_3 ;
- HSA15 $H_1 \equiv H_3 \asymp H_2 \asymp H_4$ or $H_1 \equiv H_4 \asymp H_2 \asymp H_3$ or $H_2 \equiv H_3 \asymp H_1 \asymp H_4$ or $H_2 \equiv H_4 \asymp H_1 \asymp H_3$, weight $4(v - 1)(v - 2)$, dni-coefficient Γ_4 ;
- HSA16 $H_1 \asymp H_3 \sim H_2 \asymp H_4$ or $H_1 \asymp H_4 \sim H_2 \asymp H_3$, weight $2(N_e - 1)v(v - 1)^2$, dni-coefficient Δ_1 ;
- HSA17 $H_1 \asymp H_2 \sim H_3 \asymp H_4$, weight $(N_e - 1)v(v - 1)^2$, dni-coefficient Δ_2 ;
- HSA18 $H_1 \asymp H_3 \sim H_2 \sim H_4$ or $H_1 \asymp H_4 \sim H_2 \sim H_3$ or $H_2 \asymp H_3 \sim H_1 \sim H_4$ or

290 $H_2 \asymp H_4 \sim H_1 \sim H_3$, weight $4(N_e - 1)(N_e - 2)v^2(v - 1)$, dni-coefficient Δ_3 ;
 291 HSA19 $H_1 \asymp H_2 \sim H_3 \sim H_4$ or $H_1 \sim H_2 \sim H_3 \asymp H_4$,
 292 weight $2(N_e - 1)(N_e - 2)v^2(v - 1)$, dni-coefficient Δ_4 ;
 293 HSA20 $H_1 \sim H_2 \sim H_3 \sim H_4$, weight $(N_e - 1)(N_e - 2)(N_e - 3)v^3$, dni-coefficient Δ_5 ;
 294 HSA21 $H_1 \asymp H_2 \asymp H_3 \asymp H_4$, weight $(v - 1)(v - 2)(v - 3)$, dni-coefficient Δ_6 ;
 295 HSA22 $H_1 \asymp H_2 \asymp H_3 \sim H_4$ or $H_1 \asymp H_2 \asymp H_4 \sim H_3$ or $H_1 \asymp H_3 \asymp H_4 \sim H_2$ or
 296 $H_2 \asymp H_3 \asymp H_4 \sim H_1$ weight $4(N_e - 1)v(v - 1)(v - 2)$, dni-coefficient Δ_7 .

297 Now, let $\mathbf{W}_\delta$ and $\mathbf{\Delta}$ be the row vectors consisting of 22 weights and 22 dni-
 298 coefficients in HSA1 to HSA22, respectively. Then

$$299 \quad \Delta'_1 = \Delta'_2 = \dots = \Delta'_7 = \mathbf{W}_\delta \mathbf{\Delta}^T / \mathbf{W}_\delta \mathbf{1}.$$

300 This is still a linear combination, and the products of combination coefficients times $N_e^3 v^3$
 301 are listed in the final column of Table S3.

302 The expressions in Table S3 are the essential factors to form $\mathbf{\Omega}^T$ of the transition
 303 matrix $\mathbf{\Omega}$ for the HS mating system. Moreover, the matrices $\mathbf{T}$ and $\mathbf{S}$ in the principal
 304 part of $\mathbf{\Omega}$ are listed in Appendix H.

305 Appendix D. Corrections for finite sample size

306 It is easy to see from Equations (3) and (4) that the next formula is valid:

$$307 \quad \mathbf{M} = Q\mathbf{\Phi}^T \mathbf{A}_1 + Qn^{-1}\mathbf{\Phi}^T \mathbf{A}_2 + \mathbf{\Phi}^T \mathcal{O}(n^{-2}). \quad (\text{S1})$$

308 When the sample size n is large enough, the principal part of $\mathbf{M}$ is $Q\mathbf{\Phi}^T \mathbf{A}_1$, and the
 309 remainder can be neglected, then $\mathbf{M} \approx Q\mathbf{\Phi}^T \mathbf{A}_1$, indicating that the matrix $\mathbf{A}_1$ can be used
 310 to approximate the moments of LD measurements. For example, using the fourth and the
 311 sixth column elements in $\mathbf{A}_1$ (see Table S1), we have $E(\widehat{D}^2) \approx Q(\theta_2 - 2\Gamma_3 + \Delta_5)$ and
 312 $E(\widehat{Q}) \approx Q\Delta_5$. Thus

$$313 \quad d^2 = \frac{E(\widehat{D}^2)}{E(\widehat{Q})} \approx \frac{\theta_2 - 2\Gamma_3 + \Delta_5}{\Delta_5}.$$

314 Similarly, δ^2 can be approximately expressed as

$$315 \quad \delta^2 = \frac{E(\widehat{R}^2)}{E(\widehat{R})} \approx \frac{\theta_2 + 2v_1\Gamma_1 - 2v\Gamma_3 + v_1^2\Delta_1 - 2v_1v\Delta_3 + v^2\Delta_5}{v_1^2\Delta_2 - 2v_1v\Delta_4 + v^2\Delta_5}.$$

316 In practice, sampling error will influence the estimation of $\hat{r}^2$ and $\hat{r}_\Delta^2$. For example,
 317 if the two loci are unlinked, the moments $E(\hat{r}^2)$ and $E(\hat{r}_\Delta^2)$ are greater than zero. This
 318 effect is related to the sample size n , then the term $Qn^{-1}\mathbf{\Phi}^T \mathbf{A}_2$ in Equation (S1)
 319 containing the coefficient n^{-1} cannot be neglected. To accommodate this effect, we
 320 consider the next approximate expression:

$$321 \quad \mathbf{M} \approx Q\mathbf{\Phi}^T \mathbf{A}_1 + Qn^{-1}\mathbf{\Phi}^T \mathbf{A}_2.$$

322 Denote the fourth expression in the vector $Qn^{-1}\mathbf{\Phi}^T \mathbf{A}_2$ by $M_{D/n}$, and the sixth by $M_{Q/n}$.
 323 Using the fourth and the sixth column elements in $\mathbf{A}_2$ (see Table S2), we obtain

$$324 \quad M_{D/n} = Qn^{-1} \left(\frac{v_1}{v} \theta_1 - \frac{2+v}{v} \theta_2 - \frac{2v_1}{v} \Gamma_1 - \frac{4v_1}{v} \Gamma_2 + \frac{4+6v}{v} \Gamma_3 + \frac{4v_1}{v} \Delta_3 + \frac{2v_1}{v} \Delta_4 - 6\Delta_5 \right),$$

$$M_{Q/n} = Qn^{-1} \left(\frac{4}{v} \Gamma_3 + \frac{4v_1}{v} \Delta_3 + \frac{2v_1}{v} \Delta_4 - 6\Delta_5 \right).$$

Then $d^2 \approx \frac{Q(\Theta_2 - 2\Gamma_3 + \Delta_5) + M_{D/n}}{Q\Delta_5 + M_{Q/n}}$. Because n is large, we omit $M_{Q/n}$ in the denominator for the convenience of derivation. Therefore

$$d^2 \approx \frac{\Theta_2 - 2\Gamma_3 + \Delta_5}{\Delta_5} + \frac{M_{D/n}}{Q\Delta_5}.$$

The net effect for d^2 caused by $\frac{M_{D/n}}{Q\Delta_5}$ is $\frac{1}{vn}$ if Φ is an eigenvector belonging to the maximal eigenvalue of Ω . Here, we take the HS mating system as an example to show this. In fact, for this system, according to Equation (8) and Table 4, we have

$$\omega \approx \left[1 + \frac{2c + c_1^2 v - 1}{c_2 c v_1 v N_e}, 1 + \frac{2c + c_1^2 v - 1}{c_2 c v_1 v N_e}, 1, 1, \dots, 1 \right]^T.$$

Now, replacing $1 + \frac{2c + c_1^2 v - 1}{c_2 c v_1 v N_e}$ for each of Θ_1 and Θ_2 in $\frac{M_{D/n}}{Q\Delta_5}$, and 1 for each of the other double non-identity coefficients, it follows $\frac{M_{D/n}}{Q\Delta_5} = \frac{1}{nv} \left[1 + \frac{3(2c + c_1^2 v - 1)}{v c_2 c v_1 N_e} \right]$. Hence $\frac{M_{D/n}}{Q\Delta_5} \approx \frac{1}{nv}$ by $N_e \geq n \gg 1$. Similarly, it can be shown that the net effect for δ^2 is $\frac{1}{n}$. Thus, the approximate expressions of d^2 and δ^2 considered the effect of sample size n on sampling are

$$d^2 \approx \frac{\Theta_2 - 2\Gamma_3 + \Delta_5}{\Delta_5} + \frac{1}{vn},$$

$$\delta^2 \approx \frac{\Theta_2 + 2v_1 \Gamma_1 - 2v \Gamma_3 + v_1^2 \Delta_1 - 2v_1 v \Delta_3 + v^2 \Delta_5}{v_1^2 \Delta_2 - 2v_1 v \Delta_4 + v^2 \Delta_5} + \frac{1}{n}.$$

Appendix E. Monoecious mating systems

The method to derive the expression of each element in Ω for the monoecious mating systems is the same as that for the HS mating system. It is noteworthy that unlike the HS mating system, two haplotypes sampled within the same individual need to be detected whether they are from the same gamete: (i) if they are from the same gamete, the probability is $\frac{v/2-1}{v-1}$; (ii) otherwise, the probability is $\frac{v/2}{v-1}$. We will denote $(H, H', \dots)$ for which those haplotypes within brackets are from the same gamete.

For (i), it is assumed that the chromosomes form bivalents during meiosis, and the double-reduction will never happen, then the paired chromosomes will segregate into different oocytes, which means that two haplotypes H and H' within the same gamete are copied from different haplotypes. However, this is not strictly equivalent to $H \asymp H'$. This is because the paired chromosomes will segregate into different oocytes. In order to avoid repetition, we first discuss nine situations similar to HSG1 to HSG9 in Appendix C, named MOG1 to MOG9 in turn.

- MOG1 $H_1 \equiv H_2 \equiv H_3$, weight 1, dni-coefficient 0;
- MOG2 $H_1 \equiv H_2 \asymp H_3$ or $H_1 \equiv H_3 \asymp H_2$ weight $2(v-1)$,
 - (a) not recombined, probability $1-c$, dni-coefficient 0;
 - (b) recombined, probability c , dni-coefficient $\Gamma_4/2$;

- 358 MOΓ3 $H_1 \asymp H_2 \equiv H_3$, weight $v - 1$,
 359 (a) not recombined, probability $1 - c$, dni-coefficient Θ_1 ;
 360 (b) recombined, probability c , dni-coefficient Γ_4 ;
 361 MOΓ4 $H_1 \asymp H_2 \asymp H_3$, weight $(v - 1)(v - 2)$,
 362 (a) not recombined, probability $1 - c$, dni-coefficient Γ_4 ;
 363 (b) recombined, probability c , dni-coefficient $\frac{1}{2v-4}\Gamma_4 + \frac{v-3}{v-2}\Delta_6$;
 364 MOΓ5 $H_1 \equiv H_2 \sim H_3$ or $H_1 \equiv H_3 \sim H_2$, weight $2(N_e - 1)v$,
 365 (a) not recombined, probability $1 - c$, dni-coefficient 0;
 366 (b) recombined, probability c , dni-coefficient $\Gamma_2/2$;
 367 MOΓ6 $H_2 \equiv H_3 \sim H_1$, weight $(N_e - 1)v$,
 368 (a) not recombined, probability $1 - c$, dni-coefficient Θ_2 ;
 369 (b) recombined, probability c , dni-coefficient Γ_1 ;
 370 MOΓ7 $H_1 \asymp H_2 \sim H_3$ or $H_1 \asymp H_3 \sim H_2$, weight $2(N_e - 1)v(v - 1)$,
 371 (a) not recombined, probability $1 - c$, dni-coefficient Γ_2 ;
 372 (b) recombined, probability c , dni-coefficient Δ_7 ;
 373 MOΓ8 $H_1 \sim H_2 \asymp H_3$, weight $(N_e - 1)v(v - 1)$,
 374 (a) not recombined, probability $1 - c$, dni-coefficient Γ_1 ;
 375 (b) recombined, probability c , dni-coefficient Δ_1 ;
 376 MOΓ9 $H_1 \sim H_2 \sim H_3$, weight $(N_e - 1)(N_e - 2)v^2$,
 377 (a) not recombined, probability $1 - c$, dni-coefficient Γ_3 ;
 378 (b) recombined, probability c , dni-coefficient Δ_3 .

379 For (ii), if the mating system is MS, because selfing is allowed, two haplotypes H and
 380 H' from different gametes can be copied from either the same haplotype ($H \equiv H'$), or
 381 different haplotypes in the same individual ($H \asymp H'$), or different haplotypes in different
 382 individuals ($H \sim H'$). These relationships are obviously equivalent to those in the HS
 383 mating system. If the mating system is ME, because selfing is excluded, two haplotypes
 384 from different gametes must be from different individuals ($H \sim H'$).

385 There may be more than one situation of HS0 (HSΓ, HSΔ or MOΓ) appearing in an
 386 item, and we will use some symbols to denote this phenomenon. For example, the symbol
 387 (MOΓ2/2,3,4,7/2) in the item (1) of Γ'_2 below denotes that there are four situations (i.e.
 388 MOΓ2/2, MOΓ3, MOΓ4 and MOΓ7/2) appearing in this item, in which MOΓ2/2 represents
 389 that the number of expressions describing the relations among the haplotypes is half of
 390 that for MOΓ2. This is because H_1 and H_2 are in the same gamete in the item (1) of Γ'_2 ,
 391 thus only the second expression in the two expressions in MOΓ2 ($H_1 \equiv H_2 \asymp H_3$ and $H_1 \equiv$
 392 $H_3 \asymp H_2$) can hold. The weight for MOΓ2/2 is also half of the weight for MOΓ2, and the
 393 meaning of MOΓ7/2 is analogous. It is noteworthy that MOΓ2 and MOΓ2/2 are the same
 394 except their number of expressions and weights, as are MOΓ7 and MOΓ7/2.

395 We next discuss the dni-coefficients in the next generation one by one.

- 396 Θ'_1 :
 397 (1) (H_1, H_2) , probability $\frac{v/2-1}{v-1}$,
 398 (a) none recombined, probability $(1 - c)^2$, dni-coefficient Θ_1 ;
 399 (b) one recombined, probability $2c(1 - c)$, dni-coefficient Γ_4 ;
 400 (c) both recombined, probability c^2 , dni-coefficient Δ_6 ;
 401 (2) $(H_1), (H_2)$, probability $\frac{v/2}{v-1}$,
 402 others identical to HS01-3 for MS;
 403 others identical to HS03 for ME;

404 then $\theta'_1 = m_\theta + \frac{v/2}{v-1} \mathbf{W}_\theta \boldsymbol{\theta}^T / \mathbf{W}_\theta \mathbf{1}$ for MS, or $\theta'_1 = m_\theta + \frac{v/2}{v-1} (w_{3\theta} \theta_3 / \mathbf{W}_\theta \mathbf{1})$ for ME, where

405
$$m_\theta = \frac{v/2-1}{v-1} [(1-c)^2 \theta_1 + 2c(1-c) \Gamma_4 + c^2 \Delta_6].$$

406 The expression of θ'_1 is a linear combination of dni-coefficients in the current generation,
407 whose combination coefficients are the first row of $\boldsymbol{\Omega}$ for the MS or the ME mating system.

408 θ'_2 : identical to HS01-3, and thus $\theta'_2 = \mathbf{W}_\theta \boldsymbol{\theta}^T / \mathbf{W}_\theta \mathbf{1}$ for MS or ME.

409 Γ'_1 :

410 (1) $H_1, (H_2, H_3)$, probability $\frac{v/2-1}{v-1}$, others identical to (HSF2,4,8);

411 (2) $H_1, (H_2), (H_3)$, probability $\frac{v/2}{v-1}$,
412 others identical to HSF1-9 for MS;

413 others identical to (HSF5,7,9) for ME;

414 then $\Gamma'_1 = m_\gamma + \frac{v/2}{v-1} \mathbf{W}_\gamma \boldsymbol{\Gamma}^T / \mathbf{W}_\gamma \mathbf{1}$ for MS or $\Gamma'_1 = m_\gamma + \frac{v/2}{v-1} \frac{w_{5\gamma} \gamma_5 + w_{7\gamma} \gamma_7 + w_{9\gamma} \gamma_9}{\mathbf{W}_\gamma \mathbf{1}}$ for ME, where

415
$$m_\gamma = \frac{v/2-1}{v-1} \frac{w_{2\gamma} \gamma_2 + w_{4\gamma} \gamma_4 + w_{8\gamma} \gamma_8}{\mathbf{W}_\gamma \mathbf{1}}.$$

416 In this way, the expressions of other double non-identity coefficients can be written
417 down, so can the elements in the corresponding rows of $\boldsymbol{\Omega}$. We will omit these lengthy
418 explanations from the following discussion.

419 Γ'_2 :

420 (1) $(H_1, H_2), H_3$, probability $\frac{v/2-1}{v-1}$, others identical to (MOF2/2,3,4,7/2);

421 (2) $(H_1), (H_2), H_3$, probability $\frac{v/2}{v-1}$,

422 MS: identical to HSF1-9;

423 ME: identical to (HSF5/2,6,7/2,8,9).

424 Here 'others' is omitted for brevity, the same below.

425 Γ'_3 : identical to HSF1-9.

426 Γ'_4 :

427 (1) (H_1, H_2, H_3) , probability $\frac{(v/2-1)(v/2-2)}{(v-1)(v-2)}$,

428 (a) not recombined, probability $1-c$, dni-coefficient Γ_4 ;

429 (b) recombined, probability c , dni-coefficient Δ_6 ;

430 (2) $(H_1, H_2), (H_3)$ or $(H_1, H_3), (H_2)$, probability $\frac{2(v/2-1)(v/2)}{(v-1)(v-2)}$,

431 MS: identical to (MOF2/2,3,4,7/2);

432 ME: identical to MOF7/2;

433 (3) $(H_1), (H_2, H_3)$, probability $\frac{(v/2-1)(v/2)}{(v-1)(v-2)}$,

434 MS: identical to (HSF2,4,8);

435 ME: identical to HSF8.

436 Δ'_1 :

437 (1) $(H_1, H_3), (H_2, H_4)$, probability $\frac{(v/2-1)^2}{(v-1)^2}$, identical to (HSD2,9,10/2,15/2,16/2,21);

438 (2) $(H_1, H_3), (H_2)(H_4)$ or $(H_1), (H_3), (H_2, H_4)$, probability $\frac{2(v/2-1)(v/2)}{(v-1)^2}$,

439 MS: identical to (HSD2,4/2,7/2,9,10/2,12/4,13/4,15*3/4,16/2,18/4,21,22/2);

440 ME: identical to (HSD7/2,13/4,18/4,22/2);

- 441 (3) $(H_1), (H_3), (H_2), (H_4)$, probability $\frac{(v/2)^2}{(v-1)^{2'}}$
 442 MS: identical to HSD1-22;
 443 ME: identical to (HSD3,5,8,11/2,12/2,14/2,16/2,17,18/2,19,20).
- 444 Δ'_2 :
 445 (1) $(H_1, H_2), (H_3, H_4)$, probability $\frac{(v/2-1)^2}{(v-1)^2}$, identical to (HSD10,15,17,21);
 446 (2) $(H_1, H_2), (H_3), (H_4)$ or $(H_1), (H_2), (H_3, H_4)$, probability $\frac{2(v/2-1)(v/2)}{(v-1)^2}$,
 447 MS: identical to (HSD4/2,5/2,9/2,10,13/2,15,17,19/2,21,22/2);
 448 ME: identical to (HSD13/2,19/2,22/2);
 449 (3) $(H_1), (H_2), (H_3), (H_4)$, probability $\frac{(v/2)^2}{(v-1)^{2'}}$
 450 MS: identical to HSD1-22;
 451 ME: identical to (HSD11,12,14,16,18,20).
- 452 Δ'_3 :
 453 (1) (H_1, H_3) , probability $\frac{v/2-1}{v-1}$,
 454 identical to (HSD2,4/2,7/2,9,10/2,12/4,13/4,15*3/4,16/2,18/4,21,22/2);
 455 (2) $(H_1), (H_3)$, probability $\frac{v/2}{v-1'}$
 456 MS: identical to HSD1-22;
 457 ME: identical to (HSD3,5,6/2,7/2,8,11/2,12/2,13/2,14*3/4,16/2,17,18*3/4,19,20, 22/2).
- 458 Δ'_4 :
 459 (1) (H_1, H_2) , probability $\frac{v/2-1}{v-1}$,
 460 identical to (HSD4/2,5/2,9/2,10,13/2,15,17,19/2,21,22/2);
 461 (2) $(H_1), (H_2)$, probability $\frac{v/2}{v-1'}$
 462 MS: identical to HSD1-22;
 463 ME: identical to (HSD6/2,7/2,8/2,11,12,13/2,14,16,18,19/2,20,22/2).
- 464 Δ'_5 : identical to HSD1-22.
- 465 Δ'_6 :
 466 (1) (H_1, H_2, H_3, H_4) , probability $\frac{(v-4)(v-6)}{8(v-1)(v-3)'}$, identical to HSD21;
 467 (2) $(H_1), (H_2, H_3, H_4)$ or $(H_2), (H_1, H_3, H_4)$ or $(H_3), (H_1, H_2, H_4)$
 468 or $(H_4), (H_1, H_2, H_3)$, probability $\frac{v(v-4)}{2(v-1)(v-3)'}$
 469 MS: identical to (HSD9/2,15/2,21,22/4);
 470 ME: identical to HSD22/4;
 471 (3) $(H_1, H_2), (H_3, H_4)$, probability $\frac{v(v-2)}{8(v-1)(v-3)'}$
 472 MS: identical to (HSD10,15,17,21);
 473 ME: identical to HSD17;
 474 (4) $(H_1, H_3), (H_2, H_4)$ or $(H_1, H_4), (H_2, H_3)$ probability $\frac{v(v-2)}{4(v-1)(v-3)'}$
 475 MS: identical to (HSD2,9,10/2,15/2,16/2,21);
 476 ME: identical to HSD16/2.
- 477 Δ'_7 :
 478 (1) (H_1, H_2, H_3) , probability $\frac{v-4}{4(v-1)'}$, identical to (HSD9/2,15/2,21,22/4);
 479 (2) $(H_1, H_3), (H_2)$ or $(H_1), (H_2, H_3)$, probability $\frac{2v}{4(v-1)'}$
 480 MS: identical to (HSD2,4/2,7/2,9,10/2,12/4,13/4,15*3/4,16/2,18/4,21,22/2);

481 ME: identical to (HSΔ7/4,12/4,13/8,16/2,18/4,22/4);
 482 (3) $(H_1, H_2), (H_3)$, probability $\frac{v}{4(v-1)}$,
 483 MS: identical to (HSΔ4/2,5/2,9/2,10,13/2,15,17,19/2,21,22/2);
 484 ME: identical to (HSΔ5/2,13/4,17,19/2,22/4).

485 The transition matrix Ω for the MS or the ME mating system is not shown, but the
 486 matrices $\mathbf{T}$ and $\mathbf{S}$ in the principal part of Ω are listed in Appendix H.
 487

488 Appendix F. DR mating system

489 In the dioecious mating systems, no matter whether it is DR or DH, each individual
 490 is formed by a sperm and an egg that are independently sampled from the sperm and the
 491 egg pools, respectively. We will discuss the double non-identity coefficients one by one
 492 for the DR mating system in this appendix.

493 For simplicity, we will use the symbol $\{*\}$ to be the identifier of an item, e.g. the item
 494 $\{\text{HS}\theta_2\}$ means that its contents are the same as those in HS θ_2 except for the weight, and
 495 we also use the symbol $\text{ME}\theta'_1$ to represent θ'_1 in ME, and so on.

496 θ'_1 : identical to $\text{ME}\theta'_1$.

497 θ'_2 : identical to $\text{ME}\theta'_2$.

498 Γ'_1 : identical to $\text{ME}\Gamma'_1$.

499 Γ'_2 : identical to $\text{ME}\Gamma'_2$.

500 Γ'_3 :

501 $\{\text{HS}\Gamma_1\}$ $H_1 \equiv H_2 \equiv H_3$, weight $2(1 + f^2)$;

502 $\{\text{HS}\Gamma_2\}$ $H_1 \equiv H_2 \asymp H_3$ or $H_1 \equiv H_3 \asymp H_2$, weight $4(1 + f^2)(v - 1)$;

503 $\{\text{HS}\Gamma_3\}$ $H_1 \asymp H_2 \equiv H_3$, weight $2(1 + f^2)(v - 1)$;

504 $\{\text{HS}\Gamma_4\}$ $H_1 \asymp H_2 \asymp H_3$, weight $2(1 + f^2)(v - 1)(v - 2)$;

505 $\{\text{HS}\Gamma_5\}$ $H_1 \equiv H_2 \sim H_3$ or $H_1 \equiv H_3 \sim H_2$, weight $2(1 + f)^2 v N_e - 4(1 + f^2)v$;

506 $\{\text{HS}\Gamma_6\}$ $H_2 \equiv H_3 \sim H_1$, weight $(1 + f)^2 v N_e - 2(1 + f^2)v$;

507 $\{\text{HS}\Gamma_7\}$ $H_1 \asymp H_2 \sim H_3$ or $H_1 \asymp H_3 \sim H_2$,

508 weight $2(1 + f)^2(v - 1)v N_e - 4(1 + f^2)(v - 1)v$;

509 $\{\text{HS}\Gamma_8\}$ $H_1 \sim H_2 \asymp H_3$, weight $(1 + f)^2(v - 1)v N_e - 2(1 + f^2)(v - 1)v$;

510 $\{\text{HS}\Gamma_9\}$ $H_1 \sim H_2 \sim H_3$, weight $(1 + f)^2 v^2 N_e^2 - 3(1 + f)^2 v^2 N_e + 4(1 + f^2)v^2$;

511 then $\Gamma'_3 = \mathbf{W}_\gamma^* \Gamma^T / \mathbf{W}_\gamma^* \mathbf{1}$, where $\mathbf{W}_\gamma^*$ is the row vector consisting of the above nine weights.

512 Γ'_4 : identical to $\text{ME}\Gamma'_4$.

513 Δ'_1 :

514 (1) $(H_1, H_3), (H_2, H_4)$, probability $\frac{(v/2-1)^2}{(v-1)^2}$, identical to (HSΔ2,9,10/2,15/2,16/2,21);

515 (2) $(H_1, H_3), (H_2)(H_4)$ or $(H_1), (H_3), (H_2, H_4)$, probability $\frac{2(v/2-1)(v/2)}{(v-1)^2}$,

516 identical to (HSΔ7/2,13/4,18/4,22/2);

517 (3) $(H_1), (H_3), (H_2), (H_4)$, probability $\frac{(v/2)^2}{(v-1)^2}$,

518 $\{\text{HS}\Delta_3\}$ $H_1 \equiv H_2 \sim H_3 \equiv H_4$, weight $8f$;

- 519 {HSD5} $H_1 \equiv H_2 \sim H_3 \asymp H_4$ or $H_1 \asymp H_2 \sim H_3 \equiv H_4$, weight $16f(v-1)$;
520 {HSD8} $H_1 \sim H_2 \sim H_3 \equiv H_4$ or $H_1 \equiv H_2 \sim H_3 \sim H_4$, weight $2(1+f)^2vN_e - 16fv$;
521 {HSD11/2} $H_1 \equiv H_4 \sim H_2 \equiv H_3$, weight $8f$;
522 {HSD12/2} $H_1 \equiv H_4 \sim H_2 \asymp H_3$ or $H_2 \equiv H_3 \sim H_1 \asymp H_4$, weight $16f(v-1)$;
523 {HSD14/2} $H_1 \equiv H_4 \sim H_2 \sim H_3$ or $H_2 \equiv H_3 \sim H_1 \sim H_4$,
524 weight $2(1+f)^2vN_e - 16fv$;
525 {HSD16/2} $H_1 \asymp H_4 \sim H_2 \asymp H_3$, weight $8f(v-1)^2$;
526 {HSD17} $H_1 \asymp H_2 \sim H_3 \asymp H_4$, weight $8f(v-1)^2$;
527 {HSD18/2} $H_1 \asymp H_4 \sim H_2 \sim H_3$ or $H_2 \asymp H_3 \sim H_1 \sim H_4$,
528 weight $2(1+f)^2(v-1)vN_e - 16f(v-1)v$;
529 {HSD19} $H_1 \asymp H_2 \sim H_3 \sim H_4$ or $H_1 \sim H_2 \sim H_3 \asymp H_4$,
530 weight $2(1+f)^2(v-1)vN_e - 16f(v-1)v$;
531 {HSD20} $H_1 \sim H_2 \sim H_3 \sim H_4$, weight $(1+f)^2v^2N_e^2 - 4(1+f)^2v^2N_e + 16fv^2$.
- 532 Δ'_2 :
533 (1) $(H_1, H_2), (H_3, H_4)$, probability $\frac{(v/2-1)^2}{(v-1)^2}$, identical to (HSD10,15,17,21);
534 (2) $(H_1, H_2), (H_3), (H_4)$ or $(H_1), (H_2), (H_3, H_4)$, probability $\frac{2(v/2-1)(v/2)}{(v-1)^2}$,
535 identical to (HSD13/2,19/2,22/2);
536 (3) $(H_1), (H_2), (H_3), (H_4)$, probability $\frac{(v/2)^2}{(v-1)^2}$,
- 537 {HSD11} $H_1 \equiv H_3 \sim H_2 \equiv H_4$ or $H_1 \equiv H_4 \sim H_2 \equiv H_3$, weight $16f$;
538 {HSD12} $H_1 \equiv H_3 \sim H_2 \asymp H_4$ or $H_1 \equiv H_4 \sim H_2 \asymp H_3$ or $H_2 \equiv H_3 \sim H_1 \asymp H_4$
539 or $H_2 \equiv H_4 \sim H_1 \asymp H_3$, weight $32f(v-1)$;
540 {HSD14} $H_1 \equiv H_3 \sim H_2 \sim H_4$ or $H_1 \equiv H_4 \sim H_2 \sim H_3$ or $H_2 \equiv H_3 \sim H_1 \sim H_4$
541 or $H_2 \equiv H_4 \sim H_1 \sim H_3$, weight $4(1+f)^2vN_e - 32fv$;
542 {HSD16} $H_1 \asymp H_3 \sim H_2 \asymp H_4$ or $H_1 \asymp H_4 \sim H_2 \asymp H_3$, weight $16f(v-1)^2$;
543 {HSD18} $H_1 \asymp H_3 \sim H_2 \sim H_4$ or $H_1 \asymp H_4 \sim H_2 \sim H_3$ or $H_2 \asymp H_3 \sim H_1 \sim H_4$
544 or $H_2 \asymp H_4 \sim H_1 \sim H_3$, weight $4(1+f)^2(v-1)vN_e - 32f(v-1)v$;
545 {HSD20} $H_1 \sim H_2 \sim H_3 \sim H_4$, weight $(1+f)^2v^2N_e^2 - 4(1+f)^2v^2N_e + 16fv^2$;
- 546 Δ'_3 :
547 (1) (H_1, H_3) , probability $\frac{v/2-1}{v-1}$,
548 {HSD2} $H_1 \equiv H_2 \asymp H_3 \equiv H_4$, weight $2(1+f^2)$;
549 {HSD4/2} $H_1 \equiv H_2 \equiv H_4 \asymp H_3$ or $H_1 \asymp H_2 \equiv H_3 \equiv H_4$, weight $4(1+f^2)$;
550 {HSD7/2} $H_2 \sim H_1 \asymp H_3 \equiv H_4$ or $H_1 \equiv H_2 \asymp H_3 \sim H_4$,
551 weight $2(1+f)^2vN_e - 4(1+f^2)v$;
552 {HSD9} $H_1 \asymp H_2 \asymp H_3 \equiv H_4$ or $H_1 \equiv H_2 \asymp H_3 \asymp H_4$, weight $4(1+f^2)(v-2)$;
553 {HSD10/2} $H_1 \equiv H_4 \asymp H_2 \equiv H_3$, weight $2(1+f^2)$;
554 {HSD12/4} $H_2 \equiv H_4 \sim H_1 \asymp H_3$, weight $(1+f)^2vN_e - 2(1+f^2)v$;
555 {HSD13/4} $H_2 \equiv H_3 \asymp H_1 \sim H_4$ or $H_1 \equiv H_4 \asymp H_3 \sim H_2$,
556 weight $2(1+f)^2vN_e - 4(1+f^2)v$;
557 {HSD15*3/4} $H_1 \equiv H_4 \asymp H_2 \asymp H_3$ or $H_2 \equiv H_3 \asymp H_1 \asymp H_4$ or $H_2 \equiv H_4 \asymp H_1 \asymp H_3$,
558 weight $6(1+f^2)(v-2)$;
559 {HSD16/2} $H_1 \asymp H_3 \sim H_2 \asymp H_4$, weight $(1+f)^2(v-1)vN_e - 2(1+f^2)(v-1)v$;
560 {HSD18/4} $H_1 \asymp H_3 \sim H_2 \sim H_4$,
561 weight $(1+f)^2v^2N_e^2 - 3(1+f)^2v^2N_e + 4(1+f^2)v^2$;
562 {HSD21} $H_1 \asymp H_2 \asymp H_3 \asymp H_4$, weight $2(1+f^2)(v-2)(v-3)$;
563 {HSD22/2} $H_1 \asymp H_2 \asymp H_3 \sim H_4$ or $H_1 \asymp H_3 \asymp H_4 \sim H_2$,
564 weight $2(1+f)^2(v-2)vN_e - 4(1+f^2)(v-2)v$;

565 (2) $(H_1), (H_3)$, probability $\frac{v/2}{v-1}$,
566 {HSA3} $H_1 \equiv H_2 \sim H_3 \equiv H_4$, weight $4f$;
567 {HSA5} $H_1 \equiv H_2 \sim H_3 \asymp H_4$ or $H_1 \asymp H_2 \sim H_3 \equiv H_4$, weight $8f(v-1)$;
568 {HSA6/2} $H_2 \equiv H_3 \equiv H_4 \sim H_1$ or $H_1 \equiv H_2 \equiv H_4 \sim H_3$, weight $4(1+f^2)$;
569 {HSA7/2} $H_1 \sim H_2 \asymp H_3 \equiv H_4$ or $H_1 \equiv H_2 \asymp H_4 \sim H_3$, weight $4(1+f^2)(v-1)$;
570 {HSA8} $H_1 \sim H_2 \sim H_3 \equiv H_4$ or $H_1 \equiv H_2 \sim H_3 \sim H_4$,
571 weight $2(1+f)^2vN_e - 4(1+f)^2v$;
572 {HSA11/2} $H_1 \equiv H_4 \sim H_2 \equiv H_3$, weight $4f$;
573 {HSA12/2} $H_1 \equiv H_4 \sim H_2 \asymp H_3$ or $H_2 \equiv H_3 \sim H_1 \asymp H_4$, weight $8f(v-1)$;
574 {HSA13/2} $H_1 \equiv H_4 \asymp H_2 \sim H_3$ or $H_2 \equiv H_4 \asymp H_1 \sim H_3$ or $H_2 \equiv H_3 \asymp H_4 \sim H_1$
575 or $H_2 \equiv H_4 \asymp H_3 \sim H_1$, weight $8(1+f^2)(v-1)$;
576 {HSA14*3/4} $H_1 \equiv H_4 \sim H_2 \sim H_3$ or $H_2 \equiv H_3 \sim H_1 \sim H_4$ or $H_2 \equiv H_4 \sim H_1 \sim H_3$,
577 weight $3(1+f)^2vN_e - 8(1+f+f^2)v$;
578 {HSA16/2} $H_1 \asymp H_4 \sim H_2 \asymp H_3$, weight $4f(v-1)^2$;
579 {HSA17} $H_1 \asymp H_2 \sim H_3 \asymp H_4$, weight $4f(v-1)^2$;
580 {HSA18*3/4} $H_1 \asymp H_4 \sim H_2 \sim H_3$ or $H_2 \asymp H_3 \sim H_1 \sim H_4$ or $H_2 \asymp H_4 \sim H_1 \sim H_3$,
581 weight $3(1+f)^2(v-1)vN_e - 8(1+f+f^2)(v-1)v$;
582 {HSA19} $H_1 \asymp H_2 \sim H_3 \sim H_4$ or $H_1 \sim H_2 \sim H_3 \asymp H_4$,
583 weight $2(1+f)^2(v-1)vN_e - 4(1+f)^2(v-1)v$;
584 {HSA20} $H_1 \sim H_2 \sim H_3 \sim H_4$,
585 weight $(1+f)^2v^2N_e^2 - 5(1+f)^2v^2N_e + 8(1+f+f^2)v^2$;
586 {HSA22/2} $H_1 \asymp H_2 \asymp H_4 \sim H_3$ or $H_2 \asymp H_3 \asymp H_4 \sim H_1$,
587 weight $4(1+f^2)(v-1)(v-2)$;

588 Δ'_4 :

589 (1) (H_1, H_2) , probability $\frac{v/2-1}{v-1}$,
590 {HSA4/2} $H_1 \asymp H_2 \equiv H_3 \equiv H_4$ or $H_2 \asymp H_1 \equiv H_3 \equiv H_4$, weight $4(1+f^2)$;
591 {HSA5/2} $H_1 \asymp H_2 \sim H_3 \equiv H_4$, weight $(1+f)^2vN_e - 2(1+f^2)v$;
592 {HSA9/2} $H_1 \asymp H_2 \asymp H_3 \equiv H_4$, weight $2(1+f^2)(v-2)$;
593 {HSA10} $H_1 \equiv H_3 \asymp H_2 \equiv H_4$ or $H_1 \equiv H_4 \asymp H_2 \equiv H_3$, weight $4(1+f^2)$;
594 {HSA13/2} $H_1 \equiv H_3 \asymp H_2 \sim H_4$ or $H_1 \equiv H_4 \asymp H_2 \sim H_3$ or $H_2 \equiv H_3 \asymp H_1 \sim H_4$
595 or $H_2 \equiv H_4 \asymp H_1 \sim H_3$, weight $4(1+f)^2vN_e - 8(1+f^2)v$;
596 {HSA15} $H_1 \equiv H_3 \asymp H_2 \asymp H_4$ or $H_1 \equiv H_4 \asymp H_2 \asymp H_3$ or $H_2 \equiv H_3 \asymp H_1 \asymp H_4$
597 or $H_2 \equiv H_4 \asymp H_1 \asymp H_3$, weight $8(1+f^2)(v-2)$;
598 {HSA17} $H_1 \asymp H_2 \sim H_3 \asymp H_4$, weight $(1+f)^2(v-1)vN_e - 2(1+f^2)(v-1)v$;
599 {HSA19/2} $H_1 \asymp H_2 \sim H_3 \sim H_4$,
600 weight $(1+f)^2v^2N_e^2 - 3(1+f)^2v^2N_e + 4(1+f^2)v^2$;
601 {HSA21} $H_1 \asymp H_2 \asymp H_3 \asymp H_4$, weight $2(1+f^2)(v-2)(v-3)$;
602 {HSA22/2} $H_1 \asymp H_2 \asymp H_3 \sim H_4$ or $H_1 \asymp H_2 \asymp H_4 \sim H_3$,
603 weight $2(1+f)^2(v-2)vN_e - 4(1+f^2)(v-2)v$;
604 (2) $(H_1), (H_2)$, probability $\frac{v/2}{v-1}$,
605 {HSA6/2} $H_1 \equiv H_3 \equiv H_4 \sim H_2$ or $H_2 \equiv H_3 \equiv H_4 \sim H_1$, weight $4(1+f^2)$;
606 {HSA7/2} $H_1 \sim H_2 \asymp H_3 \equiv H_4$ or $H_2 \sim H_1 \asymp H_3 \equiv H_4$, weight $4(1+f^2)(v-1)$;
607 {HSA8/2} $H_1 \sim H_2 \sim H_3 \equiv H_4$, weight $(1+f)^2vN_e - 4(1+f^2)v$;
608 {HSA11} $H_1 \equiv H_3 \sim H_2 \equiv H_4$ or $H_1 \equiv H_4 \sim H_2 \equiv H_3$, weight $8f$;
609 {HSA12} $H_1 \equiv H_3 \sim H_2 \asymp H_4$ or $H_1 \equiv H_4 \sim H_2 \asymp H_3$ or $H_2 \equiv H_3 \sim H_1 \asymp H_4$
610 or $H_2 \equiv H_4 \sim H_1 \asymp H_3$, weight $16f(v-1)$;
611 {HSA13/2} $H_1 \equiv H_3 \asymp H_4 \sim H_2$ or $H_1 \equiv H_4 \asymp H_3 \sim H_2$ or $H_2 \equiv H_3 \asymp H_4 \sim H_1$

612 or $H_2 \equiv H_4 \asymp H_3 \sim H_1$, weight $8(1+f^2)(v-1)$;
613 {HSD14} $H_1 \equiv H_3 \sim H_2 \sim H_4$ or $H_1 \equiv H_4 \sim H_2 \sim H_3$ or $H_2 \equiv H_3 \sim H_1 \sim H_4$
614 or $H_2 \equiv H_4 \sim H_1 \sim H_3$, weight $4(1+f)^2vN_e - 8(1+f)^2v$;
615 {HSD16} $H_1 \asymp H_3 \sim H_2 \asymp H_4$ or $H_1 \asymp H_4 \sim H_2 \asymp H_3$, weight $8f(v-1)^2$;
616 {HSD18} $H_1 \asymp H_3 \sim H_2 \sim H_4$ or $H_1 \asymp H_4 \sim H_2 \sim H_3$ or $H_2 \asymp H_3 \sim H_1 \sim H_4$
617 or $H_2 \asymp H_4 \sim H_1 \sim H_3$, weight $4(1+f)^2(v-1)vN_e - 8(1+f)^2(v-1)v$;
618 {HSD19/2} $H_1 \sim H_2 \sim H_3 \asymp H_4$, weight $(1+f)^2(v-1)vN_e - 4(1+f^2)(v-1)v$;
619 {HSD20} $H_1 \sim H_2 \sim H_3 \sim H_4$,
620 weight $(1+f)^2v^2N_e^2 - 5(1+f)^2v^2N_e + 8(1+f+f^2)v^2$;
621 {HSD22/2} $H_1 \asymp H_3 \asymp H_4 \sim H_2$ or $H_2 \asymp H_3 \asymp H_4 \sim H_1$,
622 weight $4(1+f^2)(v-1)(v-2)$;
623 Δ'_5 :
624 {HSD1} $H_1 \equiv H_2 \equiv H_3 \equiv H_4$, weight $4(1-f+f^2)$;
625 {HSD2} $H_1 \equiv H_2 \asymp H_3 \equiv H_4$, weight $4(1-f+f^2)(v-1)$;
626 {HSD3} $H_1 \equiv H_2 \sim H_3 \equiv H_4$, weight $(1+f)^2vN_e - 4(1-f+f^2)v$;
627 {HSD4} $H_1 \equiv H_2 \equiv H_3 \asymp H_4$ or $H_1 \equiv H_2 \equiv H_4 \asymp H_3$ or $H_1 \asymp H_2 \equiv H_3 \equiv H_4$
628 or $H_2 \asymp H_1 \equiv H_3 \equiv H_4$, weight $16(1-f+f^2)(v-1)$;
629 {HSD5} $H_1 \equiv H_2 \sim H_3 \asymp H_4$ or $H_1 \asymp H_2 \sim H_3 \equiv H_4$,
630 weight $2(1+f)^2N_e(v-1)v - 8(1-f+f^2)(v-1)v$;
631 {HSD6} $H_1 \equiv H_3 \equiv H_4 \sim H_2$ or $H_2 \equiv H_3 \equiv H_4 \sim H_1$ or $H_1 \equiv H_2 \equiv H_3 \sim H_4$
632 or $H_1 \equiv H_2 \equiv H_4 \sim H_3$, weight $8(1+f^2)N_e v - 16(1-f+f^2)v$;
633 {HSD7} $H_1 \sim H_2 \asymp H_3 \equiv H_4$ or $H_2 \sim H_1 \asymp H_3 \equiv H_4$ or $H_1 \equiv H_2 \asymp H_3 \sim H_4$ or
634 $H_1 \equiv H_2 \asymp H_4 \sim H_3$, weight $8(1+f^2)N_e v(v-1) - 16(1-f+f^2)v(v-1)$;
635 {HSD8} $H_1 \sim H_2 \sim H_3 \equiv H_4$ or $H_1 \equiv H_2 \sim H_3 \sim H_4$,
636 weight $2(1+f)^2N_e^2v^2 - 2(5+2f+5f^2)N_e v^2 + 16(1-f+f^2)v^2$;
637 {HSD9} $H_1 \asymp H_2 \asymp H_3 \equiv H_4$ or $H_1 \equiv H_2 \asymp H_3 \asymp H_4$,
638 weight $8(1-f+f^2)(v-1)(v-2)$;
639 {HSD10} $H_1 \equiv H_3 \asymp H_2 \equiv H_4$ or $H_1 \equiv H_4 \asymp H_2 \equiv H_3$, weight $8(1-f+f^2)(v-1)$;
640 {HSD11} $H_1 \equiv H_3 \sim H_2 \equiv H_4$ or $H_1 \equiv H_4 \sim H_2 \equiv H_3$,
641 weight $2(1+f)^2N_e v - 8(1-f+f^2)v$;
642 {HSD12} $H_1 \equiv H_3 \sim H_2 \asymp H_4$ or $H_1 \equiv H_4 \sim H_2 \asymp H_3$ or $H_2 \equiv H_3 \sim H_1 \asymp H_4$ or
643 $H_2 \equiv H_4 \sim H_1 \asymp H_3$, weight $4(1+f)^2N_e(v-1)v - 16(1-f+f^2)(v-1)v$;
644 {HSD13} $H_1 \equiv H_3 \asymp H_2 \sim H_4$ or $H_1 \equiv H_4 \asymp H_2 \sim H_3$ or $H_2 \equiv H_3 \asymp H_1 \sim H_4$
645 or $H_2 \equiv H_4 \asymp H_1 \sim H_3$ or $H_1 \equiv H_3 \asymp H_4 \sim H_2$ or $H_1 \equiv H_4 \asymp H_3 \sim H_2$
646 or $H_2 \equiv H_3 \asymp H_4 \sim H_1$ or $H_2 \equiv H_4 \asymp H_3 \sim H_1$,
647 weight $16(1+f^2)N_e(v-1)v - 32(1-f+f^2)(v-1)v$;
648 {HSD14} $H_1 \equiv H_3 \sim H_2 \sim H_4$ or $H_1 \equiv H_4 \sim H_2 \sim H_3$ or $H_2 \equiv H_3 \sim H_1 \sim H_4$
649 or $H_2 \equiv H_4 \sim H_1 \sim H_3$,
650 weight $4(1+f)^2N_e^2v^2 - 4(5+2f+5f^2)N_e v^2 + 32(1-f+f^2)v^2$;
651 {HSD15} $H_1 \equiv H_3 \asymp H_2 \asymp H_4$ or $H_1 \equiv H_4 \asymp H_2 \asymp H_3$ or $H_2 \equiv H_3 \asymp H_1 \asymp H_4$
652 or $H_2 \equiv H_4 \asymp H_1 \asymp H_3$, weight $16(1-f+f^2)(v-1)(v-2)$;
653 {HSD16} $H_1 \asymp H_3 \sim H_2 \asymp H_4$ or $H_1 \asymp H_4 \sim H_2 \asymp H_3$,
654 weight $2(1+f)^2N_e(v-1)^2v - 8(1-f+f^2)(v-1)^2v$;
655 {HSD17} $H_1 \asymp H_2 \sim H_3 \asymp H_4$,
656 weight $(1+f)^2N_e(v-1)^2v - 4(1-f+f^2)(v-1)^2v$;
657 {HSD18} $H_1 \asymp H_3 \sim H_2 \sim H_4$ or $H_1 \asymp H_4 \sim H_2 \sim H_3$ or $H_2 \asymp H_3 \sim H_1 \sim H_4$
658 or $H_2 \asymp H_4 \sim H_1 \sim H_3$, weight $4(1+f)^2N_e^2v^2(v-1) - 4(5+2f+5f^2)N_e v^2(v-1) + 32(1-f+f^2)v^2(v-1)$;
659

660 {HSΔ19} $H_1 \equiv H_2 \sim H_3 \sim H_4$ or $H_1 \sim H_2 \sim H_3 \equiv H_4$, weight $2(1+f)^2 N_e^2 (v-1)v^2$
661 $-2(5+2f+5f^2)N_e(v-1)v^2 + 16(1-f+f^2)(v-1)v^2$;
662 {HSΔ20} $H_1 \sim H_2 \sim H_3 \sim H_4$, weight $(1+f)^2 N_e^3 v^3 - 6(1+f)^2 N_e^2 v^3 +$
663 $(19+6f+19f^2)N_e v^3 - 24(1-f+f^2)v^3$
664 {HSΔ21} $H_1 \equiv H_2 \equiv H_3 \equiv H_4$, weight $4(1-f+f^2)(v-1)(v-2)(v-3)$;
665 {HSΔ22} $H_1 \equiv H_2 \equiv H_3 \sim H_4$ or $H_1 \equiv H_2 \equiv H_4 \sim H_3$ or $H_1 \equiv H_3 \equiv H_4 \sim H_2$
666 or $H_2 \equiv H_3 \equiv H_4 \sim H_1$,
667 weight $8(1+f^2)N_e(v-1)(v-2)v - 16(1-f+f^2)(v-1)(v-2)v$,

668 then $\Delta'_5 = \mathbf{W}_\delta^* \Delta^T / \mathbf{W}_\delta^* \mathbf{1}$ where $\mathbf{W}_\delta^*$ is the row vector consisting of the above 22 weights.

669 Δ'_6 : identical to $\text{ME}\Delta'_6$.

670 Δ'_7 : identical to $\text{ME}\Delta'_7$.

671 The transition matrix $\mathbf{\Omega}$ for the DR mating system is not shown, but the matrices $\mathbf{T}$
672 and $\mathbf{S}$ in the principal part of $\mathbf{\Omega}$ are listed in Appendix H.

673 Appendix G. DH mating system

674 For the DH mating system, because each individual remains in a reproductive unit
675 for its entire lifetime, the offspring produced within each reproductive unit are either full-
676 or half-sibs. We will denote $[H, H', \dots]$ for which those haplotypes within square
677 brackets are from the same reproductive unit.

678 Θ'_1 : identical to $\text{ME}\Theta'_1$.

679 Θ'_2 : identical to $\text{ME}\Theta'_2$.

680 Γ'_1 : identical to $\text{ME}\Gamma'_1$.

681 Γ'_2 : identical to $\text{ME}\Gamma'_2$.

682 Γ'_3 :

683 (1) $[H_1, H_2, H_3]$, probability $\frac{1}{M^2}$,

684 {HSΓ1} $H_1 \equiv H_2 \equiv H_3$, weight $\frac{1}{8v^2} + \frac{1}{8f^2v^2}$;

685 {HSΓ2} $H_1 \equiv H_2 \equiv H_3$ or $H_1 \equiv H_3 \equiv H_2$ weight $\frac{v-1}{4v^2} + \frac{v-1}{4f^2v^2}$;

686 {HSΓ3} $H_1 \equiv H_2 \equiv H_3$, weight $\frac{v-1}{8v^2} + \frac{v-1}{8f^2v^2}$;

687 {HSΓ4} $H_1 \equiv H_2 \equiv H_3$, weight $\frac{(v-1)(v-2)}{8v^2} + \frac{(v-1)(v-2)}{8f^2v^2}$;

688 {HSΓ5} $H_1 \equiv H_2 \sim H_3$ or $H_1 \equiv H_3 \sim H_2$, weight $\frac{1}{4v} + \frac{1}{4fv} + \frac{f-1}{4f^2v}$;

689 {HSΓ6} $H_2 \equiv H_3 \sim H_1$, weight $\frac{1}{8v} + \frac{1}{8fv} + \frac{f-1}{8f^2v}$;

690 {HSΓ7} $H_1 \equiv H_2 \sim H_3$ or $H_1 \equiv H_3 \sim H_2$, weight $\frac{v-1}{4v} + \frac{v-1}{4fv} + \frac{(v-1)(f-1)}{4f^2v}$;

691 {HSΓ8} $H_1 \sim H_2 \equiv H_3$, weight $\frac{v-1}{8v} + \frac{v-1}{8fv} + \frac{(v-1)(f-1)}{8f^2v}$;

692 {HSΓ9} $H_1 \sim H_2 \sim H_3$, weight $\frac{3(f-1)}{8f} + \frac{(f-1)(f-2)}{8f^2}$;

693 (2) $[H_1, H_2], [H_3]$ or $[H_1, H_3], [H_2]$, probability $\frac{2(M-1)}{M^2}$,

694 {HSΓ5/2} $H_1 \equiv H_2 \sim H_3$ or $H_1 \equiv H_3 \sim H_2$, weight $\frac{1}{4v} + \frac{1}{4fv}$;

- 695 {HSΓ7/2} $H_1 \asymp H_2 \sim H_3$ or $H_1 \asymp H_3 \sim H_2$, weight $\frac{v-1}{4v} + \frac{v-1}{4fv}$;
- 696 {HSΓ9} $H_1 \sim H_2 \sim H_3$, weight $\frac{f-1}{4f} + \frac{1}{2}$;
- 697 (3) $[H_2, H_3], [H_1]$, probability $\frac{M-1}{M^2}$,
- 698 {HSΓ6} $H_2 \equiv H_3 \sim H_1$, weight $\frac{1}{4v} + \frac{1}{4fv}$;
- 699 {HSΓ8} $H_1 \sim H_2 \asymp H_3$, weight $\frac{v-1}{4v} + \frac{v-1}{4fv}$;
- 700 {HSΓ9} $H_1 \sim H_2 \sim H_3$, weight $\frac{f-1}{4f} + \frac{1}{2}$;
- 701 (4) $[H_1], [H_2], [H_3]$, probability $\frac{(M-1)(M-2)}{M^2}$, identical to HSΓ9.
- 702 Γ'_4 :
- 703 (1) (H_1, H_2, H_3) , probability $\frac{(v/2-1)(v/2-2)}{(v-1)(v-2)}$,
- 704 (a) not recombined, probability $1 - c$, double non-identity Γ_4 ;
- 705 (b) recombined, probability c , double non-identity Δ_6 ;
- 706 (2) $(H_1, H_2), (H_3)$ or $(H_1, H_3), (H_2)$, probability $\frac{2(v/2-1)(v/2)}{(v-1)(v-2)}$, identical to MOΓ7/2;
- 707 (3) $(H_1), (H_2, H_3)$, probability $\frac{(v/2-1)(v/2)}{(v-1)(v-2)}$, identical to MOΓ8.
- 708 Δ'_1 :
- 709 (1) $[(H_1, H_3), (H_2, H_4)]$, probability $\frac{1}{M} \frac{(v/2-1)^2}{(v-1)^2}$,
- 710 {HSD2} $H_1 \equiv H_2 \asymp H_3 \equiv H_4$, weight $\frac{1}{4v(v-1)} + \frac{1}{4fv(v-1)}$;
- 711 {HSD9} $H_1 \asymp H_2 \asymp H_3 \equiv H_4$ or $H_1 \equiv H_2 \asymp H_3 \asymp H_4$, weight $\frac{v-2}{2v(v-1)} + \frac{v-2}{2fv(v-1)}$;
- 712 {HSD10/2} $H_1 \equiv H_4 \asymp H_2 \equiv H_3$, weight $\frac{1}{4v(v-1)} + \frac{1}{4fv(v-1)}$;
- 713 {HSD15/2} $H_1 \equiv H_4 \asymp H_2 \asymp H_3$ or $H_2 \equiv H_3 \asymp H_1 \asymp H_4$, weight $\frac{v-2}{2v(v-1)} + \frac{v-2}{2fv(v-1)}$;
- 714 {HSD16/2} $H_1 \asymp H_3 \sim H_2 \asymp H_4$, weight $\frac{1}{2} + \frac{f-1}{4f}$;
- 715 {HSD21} $H_1 \asymp H_2 \asymp H_3 \asymp H_4$, weight $\frac{(v-2)(v-3)}{4v(v-1)} + \frac{(v-2)(v-3)}{4fv(v-1)}$;
- 716 (2) $[(H_1, H_3), (H_2), (H_4)]$ or $[(H_1), (H_3), (H_2, H_4)]$, probability $\frac{2}{M} \frac{(v/2-1)(v/2)}{(v-1)^2}$,
- 717 {HSD7/2} $H_2 \sim H_1 \asymp H_3 \equiv H_4$ or $H_1 \equiv H_2 \asymp H_3 \sim H_4$, weight $\frac{1}{2v} + \frac{1}{2fv}$;
- 718 {HSD13/4} $H_2 \equiv H_3 \asymp H_1 \sim H_4$ or $H_1 \equiv H_4 \asymp H_3 \sim H_2$, weight $\frac{1}{2v} + \frac{1}{2fv}$;
- 719 {HSD18/4} $H_1 \asymp H_3 \sim H_2 \sim H_4$, weight $\frac{f-1}{2f}$;
- 720 {HSD22/2} $H_1 \asymp H_2 \asymp H_3 \sim H_4$ or $H_1 \asymp H_3 \asymp H_4 \sim H_2$, weight $\frac{v-2}{2v} + \frac{v-2}{2fv}$;
- 721 (3) $[(H_1), (H_3), (H_2), (H_4)]$, probability $\frac{1}{M} \frac{(v/2)^2}{(v-1)^2}$,
- 722 {HSD3} $H_1 \equiv H_2 \sim H_3 \equiv H_4$, weight $\frac{1}{2fv^2}$;
- 723 {HSD5} $H_1 \equiv H_2 \sim H_3 \asymp H_4$ or $H_1 \asymp H_2 \sim H_3 \equiv H_4$, weight $\frac{v-1}{fv^2}$;
- 724 {HSD8} $H_1 \sim H_2 \sim H_3 \equiv H_4$ or $H_1 \equiv H_2 \sim H_3 \sim H_4$, weight $\frac{f-1}{2fv}$;
- 725 {HSD11/2} $H_1 \equiv H_4 \sim H_2 \equiv H_3$, weight $\frac{1}{2fv^2}$;
- 726 {HSD12/2} $H_1 \equiv H_4 \sim H_2 \asymp H_3$ or $H_2 \equiv H_3 \sim H_1 \asymp H_4$, weight $\frac{v-1}{fv^2}$;
- 727 {HSD14/2} $H_1 \equiv H_4 \sim H_2 \sim H_3$ or $H_2 \equiv H_3 \sim H_1 \sim H_4$, weight $\frac{f-1}{2fv}$;
- 728 {HSD16/2} $H_1 \asymp H_4 \sim H_2 \asymp H_3$, weight $\frac{(v-1)^2}{2fv^2}$;
- 729 {HSD17} $H_1 \asymp H_2 \sim H_3 \asymp H_4$, weight $\frac{(v-1)^2}{2fv^2}$;
- 730 {HSD18/2} $H_1 \asymp H_4 \sim H_2 \sim H_3$ or $H_2 \asymp H_3 \sim H_1 \sim H_4$, weight $\frac{(v-1)(f-1)}{2vf}$;

- 731 {HSD19} $H_1 \asymp H_2 \sim H_3 \sim H_4$ or $H_1 \sim H_2 \sim H_3 \asymp H_4$, weight $\frac{(v-1)(f-1)}{2vf}$;
- 732 (4) $[(H_1, H_3)], [(H_2, H_4)]$, probability $\frac{M-1}{M} \frac{(v/2-1)^2}{(v-1)^2}$, identical to HSD16/2;
- 733 (5) $[(H_1, H_3)], [(H_2), (H_4)]$ or $[(H_1), (H_3)], [(H_2, H_4)]$, probability $\frac{2(M-1)}{M} \frac{(v/2-1)(v/2)}{(v-1)^2}$,
- 734 identical to HSD18/4;
- 735 (6) $[(H_1), (H_3)], [(H_2), (H_4)]$, probability $\frac{M-1}{M} \frac{(v/2)^2}{(v-1)^2}$, identical to HSD20.
- 736 Δ'_2 :
- 737 (1) $[(H_1, H_2), (H_3, H_4)]$, probability $\frac{1}{M} \frac{(v/2-1)^2}{(v-1)^2}$,
- 738 {HSD10} $H_1 \equiv H_3 \asymp H_2 \equiv H_4$ or $H_1 \equiv H_4 \asymp H_2 \equiv H_3$, weight $\frac{1}{2v(v-1)} + \frac{1}{2fv(v-1)}$;
- 739 {HSD15} $H_1 \equiv H_3 \asymp H_2 \asymp H_4$ or $H_1 \equiv H_4 \asymp H_2 \asymp H_3$ or $H_2 \equiv H_3 \asymp H_1 \asymp H_4$
- 740 or $H_2 \equiv H_4 \asymp H_1 \asymp H_3$, weight $\frac{v-2}{v(v-1)} + \frac{v-2}{fv(v-1)}$;
- 741 {HSD17} $H_1 \asymp H_2 \sim H_3 \asymp H_4$, weight $\frac{1}{2} + \frac{f-1}{4f}$;
- 742 {HSD21} $H_1 \asymp H_2 \asymp H_3 \asymp H_4$, weight $\frac{(v-2)(v-3)}{4v(v-1)} + \frac{(v-2)(v-3)}{4fv(v-1)}$;
- 743 (2) $[(H_1, H_2), (H_3), (H_4)]$ or $[(H_1), (H_2), (H_3, H_4)]$, probability $\frac{2}{M} \frac{(v/2-1)(v/2)}{(v-1)^2}$,
- 744 {HSD13/2} $H_1 \equiv H_3 \asymp H_2 \sim H_4$ or $H_1 \equiv H_4 \asymp H_2 \sim H_3$ or $H_2 \equiv H_3 \asymp H_1 \sim H_4$
- 745 or $H_2 \equiv H_4 \asymp H_1 \sim H_3$, weight $\frac{1}{v} + \frac{1}{vf}$;
- 746 {HSD19/2} $H_1 \asymp H_2 \sim H_3 \sim H_4$, weight $\frac{f-1}{2f}$;
- 747 {HSD22/2} $H_1 \asymp H_2 \asymp H_3 \sim H_4$ or $H_1 \asymp H_2 \asymp H_4 \sim H_3$, weight $\frac{v-2}{2v} + \frac{v-2}{2vf}$;
- 748 (3) $[(H_1), (H_2), (H_3), (H_4)]$, probability $\frac{1}{M} \frac{(v/2)^2}{(v-1)^2}$,
- 749 {HSD11} $H_1 \equiv H_3 \sim H_2 \equiv H_4$ or $H_1 \equiv H_4 \sim H_2 \equiv H_3$, weight $\frac{1}{fv^2}$;
- 750 {HSD12} $H_1 \equiv H_3 \sim H_2 \asymp H_4$ or $H_1 \equiv H_4 \sim H_2 \asymp H_3$ or $H_2 \equiv H_3 \sim H_1 \asymp H_4$
- 751 or $H_2 \equiv H_4 \sim H_1 \asymp H_3$, weight $\frac{2(v-1)}{fv^2}$;
- 752 {HSD14} $H_1 \equiv H_3 \sim H_2 \sim H_4$ or $H_1 \equiv H_4 \sim H_2 \sim H_3$ or $H_2 \equiv H_3 \sim H_1 \sim H_4$
- 753 or $H_2 \equiv H_4 \sim H_1 \sim H_3$, weight $\frac{f-1}{fv}$;
- 754 {HSD16} $H_1 \asymp H_3 \sim H_2 \asymp H_4$ or $H_1 \asymp H_4 \sim H_2 \asymp H_3$, weight $\frac{(v-1)^2}{fv^2}$;
- 755 {HSD18} $H_1 \asymp H_3 \sim H_2 \sim H_4$ or $H_1 \asymp H_4 \sim H_2 \sim H_3$ or $H_2 \asymp H_3 \sim H_1 \sim H_4$
- 756 or $H_2 \asymp H_4 \sim H_1 \sim H_3$, weight $\frac{(f-1)(v-1)}{fv}$;
- 757 (4) $[(H_1, H_2)], [(H_3, H_4)]$, probability $\frac{M-1}{M} \frac{(v/2-1)^2}{(v-1)^2}$, identical to HSD17;
- 758 (5) $[(H_1, H_2)], [(H_3), (H_4)]$ or $[(H_1), (H_2)], [(H_3, H_4)]$, probability $\frac{2(M-1)}{M} \frac{(v/2-1)(v/2)}{(v-1)^2}$,
- 759 identical to HSD19/2;
- 760 (6) $[(H_1), (H_2)], [(H_3), (H_4)]$, probability $\frac{M-1}{M} \frac{(v/2)^2}{(v-1)^2}$, identical to HSD20.
- 761 Δ'_3 :
- 762 (1) $[(H_1, H_3), H_2, H_4]$, probability $\frac{1}{M^2} \frac{v/2-1}{v-1}$,
- 763 {HSD2} $H_1 \equiv H_2 \asymp H_3 \equiv H_4$, weight $\frac{1}{8v^2} + \frac{1}{8v^2 f^2}$;
- 764 {HSD4/2} $H_1 \equiv H_2 \equiv H_4 \asymp H_3$ or $H_1 \asymp H_2 \equiv H_3 \equiv H_4$, weight $\frac{1}{4v^2} + \frac{1}{4v^2 f^2}$;
- 765 {HSD7/2} $H_2 \sim H_1 \asymp H_3 \equiv H_4$ or $H_1 \equiv H_2 \asymp H_3 \sim H_4$, weight $\frac{1}{4v} + \frac{1}{4vf} + \frac{f-1}{4vf^2}$;
- 766 {HSD9} $H_1 \asymp H_2 \asymp H_3 \equiv H_4$ or $H_1 \equiv H_2 \asymp H_3 \asymp H_4$, weight $\frac{v-2}{4v^2} + \frac{v-2}{4v^2 f^2}$;

$$\begin{aligned}
767 \quad \{\text{H}\Delta 10/2\} \quad & H_1 \equiv H_4 \asymp H_2 \equiv H_3, \text{ weight } \frac{1}{8v^2} + \frac{1}{8v^2 f^2}; \\
768 \quad \{\text{H}\Delta 12/4\} \quad & H_2 \equiv H_4 \sim H_1 \asymp H_3, \text{ weight } \frac{1}{8v} + \frac{1}{8fv} + \frac{f-1}{8f^2 v'}; \\
769 \quad \{\text{H}\Delta 13/4\} \quad & H_2 \equiv H_3 \asymp H_1 \sim H_4 \text{ or } H_1 \equiv H_4 \asymp H_3 \sim H_2, \text{ weight } \frac{1}{4v} + \frac{1}{4fv} + \frac{f-1}{4f^2 v'}; \\
770 \quad \{\text{H}\Delta 15^*3/4\} \quad & H_1 \equiv H_4 \asymp H_2 \asymp H_3 \text{ or } H_2 \equiv H_3 \asymp H_1 \asymp H_4 \text{ or } H_2 \equiv H_4 \asymp H_1 \asymp H_3, \\
771 \quad & \text{weight } \frac{3(v-2)}{8v^2} + \frac{3(v-2)}{8f^2 v^2}; \\
772 \quad \{\text{H}\Delta 16/2\} \quad & H_1 \asymp H_3 \sim H_2 \asymp H_4, \text{ weight } \frac{v-1}{8v} + \frac{v-1}{8fv} + \frac{(f-1)(v-1)}{8f^2 v}; \\
773 \quad \{\text{H}\Delta 18/4\} \quad & H_1 \asymp H_3 \sim H_2 \sim H_4, \text{ weight } \frac{3(f-1)}{8f} + \frac{(f-1)(f-2)}{8f^2}; \\
774 \quad \{\text{H}\Delta 21\} \quad & H_1 \asymp H_2 \asymp H_3 \asymp H_4, \text{ weight } \frac{(v-2)(v-3)}{8v^2} + \frac{(v-2)(v-3)}{8f^2 v^2}; \\
775 \quad \{\text{H}\Delta 22/2\} \quad & H_1 \asymp H_2 \asymp H_3 \sim H_4 \text{ or } H_1 \asymp H_3 \asymp H_4 \sim H_2, \\
776 \quad & \text{weight } \frac{v-2}{4v} + \frac{v-2}{4fv} + \frac{(v-2)(f-1)}{4f^2 v}; \\
777 \quad (2) \quad & [(H_1), (H_3), H_2, H_4], \text{ probability } \frac{1}{M^2} \frac{v/2}{v-1}; \\
778 \quad \{\text{H}\Delta 3\} \quad & H_1 \equiv H_2 \sim H_3 \equiv H_4, \text{ weight } \frac{1}{4fv^2}; \\
779 \quad \{\text{H}\Delta 5\} \quad & H_1 \equiv H_2 \sim H_3 \asymp H_4 \text{ or } H_1 \asymp H_2 \sim H_3 \equiv H_4, \text{ weight } \frac{v-1}{2fv^2}; \\
780 \quad \{\text{H}\Delta 6/2\} \quad & H_2 \equiv H_3 \equiv H_4 \sim H_1 \text{ or } H_1 \equiv H_2 \equiv H_4 \sim H_3, \text{ weight } \frac{1}{4v^2} + \frac{1}{4f^2 v^2}; \\
781 \quad \{\text{H}\Delta 7/2\} \quad & H_1 \sim H_2 \asymp H_3 \equiv H_4 \text{ or } H_1 \equiv H_2 \asymp H_4 \sim H_3, \text{ weight } \frac{v-1}{4v^2} + \frac{v-1}{4f^2 v^2}; \\
782 \quad \{\text{H}\Delta 8\} \quad & H_1 \sim H_2 \sim H_3 \equiv H_4 \text{ or } H_1 \equiv H_2 \sim H_3 \sim H_4, \text{ weight } \frac{f-1}{4fv} + \frac{f-1}{4f^2 v'}; \\
783 \quad \{\text{H}\Delta 11/2\} \quad & H_1 \equiv H_4 \sim H_2 \equiv H_3, \text{ weight } \frac{1}{4fv^2}; \\
784 \quad \{\text{H}\Delta 12/2\} \quad & H_1 \equiv H_4 \sim H_2 \asymp H_3 \text{ or } H_2 \equiv H_3 \sim H_1 \asymp H_4, \text{ weight } \frac{v-1}{2fv^2}; \\
785 \quad \{\text{H}\Delta 13/2\} \quad & H_1 \equiv H_4 \asymp H_2 \sim H_3 \text{ or } H_2 \equiv H_4 \asymp H_1 \sim H_3 \text{ or } H_2 \equiv H_3 \asymp H_4 \sim H_1 \\
786 \quad & \text{or } H_2 \equiv H_4 \asymp H_3 \sim H_1, \text{ weight } \frac{v-1}{2v^2} + \frac{v-1}{2f^2 v^2}; \\
787 \quad \{\text{H}\Delta 14^*3/4\} \quad & H_1 \equiv H_4 \sim H_2 \sim H_3 \text{ or } H_2 \equiv H_3 \sim H_1 \sim H_4 \text{ or } H_2 \equiv H_4 \sim H_1 \sim H_3, \\
788 \quad & \text{weight } \frac{f-1}{4fv} + \frac{f-1}{2f^2 v'}; \\
789 \quad \{\text{H}\Delta 16/2\} \quad & H_1 \asymp H_4 \sim H_2 \asymp H_3, \text{ weight } \frac{(v-1)^2}{4fv^2}; \\
790 \quad \{\text{H}\Delta 17\} \quad & H_1 \asymp H_2 \sim H_3 \asymp H_4, \text{ weight } \frac{(v-1)^2}{4fv^2}; \\
791 \quad \{\text{H}\Delta 18^*3/4\} \quad & H_1 \asymp H_4 \sim H_2 \sim H_3 \text{ or } H_2 \asymp H_3 \sim H_1 \sim H_4 \text{ or } H_2 \asymp H_4 \sim H_1 \sim H_3, \\
792 \quad & \text{weight } \frac{(v-1)(f-1)}{4fv} + \frac{(v-1)(f-1)}{2f^2 v}; \\
793 \quad \{\text{H}\Delta 19\} \quad & H_1 \asymp H_2 \sim H_3 \sim H_4 \text{ or } H_1 \sim H_2 \sim H_3 \asymp H_4, \text{ weight } \frac{(v-1)(f-1)}{4fv} + \frac{(v-1)(f-1)}{4f^2 v}; \\
794 \quad \{\text{H}\Delta 20\} \quad & H_1 \sim H_2 \sim H_3 \sim H_4, \text{ weight } \frac{(f-1)(f-2)}{4f^2}; \\
795 \quad \{\text{H}\Delta 22/2\} \quad & H_1 \asymp H_2 \asymp H_4 \sim H_3 \text{ or } H_2 \asymp H_3 \asymp H_4 \sim H_1, \text{ weight } \frac{(v-1)(v-2)}{4v^2} + \frac{(v-1)(v-2)}{4f^2 v^2}; \\
796 \quad (3) \quad & [(H_1, H_3)], [H_2, H_4], \text{ probability } \frac{M-1}{M^2} \frac{v/2-1}{v-1}; \\
797 \quad \{\text{H}\Delta 12/4\} \quad & H_2 \equiv H_4 \sim H_1 \asymp H_3, \text{ weight } \frac{1}{4v} + \frac{1}{4fv}; \\
798 \quad \{\text{H}\Delta 16/2\} \quad & H_1 \asymp H_3 \sim H_2 \asymp H_4, \text{ weight } \frac{v-1}{4v} + \frac{v-1}{4fv}; \\
799 \quad \{\text{H}\Delta 18/4\} \quad & H_1 \asymp H_3 \sim H_2 \sim H_4, \text{ weight } \frac{f-1}{4f} + \frac{1}{2}; \\
800 \quad (4) \quad & [(H_1), (H_3)], [H_2, H_4], \text{ probability } \frac{M-1}{M^2} \frac{v/2}{v-1}; \\
801 \quad \{\text{H}\Delta 14/4\} \quad & H_2 \equiv H_4 \sim H_1 \sim H_3, \text{ weight } \frac{1}{4v} + \frac{1}{4fv}; \\
802 \quad \{\text{H}\Delta 18/4\} \quad & H_2 \asymp H_4 \sim H_1 \sim H_3, \text{ weight } \frac{v-1}{4v} + \frac{v-1}{4fv}; \\
803 \quad \{\text{H}\Delta 20\} \quad & H_1 \sim H_2 \sim H_3 \sim H_4, \text{ weight } \frac{f-1}{4f} + \frac{1}{2};
\end{aligned}$$

- 804 (5) $[(H_1, H_3), H_2], [H_4]$, probability $\frac{M-1}{M^2} \frac{v/2-1}{v-1}$,
805 $\{H\Delta 7/4\}$ $H_1 \equiv H_2 \asymp H_3 \sim H_4$, weight $\frac{1}{4v} + \frac{1}{4fv}$;
806 $\{H\Delta 13/8\}$ $H_2 \equiv H_3 \asymp H_1 \sim H_4$, weight $\frac{1}{4v} + \frac{1}{4fv}$;
807 $\{H\Delta 18/4\}$ $H_1 \asymp H_3 \sim H_2 \sim H_4$, weight $\frac{f-1}{4f} + \frac{1}{2}$;
808 $\{H\Delta 22/4\}$ $H_1 \asymp H_2 \asymp H_3 \sim H_4$, weight $\frac{v-2}{4v} + \frac{v-2}{4fv}$;
809 (6) $[(H_1), (H_3), H_2], [H_4]$, probability $\frac{M-1}{M^2} \frac{v/2}{v-1}$,
810 $\{H\Delta 8/2\}$ $H_1 \equiv H_2 \sim H_3 \sim H_4$, weight $\frac{1}{4v} + \frac{1}{4fv}$;
811 $\{H\Delta 14/4\}$ $H_2 \equiv H_3 \sim H_1 \sim H_4$, weight $\frac{1}{4v} + \frac{1}{4fv}$;
812 $\{H\Delta 18/4\}$ $H_2 \asymp H_3 \sim H_1 \sim H_4$, weight $\frac{v-1}{4v} + \frac{v-1}{4fv}$;
813 $\{H\Delta 19/2\}$ $H_1 \asymp H_2 \sim H_3 \sim H_4$, weight $\frac{v-1}{4v} + \frac{v-1}{4fv}$;
814 $\{H\Delta 20\}$ $H_1 \sim H_2 \sim H_3 \sim H_4$, weight $\frac{f-1}{2f}$;
815 (7) $[(H_1, H_3), H_4], [H_2]$, probability $\frac{M-1}{M^2} \frac{v/2-1}{v-1}$,
816 $\{H\Delta 7/4\}$ $H_2 \sim H_1 \asymp H_3 \equiv H_4$, weight $\frac{1}{4v} + \frac{1}{4fv}$;
817 $\{H\Delta 13/8\}$ $H_1 \equiv H_4 \asymp H_3 \sim H_2$, weight $\frac{1}{4v} + \frac{1}{4fv}$;
818 $\{H\Delta 18/4\}$ $H_1 \asymp H_3 \sim H_2 \sim H_4$, weight $\frac{f-1}{4f} + \frac{1}{2}$;
819 $\{H\Delta 22/4\}$ $H_1 \asymp H_3 \asymp H_4 \sim H_2$, weight $\frac{v-2}{4v} + \frac{v-2}{4fv}$;
820 (8) $[(H_1), (H_3), H_4], [H_2]$, probability $\frac{M-1}{M^2} \frac{v/2}{v-1}$,
821 $\{H\Delta 8/2\}$ $H_1 \sim H_2 \sim H_3 \equiv H_4$, weight $\frac{1}{4v} + \frac{1}{4fv}$;
822 $\{H\Delta 14/4\}$ $H_1 \equiv H_4 \sim H_2 \sim H_3$, weight $\frac{1}{4v} + \frac{1}{4fv}$;
823 $\{H\Delta 18/4\}$ $H_1 \asymp H_4 \sim H_2 \sim H_3$, weight $\frac{v-1}{4v} + \frac{v-1}{4fv}$;
824 $\{H\Delta 19/2\}$ $H_1 \sim H_2 \sim H_3 \asymp H_4$, weight $\frac{v-1}{4v} + \frac{v-1}{4fv}$;
825 $\{H\Delta 20\}$ $H_1 \sim H_2 \sim H_3 \sim H_4$, weight $\frac{f-1}{2f}$;
826 (9) $[(H_1, H_3)], [H_2], [H_4]$, probability $\frac{(M-1)(M-2)}{M^2} \frac{v/2-1}{v-1}$, identical to $H\Delta 18/4$;
827 (10) $[(H_1), (H_3)], [H_2], [H_4]$, probability $\frac{(M-1)(M-2)}{M^2} \frac{v/2}{v-1}$, identical to $H\Delta 20$.
828 Δ'_4 :
829 (1) $[(H_1, H_2), H_3, H_4]$, probability $\frac{1}{M^2} \frac{v/2-1}{v-1}$,
830 $\{H\Delta 4/2\}$ $H_1 \asymp H_2 \equiv H_3 \equiv H_4$ or $H_2 \asymp H_1 \equiv H_3 \equiv H_4$, weight $\frac{1}{4v^2} + \frac{1}{4f^2v^2}$;
831 $\{H\Delta 5/2\}$ $H_1 \asymp H_2 \sim H_3 \equiv H_4$, weight $\frac{1}{8v} + \frac{1}{8fv} + \frac{f-1}{8f^2v}$;
832 $\{H\Delta 9/2\}$ $H_1 \asymp H_2 \asymp H_3 \equiv H_4$, weight $\frac{v-2}{8v^2} + \frac{v-2}{8f^2v^2}$;
833 $\{H\Delta 10\}$ $H_1 \equiv H_3 \asymp H_2 \equiv H_4$ or $H_1 \equiv H_4 \asymp H_2 \equiv H_3$, weight $\frac{1}{4v^2} + \frac{1}{4f^2v^2}$;
834 $\{H\Delta 13/2\}$ $H_1 \equiv H_3 \asymp H_2 \sim H_4$ or $H_1 \equiv H_4 \asymp H_2 \sim H_3$ or $H_2 \equiv H_3 \asymp H_1 \sim H_4$
835 or $H_2 \equiv H_4 \asymp H_1 \sim H_3$, weight $\frac{1}{2v} + \frac{1}{2fv} + \frac{f-1}{2f^2v}$;
836 $\{H\Delta 15\}$ $H_1 \equiv H_3 \asymp H_2 \asymp H_4$ or $H_1 \equiv H_4 \asymp H_2 \asymp H_3$ or $H_2 \equiv H_3 \asymp H_1 \asymp H_4$
837 or $H_2 \equiv H_4 \asymp H_1 \asymp H_3$, weight $\frac{v-2}{2v^2} + \frac{v-2}{2f^2v^2}$;
838 $\{H\Delta 17\}$ $H_1 \asymp H_2 \sim H_3 \asymp H_4$, weight $\frac{v-1}{8v} + \frac{v-1}{8fv} + \frac{(f-1)(v-1)}{8f^2v}$;
839 $\{H\Delta 19/2\}$ $H_1 \asymp H_2 \sim H_3 \sim H_4$, weight $\frac{3(f-1)}{8f} + \frac{(f-1)(f-2)}{8f^2}$;

$$\begin{aligned}
 & \{HS\Delta 21\} \quad H_1 \asymp H_2 \asymp H_3 \asymp H_4, \text{ weight } \frac{(v-2)(v-3)}{8v^2} + \frac{(v-2)(v-3)}{8f^2v^2}; \\
 & \{HS\Delta 22/2\} \quad H_1 \asymp H_2 \asymp H_3 \sim H_4 \text{ or } H_1 \asymp H_2 \asymp H_4 \sim H_3, \\
 & \quad \text{weight } \frac{v-2}{4v} + \frac{v-2}{4fv} + \frac{(v-2)(f-1)}{4f^2v}; \\
 & (2) \quad [(H_1), (H_2), H_3, H_4], \text{ probability } \frac{1}{M^2} \frac{v/2}{v-1}, \\
 & \{HS\Delta 6/2\} \quad H_1 \equiv H_3 \equiv H_4 \sim H_2 \text{ or } H_2 \equiv H_3 \equiv H_4 \sim H_1, \text{ weight } \frac{1}{4v^2} + \frac{1}{4f^2v^2}; \\
 & \{HS\Delta 7/2\} \quad H_1 \sim H_2 \asymp H_3 \equiv H_4 \text{ or } H_2 \sim H_1 \asymp H_3 \equiv H_4, \text{ weight } \frac{v-1}{4v^2} + \frac{v-1}{4f^2v^2}; \\
 & \{HS\Delta 8/2\} \quad H_1 \sim H_2 \sim H_3 \equiv H_4, \text{ weight } \frac{f-1}{4f^2v}; \\
 & \{HS\Delta 11\} \quad H_1 \equiv H_3 \sim H_2 \equiv H_4 \text{ or } H_1 \equiv H_4 \sim H_2 \equiv H_3, \text{ weight } \frac{1}{2fv^2}; \\
 & \{HS\Delta 12\} \quad H_1 \equiv H_3 \sim H_2 \asymp H_4 \text{ or } H_1 \equiv H_4 \sim H_2 \asymp H_3 \text{ or } H_2 \equiv H_3 \sim H_1 \asymp H_4 \\
 & \quad \text{or } H_2 \equiv H_4 \sim H_1 \asymp H_3, \text{ weight } \frac{v-1}{fv^2}; \\
 & \{HS\Delta 13/2\} \quad H_1 \equiv H_3 \asymp H_4 \sim H_2 \text{ or } H_1 \equiv H_4 \asymp H_3 \sim H_2 \text{ or } H_2 \equiv H_3 \asymp H_4 \sim H_1 \\
 & \quad \text{or } H_2 \equiv H_4 \asymp H_3 \sim H_1, \text{ weight } \frac{v-1}{2v^2} + \frac{v-1}{2f^2v^2}; \\
 & \{HS\Delta 14\} \quad H_1 \equiv H_3 \sim H_2 \sim H_4 \text{ or } H_1 \equiv H_4 \sim H_2 \sim H_3 \text{ or } H_2 \equiv H_3 \sim H_1 \sim H_4 \\
 & \quad \text{or } H_2 \equiv H_4 \sim H_1 \sim H_3, \text{ weight } \frac{f-1}{2vf} + \frac{f-1}{2f^2v}; \\
 & \{HS\Delta 16\} \quad H_1 \asymp H_3 \sim H_2 \asymp H_4 \text{ or } H_1 \asymp H_4 \sim H_2 \asymp H_3, \text{ weight } \frac{(v-1)^2}{2fv^2}; \\
 & \{HS\Delta 18\} \quad H_1 \asymp H_3 \sim H_2 \sim H_4 \text{ or } H_1 \asymp H_4 \sim H_2 \sim H_3 \text{ or } H_2 \asymp H_3 \sim H_1 \sim H_4 \\
 & \quad \text{or } H_2 \asymp H_4 \sim H_1 \sim H_3, \text{ weight } \frac{(v-1)(f-1)}{2fv} + \frac{(v-1)(f-1)}{2f^2v}; \\
 & \{HS\Delta 19/2\} \quad H_1 \sim H_2 \sim H_3 \asymp H_4, \text{ weight } \frac{(f-1)(v-1)}{4f^2v}; \\
 & \{HS\Delta 20\} \quad H_1 \sim H_2 \sim H_3 \sim H_4, \text{ weight } \frac{(f-1)(f-2)}{4f^2}; \\
 & \{HS\Delta 22/2\} \quad H_1 \asymp H_3 \asymp H_4 \sim H_2 \text{ or } H_2 \asymp H_3 \asymp H_4 \sim H_1, \text{ weight } \frac{(v-1)(v-2)}{4v^2} + \frac{(v-1)(v-2)}{4f^2v^2}; \\
 & (3) \quad [(H_1, H_2)], [H_3, H_4], \text{ probability } \frac{M-1}{M^2} \frac{v/2-1}{v-1}, \\
 & \{HS\Delta 5/2\} \quad H_1 \asymp H_2 \sim H_3 \equiv H_4, \text{ weight } \frac{1}{4v} + \frac{1}{4fv}; \\
 & \{HS\Delta 17\} \quad H_1 \asymp H_2 \sim H_3 \asymp H_4, \text{ weight } \frac{v-1}{4v} + \frac{v-1}{4fv}; \\
 & \{HS\Delta 19/2\} \quad H_1 \asymp H_2 \sim H_3 \sim H_4, \text{ weight } \frac{f-1}{4f} + \frac{1}{2}; \\
 & (4) \quad [(H_1), (H_2)], [H_3, H_4], \text{ probability } \frac{M-1}{M^2} \frac{v/2}{v-1}, \\
 & \{HS\Delta 8/2\} \quad H_1 \sim H_2 \sim H_3 \equiv H_4, \text{ weight } \frac{1}{4v} + \frac{1}{4fv}; \\
 & \{HS\Delta 19/2\} \quad H_1 \sim H_2 \sim H_3 \asymp H_4, \text{ weight } \frac{v-1}{4v} + \frac{v-1}{4fv}; \\
 & \{HS\Delta 20\} \quad H_1 \sim H_2 \sim H_3 \sim H_4, \text{ weight } \frac{f-1}{4f} + \frac{1}{2}; \\
 & (5) \quad [(H_1, H_2), H_3], [H_4], \text{ probability } \frac{M-1}{M^2} \frac{v/2-1}{v-1}, \\
 & \{HS\Delta 13/4\} \quad H_1 \equiv H_3 \asymp H_2 \sim H_4 \text{ or } H_2 \equiv H_3 \asymp H_1 \sim H_4, \text{ weight } \frac{1}{2v} + \frac{1}{2fv}; \\
 & \{HS\Delta 19/2\} \quad H_1 \asymp H_2 \sim H_3 \sim H_4, \text{ weight } \frac{f-1}{4f} + \frac{1}{2}; \\
 & \{HS\Delta 22/4\} \quad H_1 \asymp H_2 \asymp H_3 \sim H_4, \text{ weight } \frac{v-2}{4v} + \frac{v-2}{4fv}; \\
 & (6) \quad [(H_1), (H_2), H_3], [H_4], \text{ probability } \frac{M-1}{M^2} \frac{v/2}{v-1}, \\
 & \{HS\Delta 14/2\} \quad H_1 \equiv H_3 \sim H_2 \sim H_4 \text{ or } H_2 \equiv H_3 \sim H_1 \sim H_4, \text{ weight } \frac{1}{4v} + \frac{1}{4fv}; \\
 & \{HS\Delta 18/2\} \quad H_1 \asymp H_3 \sim H_2 \sim H_4 \text{ or } H_2 \asymp H_3 \sim H_1 \sim H_4, \text{ weight } \frac{v-1}{4v} + \frac{v-1}{4fv}; \\
 & \{HS\Delta 20\} \quad H_1 \sim H_2 \sim H_3 \sim H_4, \text{ weight } \frac{f-1}{4f} + \frac{1}{2}; \\
 & (7) \quad [(H_1, H_2), H_4], [H_3], \text{ probability } \frac{M-1}{M^2} \frac{v/2-1}{v-1},
 \end{aligned}$$

- 877 {HSΔ13/4} $H_1 \equiv H_4 \asymp H_2 \sim H_3$ or $H_2 \equiv H_4 \asymp H_1 \sim H_3$, weight $\frac{1}{2v} + \frac{1}{2fv}$;
878 {HSΔ19/2} $H_1 \asymp H_2 \sim H_3 \sim H_4$, weight $\frac{f-1}{4f} + \frac{1}{2}$;
879 {HSΔ22/4} $H_1 \asymp H_2 \asymp H_4 \sim H_3$, weight $\frac{v-2}{4v} + \frac{v-2}{4fv}$;
880 (8) $[(H_1), (H_2), H_4], [H_3]$, probability $\frac{M-1}{M^2} \frac{v/2}{v-1}$;
881 {HSΔ14/2} $H_1 \equiv H_4 \sim H_2 \sim H_3$ or $H_2 \equiv H_4 \sim H_1 \sim H_3$, weight $\frac{1}{2v} + \frac{1}{2fv}$;
882 {HSΔ18/2} $H_1 \asymp H_4 \sim H_2 \sim H_3$ or $H_2 \asymp H_4 \sim H_1 \sim H_3$, weight $\frac{v-1}{2v} + \frac{v-1}{2fv}$;
883 {HSΔ20} $H_1 \sim H_2 \sim H_3 \sim H_4$, weight $\frac{f-1}{2f}$;
884 (9) $[(H_1, H_2)], [H_3], [H_4]$, probability $\frac{(M-1)(M-2)}{M^2} \frac{v/2-1}{v-1}$, identical to HSΔ19/2;
885 (10) $[(H_1), (H_2)], [H_3], [H_4]$, probability $\frac{(M-1)(M-2)}{M^2} \frac{v/2}{v-1}$, identical to HSΔ20.
- 886 Δ'_5 :
887 (1) $[H_1, H_2, H_3, H_4]$, probability $\frac{1}{M^3}$;
888 {HSΔ1} $H_1 \equiv H_2 \equiv H_3 \equiv H_4$, weight $\frac{1}{16v^3} + \frac{1}{16f^3v^3}$;
889 {HSΔ2} $H_1 \equiv H_2 \asymp H_3 \equiv H_4$, weight $\frac{v-1}{16v^3} + \frac{v-1}{16f^3v^3}$;
890 {HSΔ3} $H_1 \equiv H_2 \sim H_3 \equiv H_4$, weight $\frac{1}{8fv^2} + \frac{f-1}{16f^3v^2}$;
891 {HSΔ4} $H_1 \equiv H_2 \equiv H_3 \asymp H_4$ or $H_1 \equiv H_2 \equiv H_4 \asymp H_3$ or $H_1 \asymp H_2 \equiv H_3 \equiv H_4$
892 or $H_2 \asymp H_1 \equiv H_3 \equiv H_4$, weight $\frac{v-1}{4v^3} + \frac{v-1}{4f^3v^3}$;
893 {HSΔ5} $H_1 \equiv H_2 \sim H_3 \asymp H_4$ or $H_1 \asymp H_2 \sim H_3 \equiv H_4$, weight $\frac{v-1}{4fv^2} + \frac{(f-1)(v-1)}{8f^3v^2}$;
894 {HSΔ6} $H_1 \equiv H_3 \equiv H_4 \sim H_2$ or $H_2 \equiv H_3 \equiv H_4 \sim H_1$ or $H_1 \equiv H_2 \equiv H_3 \sim H_4$
895 or $H_1 \equiv H_2 \equiv H_4 \sim H_3$, weight $\frac{1}{4v^2} + \frac{1}{4f^2v^2} + \frac{f-1}{4f^3v^2}$;
896 {HSΔ7} $H_1 \sim H_2 \asymp H_3 \equiv H_4$ or $H_2 \sim H_1 \asymp H_3 \equiv H_4$ or $H_1 \equiv H_2 \asymp H_3 \sim H_4$
897 or $H_1 \equiv H_2 \asymp H_4 \sim H_3$, weight $\frac{v-1}{4v^2} + \frac{v-1}{4f^2v^2} + \frac{(f-1)(v-1)}{4f^3v^2}$;
898 {HSΔ8} $H_1 \sim H_2 \sim H_3 \equiv H_4$ or $H_1 \equiv H_2 \sim H_3 \sim H_4$, weight $\frac{f-1}{8fv} + \frac{f-1}{4f^2v} + \frac{(f-1)(f-2)}{8f^3v}$;
899 {HSΔ9} $H_1 \asymp H_2 \asymp H_3 \equiv H_4$ or $H_1 \equiv H_2 \asymp H_3 \asymp H_4$, weight $\frac{(v-1)(v-2)}{8v^3} + \frac{(v-1)(v-2)}{8f^3v^3}$;
900 {HSΔ10} $H_1 \equiv H_3 \asymp H_2 \equiv H_4$ or $H_1 \equiv H_4 \asymp H_2 \equiv H_3$, weight $\frac{v-1}{8v^3} + \frac{v-1}{8f^3v^3}$;
901 {HSΔ11} $H_1 \equiv H_3 \sim H_2 \equiv H_4$ or $H_1 \equiv H_4 \sim H_2 \equiv H_3$, weight $\frac{1}{4fv^2} + \frac{f-1}{8f^3v^2}$;
902 {HSΔ12} $H_1 \equiv H_3 \sim H_2 \asymp H_4$ or $H_1 \equiv H_4 \sim H_2 \asymp H_3$ or $H_2 \equiv H_3 \sim H_1 \asymp H_4$
903 or $H_2 \equiv H_4 \sim H_1 \asymp H_3$, weight $\frac{v-1}{2fv^2} + \frac{(f-1)(v-1)}{4f^3v^2}$;
904 {HSΔ13} $H_1 \equiv H_3 \asymp H_2 \sim H_4$ or $H_1 \equiv H_4 \asymp H_2 \sim H_3$ or $H_2 \equiv H_3 \asymp H_1 \sim H_4$
905 or $H_2 \equiv H_4 \asymp H_1 \sim H_3$ or $H_1 \equiv H_3 \asymp H_4 \sim H_2$ or $H_1 \equiv H_4 \asymp H_3 \sim H_2$
906 or $H_2 \equiv H_3 \asymp H_4 \sim H_1$ or $H_2 \equiv H_4 \asymp H_3 \sim H_1$,
907 weight $\frac{v-1}{2v^2} + \frac{v-1}{2f^2v^2} + \frac{(f-1)(v-1)}{2f^3v^2}$;
908 {HSΔ14} $H_1 \equiv H_3 \sim H_2 \sim H_4$ or $H_1 \equiv H_4 \sim H_2 \sim H_3$ or $H_2 \equiv H_3 \sim H_1 \sim H_4$
909 or $H_2 \equiv H_4 \sim H_1 \sim H_3$, weight $\frac{f-1}{4fv} + \frac{f-1}{2f^2v} + \frac{(f-1)(f-2)}{4f^3v}$;
910 {HSΔ15} $H_1 \equiv H_3 \asymp H_2 \asymp H_4$ or $H_1 \equiv H_4 \asymp H_2 \asymp H_3$ or $H_2 \equiv H_3 \asymp H_1 \asymp H_4$
911 or $H_2 \equiv H_4 \asymp H_1 \asymp H_3$, weight $\frac{(v-1)(v-2)}{4v^3} + \frac{(v-1)(v-2)}{4f^3v^3}$;
912 {HSΔ16} $H_1 \asymp H_3 \sim H_2 \asymp H_4$ or $H_1 \asymp H_4 \sim H_2 \asymp H_3$, weight $\frac{(v-1)^2}{4fv^2} + \frac{(f-1)(v-1)^2}{8f^3v^2}$;
913 {HSΔ17} $H_1 \asymp H_2 \sim H_3 \asymp H_4$, weight $\frac{(v-1)^2}{8fv^2} + \frac{(f-1)(v-1)^2}{16f^3v^2}$;
914 {HSΔ18} $H_1 \asymp H_3 \sim H_2 \sim H_4$ or $H_1 \asymp H_4 \sim H_2 \sim H_3$ or $H_2 \asymp H_3 \sim H_1 \sim H_4$

$$\begin{aligned}
& \text{or } H_2 \asymp H_4 \sim H_1 \sim H_3, \text{ weight } \frac{(f-1)(v-1)}{4fv} + \frac{(f-1)(v-1)}{2f^2v} + \frac{(f-1)(f-2)(v-1)}{4f^3v}, \\
\{HS\Delta 19\} & H_1 \asymp H_2 \sim H_3 \sim H_4 \text{ or } H_1 \sim H_2 \sim H_3 \asymp H_4, \\
& \text{weight } \frac{(f-1)(v-1)}{8fv} + \frac{(f-1)(v-1)}{4f^2v} + \frac{(f-1)(f-2)(v-1)}{8f^3v}, \\
\{HS\Delta 20\} & H_1 \sim H_2 \sim H_3 \sim H_4, \text{ weight } \frac{(f-1)(f-2)}{4f^2} + \frac{(f-1)(f-2)(f-3)}{16f^3}, \\
\{HS\Delta 21\} & H_1 \asymp H_2 \asymp H_3 \asymp H_4, \text{ weight } \frac{(v-1)(v-2)(v-3)}{16v^3} + \frac{(v-1)(v-2)(v-3)}{16f^3v^3}, \\
\{HS\Delta 22\} & H_1 \asymp H_2 \asymp H_3 \sim H_4 \text{ or } H_1 \asymp H_2 \asymp H_4 \sim H_3 \text{ or } H_1 \asymp H_3 \asymp H_4 \sim H_2 \\
& \text{or } H_2 \asymp H_3 \asymp H_4 \sim H_1, \text{ weight } \frac{(v-1)(v-2)}{4v^2} + \frac{(v-1)(v-2)}{4f^2v^2} + \frac{(f-1)(v-1)(v-2)}{4f^3v^2}, \\
(2) & [H_1, H_2, H_3], [H_4] \text{ or } [H_1, H_2, H_4], [H_3] \text{ or } [H_1, H_3, H_4], [H_2] \text{ or } [H_2, H_3, H_4], [H_1], \\
& \text{probability } \frac{4(M-1)}{M^3}, \\
\{HS\Delta 6/4\} & H_1 \equiv H_3 \equiv H_4 \sim H_2 \text{ or } H_2 \equiv H_3 \equiv H_4 \sim H_1 \text{ or } H_1 \equiv H_2 \equiv H_3 \sim H_4 \\
& \text{or } H_1 \equiv H_2 \equiv H_4 \sim H_3, \text{ weight } \frac{1}{8v^2} + \frac{1}{8f^2v^2}, \\
\{HS\Delta 7/4\} & H_1 \sim H_2 \asymp H_3 \equiv H_4 \text{ or } H_2 \sim H_1 \asymp H_3 \equiv H_4 \text{ or } H_1 \equiv H_2 \asymp H_3 \sim H_4 \\
& \text{or } H_1 \equiv H_2 \asymp H_4 \sim H_3, \text{ weight } \frac{v-1}{8v^2} + \frac{v-1}{8f^2v^2}, \\
\{HS\Delta 8/2\} & H_1 \sim H_2 \sim H_3 \equiv H_4 \text{ or } H_1 \equiv H_2 \sim H_3 \sim H_4, \text{ weight } \frac{1}{8v} + \frac{1}{8fv} + \frac{f-1}{8f^2v}, \\
\{HS\Delta 13/4\} & H_1 \equiv H_3 \asymp H_2 \sim H_4 \text{ or } H_1 \equiv H_4 \asymp H_2 \sim H_3 \text{ or } H_2 \equiv H_3 \asymp H_1 \sim H_4 \\
& \text{or } H_2 \equiv H_4 \asymp H_1 \sim H_3 \text{ or } H_1 \equiv H_3 \asymp H_4 \sim H_2 \text{ or } H_1 \equiv H_4 \asymp H_3 \sim H_2 \\
& \text{or } H_2 \equiv H_3 \asymp H_4 \sim H_1 \text{ or } H_2 \equiv H_4 \asymp H_3 \sim H_1, \text{ weight } \frac{v-1}{4v^2} + \frac{v-1}{4f^2v^2}, \\
\{HS\Delta 14/2\} & H_1 \equiv H_3 \sim H_2 \sim H_4 \text{ or } H_1 \equiv H_4 \sim H_2 \sim H_3 \text{ or } H_2 \equiv H_3 \sim H_1 \sim H_4 \\
& \text{or } H_2 \equiv H_4 \sim H_1 \sim H_3, \text{ weight } \frac{1}{4v} + \frac{1}{4fv} + \frac{f-1}{4f^2v}, \\
\{HS\Delta 18/2\} & H_1 \asymp H_3 \sim H_2 \sim H_4 \text{ or } H_1 \asymp H_4 \sim H_2 \sim H_3 \text{ or } H_2 \asymp H_3 \sim H_1 \sim H_4 \\
& \text{or } H_2 \asymp H_4 \sim H_1 \sim H_3, \text{ weight } \frac{v-1}{4v} + \frac{v-1}{4fv} + \frac{(f-1)(v-1)}{4f^2v}, \\
\{HS\Delta 19/2\} & H_1 \asymp H_2 \sim H_3 \sim H_4 \text{ or } H_1 \sim H_2 \sim H_3 \asymp H_4, \text{ weight } \frac{v-1}{8v} + \frac{v-1}{8fv} + \frac{(f-1)(v-1)}{8f^2v}, \\
\{HS\Delta 20\} & H_1 \sim H_2 \sim H_3 \sim H_4, \text{ weight } \frac{3(f-1)}{8f} + \frac{(f-1)(f-2)}{8f^2}, \\
\{HS\Delta 22/4\} & H_1 \asymp H_2 \asymp H_3 \sim H_4 \text{ or } H_1 \asymp H_2 \asymp H_4 \sim H_3 \text{ or } H_1 \asymp H_3 \asymp H_4 \sim H_2 \\
& \text{or } H_2 \asymp H_3 \asymp H_4 \sim H_1, \text{ weight } \frac{(v-1)(v-2)}{8v^2} + \frac{(v-1)(v-2)}{8f^2v^2}, \\
(3) & [H_1, H_2], [H_3, H_4], \text{ probability } \frac{(M-1)}{M^3}, \\
\{HS\Delta 3\} & H_1 \equiv H_2 \sim H_3 \equiv H_4, \text{ weight } \frac{1}{16v^2} + \frac{1}{8fv^2} + \frac{1}{16f^2v^2}, \\
\{HS\Delta 5\} & H_1 \equiv H_2 \sim H_3 \asymp H_4 \text{ or } H_1 \asymp H_2 \sim H_3 \equiv H_4, \text{ weight } \frac{v-1}{8v^2} + \frac{v-1}{4fv^2} + \frac{v-1}{8f^2v^2}, \\
\{HS\Delta 8\} & H_1 \sim H_2 \sim H_3 \equiv H_4 \text{ or } H_1 \equiv H_2 \sim H_3 \sim H_4, \text{ weight } \frac{1}{4v} + \frac{1}{4fv} + \frac{f-1}{8fv} + \frac{f-1}{8f^2v}, \\
\{HS\Delta 17\} & H_1 \asymp H_2 \sim H_3 \asymp H_4, \text{ weight } \frac{(v-1)^2}{16v^2} + \frac{(v-1)^2}{8fv^2} + \frac{(v-1)^2}{16f^2v^2}, \\
\{HS\Delta 19\} & H_1 \asymp H_2 \sim H_3 \sim H_4 \text{ or } H_1 \sim H_2 \sim H_3 \asymp H_4, \\
& \text{weight } \frac{v-1}{4v} + \frac{v-1}{4fv} + \frac{(f-1)(v-1)}{8fv} + \frac{(f-1)(v-1)}{8f^2v}, \\
\{HS\Delta 20\} & H_1 \sim H_2 \sim H_3 \sim H_4, \text{ weight } \frac{1}{4} + \frac{f-1}{4f} + \frac{(f-1)^2}{16f^2}, \\
(4) & [H_1, H_3], [H_2, H_4] \text{ or } [H_1, H_4], [H_2, H_3], \text{ probability } \frac{2(M-1)}{M^3}, \\
\{HS\Delta 11/2\} & H_1 \equiv H_3 \sim H_2 \equiv H_4 \text{ or } H_1 \equiv H_4 \sim H_2 \equiv H_3, \text{ weight } \frac{1}{16v^2} + \frac{1}{8fv^2} + \frac{1}{16f^2v^2}, \\
\{HS\Delta 12/2\} & H_1 \equiv H_3 \sim H_2 \asymp H_4 \text{ or } H_1 \equiv H_4 \sim H_2 \asymp H_3 \text{ or } H_2 \equiv H_3 \sim H_1 \asymp H_4 \\
& \text{or } H_2 \equiv H_4 \sim H_1 \asymp H_3, \text{ weight } \frac{v-1}{8v^2} + \frac{v-1}{4fv^2} + \frac{v-1}{8f^2v^2}, \\
\{HS\Delta 14/2\} & H_1 \equiv H_3 \sim H_2 \sim H_4 \text{ or } H_1 \equiv H_4 \sim H_2 \sim H_3 \text{ or } H_2 \equiv H_3 \sim H_1 \sim H_4 \\
& \text{or } H_2 \equiv H_4 \sim H_1 \sim H_3, \text{ weight } \frac{1}{4v} + \frac{1}{4fv} + \frac{f-1}{8fv} + \frac{f-1}{8f^2v},
\end{aligned}$$

- 954 {HSA16/2} $H_1 \asymp H_3 \sim H_2 \asymp H_4$ or $H_1 \asymp H_4 \sim H_2 \asymp H_3$, weight $\frac{(v-1)^2}{16v^2} + \frac{(v-1)^2}{8fv^2} + \frac{(v-1)^2}{16f^2v^2}$;
- 955 {HSA18/2} $H_1 \asymp H_3 \sim H_2 \sim H_4$ or $H_1 \asymp H_4 \sim H_2 \sim H_3$ or $H_2 \asymp H_3 \sim H_1 \sim H_4$
- 956 or $H_2 \asymp H_4 \sim H_1 \sim H_3$, weight $\frac{v-1}{4v} + \frac{v-1}{4fv} + \frac{(f-1)(v-1)}{8fv} + \frac{(f-1)(v-1)}{8f^2v}$;
- 957 {HSA20} $H_1 \sim H_2 \sim H_3 \sim H_4$, weight $\frac{1}{4} + \frac{f-1}{4f} + \frac{(f-1)^2}{16f^2}$;
- 958 (5) $[H_1, H_2], [H_3], [H_4]$ or $[H_3, H_4], [H_1], [H_2]$, probability $\frac{2(M-1)(M-2)}{M^3}$,
- 959 {HSA8/2} $H_1 \sim H_2 \sim H_3 \equiv H_4$ or $H_1 \equiv H_2 \sim H_3 \sim H_4$, weight $\frac{1}{4v} + \frac{1}{4fv}$;
- 960 {HSA19/2} $H_1 \asymp H_2 \sim H_3 \sim H_4$ or $H_1 \sim H_2 \sim H_3 \asymp H_4$, weight $\frac{v-1}{4v} + \frac{v-1}{4fv}$;
- 961 {HSA20} $H_1 \sim H_2 \sim H_3 \sim H_4$, weight $\frac{1}{2} + \frac{f-1}{4f}$;
- 962 (6) $[H_1, H_3], [H_2], [H_4]$ or $[H_1, H_4], [H_2], [H_3]$ or $[H_2, H_3], [H_1], [H_4]$
- 963 or $[H_2, H_4], [H_1], [H_3]$, probability $\frac{4(M-1)(M-2)}{M^3}$,
- 964 {HSA14/4} $H_1 \equiv H_3 \sim H_2 \sim H_4$ or $H_1 \equiv H_4 \sim H_2 \sim H_3$ or $H_2 \equiv H_3 \sim H_1 \sim H_4$
- 965 or $H_2 \equiv H_4 \sim H_1 \sim H_3$, weight $\frac{1}{4v} + \frac{1}{4fv}$;
- 966 {HSA18/4} $H_1 \asymp H_3 \sim H_2 \sim H_4$ or $H_1 \asymp H_4 \sim H_2 \sim H_3$ or $H_2 \asymp H_3 \sim H_1 \sim H_4$
- 967 or $H_2 \asymp H_4 \sim H_1 \sim H_3$, weight $\frac{v-1}{4v} + \frac{v-1}{4fv}$;
- 968 {HSA20} $H_1 \sim H_2 \sim H_3 \sim H_4$, weight $\frac{1}{2} + \frac{f-1}{4f}$;
- 969 (7) $[H_1], [H_2], [H_3], [H_4]$, probability $\frac{(M-1)(M-2)(M-3)}{M^3}$, identical to HSA20.
- 970 Δ'_6 :
- 971 (1) (H_1, H_2, H_3, H_4) , probability $\frac{(v/2-1)(v/2-2)(v/2-3)}{(v-1)(v-2)(v-3)}$, identical to HSA21;
- 972 (2) $(H_1, H_2, H_3), (H_4)$ or $(H_1, H_2, H_4), (H_3)$ or $(H_1, H_3, H_4), (H_2)$
- 973 or $(H_2, H_3, H_4), (H_1)$, probability $\frac{4(v/2-1)(v/2-2)(v/2)}{(v-1)(v-2)(v-3)}$, identical to HSA22/4;
- 974 (3) $(H_1, H_2), (H_3, H_4)$, probability $\frac{(v/2-1)^2(v/2)}{(v-1)(v-2)(v-3)}$, identical to HSA17;
- 975 (4) $(H_1, H_3), (H_2, H_4)$ or $(H_1, H_4), (H_2, H_3)$, probability $\frac{2(v/2-1)^2(v/2)}{(v-1)(v-2)(v-3)}$,
- 976 identical to HSA16/2.
- 977 Δ'_7 :
- 978 (1) $[(H_1, H_2, H_3), H_4]$, probability $\frac{1}{M} \frac{(v/2-1)(v/2-2)}{(v-1)(v-2)}$,
- 979 {HSA9/2} $H_1 \asymp H_2 \asymp H_3 \equiv H_4$, weight $\frac{1}{4v} + \frac{1}{4fv}$;
- 980 {HSA15/2} $H_1 \equiv H_4 \asymp H_2 \asymp H_3$ or $H_2 \equiv H_4 \asymp H_1 \asymp H_3$, weight $\frac{1}{2v} + \frac{1}{2fv}$;
- 981 {HSA21} $H_1 \asymp H_2 \asymp H_3 \asymp H_4$, weight $\frac{v-3}{4v} + \frac{v-3}{4fv}$;
- 982 {HSA22/4} $H_1 \asymp H_2 \asymp H_3 \sim H_4$, weight $\frac{1}{2} + \frac{f-1}{4f}$;
- 983 (2) $[(H_1, H_2, H_3)], [H_4]$, probability $\frac{M-1}{M} \frac{(v/2-1)(v/2-2)}{(v-1)(v-2)}$, identical to HSA22/4;
- 984 (3) $[(H_1, H_2), (H_3), H_4]$, probability $\frac{1}{M} \frac{(v/2-1)(v/2)}{(v-1)(v-2)}$,
- 985 {HSA5/2} $H_1 \asymp H_2 \sim H_3 \equiv H_4$, weight $\frac{1}{4v} + \frac{1}{4fv}$;
- 986 {HSA13/4} $H_1 \equiv H_4 \asymp H_2 \sim H_3$ or $H_2 \equiv H_4 \asymp H_1 \sim H_3$, weight $\frac{1}{2v} + \frac{1}{2fv}$;
- 987 {HSA17} $H_1 \asymp H_2 \sim H_3 \asymp H_4$, weight $\frac{v-1}{4v} + \frac{v-1}{4fv}$;
- 988 {HSA19/2} $H_1 \asymp H_2 \sim H_3 \sim H_4$, weight $\frac{f-1}{2f}$;
- 989 {HSA22/4} $H_1 \asymp H_2 \asymp H_4 \sim H_3$, weight $\frac{v-2}{4v} + \frac{v-2}{4fv}$;
- 990 (4) $[(H_1, H_2), (H_3)], [H_4]$, probability $\frac{M-1}{M} \frac{(v/2-1)(v/2)}{(v-1)(v-2)}$, identical to HSA19/2;

- 991 (5) $[(H_1, H_3), (H_2), H_4]$ or $[(H_2, H_3), (H_1), H_4]$, probability $\frac{2}{M} \frac{(v/2-1)(v/2)}{(v-1)(v-2)}$,
992 $\{HS\Delta 7/4\}$ $H_2 \sim H_1 \asymp H_3 \equiv H_4$, weight $\frac{1}{4v} + \frac{1}{4fv}$;
993 $\{HS\Delta 12/4\}$ $H_2 \equiv H_4 \sim H_1 \asymp H_3$, weight $\frac{1}{4v} + \frac{1}{4fv}$;
994 $\{HS\Delta 13/8\}$ $H_1 \equiv H_4 \asymp H_3 \sim H_2$, weight $\frac{1}{4v} + \frac{1}{4fv}$;
995 $\{HS\Delta 16/2\}$ $H_1 \asymp H_3 \sim H_2 \asymp H_4$, weight $\frac{v-1}{4v} + \frac{v-1}{4fv}$;
996 $\{HS\Delta 18/4\}$ $H_1 \asymp H_3 \sim H_2 \sim H_4$, weight $\frac{f-1}{2f}$;
997 $\{HS\Delta 22/4\}$ $H_1 \asymp H_3 \asymp H_4 \sim H_2$, weight $\frac{v-2}{4v} + \frac{v-2}{4fv}$;
998 (6) $[(H_1, H_3), (H_2)], [H_4]$ or $[(H_2, H_3), (H_1)], [H_4]$, probability $\frac{2(M-1)}{M} \frac{(v/2-1)(v/2)}{(v-1)(v-2)}$,
999 identical to $HS\Delta 18/4$.
1000 The transition matrix $\mathbf{\Omega}$ for the DH mating system is not shown, but the matrices $\mathbf{T}$
1001 and $\mathbf{S}$ in the principal part of $\mathbf{\Omega}$ are listed in Appendix H.

1002 Appendix H. Matrices **T** and **S** for various mating systems

1003 HS mating system

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$$\mathbf{T}_{\text{HS}} = \begin{bmatrix} \frac{c_1^2 v_2}{2v_1} & \frac{vc_1^2}{2v_1} & -\frac{cvc_1}{v_1} & 0 & 0 & -\frac{cc_1 v_2}{v_1} & \frac{c^2 v}{2v_1} & 0 & 0 & 0 & 0 & \frac{c^2 v_2}{2v_1} & 0 \\ 0 & c_1^2 & -2cc_1 & 0 & 0 & 0 & c^2 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & -\frac{c_1 v_2}{2v_1} & 0 & -\frac{vc_1}{2v_1} & 0 & \frac{cv_2}{2v_1} & 0 & \frac{cv}{2v_1} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & -\frac{c_1 v_2}{2v_1} & -\frac{vc_1}{2v_1} & 0 & 0 & 0 & \frac{cv}{2v_1} & 0 & 0 & 0 & \frac{cv_2}{2v_1} \\ 0 & 0 & 0 & 0 & -c_1 & 0 & 0 & 0 & c & 0 & 0 & 0 & 0 \\ 0 & 0 & -\frac{vc_1}{4v_1} & -\frac{vc_1}{2v_1} & 0 & -\frac{c_1 v_4}{4v_1} & \frac{cv}{4v_1} & 0 & 0 & 0 & 0 & \frac{cv_4}{4v_1} & \frac{cv}{2v_1} \\ 0 & 0 & 0 & 0 & 0 & 0 & \frac{v_2^2}{4v_1^2} & 0 & \frac{vv_2}{2v_1^2} & 0 & \frac{v^2}{4v_1^2} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{v_2^2}{4v_1^2} & 0 & \frac{vv_2}{2v_1^2} & \frac{v^2}{4v_1^2} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{v_2}{2v_1} & 0 & \frac{v}{2v_1} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{v_2}{2v_1} & \frac{v}{2v_1} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & \frac{vv_2}{4v_1 v_3} & \frac{vv_2}{8v_1 v_3} & 0 & 0 & 0 & \frac{v_4 v_6}{8v_1 v_3} & \frac{vv_4}{2v_1 v_3} \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{v}{2v_1} & \frac{v}{4v_1} & 0 & 0 & \frac{v_4}{4v_1} \end{bmatrix},$$

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$$\mathbf{S}_{\text{HS}} = \begin{bmatrix} \frac{1}{2} + \frac{c}{2} \left(c_2 + \frac{c}{v_1^2} \right) & -\frac{vc_1^2}{2v_1} & \frac{cvc_1}{v_1} & 0 & 0 & \frac{cv_2(v_1 - cv_2)}{v_1^2} & -\frac{c^2v}{2v_1} & 0 & 0 & 0 & 0 & \frac{c^2v_2v_3}{2v_1^2} & 0 \\ c_1^2 - \frac{1 + 2cc_1}{v} + \frac{c^2}{v_1} & -c_1^2 & 2cc_1 & 0 & 0 & \frac{2cv_2(v_1 - cv_2)}{vv_1} & -c^2 & 0 & 0 & 0 & 0 & \frac{c^2v_2v_3}{vv_1} & 0 \\ \frac{cv_2}{2vv_1^2} & -\frac{c_1}{2v_1} & \frac{1}{2v_1} & \frac{c - c_1v_1}{v_1} & \frac{3vc_1}{2v_1} & \frac{v_2^2(v_1 - cv_3)}{2vv_1^2} & \frac{c}{2v_1} & 0 & \frac{-3cv}{2v_1} & 0 & 0 & \frac{cv_2^2v_3}{2vv_1^2} & \frac{cv_2}{v_1} \\ -\frac{c_1v_2}{2vv_1} & -\frac{c_1}{2v_1} & \frac{v_1 - cv_2}{2v_1} & \frac{v - cv_2}{2v_1} & \frac{3vc_1}{2v_1} & \frac{(v_2 - cv_4)v_2}{2v_1v} & \frac{c}{2} & 0 & \frac{-3cv}{2v_1} & 0 & 0 & \frac{cv_2v_3}{2v_1v} & \frac{cv_2}{2v_1} \\ 0 & -\frac{c_1}{v} & \frac{v_1 - cv_2}{v} & \frac{2v_1 - 2cv_2}{v} & 3c_1 & 0 & \frac{cv_1}{v} & 0 & -3c & 0 & 0 & 0 & \frac{2cv_2}{v} \\ \frac{3c + 2v_1 - 2cv}{4v_1^2} & 0 & \frac{vc_1}{4v_1} & \frac{vc_1}{2v_1} & 0 & \frac{3v_1v_2 - c(3v_5v + 14)}{4v_1^2} & -\frac{cv}{4v_1} & 0 & 0 & 0 & 0 & \frac{cv_3(3v - 4)}{4v_1^2} & -\frac{cv}{2v_1} \\ \frac{v_2^2}{4vv_1^3} & 0 & \frac{v_2}{2v_1^2} & \frac{v_2}{v_1^2} & \frac{v}{v_1^2} & \frac{v_2^3}{2vv_1^3} & \frac{vv_2}{4v_1^2} & 0 & -\frac{vv_4}{2v_1^2} & \frac{v}{2v_1} & -\frac{3v^2}{2v_1^2} & \frac{v_2^3v_3}{4vv_1^3} & \frac{v_2^2}{v_1^2} \\ \frac{v_2^2}{2vv_1^3} & 0 & 0 & \frac{2v_2}{v_1^2} & \frac{v}{v_1^2} & \frac{v_2^3}{vv_1^3} & 0 & \frac{vv_2}{4v_1^2} & \frac{v}{v_1} & \frac{(5 - 2v)v}{2v_1^2} & -\frac{3v^2}{2v_1^2} & \frac{v_2^3v_3}{4vv_1^3} & \frac{v_2^2}{v_1^2} \\ 0 & 0 & \frac{1}{v} - \frac{1}{2v_1} & \frac{v_2}{vv_1} & \frac{2}{v_1} & 0 & \frac{1}{2} - \frac{1}{v} & 0 & \frac{2 + v}{2v_1} & 1 & -\frac{3v}{v_1} & 0 & 1 - \frac{4}{v} + \frac{1}{v_1} \\ 0 & 0 & 0 & \frac{2v_2}{vv_1} & \frac{2}{v_1} & 0 & 0 & \frac{1}{2} - \frac{1}{v} & 2 & -\frac{v_4}{2v_1} & -\frac{3v}{v_1} & 0 & 1 - \frac{4}{v} + \frac{1}{v_1} \\ 0 & 0 & 0 & 0 & \frac{4}{v} & 0 & 0 & 0 & 4 - \frac{4}{v} & 2 - \frac{2}{v} & -6 & 0 & 0 \\ \frac{v_2}{2v_1^2v_3} & 0 & 0 & 0 & 0 & \frac{8 + v(2v - 9)}{v_1^2v_3} & -\frac{vv_2}{4v_1v_3} & -\frac{vv_2}{8v_1v_3} & 0 & 0 & 0 & \frac{28 + v(7v - 32)}{8v_1^2} & -\frac{vv_4}{2v_1v_3} \\ 0 & 0 & \frac{1}{2v_1} & \frac{2}{v_1} & 0 & \frac{v_4}{2vv_1} & \frac{1}{2} & \frac{1}{4} & -\frac{3v}{2v_1} & -\frac{3v}{4v_1} & 0 & \frac{5 + v}{4v_1} - \frac{3}{v} & \frac{8 - 5v}{4 - 4v} \end{bmatrix},$$

1010 **MS mating system**

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$$\mathbf{T}_{\text{MS}} = \begin{bmatrix} \frac{c_1^2 v_2}{2v_1} & \frac{vc_1^2}{2v_1} & -\frac{cvc_1}{v_1} & 0 & 0 & -\frac{cc_1 v_2}{v_1} & \frac{c^2 v}{2v_1} & 0 & 0 & 0 & 0 & \frac{c^2 v_2}{2v_1} & 0 \\ 0 & c_1^2 & -2cc_1 & 0 & 0 & 0 & c^2 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & -\frac{c_1 v_2}{2v_1} & 0 & -\frac{vc_1}{2v_1} & 0 & \frac{cv_2}{2v_1} & 0 & \frac{cv}{2v_1} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & -\frac{c_1 v_2}{2v_1} & -\frac{vc_1}{2v_1} & 0 & 0 & 0 & \frac{cv}{2v_1} & 0 & 0 & 0 & \frac{cv_2}{2v_1} \\ 0 & 0 & 0 & 0 & -c_1 & 0 & 0 & 0 & c & 0 & 0 & 0 & 0 \\ 0 & 0 & -\frac{vc_1}{4v_1} & -\frac{vc_1}{2v_1} & 0 & -\frac{c_1 v_4}{4v_1} & \frac{cv}{4v_1} & 0 & 0 & 0 & 0 & \frac{cv_4}{4v_1} & \frac{cv}{2v_1} \\ 0 & 0 & 0 & 0 & 0 & 0 & \frac{v_2^2}{4v_1^2} & 0 & \frac{vv_2}{2v_1^2} & 0 & \frac{v^2}{4v_1^2} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{v_2^2}{4v_1^2} & 0 & \frac{vv_2}{2v_1^2} & \frac{v^2}{4v_1^2} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{v_2}{2v_1} & 0 & \frac{v}{2v_1} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{v_2}{2v_1} & \frac{v}{2v_1} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & \frac{vv_2}{4v_1 v_3} & \frac{vv_2}{8v_1 v_3} & 0 & 0 & 0 & \frac{v_4 v_6}{8v_1 v_3} & \frac{vv_4}{2v_1 v_3} \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{v}{2v_1} & \frac{v}{4v_1} & 0 & 0 & \frac{v_4}{4v_1} \end{bmatrix},$$

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$$\mathbf{S}_{\text{MS}} = \begin{bmatrix} c_1^2 - \frac{1+2cc_1}{v} + \frac{c^2}{v_1} & 0 & 0 & 0 & 0 & \frac{2cv_2(v_1 - cv_2)}{vv_1} & 0 & 0 & 0 & 0 & 0 & 0 & \frac{c^2v_2v_3}{vv_1} & 0 \\ \frac{cv_2}{2vv_1^2} & 0 & \frac{c_1v_2}{2v_1} & \frac{v_1 + c - cv_1}{v_1} & \frac{vc_1}{v_1} & \frac{v_2^2(v_1 - cv_3)}{2vv_1^2} & -\frac{cv_2}{2v_1} & 0 & -\frac{cv}{v_1} & 0 & 0 & \frac{cv_2^2v_3}{2vv_1^2} & \frac{cv_2}{v_1} \\ -\frac{c_1v_2}{2vv_1} & -\frac{c_1}{2v_1} & \frac{v_1 - cv_2}{2v_1} & \frac{1}{2v_1} & \frac{vc_1}{v_1} & \frac{v_2(v_2 - cv_4)}{2v_1v} & \frac{c}{2} & 0 & -\frac{cv}{v_1} & 0 & 0 & \frac{cv_2v_3}{2v_1v} & 0 \\ 0 & -\frac{c_1}{v} & \frac{v_1 - cv_2}{v} & \frac{2v_1 - 2cv_2}{v} & 3c_1 & 0 & \frac{cv_1}{v} & 0 & -3c & 0 & 0 & 0 & \frac{2cv_2}{v} \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \frac{v_2^2}{4vv_1^3} & 0 & 0 & \frac{v_2}{v_1^2} & \frac{v}{2v_1^2} & \frac{v_2^3}{2vv_1^3} & -\frac{v_2^2}{4v_1^2} & 0 & -\frac{vv_3}{2v_1^2} & \frac{v}{2v_1} & -\frac{v^2}{v_1^2} & \frac{v_2^3v_3}{4vv_1^3} & \frac{v_2^2}{v_1^2} \\ \frac{v_2^2}{2vv_1^3} & 0 & 0 & \frac{2v_2}{v_1^2} & \frac{v}{v_1^2} & \frac{v_2^3}{vv_1^3} & 0 & -\frac{v_2^2}{4v_1^2} & \frac{v}{v_1} & \frac{1-v_1^2}{v_1^2} & -\frac{v^2}{v_1^2} & \frac{v_2^3v_3}{4vv_1^3} & \frac{v_2^2}{v_1^2} \\ 0 & 0 & \frac{v_2}{2vv_1} & \frac{v_2}{vv_1} & \frac{3}{2v_1} & 0 & \frac{v_2}{2v} & 0 & \frac{3}{2v_1} & 1 & -\frac{5v}{2v_1} & 0 & 1 - \frac{4}{v} + \frac{1}{v_1} \\ 0 & 0 & 0 & \frac{2v_2}{vv_1} & \frac{2}{v_1} & 0 & 0 & \frac{v_2}{2v} & 2 & \frac{5-2v}{2v_1} & -\frac{5v}{2v_1} & 0 & 1 - \frac{4}{v} + \frac{1}{v_1} \\ 0 & 0 & 0 & 0 & \frac{4}{v} & 0 & 0 & 0 & \frac{4v_1}{v} & \frac{2v_1}{v} & -6 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \frac{1}{2v_1} & \frac{1}{v_1} & 0 & \frac{v_4}{2vv_1} & \frac{1}{2} & \frac{1}{4} & -\frac{v}{v_1} & -\frac{v}{2v_1} & 0 & \frac{v+5}{4v_1} - \frac{3}{v} & \frac{1}{2} \end{bmatrix},$$

1017 **ME and DR mating systems**

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$$\mathbf{T}_{\text{ME/DR}} = \begin{bmatrix} \frac{c_1^2 v_2}{2v_1} & \frac{vc_1^2}{2v_1} & -\frac{cvc_1}{v_1} & 0 & 0 & -\frac{cc_1 v_2}{v_1} & \frac{c^2 v}{2v_1} & 0 & 0 & 0 & 0 & \frac{c^2 v_2}{2v_1} & 0 \\ 0 & c_1^2 & -2cc_1 & 0 & 0 & 0 & c^2 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & -\frac{c_1 v_2}{2v_1} & 0 & -\frac{vc_1}{2v_1} & 0 & \frac{cv_2}{2v_1} & 0 & \frac{cv}{2v_1} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & -\frac{c_1 v_2}{2v_1} & -\frac{vc_1}{2v_1} & 0 & 0 & 0 & \frac{cv}{2v_1} & 0 & 0 & 0 & \frac{cv_2}{2v_1} \\ 0 & 0 & 0 & 0 & -c_1 & 0 & 0 & 0 & c & 0 & 0 & 0 & 0 \\ 0 & 0 & -\frac{vc_1}{4v_1} & -\frac{vc_1}{2v_1} & 0 & -\frac{c_1 v_4}{4v_1} & \frac{cv}{4v_1} & 0 & 0 & 0 & 0 & \frac{cv_4}{4v_1} & \frac{cv}{2v_1} \\ 0 & 0 & 0 & 0 & 0 & 0 & \frac{v_2^2}{4v_1^2} & 0 & \frac{vv_2}{2v_1^2} & 0 & \frac{v^2}{4v_1^2} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{v_2^2}{4v_1^2} & 0 & \frac{vv_2}{2v_1^2} & \frac{v^2}{4v_1^2} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{v_2}{2v_1} & 0 & \frac{v}{2v_1} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{v_2}{2v_1} & \frac{v}{2v_1} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & \frac{vv_2}{4v_1 v_3} & \frac{vv_2}{8v_1 v_3} & 0 & 0 & 0 & \frac{v_4 v_6}{8v_1 v_3} & \frac{vv_4}{2v_1 v_3} \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{v}{2v_1} & \frac{v}{4v_1} & 0 & 0 & \frac{v_4}{4v_1} \end{bmatrix},$$

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$$\mathbf{S}_{\text{ME/DR}} = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ c_1^2 - \frac{1+2cc_1}{v} + \frac{c^2}{v_1} & -c_1^2 & 2cc_1 & 0 & 0 & \frac{2cv_2(v_1-cv_2)}{vv_1} & -c^2 & 0 & 0 & 0 & 0 & \frac{c^2v_2v_3}{vv_1} & 0 \\ \frac{cv_2}{2vv_1^2} & 0 & \frac{c_1v_2}{2v_1} & \frac{v_1+c-cv_1}{v_1} & \frac{vc_1}{v_1} & \frac{v_2^2(v_1-cv_3)}{2vv_1^2} & -\frac{cv_2}{2v_1} & 0 & -\frac{cv}{v_1} & 0 & 0 & \frac{cv_2^2v_3}{2vv_1^2} & \frac{cv_2}{v_1} \\ -\frac{c_1v_2}{2vv_1} & -\frac{c_1}{2v_1} & \frac{v_1-cv_2}{2v_1} & \frac{1}{2v_1} & \frac{vc_1}{v_1} & \frac{v_2(v_2-cv_4)}{2v_1v} & \frac{c}{2} & 0 & -\frac{cv}{v_1} & 0 & 0 & \frac{cv_2v_3}{2v_1v} & 0 \\ 0 & -\frac{c_1}{v} & \frac{v_1-cv_2}{v} & \frac{2v_1-2cv_2}{v} & 3c_1 & 0 & \frac{cv_1}{v} & 0 & -3c & 0 & 0 & 0 & \frac{2cv_2}{v} \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \frac{v_2^2}{4vv_1^3} & 0 & 0 & \frac{v_2}{v_1^2} & \frac{v}{2v_1^2} & \frac{v_2^3}{2vv_1^3} & -\frac{v_2^2}{4v_1^2} & 0 & -\frac{vv_3}{2v_1^2} & \frac{v}{2v_1} & -\frac{v^2}{v_1^2} & \frac{v_2^3v_3}{4vv_1^3} & \frac{v_2^2}{v_1^2} \\ \frac{v_2^2}{2vv_1^3} & 0 & 0 & \frac{2v_2}{v_1^2} & \frac{v}{v_1^2} & \frac{v_2^3}{vv_1^3} & 0 & -\frac{v_2^2}{4v_1^2} & \frac{v}{v_1} & \frac{1-v_1^2}{v_1^2} & -\frac{v^2}{v_1^2} & \frac{v_2^3v_3}{4vv_1^3} & \frac{v_2^2}{v_1^2} \\ 0 & 0 & \frac{v_2}{2vv_1} & \frac{v_2}{vv_1} & \frac{3}{2v_1} & 0 & \frac{v_2}{2v} & 0 & \frac{3}{2v_1} & 1 & -\frac{5v}{2v_1} & 0 & 1 - \frac{4}{v} + \frac{1}{v_1} \\ 0 & 0 & 0 & \frac{2v_2}{vv_1} & \frac{2}{v_1} & 0 & 0 & \frac{v_2}{2v} & 2 & \frac{5-2v}{2v_1} & -\frac{5v}{2v_1} & 0 & 1 - \frac{4}{v} + \frac{1}{v_1} \\ 0 & 0 & 0 & 0 & \frac{4}{v} & 0 & 0 & 0 & \frac{4v_1}{v} & \frac{2v_1}{v} & -6 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \frac{1}{2v_1} & \frac{1}{v_1} & 0 & \frac{v_4}{2vv_1} & \frac{1}{2} & \frac{1}{4} & -\frac{v}{v_1} & -\frac{v}{2v_1} & 0 & \frac{v+5}{4v_1} - \frac{3}{v} & \frac{1}{2} \end{bmatrix},$$

1024 **DH mating system**

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$$\mathbf{T}_{\text{DH}} = \begin{bmatrix} \frac{c_1^2 v_2}{2v_1} & \frac{vc_1^2}{2v_1} & -\frac{cvc_1}{v_1} & 0 & 0 & -\frac{cc_1 v_2}{v_1} & \frac{c^2 v}{2v_1} & 0 & 0 & 0 & 0 & \frac{c^2 v_2}{2v_1} & 0 \\ 0 & c_1^2 & -2cc_1 & 0 & 0 & 0 & c^2 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & -\frac{c_1 v_2}{2v_1} & 0 & -\frac{vc_1}{2v_1} & 0 & \frac{cv_2}{2v_1} & 0 & \frac{cv}{2v_1} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & -\frac{c_1 v_2}{2v_1} & -\frac{vc_1}{2v_1} & 0 & 0 & 0 & \frac{cv}{2v_1} & 0 & 0 & 0 & \frac{cv_2}{2v_1} \\ 0 & 0 & 0 & 0 & -c_1 & 0 & 0 & 0 & c & 0 & 0 & 0 & 0 \\ 0 & 0 & -\frac{vc_1}{4v_1} & -\frac{vc_1}{2v_1} & 0 & -\frac{c_1 v_4}{4v_1} & \frac{cv}{4v_1} & 0 & 0 & 0 & 0 & \frac{cv_4}{4v_1} & \frac{cv}{2v_1} \\ 0 & 0 & 0 & 0 & 0 & 0 & \frac{v_2^2}{4v_1^2} & 0 & \frac{vv_2}{2v_1^2} & 0 & \frac{v^2}{4v_1^2} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{v_2^2}{4v_1^2} & 0 & \frac{vv_2}{2v_1^2} & \frac{v^2}{4v_1^2} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{v_2}{2v_1} & 0 & \frac{v}{2v_1} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{v_2}{2v_1} & \frac{v}{2v_1} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & \frac{vv_2}{4v_1 v_3} & \frac{vv_2}{8v_1 v_3} & 0 & 0 & 0 & \frac{v_4 v_6}{8v_1 v_3} & \frac{vv_4}{2v_1 v_3} \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{v}{2v_1} & \frac{v}{4v_1} & 0 & 0 & \frac{v_4}{4v_1} \end{bmatrix},$$

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$$\mathbf{s}_{\text{DH}} = \begin{bmatrix} c_1^2 - \frac{1+2cc_1}{v} + \frac{c^2}{v_1} & 0 & 0 & 0 & 0 & \frac{2cv_2(v_1 - cv_2)}{vv_1} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ -c_1^2 & -c_1^2 & 2cc_1 & 0 & 0 & -c^2 & 0 & 0 & 0 & 0 & 0 & \frac{cv_2^2 v_3}{2vv_1^2} & \frac{cv_2}{v_1} \\ \frac{cv_2}{2vv_1^2} & 0 & \frac{c_1 v_2}{2v_1} & \frac{v_1 + c(1 - v_1)}{v_1} & \frac{vc_1}{v_1} & \frac{v_2^2(v_1 - cv_3)}{2vv_1^2} & -\frac{cv_2}{2v_1} & 0 & -\frac{cv}{v_1} & 0 & 0 & \frac{cv_2^2 v_3}{2vv_1^2} & \frac{cv_2}{v_1} \\ -\frac{c_1 v_2}{2vv_1} & -\frac{c_1}{2v_1} & \frac{v_1 - cv_2}{2v_1} & \frac{1}{2v_1} & \frac{vc_1}{v_1} & \frac{v_2(v_2 - cv_4)}{2vv_1} & \frac{c}{2} & 0 & -\frac{cv}{v_1} & 0 & 0 & \frac{cv_2 v_3}{2v_1 v} & 0 \\ 0 & -\frac{c_1}{v} & \frac{v_1 - cv_2}{v} & \frac{2v_1 - 2cv_2}{v} & 3c_1 & 0 & \frac{cv_1}{v} & 0 & -3c & 0 & 0 & 0 & \frac{2cv_2}{v} \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \frac{v_2^2}{4vv_1^3} & \frac{1}{2(1+f)v_1^2} & \frac{1}{(1+f)v_1} & \frac{v_2}{v_1^2} & \frac{vf_1}{2(1+f)v_1^2} & \frac{v_2^3}{2vv_1^3} & \frac{v^2 - fv_2^2 - 2}{4(1+f)v_1^2} & \frac{1}{2+2f} & \frac{v[5+3f-(3+f)v]}{2(1+f)v_1^2} & \frac{vf_1}{2(1+f)v_1} & -\frac{fv^2}{(1+f)v_1^2} & \frac{v_2^3 v_3}{4vv_1^3} & \frac{v_2^2}{v_1^2} \\ \frac{v_2^2}{2vv_1^3} & \frac{1}{(1+f)v_1^2} & \frac{2}{(1+f)v_1} & \frac{2v_2}{v_1^2} & \frac{vf_1}{(1+f)v_1^2} & \frac{v_2^3}{vv_1^3} & \frac{1}{1+f} & -\frac{v_2^2}{4v_1^2} & \frac{vf_1}{(1+f)v_1} & \frac{1-v_1^2}{v_1^2} & -\frac{fv^2}{(1+f)v_1^2} & \frac{v_2^3 v_3}{4vv_1^3} & \frac{v_2^2}{v_1^2} \\ 0 & 0 & \frac{1}{v} - \frac{1}{2v_1} & \frac{v_2}{vv_1} & \frac{3}{2v_1} & 0 & \frac{1}{2} - \frac{1}{v} & 0 & \frac{3}{2v_1} & 1 & -\frac{5v}{2v_1} & 0 & 1 - \frac{4}{v} + \frac{1}{v_1} \\ 0 & 0 & 0 & \frac{2v_2}{vv_1} & \frac{3}{2v_1} & 0 & 0 & \frac{1}{2} - \frac{1}{v} & \frac{3}{2} & \frac{3-2v_1}{2v_1} & -\frac{2v}{v_1} & 0 & 1 - \frac{4}{v} + \frac{1}{v_1} \\ 0 & 0 & 0 & 0 & \frac{4}{v} & 0 & 0 & 0 & 4 - \frac{4}{v} & 2 - \frac{2}{v} & -6 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \frac{1}{2v_1} & \frac{1}{v_1} & 0 & \frac{v_4}{2vv_1} & \frac{1}{2} & \frac{1}{4} & -\frac{v}{v_1} & -\frac{v}{2v_1} & 0 & -\frac{3}{v} + \frac{5+v}{4v_1} & \frac{1}{2} \end{bmatrix}.$$

Appendix I. Bias correction for D and Δ

If the allele frequency is estimated from the samples, the estimates $\hat{p}$ and $\hat{q}$ are unbiased, but their product $\hat{p}\hat{q}$ is biased. Because pq appears in the expressions of D and Δ , we should consider the correction of biases during estimating D and Δ . In this appendix, we will follow the method for the unbiased estimation of Weir (1979) to give the unbiased estimate formulas for D and Δ , where D , Δ , p and q are short for D_{AB} , Δ_{AB} , p_A and q_B in turn.

We begin our discussion with the expectation $E[\hat{p}_A\hat{q}_B]$. According to the facts that

$\hat{p}_A = \frac{1}{nv} \sum_{i,j=1}^v x_{ij}$ and $\hat{q}_B = \frac{1}{nv} \sum_{i,j=1}^v y_{ij}$, we have

$$E[\hat{p}_A\hat{q}_B] = \frac{1}{n^2v^2} E\left[\left(\sum_{i,j=1}^v x_{ij}\right)\left(\sum_{i,j=1}^v y_{ij}\right)\right] = p_Aq_B + \frac{1}{nv} [D_s^{AB} + (v-1)D_d^{AB}].$$

For the case of phased genotypes, since $D_{AB} = D_s^{AB}$, the following holds:

$$E[\hat{p}_A\hat{q}_B] = p_Aq_B + \frac{1}{nv} [D_{AB} + (v-1)D_d^{AB}].$$

In addition, $D_s^{AB} = P_s^{AB} - p_Aq_B$ and $D_d^{AB} = P_d^{AB} - p_Aq_B$, we obtain

$$\begin{aligned} E[\tilde{D}_s^{AB}] &= E[\hat{P}_s^{AB}] - E[\hat{p}_A\hat{q}_B] \\ &= P_s^{AB} - p_Aq_B - \frac{1}{nv} [D_{AB} + (v-1)D_d^{AB}] \\ &= \frac{nv-1}{nv} D_{AB} - \frac{v-1}{nv} D_d^{AB}, \end{aligned}$$

$$\begin{aligned} E[\tilde{D}_d^{AB}] &= E[\hat{P}_d^{AB}] - E[\hat{p}_A\hat{q}_B] \\ &= P_d^{AB} - p_Aq_B - \frac{1}{nv} [D_{AB} + (v-1)D_d^{AB}] \\ &= -\frac{1}{nv} D_{AB} + \frac{nv-v+1}{nv} D_d^{AB}. \end{aligned}$$

Replacing $E[\tilde{D}_s^{AB}]$ by $\tilde{D}_s^{AB}$, $E[\tilde{D}_d^{AB}]$ by $\tilde{D}_d^{AB}$, D_{AB} by $\hat{D}_{AB}$ and D_d^{AB} by $\hat{D}_d^{AB}$, it follows

$$\begin{aligned} \tilde{D}_s^{AB} &= \frac{nv-1}{nv} \hat{D}_{AB} - \frac{v-1}{nv} \hat{D}_d^{AB}, \\ \tilde{D}_d^{AB} &= -\frac{1}{nv} \hat{D}_{AB} + \frac{nv-v+1}{nv} \hat{D}_d^{AB}. \end{aligned}$$

This is a linear equation set with $\hat{D}_{AB}$ and $\hat{D}_d^{AB}$ as the unknowns, the solution of which for $\hat{D}_{AB}$ is the unbiased estimate for D_{AB} , and its expression is as follows:

$$\hat{D}_{AB} = \frac{(n-1)v+1}{(n-1)v} \tilde{D}_s^{AB} + \frac{v-1}{(n-1)v} \tilde{D}_d^{AB}.$$

For the case of unphased genotypes, by $\Delta_{AB} = D_s^{AB} + (v-1)D_d^{AB}$, the following holds:

$$E[\hat{p}_A \hat{q}_B] = p_A q_B + \frac{1}{nv} \Delta_{AB}.$$

In addition, $\Delta_{AB} = \left(\sum_{i,j=1}^v \frac{ij}{v} G_{B^j X^{v-i}}^{A^i X^{v-i}} \right) - vp_A q_B$ by Equation (1). Hence

$$\begin{aligned} E[\tilde{\Delta}_{AB}] &= \left(\sum_{i,j=1}^v \frac{ij}{v} E \left[\hat{G}_{B^j X^{v-i}}^{A^i X^{v-i}} \right] \right) - vE[\hat{p}_A \hat{q}_B] \\ &= \left(\sum_{i,j=1}^v \frac{ij}{v} G_{B^j X^{v-i}}^{A^i X^{v-i}} \right) - vp_A q_B - \frac{1}{n} \Delta_{AB} \\ &= \frac{n-1}{n} \Delta_{AB}. \end{aligned}$$

Now, replacing $E[\tilde{\Delta}_{AB}]$ by $\tilde{\Delta}_{AB}$ and Δ_{AB} by $\hat{\Delta}_{AB}$, it follows the unbiased estimate formula for Δ_{AB} as follows:

$$\hat{\Delta}_{AB} = \frac{n}{n-1} \tilde{\Delta}_{AB}.$$

1065 **Supplementary Tables**

1066 **Table S1. Elements in combination matrix A_1**

	$E(\widehat{D}_w^2)$	$E(\widehat{D}_b^2)$	$E(\widehat{D}_w\widehat{D}_b)$	$E(\widehat{D}^2)$	$E(\widehat{\Delta}^2)$	$E(\widehat{Q})$	$E(\widehat{R})$
Θ_1	0	0	0	0	0	0	0
Θ_2	1	0	0	1	1	0	0
Γ_1	-2	0	1	0	$2v_1$	0	0
Γ_2	0	0	0	0	0	0	0
Γ_3	0	0	-1	-2	$-2v$	0	0
Γ_4	0	0	0	0	0	0	0
Δ_1	1	1	-1	0	v_1^2	0	0
Δ_2	0	0	0	0	0	0	v_1^2
Δ_3	0	-2	1	0	$-2v_1v$	0	0
Δ_4	0	0	0	0	0	0	$-2v_1v$
Δ_5	0	1	0	1	v^2	1	v^2
Δ_6	0	0	0	0	0	0	0
Δ_7	0	0	0	0	0	0	0

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Table S2. Elements in combination matrix A_2

	$E(\widehat{D}_w^2)$	$E(\widehat{D}_b^2)$	$E(\widehat{D}_w\widehat{D}_b)$	$E(\widehat{D}^2)$	$E(\widehat{\Delta}^2)$	$E(\widehat{Q})$	$E(\widehat{R})$
Θ_1	$\frac{v_1^2 + 1}{vv_1}$	$\frac{1}{vv_1}$	$-\frac{1}{vv_1}$	$\frac{v_1}{v}$	$\frac{2v_1}{v}$	0	$\frac{2v_1}{v}$
Θ_2	-1	0	$-\frac{1}{v}$	$-\frac{2+v}{v}$	-3	0	0
Γ_1	2	$-\frac{2}{v}$	$-\frac{2v_1}{v}$	$-\frac{2v_1}{v}$	$-6v_1$	0	0
Γ_2	0	$-\frac{4}{v}$	$-\frac{2v_2}{v}$	$-\frac{4v_1}{v}$	$-8v_1$	0	$-8v_1$
Γ_3	0	$\frac{4}{v}$	3	$\frac{4+6v}{v}$	$10v$	$\frac{4}{v}$	$4v$
Γ_4	$-\frac{2v_2^2}{vv_1}$	$\frac{2v_2}{vv_1}$	$\frac{v_2v_3}{vv_1}$	0	$\frac{4v_1v_2}{v}$	0	$\frac{4v_1v_2}{v}$
Δ_1	-1	$\frac{2-3v}{v}$	$\frac{2v-1}{v}$	0	$-3v_1^2$	0	0
Δ_2	0	0	0	0	0	0	$-3v_1^2$
Δ_3	0	$\frac{10v-4}{v}$	-3	$\frac{4v_1}{v}$	$10vv_1$	$\frac{4v_1}{v}$	$4vv_1$
Δ_4	0	$\frac{2v_1}{v}$	0	$\frac{2v_1}{v}$	$2vv_1$	$\frac{2v_1}{v}$	$8vv_1$
Δ_5	0	-6	0	-6	$-6v^2$	-6	$-6v^2$
Δ_6	$\frac{v_2v_3}{vv_1}$	$\frac{v_2v_3}{vv_1}$	$-\frac{v_2v_3}{vv_1}$	0	$\frac{v_1v_2v_3}{v}$	0	$\frac{v_1v_2v_3}{v}$
Δ_7	0	$-\frac{4v_2}{v}$	$\frac{2v_2}{v}$	0	$-4v_1v_2$	0	$-4v_1v_2$

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Table S3. Essential factors to form Ω^T for HS mating system

	Θ'_1 to Θ'_2	Γ'_1 to Γ'_4	Δ'_1 to Δ'_7
Θ_1	$c^2 + c_1^2 v_1^2$	$v_1 - cv_2$	$2v_1$
Θ_2	$vc_1^2 N_1 v_1$	$-c_1 N_1 v$	$2vN_1$
Γ_1	$-2cvc_1 N_1 v_1$	$vN_1(v_1 - cv_2)$	$4vN_1 v_1$
Γ_2	0	$2vN_1(v_1 - cv_2)$	$8vN_1 v_1$
Γ_3	0	$-v^2 c_1 N_1 N_2$	$4v^2 N_1 N_2$
Γ_4	$-2cv_2(cv_2 - v_1)$	$(v_1 - cv_4)v_2$	$4v_1 v_2$
Δ_1	$c^2 v N_1 v_1$	$cvN_1 v_1$	$2vN_1 v_1^2$
Δ_2	0	0	$vN_1 v_1^2$
Δ_3	0	$cv^2 N_1 N_2$	$4v^2 N_1 N_2 v_1$
Δ_4	0	0	$2v^2 N_1 N_2 v_1$
Δ_5	0	0	$v^3 N_1 N_2 N_3$
Δ_6	$c^2 v_2 v_3$	$cv_2 v_3$	$v_1 v_2 v_3$
Δ_7	0	$2cvN_1 v_2$	$4vN_1 v_1 v_2$
Divisor	Nvv_1	$N^2 v^2$	$N^3 v^3$

1073 There are 13 columns for Ω^T , the first two columns are the same, each of which is Nvv_1
1074 times of the combination coefficients of Θ'_1 or Θ'_2 . Similarly, the next four columns are
1075 the same, so are the last seven columns. Moreover, $c - 1$ is denoted by c_1 , $N - i$ by N_i
1076 and $v - i$ by v_i , $i = 1, 2, 3$.

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Table S4. Approximations of d^2

v	HS	MS/ME/DR	DH
2	$\frac{1 - 2c + 2c^2}{4cN_e - 2c^2N_e}$	$\frac{1 - 2c + 2c^2}{4cN_e - 2c^2N_e}$	$-\frac{1 + f - 2c(1 + f) + c^2(3 + 2f)}{2(-2 + c)c(1 + f)N_e}$
4	$\frac{3 - 6c + 4c^2}{24cN_e - 12c^2N_e}$	$\frac{16 - 24c + 12c^2 + 5c^3}{128cN_e - 32c^3N_e}$	$-\frac{16(1 + f) - 24c(1 + f) + 4c^2(5 + 3f) + c^3(3 + 5f)}{32c(-4 + c^2)(1 + f)N_e}$
6	$\frac{5 - 10c + 6c^2}{60cN_e - 30c^2N_e}$	$\frac{63 - 84c + 14c^2 + 32c^3}{126c(6 + c - 2c^2)N_e}$	$-\frac{63(1 + f) - 84c(1 + f) + 7c^2(5 + 2f) + c^3(26 + 32f)}{126c(-6 - c + 2c^2)(1 + f)N_e}$
8	$\frac{7 - 14c + 8c^2}{112cN_e - 56c^2N_e}$	$\frac{160 - 200c - 10c^2 + 99c^3}{2560cN_e + 640c^2N_e - 960c^3N_e}$	$-\frac{-10c^2(-3 + f) + 160(1 + f) - 200c(1 + f) + c^3(87 + 99f)}{320c(-8 - 2c + 3c^2)(1 + f)N_e}$
10	$\frac{9 - 18c + 10c^2}{180cN_e - 90c^2N_e}$	$\frac{-325 + 390c + 78c^2 - 224c^3}{650c(-10 - 3c + 4c^2)N_e}$	$-\frac{-325(1 + f) + 390c(1 + f) + 13c^2(1 + 6f) - 4c^3(51 + 56f)}{650c(-10 - 3c + 4c^2)(1 + f)N_e}$

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Each expression should be added $\mathbf{1}/(vn)$ in order to consider the sampling variance.

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Table S5. Approximations of δ^2

v	HS	MS/ME/DR	DH
2	$\frac{1 - 2c + 2c^2}{4cN_e - 2c^2N_e}$	$\frac{-1 + 2c - 2c^2}{2(-2 + c)c(N_e - v^2\eta)}$	$-\frac{1 + f - 2cf + 2c^2(1 + f)}{2(-2 + c)c(1 + f)(N_e - v^2\eta)}$
4	$\frac{3 - 6c + 4c^2}{24cN_e - 12c^2N_e}$	$\frac{-4 + 3c - 12c^2 + 4c^3}{2c(-4 + c^2)(4N_e - v^2\eta)}$	$\frac{3c(-5 + f) - 4(1 + f) + 4c^3(3 + f) - 4c^2(5 + 3f)}{2c(-4 + c^2)(1 + f)(4N_e - v^2\eta)}$
6	$\frac{5 - 10c + 6c^2}{60cN_e - 30c^2N_e}$	$\frac{9(-7 - 4c - 26c^2 + 12c^3)}{14c(-6 - c + 2c^2)(9N_e - v^2\eta)}$	$\frac{9[-7(1 + f) + 12c^3(3 + f) - 2c(27 + 2f) - 2c^2(25 + 13f)]}{14c(-6 - c + 2c^2)(1 + f)(9N_e - v^2\eta)}$
8	$\frac{7 - 14c + 8c^2}{112cN_e - 56c^2N_e}$	$\frac{4(-10 - 19c - 44c^2 + 24c^3)}{5c(-8 - 2c + 3c^2)(16N_e - v^2\eta)}$	$\frac{4[-10(1 + f) + 24c^3(3 + f) - 4c^2(23 + 11f) - c(117 + 19f)]}{5c(-8 - 2c + 3c^2)(1 + f)(16N_e - v^2\eta)}$
10	$\frac{9 - 18c + 10c^2}{180cN_e - 90c^2N_e}$	$\frac{25(-13 - 42c - 66c^2 + 40c^3)}{26c(-10 - 3c + 4c^2)(25N_e - v^2\eta)}$	$\frac{25[-13(1 + f) + 40c^3(3 + f) - 6c(34 + 7f) - 2c^2(73 + 33f)]}{26c(-10 - 3c + 4c^2)(1 + f)(25N_e - v^2\eta)}$

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Where $\eta = \frac{2(v-2)(v-1)}{v^2}$ for the MS mating system, or $\eta = \frac{4(v-1)^2}{v^2}$ for the ME/DR/DH mating systems. Each expression

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should be added $1/n$ in order to consider the sampling variance.

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Table S6. Exact d^2 and δ^2

Mating System	v	$d^2_{c=0.5}$	$d^2_{c=1-1/v}$	Error rate	$\delta^2_{c=0.5}$	$\delta^2_{c=1-1/v}$	Error rate
HS	2	0.0083	0.0083	0.00%	0.0134	0.0134	0.00%
	4	0.0036	0.0032	13.95%	0.0112	0.0108	4.13%
	6	0.0023	0.0020	19.45%	0.0108	0.0104	3.69%
	8	0.0017	0.0014	22.49%	0.0106	0.0103	3.11%
	10	0.0014	0.0011	24.43%	0.0105	0.0102	2.66%
MS	2	0.0083	0.0083	0.00%	0.0134	0.0134	0.00%
	4	0.0038	0.0033	13.06%	0.0134	0.0134	0.13%
	6	0.0024	0.0020	18.63%	0.0134	0.0135	-0.41%
	8	0.0018	0.0015	21.81%	0.0134	0.0135	-0.51%
	10	0.0014	0.0011	23.85%	0.0134	0.0135	-0.51%
ME	2	0.0083	0.0083	0.00%	0.0133	0.0133	0.00%
	4	0.0037	0.0033	12.99%	0.0133	0.0133	0.06%
	6	0.0024	0.0020	18.55%	0.0133	0.0133	-0.47%
	8	0.0018	0.0014	21.71%	0.0133	0.0133	-0.57%
	10	0.0014	0.0011	23.74%	0.0133	0.0133	-0.56%
DR ($f = 1$)	2	0.0083	0.0083	0.00%	0.0133	0.0133	0.00%
	4	0.0037	0.0033	12.96%	0.0133	0.0133	0.04%
	6	0.0024	0.0020	18.52%	0.0133	0.0134	-0.48%
	8	0.0018	0.0014	21.69%	0.0133	0.0134	-0.58%
	10	0.0014	0.0011	23.72%	0.0133	0.0134	-0.56%
DR ($f = 2$)	2	0.0083	0.0083	0.00%	0.0133	0.0133	0.00%
	4	0.0037	0.0033	12.95%	0.0133	0.0133	0.04%
	6	0.0024	0.0020	18.51%	0.0133	0.0134	-0.49%
	8	0.0018	0.0014	21.68%	0.0133	0.0134	-0.58%
	10	0.0014	0.0011	23.72%	0.0133	0.0134	-0.57%
DR ($f = 5$)	2	0.0082	0.0082	0.00%	0.0133	0.0133	0.00%
	4	0.0037	0.0033	12.93%	0.0133	0.0133	0.02%
	6	0.0024	0.0020	18.50%	0.0133	0.0133	-0.50%
	8	0.0018	0.0014	21.67%	0.0133	0.0134	-0.59%
	10	0.0014	0.0011	23.71%	0.0133	0.0134	-0.58%
DH ($f = 1$)	2	0.0091	0.0091	0.00%	0.0166	0.0166	0.00%
	4	0.0039	0.0035	10.13%	0.0166	0.0168	-1.20%
	6	0.0024	0.0021	16.04%	0.0165	0.0168	-1.35%
	8	0.0018	0.0015	19.59%	0.0165	0.0167	-1.22%
	10	0.0014	0.0012	21.92%	0.0165	0.0167	-1.07%
DH ($f = 2$)	2	0.0088	0.0088	0.00%	0.0155	0.0155	0.00%
	4	0.0038	0.0034	11.04%	0.0154	0.0156	-0.85%
	6	0.0024	0.0021	16.85%	0.0154	0.0156	-1.10%
	8	0.0018	0.0015	20.28%	0.0154	0.0156	-1.03%

	10	0.0014	0.0011	22.51%	0.0154	0.0156	-0.93%
	2	0.0085	0.0085	0.00%	0.0144	0.0144	0.00%
	4	0.0038	0.0034	11.96%	0.0143	0.0144	-0.45%
DH	6	0.0024	0.0020	17.66%	0.0143	0.0145	-0.83%
($f = 5$)	8	0.0018	0.0015	20.96%	0.0143	0.0145	-0.83%
	10	0.0014	0.0011	23.10%	0.0143	0.0144	-0.77%

1087 Where the effective population size N_e and the sample size n are 100, and the error
1088 rate is calculated by $(d_{c=0.5}^2 - d_{c=1-1/v}^2)/d_{c=1-1/v}^2$ or $(\delta_{c=0.5}^2 - \delta_{c=1-1/v}^2)/\delta_{c=1-1/v}^2$.

Supplementary Figures

Figure S1. The behaviors of $\hat{r}^2$ and $\hat{r}_\Delta^2$ for various mating systems (set $N_e = 40$, $v = 2$, 4, 6 or 8, $L = 200$ and $c = 0.1$; for DR and DH, also set $f = 2$ or 5). Each column shows the results under a different mating system. Each row shows the results under a different ploidy level. Solid gray lines denote the approximate d^2 or δ^2 , dotted gray lines denote the exact d^2 or δ^2 , and solid lines denote $\hat{r}^2$ and $\hat{r}_\Delta^2$, where the lines denoting δ^2 (or $\hat{r}_\Delta^2$) are above those denoting d^2 (or $\hat{r}^2$) for each situation.

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1100 **Figure S2.** The behaviors of $\hat{r}^2$ and $\hat{r}_{\Delta}^2$ for the MS mating system under different
 1101 recombination rates (set $N_e = 80$ and $L = 200$). The number above a line represents a
 1102 recombination rate.

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1106 **Figure S3.** The relationship between d^2 (or δ^2) and the recombination rate c for various
1107 mating systems (set $N_e = 100$ and $n = 100$). The line styles are the same as those in
1108 Figure 2. Each subscript of d^2 or δ^2 denotes a mating system, e.g. the subscript DR1 is
1109 the DR mating system with $f = 1$.

Figure S4. The relationship between the bias of $\hat{V}$ and the sample size n . The figure layout and the line style are the same as those in Figure 3.