Fst between haploids and diploids in species with discrete ploidal generations

Here we put supplementary information for our manuscript, “Fst between haploids and diploids in species with discrete ploidal generations”.
Note that, you might have to reset the variables as necessary because we reuse same variables in the different sections.

Appendix

Appendix A

Equations

We define the probabilities of identities Qij of genes sampled in deme i and j (QHD=QDH).
When we derive the recursions for Q, we assume that the number of haploid and diploid individuals are fixed as $NH = N\,\rho_H$ and $ND = N\,\rho_D$. We also assume that the probability of identity from diploid population is independent of whether the two alleles are sampled from the same individual or different individuals (no inbreeding).

$$\text{NextQHH} = (1-\mu)^2 * \left(\text{mHfromH}^2 * \left(\frac{1}{\text{Hap}} + \left(1 - \frac{1}{\text{Hap}}\right) * \text{QHH}\right) + \text{mHfromH} * \text{mHfromD} * \text{QHD} + \text{mHfromD} * \text{mHfromH} * \text{QDH} + \text{mHfromD}^2 * \left(\frac{1}{2 * \text{Dip}} + \left(1 - \frac{1}{2 * \text{Dip}}\right) * \text{QDD}\right)\right);$$

$$\text{NextQHD} = (1-\mu)^2 * \left(\text{mHfromH} * \text{mDfromH} * \left(\frac{1}{\text{Hap}} + \left(1 - \frac{1}{\text{Hap}}\right) * \text{QHH}\right) + \text{mHfromH} * \text{mDfromD} * \text{QHD} + \text{mHfromD} * \text{mDfromH} * \text{QDH} + \text{mHfromD} * \text{mDfromD} * \left(\frac{1}{2 * \text{Dip}} + \left(1 - \frac{1}{2 * \text{Dip}}\right) * \text{QDD}\right)\right);$$

$$\text{NextQDH} = (1-\mu)^2 * \left(\text{mDfromH} * \text{mHfromH} * \left(\frac{1}{\text{Hap}} + \left(1 - \frac{1}{\text{Hap}}\right) * \text{QHH}\right) + \text{mDfromH} * \text{mHfromD} * \text{QHD} + \text{mDfromD} * \text{mHfromH} * \text{QDH} + \text{mDfromD} * \text{mHfromD} * \left(\frac{1}{2 * \text{Dip}} + \left(1 - \frac{1}{2 * \text{Dip}}\right) * \text{QDD}\right)\right);$$

$$\text{NextQDD} = (1-\mu)^2 * \left(\text{mDfromD}^2 * \left(\frac{1}{2 * \text{Dip}} + \left(1 - \frac{1}{2 * \text{Dip}}\right) * \text{QDD}\right) + \text{mDfromH} * \text{mDfromD} * \text{QHD} + \text{mDfromD} * \text{mDfromH} * \text{QDH} + \text{mDfromH}^2 * \left(\frac{1}{\text{Hap}} + \left(1 - \frac{1}{\text{Hap}}\right) * \text{QHH}\right)\right);$$

The recursion equations for Q can be described as, $(1-\mu)^2 A\,(Q+c)$;
(this equation corresponds to Eq. (9.30) in Rousset (2004))

$$\text{MatrixA} = \begin{pmatrix} \text{mHfromH} * \text{mHfromH} & \text{mHfromH} * \text{mHfromD} & \text{mHfromD} * \text{mHfromH} & \text{mHfromD} * \text{mHfromD} \\ \text{mHfromH} * \text{mDfromH} & \text{mHfromH} * \text{mDfromD} & \text{mHfromD} * \text{mDfromH} & \text{mHfromD} * \text{mDfromD} \\ \text{mDfromH} * \text{mHfromH} & \text{mDfromH} * \text{mHfromD} & \text{mDfromD} * \text{mHfromH} & \text{mDfromD} * \text{mHfromD} \\ \text{mDfromH} * \text{mDfromH} & \text{mDfromH} * \text{mDfromD} & \text{mDfromD} * \text{mDfromH} & \text{mDfromD} * \text{mDfromD} \end{pmatrix};$$

$$\text{VectC} = \begin{pmatrix} \frac{1}{\text{Hap}} * (1 - \text{QHH}) \\ 0 \\ 0 \\ \frac{1}{2*\text{Dip}} * (1 - \text{QDD}) \end{pmatrix};$$

$$\begin{pmatrix} \text{NextQHH} \\ \text{NextQHD} \\ \text{NextQDH} \\ \text{NextQDD} \end{pmatrix} - (1-\mu)^2 * \text{MatrixA}. \left(\begin{pmatrix} \text{QHH} \\ \text{QHD} \\ \text{QDH} \\ \text{QDD} \end{pmatrix} + \text{VectC} \right) \text{ // Simplify}$$

```
{{0}, {0}, {0}, {0}}
```

Note that, we can write, A = TensorProduct[F, F]

$$\text{MatrixF} = \begin{pmatrix} \text{mHfromH} & \text{mHfromD} \\ \text{mDfromH} & \text{mDfromD} \end{pmatrix};$$

```
TensorProduct[MatrixF, MatrixF] // MatrixForm
MatrixA // MatrixForm
```

$$\begin{pmatrix} \begin{pmatrix} \text{mHfromH}^2 & \text{mHfromD mHfromH} \\ \text{mDfromH mHfromH} & \text{mDfromD mHfromH} \end{pmatrix} & \begin{pmatrix} \text{mHfromD mHfromH} & \text{mHfromD}^2 \\ \text{mDfromH mHfromD} & \text{mDfromD mHfromD} \end{pmatrix} \\ \begin{pmatrix} \text{mDfromH mHfromH} & \text{mDfromH mHfromD} \\ \text{mDfromH}^2 & \text{mDfromD mDfromH} \end{pmatrix} & \begin{pmatrix} \text{mDfromD mHfromH} & \text{mDfromD mHfromD} \\ \text{mDfromD mDfromH} & \text{mDfromD}^2 \end{pmatrix} \end{pmatrix}$$

$$\begin{pmatrix} \text{mHfromH}^2 & \text{mHfromD mHfromH} & \text{mHfromD mHfromH} & \text{mHfromD}^2 \\ \text{mDfromH mHfromH} & \text{mDfromD mHfromH} & \text{mDfromH mHfromD} & \text{mDfromD mHfromD} \\ \text{mDfromH mHfromH} & \text{mDfromH mHfromD} & \text{mDfromD mHfromH} & \text{mDfromD mHfromD} \\ \text{mDfromH}^2 & \text{mDfromD mDfromH} & \text{mDfromD mDfromH} & \text{mDfromD}^2 \end{pmatrix}$$

Note that, the matrix A is a probability matrix;

$$\text{MatrixA}. \begin{pmatrix} 1 \\ 1 \\ 1 \\ 1 \end{pmatrix} \text{ /. mHfromD} \to 1 - \text{mHfromH /. mDfromH} \to 1 - \text{mDfromD // Simplify}$$

```
{{1}, {1}, {1}, {1}}
```

Furthermore, this can be represented as, $(1-\mu)^2$ (GQ + Aδ) and $(1-\mu)^2$ (GQ + $(I - G)$ 1); (this equation corresponds to Eq. (4.4) in Rousset (2004))

```
MatrixG =
```

$$\begin{pmatrix} mHfromH^2*\left(1-\frac{1}{Hap}\right) & mHfromH*mHfromD & mHfromD*mHfromH & mHfromD^2*\left(1-\frac{1}{2*D}\right. \\ mHfromH*mDfromH*\left(1-\frac{1}{Hap}\right) & mHfromH*mDfromD & mHfromD*mDfromH & mHfromD*mDfromD*(1 \\ mDfromH*mHfromH*\left(1-\frac{1}{Hap}\right) & mDfromH*mHfromD & mDfromD*mHfromH & mDfromD*mHfromD*(1 \\ mDfromH^2*\left(1-\frac{1}{Hap}\right) & mDfromH*mDfromD & mDfromD*mDfromH & mDfromD^2*\left(1-\frac{1}{2*D}\right. \end{pmatrix};$$

$$Vect\delta = \begin{pmatrix} \frac{1}{Hap} \\ 0 \\ 0 \\ \frac{1}{2*Dip} \end{pmatrix};$$

$$\begin{pmatrix} NextQHH \\ NextQHD \\ NextQDH \\ NextQDD \end{pmatrix} - (1-\mu)^2 * \left(MatrixG.\begin{pmatrix} QHH \\ QHD \\ QDH \\ QDD \end{pmatrix} + MatrixA.Vect\delta \right) \text{ // Simplify}$$

$$\begin{pmatrix} NextQHH \\ NextQHD \\ NextQDH \\ NextQDD \end{pmatrix} - (1-\mu)^2 * \left(MatrixG.\begin{pmatrix} QHH \\ QHD \\ QDH \\ QDD \end{pmatrix} + \left(\begin{pmatrix} 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \end{pmatrix} - MatrixG \right).\begin{pmatrix} 1 \\ 1 \\ 1 \\ 1 \end{pmatrix} \right) \text{ /.}$$

```
    mHfromD → 1 - mHfromH /. mDfromH → 1 - mDfromD // Simplify
```

```
{{0}, {0}, {0}, {0}}
{{0}, {0}, {0}, {0}}
```

Exact Fst

Recall that these are backwards rates so that mDD+mHD sum to one:

```
constraints = {mHfromH + mHfromD == 1, mDfromH + mDfromD == 1, ρD + ρH == 1};
subconstraints = {mHfromH → 1 - mHfromD, mDfromD → 1 - mDfromH};
```

At equilibrium, we have

```
sol = Simplify[Solve[(NextQHH == QHH && NextQDD == QDD && NextQHD == QHD && NextQDH == QDH),
    {QHH, QHD, QDH, QDD}], constraints];
```

When there is not mutation, because of a finite population size, Q must be 1.

```
sol /. μ → 0 // Simplify
```

```
{{QHH → 1, QHD → 1, QDH → 1, QDD → 1}}
```

```
EqQHH = Simplify[QHH /. sol[[1]], constraints]
EqQHD = Simplify[QHD /. sol[[1]], constraints]
EqQDH = Simplify[QDH /. sol[[1]], constraints]
EqQDD = Simplify[QDD /. sol[[1]], constraints]
```

Note that, we can show QHD = QDH, as expected:

```
EqQHD == EqQDH
```

```
True
```

Using Q, we define the F-like measures for the haploid-diploid population.

```
FaiHHstrict =
  Simplify[Limit[(EqQHH - EqQHD)/(1 - EqQHD) /. Dip → ρD * Ntot /. Hap → ρH * Ntot, μ → 0], constraints]
FaiDDstrict = Simplify[
   Limit[(EqQDD - EqQHD)/(1 - EqQHD) /. Dip → ρD * Ntot /. Hap → ρH * Ntot, μ → 0], constraints]
```

```
- (((mDfromH - mHfromH) (mDfromH mHfromH (2 - 4 Ntot ρD) + mDfromH^2 (-1 + 2 Ntot ρD) +
        mHfromH^2 (-1 + 2 Ntot ρD) + mHfromH Ntot (-2 + ρH) + Ntot ρH)) /
    (mDfromH^3 (-1 + 2 Ntot ρD) (-1 + Ntot ρH) + mDfromH^2 (1 + 2 Ntot (-1 + ρH))
       (-Ntot ρH + 3 mHfromH (-1 + Ntot ρH)) -
      (-2 Ntot ρD + mHfromH (-1 + 2 Ntot ρD)) (-Ntot ρH + mHfromH^2 (-1 + Ntot ρH)) +
      mDfromH (Ntot (1 - 2 Ntot ρD) ρH + 3 mHfromH^2 (-1 + 2 Ntot ρD) (-1 + Ntot ρH) +
         mHfromH Ntot (2 ρD + ρH - 4 Ntot ρD ρH))))
```

```
- (((mDfromH - mHfromH) (-Ntot ρH + mDfromH^2 (-1 + Ntot ρH) +
        mHfromH^2 (-1 + Ntot ρH) + mDfromH (Ntot (2 ρD + ρH) + mHfromH (2 - 2 Ntot ρH)))) /
    (mDfromH^3 (-1 + 2 Ntot ρD) (-1 + Ntot ρH) + mDfromH^2 (1 + 2 Ntot (-1 + ρH))
       (-Ntot ρH + 3 mHfromH (-1 + Ntot ρH)) -
      (-2 Ntot ρD + mHfromH (-1 + 2 Ntot ρD)) (-Ntot ρH + mHfromH^2 (-1 + Ntot ρH)) +
      mDfromH (Ntot (1 - 2 Ntot ρD) ρH + 3 mHfromH^2 (-1 + 2 Ntot ρD) (-1 + Ntot ρH) +
         mHfromH Ntot (2 ρD + ρH - 4 Ntot ρD ρH))))
```

Through a series of collecting factors, as in the following command, and gathering terms

```
Collect[Numerator[FaiHHstrict], {Ntot}, Factor]
```

```
(mDfromH - mHfromH)^3 - (mDfromH - mHfromH) Ntot
  (-2 mHfromH + 2 mDfromH^2 ρD - 4 mDfromH mHfromH ρD + 2 mHfromH^2 ρD + ρH + mHfromH ρH)
```

we can rewrite FaiHHstrict and FaiDDstrict as:

```
Eq4a = ((1 - X)^3 + Ntot * (1 - X) * ((2 - X) * X * (2 * ρD) - mHfromD * (ρH + 2 * ρD))) /
    ((1 - X)^3 - Ntot * (1 - X) * ((1 - X)^2 * (ρH + 2 * ρD) - mDfromD * ρH - mHfromH * (2 * ρD)) +
      Ntot^2 * X^2 * (2 - X) * (2 * ρD) * ρH);
% - FaiHHstrict /. X → mHfromD + mDfromH /. subconstraints /. ρD → 1 - ρH // Factor
```

0

```
Eq4b = ((1 - X)^3 + Ntot * (1 - X) * ((2 - X) * X * ρH - mDfromH * (ρH + 2 * ρD))) /
    ((1 - X)^3 - Ntot * (1 - X) * ((1 - X)^2 * (ρH + 2 ρD) - mDfromD * ρH - mHfromH * (2 * ρD)) +
      Ntot^2 * X^2 * (2 - X) * (2 * ρD) * ρH);
% - FaiDDstrict /. X → mDfromH + mHfromD /. subconstraints /. ρD → 1 - ρH // Factor
```

0

where X = mDH+mHD, the sum of the movement rates.

```
Fexact = {((1 - X)^3 + Ntot * (1 - X) * ((2 - X) * X * (2 * ρD) - mHfromD * (ρH + 2 * ρD))) /
     ((1 - X)^3 - Ntot * (1 - X) * ((1 - X)^2 * (ρH + 2 * ρD) - mDfromD * ρH - mHfromH * (2 * ρD)) +
       Ntot^2 * X^2 * (2 - X) * (2 * ρD) * ρH),
    ((1 - X)^3 + Ntot * (1 - X) * ((2 - X) * X * ρH - mDfromH * (ρH + 2 * ρD))) /
     ((1 - X)^3 - Ntot * (1 - X) * ((1 - X)^2 * (ρH + 2 ρD) - mDfromD * ρH - mHfromH * (2 * ρD)) +
       Ntot^2 * X^2 * (2 - X) * (2 * ρD) * ρH)};
```

If the movement rates are neither near zero nor near one and the population size is large

If N is large (total population size) relative to the migration rates (i.e., none of the migration rates is very rare) these reduce to [dropping terms not involving Ntot] for {haploids, diploids}:

```
Series[Fexact /. Ntot → Ntot/ϵ, {ϵ, 0, 1}]
Factor[Normal[Series[Fexact /. Ntot → Ntot/ϵ, {ϵ, 0, 1}]]] /. ϵ → 1
```

$$\left\{-\frac{\left((-1+X)\left(2\,\text{mHfromD}\,\rho D-4\,X\,\rho D+2\,X^2\,\rho D+\text{mHfromD}\,\rho H\right)\right)\epsilon}{2\left(\text{Ntot}\,(-2+X)\,X^2\,\rho D\,\rho H\right)}+O[\epsilon]^2,\right.$$
$$\left.-\frac{\left((-1+X)\left(2\,\text{mDfromH}\,\rho D+\text{mDfromH}\,\rho H-2\,X\,\rho H+X^2\,\rho H\right)\right)\epsilon}{2\left(\text{Ntot}\,(-2+X)\,X^2\,\rho D\,\rho H\right)}+O[\epsilon]^2\right\}$$

$$\left\{-\frac{(-1+X)\left(2\,\text{mHfromD}\,\rho D-4\,X\,\rho D+2\,X^2\,\rho D+\text{mHfromD}\,\rho H\right)}{2\,\text{Ntot}\,(-2+X)\,X^2\,\rho D\,\rho H},\right.$$
$$\left.-\frac{(-1+X)\left(2\,\text{mDfromH}\,\rho D+\text{mDfromH}\,\rho H-2\,X\,\rho H+X^2\,\rho H\right)}{2\,\text{Ntot}\,(-2+X)\,X^2\,\rho D\,\rho H}\right\}$$

```
FNlarge = {((1 - X) * ((2 - X) * X * (2 * ρD) - mHfromD (ρH + 2 * ρD))) / ((2 - X) * X^2 * ρH * (2 * ρD) * Ntot),
    ((1 - X) * ((2 - X) * X * ρH - mDfromH * (ρH + 2 * ρD))) / ((2 - X) * X^2 * ρH * (2 * ρD) * Ntot)};
Simplify[% - %%, constraints]
```

```
{0, 0}
```

We can use the above general Fst result when Ntot is large to estimate the degree of sexuality, although this is too complicated to present in the main paper:

```
FNlarge /. X → mHfromD + mDfromH /. mHfromD → 1 - mHfromH /. mDfromH → 1 - mDfromD /.
    mHfromH → θHH/Ntot /. mDfromD → θDD/Ntot // Simplify;
Simplify[Solve[{%[[1]] == ϕH, %[[2]] == ϕD}, {θHH, θDD}], constraints]
```

$$\Big\{\Big\{\theta HH \to \Big(2\,Ntot\,\rho H\,(1+2\,Ntot\,\phi D)\,(\phi D+\phi H) + 4\,Ntot^3\,\rho H^4\,\phi D\,(\phi D+\phi H)^2 - 2\,Ntot^2\,\rho H^3\,(\phi D+\phi H)\,(\phi H+4\,Ntot\,\phi D\,(\phi D+\phi H)) + Ntot\,\rho H^2\,(\phi D+\phi H)\,\big(-1+4\,Ntot^2\,\phi D\,(\phi D+\phi H)+Ntot\,(-4\,\phi D+2\,\phi H)\big) - \sqrt{2}\,\sqrt{Ntot^3\,\rho D\,\rho H\,\phi H^2\,(\phi D+\phi H)\,(\rho H+2\,\rho D\,(1+Ntot\,\rho H\,(\phi D+\phi H)))^3}\Big) \Big/ \Big((\phi D+\phi H)\,(\rho H+2\,\rho D\,(1+Ntot\,\rho H\,(\phi D+\phi H)))^2\Big),$$

$$\theta DD \to \Big(4\,Ntot\,\phi D\,\phi H + 4\,Ntot\,\phi H^2 + 4\,Ntot^3\,\rho H^4\,\phi H^2\,(\phi D+\phi H)^2 + 2\,Ntot\,\rho H\,\phi H\,(\phi D+\phi H)\,(-3+2\,Ntot\,(\phi D+2\,\phi H)) + 2\,Ntot\,\rho H^2\,\phi H\,(\phi D+\phi H)\,\big(1+2\,Ntot^2\,\phi H\,(\phi D+\phi H)-Ntot\,(4\,\phi D+7\,\phi H)\big) - 2\,Ntot^2\,\rho H^3\,\phi H\,(\phi D+\phi H)\,(\phi H\,(-3+4\,Ntot\,\phi H)+\phi D\,(-2+4\,Ntot\,\phi H)) - \sqrt{2}\,\phi D\,\sqrt{Ntot^3\,\rho D\,\rho H\,\phi H^2\,(\phi D+\phi H)\,(\rho H+2\,\rho D\,(1+Ntot\,\rho H\,(\phi D+\phi H)))^3}\Big) \Big/ \Big(\phi H\,(\phi D+\phi H)\,(\rho H+2\,\rho D\,(1+Ntot\,\rho H\,(\phi D+\phi H)))^2\Big)\Big\},$$

$$\Big\{\theta HH \to \Big(2\,Ntot\,\rho H\,(1+2\,Ntot\,\phi D)\,(\phi D+\phi H) + 4\,Ntot^3\,\rho H^4\,\phi D\,(\phi D+\phi H)^2 - 2\,Ntot^2\,\rho H^3\,(\phi D+\phi H)\,(\phi H+4\,Ntot\,\phi D\,(\phi D+\phi H)) + Ntot\,\rho H^2\,(\phi D+\phi H)\,\big(-1+4\,Ntot^2\,\phi D\,(\phi D+\phi H)+Ntot\,(-4\,\phi D+2\,\phi H)\big) + \sqrt{2}\,\sqrt{Ntot^3\,\rho D\,\rho H\,\phi H^2\,(\phi D+\phi H)\,(\rho H+2\,\rho D\,(1+Ntot\,\rho H\,(\phi D+\phi H)))^3}\Big) \Big/ \Big((\phi D+\phi H)\,(\rho H+2\,\rho D\,(1+Ntot\,\rho H\,(\phi D+\phi H)))^2\Big),$$

$$\theta DD \to \Big(4\,Ntot\,\phi D\,\phi H + 4\,Ntot\,\phi H^2 + 4\,Ntot^3\,\rho H^4\,\phi H^2\,(\phi D+\phi H)^2 + 2\,Ntot\,\rho H\,\phi H\,(\phi D+\phi H)\,(-3+2\,Ntot\,(\phi D+2\,\phi H)) + 2\,Ntot\,\rho H^2\,\phi H\,(\phi D+\phi H)\,\big(1+2\,Ntot^2\,\phi H\,(\phi D+\phi H)-Ntot\,(4\,\phi D+7\,\phi H)\big) - 2\,Ntot^2\,\rho H^3\,\phi H\,(\phi D+\phi H)\,(\phi H\,(-3+4\,Ntot\,\phi H)+\phi D\,(-2+4\,Ntot\,\phi H)) + \sqrt{2}\,\phi D\,\sqrt{Ntot^3\,\rho D\,\rho H\,\phi H^2\,(\phi D+\phi H)\,(\rho H+2\,\rho D\,(1+Ntot\,\rho H\,(\phi D+\phi H)))^3}\Big) \Big/ \Big(\phi H\,(\phi D+\phi H)\,(\rho H+2\,\rho D\,(1+Ntot\,\rho H\,(\phi D+\phi H)))^2\Big)\Big\}\Big\}$$

In the primarily sexual case (mDD and mHH small):

```
Factor[Normal[Series[
   Fexact /. X → mHfromD + mDfromH /. mHfromD → 1 - mHfromH /. mDfromH → 1 - mDfromD /.
     mHfromH → θHH/Ntot /. mDfromD → θDD/Ntot /. Ntot → Ntot/ϵ, {ϵ, 0, 0}]]]
```

$$\left\{\frac{2\,\rho D+\rho H}{2\,\rho D+\rho H+8\,\theta DD\,\rho D\,\rho H+8\,\theta HH\,\rho D\,\rho H},\ \frac{2\,\rho D+\rho H}{2\,\rho D+\rho H+8\,\theta DD\,\rho D\,\rho H+8\,\theta HH\,\rho D\,\rho H}\right\}$$

```
%[[1]] - (ρH + (2 * ρD))/(ρH + (2 * ρD) + 4 * ρH * (2 * ρD) * (θHH + θDD)) // Simplify
```

0

Consistent with (B.1).

In the fully symmetric case with ρH=2/3:

```
Factor[
  Fexact /. X → mHfromD + mDfromH /. mHfromH → 1 - m /. mDfromD → 1 - m /. mHfromD → m /.
    mDfromH → m /. ρD → 1 - ρH /. ρH → 2/3] // Simplify
```

$$\left\{-\frac{3\,(1-2\,m)^2}{-3+m\,(12-8\,Ntot)+4\,m^2\,(-3+2\,Ntot)},\ -\frac{3\,(1-2\,m)^2}{-3+m\,(12-8\,Ntot)+4\,m^2\,(-3+2\,Ntot)}\right\}$$

In agreement with equation (6):

```
(1 - 2 * m)^2/(2/3 * Ntot - (1 - 2 * m)^2 (2/3 * Ntot - 1));
%% - % // Factor
```

{0, 0}

Extreme values of Fst

```
Simplify[FaiHHstrict /. subconstraints /. mHfromD → 0 /. mDfromH → 0, constraints]
Simplify[FaiDDstrict /. subconstraints /. mHfromD → 0 /. mDfromH → 0, constraints]
```

1

1

```
Simplify[FaiHHstrict /. subconstraints /. mHfromD → 1/2 /. mDfromH → 1/2, constraints]
Simplify[FaiDDstrict /. subconstraints /. mHfromD → 1/2 /. mDfromH → 1/2, constraints]
```

0

0

```
Simplify[FaiHHstrict /. subconstraints /. mHfromD → 1 /. mDfromH → 1, constraints]
Simplify[FaiDDstrict /. subconstraints /. mHfromD → 1 /. mDfromH → 1, constraints]
```

1

1

```
Simplify[FaiHHstrict /. subconstraints /. mHfromD → 0 /. mDfromH → 1, constraints]
Simplify[FaiDDstrict /. subconstraints /. mHfromD → 0 /. mDfromH → 1, constraints]
```

0

0

```
Simplify[FaiHHstrict /. subconstraints /. mHfromD → 1 /. mDfromH → 0, constraints]
Simplify[FaiDDstrict /. subconstraints /. mHfromD → 1 /. mDfromH → 0, constraints]
```

0

0

```
Simplify[FaiHHstrict /. subconstraints /. mHfromD → 1 - mDfromH, constraints]
Simplify[FaiDDstrict /. subconstraints /. mHfromD → 1 - mDfromH, constraints]
```

0

0

Appendix B

Equations

```
FaiHHstrict = ((1 - X)^3 + Ntot * (1 - X) * ((2 - X) * X * (2 * ρD) - mHfromD * (ρH + 2 * ρD))) /
    ((1 - X)^3 - Ntot * (1 - X) * ((1 - X)^2 * (ρH + 2 * ρD) - mDfromD * ρH - mHfromH * (2 * ρD)) +
      Ntot^2 * X^2 * (2 - X) * (2 * ρD) * ρH) /. X → mHfromD + mDfromH // Simplify;
FaiDDstrict = ((1 - X)^3 + Ntot * (1 - X) * ((2 - X) * X * ρH - mDfromH * (ρH + 2 * ρD))) /
    ((1 - X)^3 - Ntot * (1 - X) * ((1 - X)^2 * (ρH + 2 ρD) - mDfromD * ρH - mHfromH * (2 * ρD)) +
      Ntot^2 * X^2 * (2 - X) * (2 * ρD) * ρH) /. X → mHfromD + mDfromH // Simplify;
```

```
constraints = {mHfromH + mHfromD == 1, mDfromH + mDfromD == 1, ρD + ρH == 1};
subconstraints = {mHfromH → 1 - mHfromD, mDfromD → 1 - mDfromH};
```

Complete symmetry case

```
Simplify[
 FaiHHstrict /. subconstraints /. mHfromD → m /. mDfromH → m /. ρD → 1 - ρH /. ρH → 2/3,
 constraints]
Simplify[FaiDDstrict /. subconstraints /. mHfromD → m /. mDfromH → m /. ρD → 1 - ρH /.
  ρH → 2/3, constraints]
```

$$-\frac{3\,(1-2\,m)^2}{-3+m\,(12-8\,Ntot)+4\,m^2\,(-3+2\,Ntot)}$$

$$-\frac{3\,(1-2\,m)^2}{-3+m\,(12-8\,Ntot)+4\,m^2\,(-3+2\,Ntot)}$$

```
Eq6 = (1 - 2 * m)^2 / (2/3 * Ntot - (1 - 2 * m)^2 * (2/3 * Ntot - 1));
Eq6 - %% // Simplify
```

0

If we assume N large and N m of order one, we get

```
Simplify[Normal[Series[Eq6 /. m → θ/Ntot /. Ntot → Ntot/ϵ, {ϵ, 0, 0}]]]
```

$$\frac{3}{3+8\,\theta}$$

which reduces to the classic Fst prediction when expressing the total population size in terms of the effective number of diploids:

```
Simplify[% /. θ → 3/2 * m * cNtot]
```

$$\frac{1}{1+4\,cNtot\,m}$$

```
Limit[Eq6, m → 0]
Limit[Eq6, m → 1/2]
Limit[Eq6, m → 1]
```

1

0

1

Rare sexuality in a large population

We consider the case when there is frequent asexual reproduction (a≒1, and then mHfromD and mDfromH is small), and large population size. We assume;

- mHfromD = $O(\epsilon)$
- mDfromH = $O(\epsilon)$
- Ntot = $O(1/\epsilon)$

These assumptions indicates, θHD = mHfromD Ntot = $O(1)$ and θDH = mDfromH Ntot = $O(1)$.

```
FNlarge[[1]] /. X → mHfromD + mDfromH
```

$$\frac{(1-\text{mDfromH}-\text{mHfromD})\,(2\,(2-\text{mDfromH}-\text{mHfromD})\,(\text{mDfromH}+\text{mHfromD})\,\rho D-\text{mHfromD}\,(2\,\rho D+\rho H))}{2\,(2-\text{mDfromH}-\text{mHfromD})\,(\text{mDfromH}+\text{mHfromD})^2\,\text{Ntot}\,\rho D\,\rho H}$$

```
FaiHH◆RS = Simplify[
  Normal[Series[FaiHHstrict /. subconstraints /. ρD → 1 - ρH /. mHfromD → θHD/Ntot /.
      mDfromH → θDH/Ntot /. Ntot → cNtot * 1/ϵ, {ϵ, 0, 0}]]]
```

$$-\frac{1+\theta HD\,(2-3\,\rho H)-4\,\theta DH\,(-1+\rho H)}{-1-4\,\theta DH-2\,\theta HD+3\,\theta DH\,\rho H+4\,(\theta DH+\theta HD)^2\,(-1+\rho H)\,\rho H}$$

```
FaiDD◆RS = Simplify[
  Normal[Series[FaiDDstrict /. subconstraints /. ρD → 1 - ρH /. mHfromD → θHD/Ntot /.
      mDfromH → θDH/Ntot /. Ntot → cNtot * 1/ϵ, {ϵ, 0, 0}]]]
```

$$-\frac{1+2\,\theta HD\,\rho H+\theta DH\,(-2+3\,\rho H)}{-1-4\,\theta DH-2\,\theta HD+3\,\theta DH\,\rho H+4\,(\theta DH+\theta HD)^2\,(-1+\rho H)\,\rho H}$$

```
Eq9a = (1 + (2 * ρD) * (θHD + θDH) - (ρH * θHD - (2 * ρD) * θDH)) /
   (1 + 2 * (θHD + θDH) + 2 * ρH * (2 * ρD) * (θHD + θDH)^2 - (ρH - (2 * ρD)) * θDH);
Eq9b = (1 + ρH * (θHD + θDH) + (ρH * θHD - (2 * ρD) * θDH)) /
   (1 + 2 * (θHD + θDH) + 2 * ρH * (2 * ρD) * (θHD + θDH)^2 - (ρH - (2 * ρD)) * θDH);
FaiHH◆RS - Eq9a /. ρD → 1 - ρH // Simplify
FaiDD◆RS - Eq9b /. ρD → 1 - ρH // Simplify
```

```
0
```

```
0
```

```
FaiHH◆RS /. ρH → 2/3 /. θHD → m * Ntot /. θDH → m * Ntot /. Ntot → 3/2 * Nlocal // Factor
FaiDD◆RS /. ρH → 2/3 /. θHD → m * Ntot /. θDH → m * Ntot /. Ntot → 3/2 * Nlocal // Factor
```

$$\frac{1}{1+4\,m\,Nlocal}$$

$$\frac{1}{1+4\,m\,Nlocal}$$

```
sol = Simplify[
  Solve[(Eq9a /. ρD → 1 - ρH) == φH && (Eq9b /. ρD → 1 - ρH) == φD, {θHD, θDH}], 0 < ρH < 1]
```

$$\left\{\left\{\theta HD \to \frac{\varphi D\ (-4+4\,\rho H+4\,\varphi H-5\,\rho H\,\varphi H)+\varphi H\ (-2+3\,\rho H+2\,\varphi H-2\,\rho H\,\varphi H)}{4\ (-1+\rho H)\ \rho H\ (\varphi D+\varphi H)^2},\right.\right.$$
$$\left.\left.\theta DH \to \frac{\rho H\,\varphi D^2-2\,\rho H\,\varphi H+\varphi D\ (2-2\,\varphi H+\rho H\ (-3+4\,\varphi H))}{4\ (-1+\rho H)\ \rho H\ (\varphi D+\varphi H)^2}\right\}\right\}$$

```
Eq10a = ((2 * ρD) * (1 - φH) * (φH + 2 * φD) - ρH * φH * (1 - φD)) / (2 * ρH * (2 * ρD) * (φH + φD)^2);
Eq10b = (ρH * (1 - φD) * (2 * φH + φD) - (2 ρD) * φD * (1 - φH)) / (2 * ρH * (2 * ρD) * (φH + φD)^2);
(θHD /. sol[[1]]) - Eq10a /. ρD → 1 - ρH // Simplify
(θDH /. sol[[1]]) - Eq10b /. ρD → 1 - ρH // Simplify
```

0

0

This matches equation 10.

Common sexuality in a large population

We consider the case when the species has frequent sexual reproduction (a≒0, and then mHH and mDD is small), large population size.
We assume mHH = $O(\epsilon)$, mDD = $O(\epsilon)$, N = $O(1/\epsilon)$, mHH N = $O(1)$, and mDD N = $O(1)$.

```
FaiHH◆RA =
 Simplify[Normal[Series[FaiHHstrict /. mHfromD → 1 - mHfromH /. mDfromH → 1 - mDfromD /.
      mHfromH → θHH/Ntot /. mDfromD → θDD/Ntot /. Ntot → cNtot * 1/ϵ, {ϵ, 0, 0}]]]
```

$$\frac{2\,\rho D+\rho H}{\rho H+\rho D\ (2+8\,\theta DD\,\rho H+8\,\theta HH\,\rho H)}$$

```
FaiDD◆RA =
 Simplify[Normal[Series[FaiDDstrict /. mHfromD → 1 - mHfromH /. mDfromH → 1 - mDfromD /.
      mHfromH → θHH/Ntot /. mDfromD → θDD/Ntot /. Ntot → cNtot * 1/ϵ, {ϵ, 0, 0}]]]
```

$$\frac{2\,\rho D + \rho H}{\rho H + \rho D\,(2 + 8\,\theta DD\,\rho H + 8\,\theta HH\,\rho H)}$$

These are equal to one another.

```
EqB1 = (ρH + (2 * ρD)) / (ρH + (2 * ρD) + 4 * ρH * (2 * ρD) * (θHH + θDD));
FaiHH◆RA - EqB1 /. ρD → 1 - ρH // Simplify
FaiDD◆RA - EqB1 /. ρD → 1 - ρH // Simplify
```

0

0

```
sol = Simplify[Solve[(ρH + (2 * ρD)) / (ρH + (2 * ρD) + 4 * ρH * (2 * ρD) * sum) == φ, {sum}], 0 < ρH < 1]
```

$$\left\{\left\{\text{sum} \to -\frac{(2\,\rho D + \rho H)\,(-1 + \varphi)}{8\,\rho D\,\rho H\,\varphi}\right\}\right\}$$

```
(sum /. sol[[1]]) - ((1 - φ) * (ρH + (2 * ρD))) / (4 * φ * ρH * (2 * ρD)) /. ρD → 1 - ρH // Simplify
```

0

which matches equation (B.2).

Rare sexuality in a very large population

We consider the case when the specie represents frequent asexual reproduction (a≒1, and then mDtoH and mHtoD is small), large population size.
We assume mDtoH = O(ϵ), mHtoD = O(ϵ), N = O($1/\epsilon^2$), mDtoH N = O($1/\epsilon$), and mHtoD N = O($1/\epsilon$).

```
Series[FaiHHstrict /. X → mHfromD + mDfromH /. subconstraints /. ρD → 1 - ρH /.
    mHfromD → cmHfromD * ϵ /. mDfromH → cmDfromH * ϵ /.
  Ntot → cNtot * 1/ϵ^2, {ϵ, 0, 1}] // FullSimplify
FaiHH◆RSlargemN = Normal[%] /. cmDfromH → mDfromH/ϵ /. cmHfromD → mHfromD/ϵ /.
    cNtot → Ntot * ϵ^2 /. mHfromD → θHD/Ntot /. mDfromH → θDH/Ntot // FullSimplify
```

$$\frac{(4\,\text{cmDfromH}\,(-1+\rho H)+\text{cmHfromD}\,(-2+3\,\rho H))\,\epsilon}{4\,(\text{cmDfromH}+\text{cmHfromD})^2\,\text{cNtot}\,(-1+\rho H)\,\rho H}+O[\epsilon]^2$$

$$\frac{4\,\theta DH\,(-1+\rho H)+\theta HD\,(-2+3\,\rho H)}{4\,(\theta DH+\theta HD)^2\,(-1+\rho H)\,\rho H}$$

```
Series[FaiDDstrict /. X → mHfromD + mDfromH /. subconstraints /. ρD → 1 - ρH /.
    mHfromD → cmHfromD * ϵ /. mDfromH → cmDfromH * ϵ /.
  Ntot → cNtot * 1/ϵ^2, {ϵ, 0, 1}] // FullSimplify
FaiDD◆RSlargemN = Normal[%] /. cmDfromH → mDfromH/ϵ /. cmHfromD → mHfromD/ϵ /.
    cNtot → Ntot * ϵ^2 /. mHfromD → θHD/Ntot /. mDfromH → θDH/Ntot // FullSimplify
```

$$\frac{(\text{cmDfromH}\,(2-3\,\rho H)-2\,\text{cmHfromD}\,\rho H)\,\epsilon}{4\,(\text{cmDfromH}+\text{cmHfromD})^2\,\text{cNtot}\,(-1+\rho H)\,\rho H}+O[\epsilon]^2$$

$$\frac{\theta DH\,(2-3\,\rho H)-2\,\theta HD\,\rho H}{4\,(\theta DH+\theta HD)^2\,(-1+\rho H)\,\rho H}$$

```
FaiHH◆RSlargemN - ((2 * θDH + θHD) * (2 * ρD) - θHD * ρH)/(4 * (θDH + θHD)^2 * ρH * ρD) /. ρD → 1 - ρH // Simplify
FaiDD◆RSlargemN - ((2 * θHD + θDH) * ρH - θDH * (2 * ρD))/(4 * (θDH + θHD)^2 * ρH * ρD) /. ρD → 1 - ρH // Simplify
```

0

0

```
sol = Simplify[Solve[(FaiHH◆RSlargemN /. ρD → 1 - ρH) == φH &&
    (FaiDD◆RSlargemN /. ρD → 1 - ρH) == φD, {θHD, θDH}], 0 < ρH < 1]
```

$$\left\{\left\{\theta HD\to\frac{4\,(-1+\rho H)\,\varphi D+(-2+3\,\rho H)\,\varphi H}{4\,(-1+\rho H)\,\rho H\,(\varphi D+\varphi H)^2},\ \theta DH\to\frac{(2-3\,\rho H)\,\varphi D-2\,\rho H\,\varphi H}{4\,(-1+\rho H)\,\rho H\,(\varphi D+\varphi H)^2}\right\}\right\}$$

```
θHD + θDH /. sol[[1]] // Simplify
```

$$\frac{-2+\rho H}{4\ (-1+\rho H)\ \rho H\ (\varphi D+\varphi H)}$$

We note, this approximation can be derived from the approximation of large N limit.

```
Simplify[
 Normal[Series[FNlarge /. X → mHfromD + mDfromH /. subconstraints /. ρD → 1 - ρH /.
     mHfromD → θHD/Ntot /. mDfromH → θDH/Ntot /. Ntot → cNtot * 1/ϵ, {ϵ, 0, 0}]]]
% - {FaiHH◆RSlargemN, FaiDD◆RSlargemN}
```

$$\left\{\frac{4\,\theta DH\ (-1+\rho H)+\theta HD\ (-2+3\,\rho H)}{4\ (\theta DH+\theta HD)^2\ (-1+\rho H)\ \rho H},\ \frac{\theta DH\ (2-3\,\rho H)-2\,\theta HD\,\rho H}{4\ (\theta DH+\theta HD)^2\ (-1+\rho H)\ \rho H}\right\}$$

{0, 0}

Appendix C

Definition of Fst in Whitlock and Barton (1997)

The generalized Wright’s Fst coefficient can be defined as;

$$\mathrm{Corr}[ij] = \frac{Fij - Fave}{1 - Fave}$$

Because Fij could be approximated as;

$$Fij\ (t) = 1 - rij\lambda^t$$

$$Fave = \frac{H^2}{(H+2D)^2}\,FHH + \frac{H\ (2D)}{(H+2D)^2}\,FHD + \frac{(2D)\ H}{(H+2D)^2}\,FDH + \frac{(2D)^2}{(H+2D)^2}\,FHH$$

using leading eigenvalue λ and right eigenvector u for matrix G, the Fst becomes

$$\mathrm{Corrijave}[ij] = \frac{Fij - Fave}{1 - Fave} =$$

$$\frac{\left(\frac{H^2}{(H+2D)^2}\,rHH+\frac{H\ (2D)}{(H+2D)^2}\,rHD+\frac{(2D)\ H}{(H+2D)^2}\,rDH+\frac{(2D)^2}{(H+2D)^2}\,rHH-rij\right)\lambda^t}{\left(\frac{H^2}{(H+2D)^2}\,rHH+\frac{H\ (2D)}{(H+2D)^2}\,rHD+\frac{(2D)\ H}{(H+2D)^2}\,rDH+\frac{(2D)^2}{(H+2D)^2}\,rHH\right)\lambda^t} = 1 - \frac{rij}{\frac{H^2}{(H+2D)^2}\,rHH+\frac{H\ (2D)}{(H+2D)^2}\,rHD+\frac{(2D)\ H}{(H+2D)^2}\,rDH+\frac{(2D)^2}{(H+2D)^2}\,rHH}$$

Hence, we will need the leading right eigenvector for the matrix G.

```
MatrixG =
  ( mHfromH^2 * (1 - 1/Hap)              mHfromH * mHfromD   mHfromD * mHfromH   mHfromD^2 * (1 - 1/(2*D
    mHfromH * mDfromH * (1 - 1/Hap)      mHfromH * mDfromD   mHfromD * mDfromH   mHfromD * mDfromD * (1
    mDfromH * mHfromH * (1 - 1/Hap)      mDfromH * mHfromD   mDfromD * mHfromH   mDfromD * mHfromD * (1
    mDfromH^2 * (1 - 1/Hap)              mDfromH * mDfromD   mDfromD * mDfromH   mDfromD^2 * (1 - 1/(2*D
  );
```

We first consider the right leading eigenvalue of matrix G.

```
MatrixG /. subconstraints /. Hap → ρH * Ntot /. Dip → (1 - ρH) * Ntot /. Ntot → cNtot * 1/ϵ;
Limit[%, ϵ → 0];
% // MatrixForm
Eigenvalues[%%]
Eigenvectors[%%%]
```

```
( (-1 + mHfromD)^2                   -(-1 + mHfromD) mHfromD            -(-1 + mHfromD) mHfromD
  mDfromH - mDfromH mHfromD          (-1 + mDfromH) (-1 + mHfromD)      mDfromH mHfromD                    mH
  mDfromH - mDfromH mHfromD          mDfromH mHfromD                    (-1 + mDfromH) (-1 + mHfromD)      mH
  mDfromH^2                          -(-1 + mDfromH) mDfromH            -(-1 + mDfromH) mDfromH
```

$\{1,\ 1 - mDfromH - mHfromD,\ 1 - mDfromH - mHfromD,\ (-1 + mDfromH + mHfromD)^2\}$

$\left\{\{1, 1, 1, 1\},\ \left\{-\frac{mHfromD}{mDfromH},\ -\frac{-mDfromH + mHfromD}{mDfromH},\ 0,\ 1\right\},\right.$
$\left.\{0, -1, 1, 0\},\ \left\{\frac{mHfromD^2}{mDfromH^2},\ -\frac{mHfromD}{mDfromH},\ -\frac{mHfromD}{mDfromH},\ 1\right\}\right\}$

```
CharEq = Det[MatrixG - λ * IdentityMatrix[4]] /. subconstraints /. Hap → ρH * Ntot /.
    Dip → (1 - ρH) * Ntot // Simplify;
```

```
CharEqlargeN =
  CharEq /. Ntot → cNtot * 1/ϵ /. λ → λ0 + λ1 * ϵ + λ2 * ϵ^2 + λ3 * ϵ^3 + λ4 * ϵ^4 + λ5 * ϵ^5 +
      λ6 * ϵ^6 + λ7 * ϵ^7 + λ8 * ϵ^8 + λ9 * ϵ^9 + λ10 * ϵ^10 // Simplify;
Limit[%, ϵ → 0]
Solve[% == 0, λ0]
```

$$-\left(1 + \text{mDfromH}^2 + 2\,\text{mDfromH}\,(-1 + \text{mHfromD}) - 2\,\text{mHfromD} + \text{mHfromD}^2 - \lambda 0\right)(-1 + \lambda 0)\,(-1 + \text{mDfromH} + \text{mHfromD} + \lambda 0)^2$$

$$\{\{\lambda 0 \to 1\}, \{\lambda 0 \to 1 - \text{mDfromH} - \text{mHfromD}\}, \{\lambda 0 \to 1 - \text{mDfromH} - \text{mHfromD}\}, \{\lambda 0 \to (-1 + \text{mDfromH} + \text{mHfromD})^2\}\}$$

```
Series[CharEqlargeN, {ϵ, 0, 1}];
% /. λ0 → 1 // Simplify
```

$$-\frac{1}{2\,(\text{cNtot}\,(-1 + \rho H)\,\rho H)}\Big((-2 + \text{mDfromH} + \text{mHfromD})\,(\text{mDfromH} + \text{mHfromD})\Big(\text{mHfromD}^2\,(-1 + 2\,\text{cNtot}\,\lambda 1\,(-1 + \rho H))\,\rho H + 4\,\text{cNtot}\,\text{mDfromH}\,\text{mHfromD}\,\lambda 1\,(-1 + \rho H)\,\rho H + 2\,\text{mDfromH}^2\,(-1 + \rho H)\,(1 + \text{cNtot}\,\lambda 1\,\rho H)\Big)\Big)\,\epsilon + O[\epsilon]^2$$

```
solλ1 = Simplify[Solve[(Normal[%]) == 0, λ1], 0 < cNtot]
```

$$\left\{\left\{\lambda 1 \to \frac{-2\,\text{mDfromH}^2\,(-1 + \rho H) + \text{mHfromD}^2\,\rho H}{2\,\text{cNtot}\,(\text{mDfromH} + \text{mHfromD})^2\,(-1 + \rho H)\,\rho H}\right\}\right\}$$

```
Order0λ = 1;
Order1λ = λ1 /. solλ1[[1]];
```

```
λGapprox = Order0λ + Order1λ * ϵ /. cNtot → Ntot * ϵ // Simplify
```

$$1 + \frac{-2\,\text{mDfromH}^2\,(-1 + \rho H) + \text{mHfromD}^2\,\rho H}{2\,(\text{mDfromH} + \text{mHfromD})^2\,\text{Ntot}\,(-1 + \rho H)\,\rho H}$$

We next derive the right leading eigenvector of matrix G.

$$\text{RightVapprox} = \begin{pmatrix} \text{rHHorder0} + \text{rHHorder1} * \epsilon + \text{rHHorder2} * \epsilon^2 \\ \text{rHDorder0} + \text{rHDorder1} * \epsilon + \text{rHDorder2} * \epsilon^2 \\ \text{rDHorder0} + \text{rDHorder1} * \epsilon + \text{rDHorder2} * \epsilon^2 \\ \text{rDDorder0} + \text{rDDorder1} * \epsilon + \text{rDDorder2} * \epsilon^2 \end{pmatrix};$$

```
condRightV = (MatrixG.RightVapprox) - (λ * RightVapprox) /. λ → λGapprox + λ2 * ϵ^2 /.
      subconstraints /. Hap → ρH * Ntot /.
    Dip → (1 - ρH) * Ntot /. Ntot → cNtot * 1/ϵ // Simplify;
```

We consider order 0, we have

```
Series[condRightV, {ϵ, 0, 0}];
Normal[%] // Simplify
```

```
{{mHfromD (rDHorder0 + rHDorder0 - 2 rHHorder0 +
     mHfromD (rDDorder0 - rDHorder0 - rHDorder0 + rHHorder0))},
 {mHfromD (rDDorder0 - mDfromH rDDorder0 - rHDorder0 +
      mDfromH (rDHorder0 + rHDorder0 - rHHorder0)) + mDfromH (-rHDorder0 + rHHorder0)},
 {mHfromD (rDDorder0 - mDfromH rDDorder0 + (-1 + mDfromH) rDHorder0 +
      mDfromH (rHDorder0 - rHHorder0)) + mDfromH (-rDHorder0 + rHHorder0)},
 {mDfromH ((-2 + mDfromH) rDDorder0 + rDHorder0 - mDfromH rDHorder0 +
     rHDorder0 - mDfromH rHDorder0 + mDfromH rHHorder0)}}
```

```
sol0 = Solve[% == {{0}, {0}, {0}, {0}} && rHHorder0 + rHDorder0 + rDHorder0 + rDDorder0 == const,
  {rHHorder0, rHDorder0, rDHorder0, rDDorder0}]
```

$$\left\{\left\{rHHorder0 \to \frac{const}{4},\ rHDorder0 \to \frac{const}{4},\ rDHorder0 \to \frac{const}{4},\ rDDorder0 \to \frac{const}{4}\right\}\right\}$$

First order term

```
Series[condRightV, {ϵ, 0, 1}];
Normal[%] /. sol0[[1]] // Simplify
```

$$\Bigg\{\Bigg\{\epsilon\,\Bigg(\mathrm{mHfromD}^2\,\mathrm{rDDorder1}+\mathrm{mHfromD}\,\mathrm{rDHorder1}-\mathrm{mHfromD}^2\,\mathrm{rDHorder1}+\mathrm{mHfromD}\,\mathrm{rHDorder1}-\mathrm{mHfromD}^2\,\mathrm{rHDorder1}-\mathrm{rHHorder1}+(-1+\mathrm{mHfromD})^2\left(\mathrm{rHHorder1}-\frac{\mathrm{const}}{4\,\mathrm{cNtot}\,\rho\mathrm{H}}\right)-\frac{\mathrm{const}\,\mathrm{mHfromD}^2}{8\,\mathrm{cNtot}-8\,\mathrm{cNtot}\,\rho\mathrm{H}}-\frac{\mathrm{const}\left(-2\,\mathrm{mDfromH}^2\,(-1+\rho\mathrm{H})+\mathrm{mHfromD}^2\,\rho\mathrm{H}\right)}{8\,\mathrm{cNtot}\,(\mathrm{mDfromH}+\mathrm{mHfromD})^2\,(-1+\rho\mathrm{H})\,\rho\mathrm{H}}\Bigg)\Bigg\},$$

$$\Bigg\{\frac{1}{8\,\mathrm{cNtot}}\,\epsilon\,\Bigg(-\frac{\mathrm{const}\,\mathrm{mHfromD}^2}{(\mathrm{mDfromH}+\mathrm{mHfromD})^2\,(-1+\rho\mathrm{H})}-\frac{1}{(\mathrm{mDfromH}+\mathrm{mHfromD})^2\,\rho\mathrm{H}}\,2\,\mathrm{mDfromH}\left(\mathrm{const}\left(\mathrm{mDfromH}^2+\mathrm{mHfromD}^2+\mathrm{mDfromH}\,(-1+2\,\mathrm{mHfromD})\right)+4\,\mathrm{cNtot}\,(\mathrm{mDfromH}+\mathrm{mHfromD})^2\,(\mathrm{rHDorder1}-\mathrm{rHHorder1})\,\rho\mathrm{H}\right)+\frac{1}{(-1+\rho\mathrm{H})\,\rho\mathrm{H}}\,\mathrm{mHfromD}\,(-8\,\mathrm{cNtot}\,((-1+\mathrm{mDfromH})\,\mathrm{rDDorder1}+\mathrm{rHDorder1}-\mathrm{mDfromH}\,(\mathrm{rDHorder1}+\mathrm{rHDorder1}-\mathrm{rHHorder1}))\,(-1+\rho\mathrm{H})\,\rho\mathrm{H}+\mathrm{const}\,(\mathrm{mDfromH}\,(-2+\rho\mathrm{H})+\rho\mathrm{H}))\Bigg)\Bigg\},$$

$$\Bigg\{\frac{1}{8\,\mathrm{cNtot}}\,\epsilon\,\Bigg(-\frac{\mathrm{const}\,\mathrm{mHfromD}^2}{(\mathrm{mDfromH}+\mathrm{mHfromD})^2\,(-1+\rho\mathrm{H})}-\frac{1}{(\mathrm{mDfromH}+\mathrm{mHfromD})^2\,\rho\mathrm{H}}\,2\,\mathrm{mDfromH}\left(\mathrm{const}\left(\mathrm{mDfromH}^2+\mathrm{mHfromD}^2+\mathrm{mDfromH}\,(-1+2\,\mathrm{mHfromD})\right)+4\,\mathrm{cNtot}\,(\mathrm{mDfromH}+\mathrm{mHfromD})^2\,(\mathrm{rDHorder1}-\mathrm{rHHorder1})\,\rho\mathrm{H}\right)+\frac{1}{(-1+\rho\mathrm{H})\,\rho\mathrm{H}}\,\mathrm{mHfromD}\,(-8\,\mathrm{cNtot}\,((-1+\mathrm{mDfromH})\,\mathrm{rDDorder1}+\mathrm{rDHorder1}-\mathrm{mDfromH}\,\mathrm{rDHorder1}+\mathrm{mDfromH}\,(-\mathrm{rHDorder1}+\mathrm{rHHorder1}))\,(-1+\rho\mathrm{H})\,\rho\mathrm{H}+\mathrm{const}\,(\mathrm{mDfromH}\,(-2+\rho\mathrm{H})+\rho\mathrm{H}))\Bigg)\Bigg\},$$

$$\Bigg\{\epsilon\,\Bigg(-\mathrm{rDDorder1}+\mathrm{mDfromH}\,\mathrm{rDHorder1}-\mathrm{mDfromH}^2\,\mathrm{rDHorder1}+\mathrm{mDfromH}\,\mathrm{rHDorder1}-\mathrm{mDfromH}^2\,\mathrm{rHDorder1}+\mathrm{mDfromH}^2\,\mathrm{rHHorder1}+\frac{(-1+\mathrm{mDfromH})^2\,(\mathrm{const}+8\,\mathrm{cNtot}\,\mathrm{rDDorder1}\,(-1+\rho\mathrm{H}))}{8\,\mathrm{cNtot}\,(-1+\rho\mathrm{H})}-\frac{\mathrm{const}\,\mathrm{mDfromH}^2}{4\,\mathrm{cNtot}\,\rho\mathrm{H}}-\frac{\mathrm{const}\left(-2\,\mathrm{mDfromH}^2\,(-1+\rho\mathrm{H})+\mathrm{mHfromD}^2\,\rho\mathrm{H}\right)}{8\,\mathrm{cNtot}\,(\mathrm{mDfromH}+\mathrm{mHfromD})^2\,(-1+\rho\mathrm{H})\,\rho\mathrm{H}}\Bigg)\Bigg\}\Bigg\}$$

```
sol1 = Solve[% == {{0}, {0}, {0}, {0}} && rHHorder1 + rHDorder1 + rDHorder1 + rDDorder1 == 0,
  {rHHorder1, rHDorder1, rDHorder1, rDDorder1}]

{{rHHorder1 →
   (const (-14 mDfromH + 20 mDfromH^2 - 6 mDfromH^3 - 6 mHfromD + 32 mDfromH mHfromD -
        18 mDfromH^2 mHfromD + 12 mHfromD^2 - 18 mDfromH mHfromD^2 - 6 mHfromD^3 + 15 mDfromH
         ρH - 22 mDfromH^2 ρH + 7 mDfromH^3 ρH + 11 mHfromD ρH - 40 mDfromH mHfromD ρH +
        21 mDfromH^2 mHfromD ρH - 18 mHfromD^2 ρH + 21 mDfromH mHfromD^2 ρH + 7 mHfromD^3 ρH)) /
    (32 cNtot (-2 + mDfromH + mHfromD) (mDfromH + mHfromD)^2 (-1 + ρH) ρH), rHDorder1 →
   -((const (-2 + 4 mDfromH - 2 mDfromH^2 + 4 mHfromD - 4 mDfromH mHfromD - 2 mHfromD^2 + ρH -
          2 mDfromH ρH + mDfromH^2 ρH - 2 mHfromD ρH + 2 mDfromH mHfromD ρH + mHfromD^2 ρH)) /
      (32 cNtot (-2 + mDfromH + mHfromD) (mDfromH + mHfromD) (-1 + ρH) ρH)), rDHorder1 →
   -((const (-2 + 4 mDfromH - 2 mDfromH^2 + 4 mHfromD - 4 mDfromH mHfromD - 2 mHfromD^2 + ρH -
          2 mDfromH ρH + mDfromH^2 ρH - 2 mHfromD ρH + 2 mDfromH mHfromD ρH + mHfromD^2 ρH)) /
      (32 cNtot (-2 + mDfromH + mHfromD) (mDfromH + mHfromD) (-1 + ρH) ρH)),
  rDDorder1 → -((const (-10 mDfromH + 12 mDfromH^2 - 2 mDfromH^3 - 2 mHfromD +
          16 mDfromH mHfromD - 6 mDfromH^2 mHfromD + 4 mHfromD^2 - 6 mDfromH mHfromD^2 -
          2 mHfromD^3 + 13 mDfromH ρH - 18 mDfromH^2 ρH + 5 mDfromH^3 ρH +
          9 mHfromD ρH - 32 mDfromH mHfromD ρH + 15 mDfromH^2 mHfromD ρH -
          14 mHfromD^2 ρH + 15 mDfromH mHfromD^2 ρH + 5 mHfromD^3 ρH)) /
      (32 cNtot (-2 + mDfromH + mHfromD) (mDfromH + mHfromD)^2 (-1 + ρH) ρH))}}
```

```
rightVapprox =
  {{rHHorder0 + rHHorder1 * ϵ}, {rHDorder0 + rHDorder1 * ϵ}, {rDHorder0 + rDHorder1 * ϵ}, {rDDorder0 + rDDorder1 * ϵ}} /. sol0[[1]] /. sol1[[1]] /. cNtot → Ntot * ϵ // Simplify
```

$$\left\{\left\{\frac{1}{32}\,\text{const}\left(8+\left((-1+\text{mDfromH}+\text{mHfromD})\left(\text{mDfromH}^2(-6+7\rho H)+\text{mHfromD}(6-11\rho H+\text{mHfromD}(-6+7\rho H))+\text{mDfromH}(14-15\rho H+2\,\text{mHfromD}(-6+7\rho H))\right)\right)\Big/\left((-2+\text{mDfromH}+\text{mHfromD})(\text{mDfromH}+\text{mHfromD})^2\,\text{Ntot}(-1+\rho H)\rho H\right)\right)\right\},\right.$$

$$\left\{\frac{1}{32}\,\text{const}\left(8-\frac{(-1+\text{mDfromH}+\text{mHfromD})^2(-2+\rho H)}{(-2+\text{mDfromH}+\text{mHfromD})(\text{mDfromH}+\text{mHfromD})\,\text{Ntot}(-1+\rho H)\rho H}\right)\right\},$$

$$\left\{\frac{1}{32}\,\text{const}\left(8-\frac{(-1+\text{mDfromH}+\text{mHfromD})^2(-2+\rho H)}{(-2+\text{mDfromH}+\text{mHfromD})(\text{mDfromH}+\text{mHfromD})\,\text{Ntot}(-1+\rho H)\rho H}\right)\right\},$$

$$\left.\left\{\frac{1}{32}\,\text{const}\left(8-\left((-1+\text{mDfromH}+\text{mHfromD})\left(\text{mDfromH}^2(-2+5\rho H)+\text{mHfromD}(2-9\rho H+\text{mHfromD}(-2+5\rho H))+\text{mDfromH}(10-13\rho H+2\,\text{mHfromD}(-2+5\rho H))\right)\right)\Big/\left((-2+\text{mDfromH}+\text{mHfromD})(\text{mDfromH}+\text{mHfromD})^2\,\text{Ntot}(-1+\rho H)\rho H\right)\right)\right\}\right\}$$

```
Total[rightVapprox] // Simplify
rightVapprox[[2]] == rightVapprox[[3]]
```

```
{const}
```

```
True
```

Using eigenvectors, we define Fst

```
CorrHHave =
  1 - rHH / (Hap^2/(Hap+2*Dip)^2 * rHH + 2*Hap*(2*Dip)/(Hap+2*Dip)^2 * rHD + (2*Dip)^2/(Hap+2*Dip)^2 * rDD) /. rHH → rightVapprox[[1, 1]] /.
      rHD → rightVapprox[[2, 1]] /. rDD → rightVapprox[[4, 1]] /. Hap → Ntot * ρH /.
    Dip → Ntot * (1 - ρH) /. Ñtot → Ntot * ϵ // FullSimplify
CorrHDave = 1 - rHD / (Hap^2/(Hap+2*Dip)^2 * rHH + 2*Hap*(2*Dip)/(Hap+2*Dip)^2 * rHD + (2*Dip)^2/(Hap+2*Dip)^2 * rDD) /.
      rHH → rightVapprox[[1, 1]] /. rHD → rightVapprox[[2, 1]] /.
    rDD → rightVapprox[[4, 1]] /. Hap → Ntot * ρH /.
    Dip → Ntot * (1 - ρH) /. Ñtot → Ntot * ϵ // FullSimplify
CorrDDave = 1 - rDD / (Hap^2/(Hap+2*Dip)^2 * rHH + 2*Hap*(2*Dip)/(Hap+2*Dip)^2 * rHD + (2*Dip)^2/(Hap+2*Dip)^2 * rDD) /.
      rHH → rightVapprox[[1, 1]] /. rHD → rightVapprox[[2, 1]] /.
    rDD → rightVapprox[[4, 1]] /. Hap → Ntot * ρH /.
    Dip → Ntot * (1 - ρH) /. Ñtot → Ntot * ϵ // FullSimplify
```

For large values of the population size, we do not obtain the same measure of Fst as Rousset’s method (by contrast to the Whitlock & Barton method using HD as a comparator, rather than the average, see below):

```
Factor[Normal[Series[{CorrHHave, CorrDDave} /. Ntot → Ntot/ϵ, {ϵ, 0, 1}]] /. ϵ → 1]
```

$$\Big\{-\Big(\big(2\,(-1+\text{mDfromH}+\text{mHfromD})\,\big(3\,\text{mDfromH}-\text{mDfromH}^2+\text{mHfromD}-2\,\text{mDfromH}\,\text{mHfromD}-\text{mHfromD}^2-3\,\text{mDfromH}\,\rho\text{H}+\text{mDfromH}^2\,\rho\text{H}-2\,\text{mHfromD}\,\rho\text{H}+2\,\text{mDfromH}\,\text{mHfromD}\,\rho\text{H}+\text{mHfromD}^2\,\rho\text{H}\big)\big)\Big/\big((-2+\text{mDfromH}+\text{mHfromD})\,(\text{mDfromH}+\text{mHfromD})^2\,\text{Ntot}\,(-2+\rho\text{H})\,\rho\text{H}\big)\Big),$$
$$-\Big(\big((-1+\text{mDfromH}+\text{mHfromD})\,\big(4\,\text{mDfromH}-5\,\text{mDfromH}\,\rho\text{H}+\text{mDfromH}^2\,\rho\text{H}-3\,\text{mHfromD}\,\rho\text{H}+2\,\text{mDfromH}\,\text{mHfromD}\,\rho\text{H}+\text{mHfromD}^2\,\rho\text{H}\big)\big)\Big/\big(2\,(-2+\text{mDfromH}+\text{mHfromD})\,(\text{mDfromH}+\text{mHfromD})^2\,\text{Ntot}\,(-2+\rho\text{H})\,(-1+\rho\text{H})\big)\Big)\Big\}$$

```
Factor[% / FNlarge /. X → mHfromD + mDfromH /. subconstraints /. ρD → 1 - ρH] // FullSimplify
```

$$\Big\{\Big(4\,\big(\text{mHfromD}\,(1+\text{mHfromD}\,(-1+\rho\text{H})-2\,\rho\text{H})+\text{mDfromH}^2\,(-1+\rho\text{H})+\text{mDfromH}\,(-3+2\,\text{mHfromD})\,(-1+\rho\text{H})\big)\,(-1+\rho\text{H})\Big)\Big/\Big(\big(\text{mHfromD}\,(2+2\,\text{mHfromD}\,(-1+\rho\text{H})-3\,\rho\text{H})+2\,\text{mDfromH}^2\,(-1+\rho\text{H})+4\,\text{mDfromH}\,(-1+\text{mHfromD})\,(-1+\rho\text{H})\big)\,(-2+\rho\text{H})\Big),$$
$$\frac{\rho\text{H}\,\big(-4\,\text{mDfromH}-\big(\text{mDfromH}^2+(-3+\text{mHfromD})\,\text{mHfromD}+\text{mDfromH}\,(-5+2\,\text{mHfromD})\big)\,\rho\text{H}\big)}{(-2+\rho\text{H})\,\big(2\,\text{mDfromH}+\big((-3+\text{mDfromH})\,\text{mDfromH}+2\,(-1+\text{mDfromH})\,\text{mHfromD}+\text{mHfromD}^2\big)\,\rho\text{H}\big)}\Big\}$$

For example, in the symmetric case with large N and small (but not very small) movement rates, this measure yields Fst values that are half as large:

```
Normal[Series[% /. mHfromD → m /. mDfromH → m /. ρH → 2/3, {m, 0, 1}]] // Factor
```

$$\left\{\frac{1}{2}, \frac{1}{2}\right\}$$

Alternatively, we can focus on the case where sexuality is nearly complete (asexuality rare, with mHfromH and mDfromD of order ϵ):

```
Simplify[Normal[
  Series[CorrHHave /. mHfromD → 1 - mDfromD /. mDfromH → 1 - mHfromH /. mHfromH → θHH/Ntot /.
     mDfromD → θDD/Ntot /. Ntot → cNtot * 1/ϵ, {ϵ, 0, 0}]], constraints]
```

$$-\frac{8\ (-1+\rho H)\ \rho H}{-4+4\ (3+8\ \theta DD+8\ \theta HH)\ \rho H-3\ (3+16\ \theta DD+16\ \theta HH)\ \rho H^{2}+16\ (\theta DD+\theta HH)\ \rho H^{3}}$$

which can be written as:

```
EqB1WB = (4 * ρH (2 * ρD)) / (-(ρH - (2 * ρD))^2 + 8 * ρH * (2 * ρD) * (ρH + (2 * ρD)) * (θHH + θDD));
%% - % /. ρD → 1 - ρH // Factor
```

0

This differs substantially from Eq. (B.1) based on Rousset's method (becoming negative as sexuality approaches one rather than approaching one as does Eq. (B.1)), likely because the coalescent events are poorly described by the leading eigenvalue only when the populations are nearly fully sexual:

```
EqB1 = (ρH + (2 * ρD)) / (ρH + (2 * ρD) + 4 * ρH * (2 * ρD) * (θHH + θDD));
```

Fst measured relative to HD by Whitlock and Barton (1997)

Using the eigenvectors obtained above, we define Fst

```
CorrHHhd = 1 - rHH/rHD /. rHH → rightVapprox[[1, 1]] /. rHD → rightVapprox[[2, 1]] /.
    rDD → rightVapprox[[4, 1]] /. Hap → Ntot * ρH /.
   Dip → Ntot * (1 - ρH) /. cNtot → Ntot * ϵ // FullSimplify
CorrHDhd = 1 - rHD/rHD /. rHH → rightVapprox[[1, 1]] /. rHD → rightVapprox[[2, 1]] /.
    rDD → rightVapprox[[4, 1]] /. Hap → Ntot * ρH /.
   Dip → Ntot * (1 - ρH) /. cNtot → Ntot * ϵ // FullSimplify
CorrDDhd = 1 - rDD/rHD /. rHH → rightVapprox[[1, 1]] /. rHD → rightVapprox[[2, 1]] /.
    rDD → rightVapprox[[4, 1]] /. Hap → Ntot * ρH /.
   Dip → Ntot * (1 - ρH) /. cNtot → Ntot * ϵ // FullSimplify
```

$$-\left(\left(4\,(-1+\text{mDfromH}+\text{mHfromD})\left(\text{mHfromD}\,(2+2\,\text{mHfromD}\,(-1+\rho H)-3\,\rho H)+2\,\text{mDfromH}^2\,(-1+\rho H)+4\,\text{mDfromH}\,(-1+\text{mHfromD})\,(-1+\rho H)\right)\right)\Big/\left((\text{mDfromH}+\text{mHfromD})\left(2\,(-1+\text{mDfromH}+\text{mHfromD})^2-\left((-1+\text{mDfromH}+\text{mHfromD})^2+8\,(-2+\text{mDfromH}+\text{mHfromD})\,(\text{mDfromH}+\text{mHfromD})\,\text{Ntot}\right)\rho H+8\,(-2+\text{mDfromH}+\text{mHfromD})\,(\text{mDfromH}+\text{mHfromD})\,\text{Ntot}\,\rho H^2\right)\right)\right)$$

$$0$$

$$\left(4\,(-1+\text{mDfromH}+\text{mHfromD})\left(2\,\text{mDfromH}+\left((-3+\text{mDfromH})\,\text{mDfromH}+2\,(-1+\text{mDfromH})\,\text{mHfromD}+\text{mHfromD}^2\right)\rho H\right)\right)\Big/\left((\text{mDfromH}+\text{mHfromD})\left(2\,(-1+\text{mDfromH}+\text{mHfromD})^2-\left((-1+\text{mDfromH}+\text{mHfromD})^2+8\,(-2+\text{mDfromH}+\text{mHfromD})\,(\text{mDfromH}+\text{mHfromD})\,\text{Ntot}\right)\rho H+8\,(-2+\text{mDfromH}+\text{mHfromD})\,(\text{mDfromH}+\text{mHfromD})\,\text{Ntot}\,\rho H^2\right)\right)$$

For large values of the population size, we obtain the same measure of Fst as Rousset’s method:

```
Factor[Normal[Series[{CorrHHhd, CorrDDhd} /. Ntot → Ntot/ϵ, {ϵ, 0, 1}]] /. ϵ → 1]
```

$$\Big\{-\Big(\Big((-1+\text{mDfromH}+\text{mHfromD})\left(4\,\text{mDfromH}-2\,\text{mDfromH}^2+2\,\text{mHfromD}-4\,\text{mDfromH}\,\text{mHfromD}-2\,\text{mHfromD}^2-4\,\text{mDfromH}\,\rho H+2\,\text{mDfromH}^2\,\rho H-3\,\text{mHfromD}\,\rho H+4\,\text{mDfromH}\,\text{mHfromD}\,\rho H+2\,\text{mHfromD}^2\,\rho H\right)\Big)\Big/\left(2\,(-2+\text{mDfromH}+\text{mHfromD})\,(\text{mDfromH}+\text{mHfromD})^2\,\text{Ntot}\,(-1+\rho H)\,\rho H\right)\Big),$$
$$\Big((-1+\text{mDfromH}+\text{mHfromD})\left(2\,\text{mDfromH}-3\,\text{mDfromH}\,\rho H+\text{mDfromH}^2\,\rho H-2\,\text{mHfromD}\,\rho H+2\,\text{mDfromH}\,\text{mHfromD}\,\rho H+\text{mHfromD}^2\,\rho H\right)\Big)\Big/\left(2\,(-2+\text{mDfromH}+\text{mHfromD})\,(\text{mDfromH}+\text{mHfromD})^2\,\text{Ntot}\,(-1+\rho H)\,\rho H\right)\Big\}$$

```
Factor[% - FNlarge /. X → mHfromD + mDfromH /. subconstraints /. ρD → 1 - ρH]
```

$$\{0,\,0\}$$

Alternatively, we can focus on the case where sexuality is nearly complete (asexuality rare, with mHfromH and mDfromD of order ϵ):

```
Simplify[Normal[
  Series[CorrHHhd /. mHfromD → 1 - mDfromD /. mDfromH → 1 - mHfromH /. mHfromH → θHH/Ntot /.
     mDfromD → θDD/Ntot /. Ntot → cNtot * 1/ϵ, {ϵ, 0, 0}]], constraints]
```

$$\frac{2\ (-2+\rho H)}{-2+(1-16\,\theta DD-16\,\theta HH)\ \rho H+16\ (\theta DD+\theta HH)\ \rho H^2}$$

```
altEqB1WB = 2 * (ρH + (2 * ρD))/(ρH + (2 * ρD) + 8 * ρH * (2 * ρD) * (θDD + θHH));
%% - % /. ρD → 1 - ρH // Factor
```

0

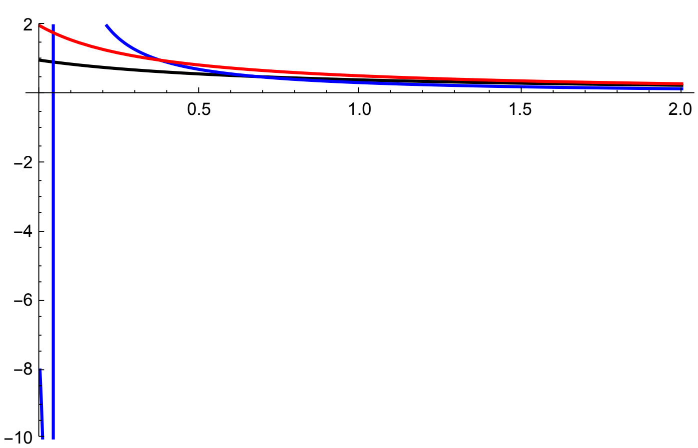
```
EqB1WB
```

$$\frac{8\ \rho D\ \rho H}{-(-2\ \rho D+\rho H)^2+16\ (\theta DD+\theta HH)\ \rho D\ \rho H\ (2\ \rho D+\rho H)}$$

This differs substantially from Eq. (B.1) based on Rousset’s method (being nearly twice as large when asexuality is very rare and θDD+θHH near zero) , likely because the coalescent events are poorly described by the leading eigenvalue only when the populations are nearly fully sexual, as assumed by the Whitlock and Barton method.

The following graph illustrates the discrepancies that arise with the Whitlock & Barton method when asexuality is very rare, where the asymptotic properties focusing on the leading eigenvalue fail to capture the dynamics when there is a nearly strict alternation of generations.

```
Plot[Evaluate[{EqB1, EqB1WB, altEqB1WB} /. ρD → 1 - ρH /. (θHH + θDD) → sum /. ρH → 1/2],
 {sum, 0, 2}, PlotRange → {All, {-10, 2}}, PlotStyle → {{Black}, {Blue}, {Red}}]
```



Complete symmetry case

```
MatrixG /. subconstraints /. mHfromD → m /. mDfromH → m /. Hap → ρH * Ntot /.
    Dip → (1 - ρH) * Ntot /. ρH → 2/3 // Simplify;
% // MatrixForm
FullSimplify[Eigenvalues[%%], 0 < Ntot]
RightV = FullSimplify[Eigenvectors[%%%], 0 < Ntot]
```

$$\begin{pmatrix} \frac{(-1+m)^2(-3+2\,Ntot)}{2\,Ntot} & -(-1+m)\,m & -(-1+m)\,m & m^2\left(1-\frac{3}{2\,Ntot}\right) \\ (1-m)\,m\left(1-\frac{3}{2\,Ntot}\right) & (-1+m)^2 & m^2 & (1-m)\,m\left(1-\frac{3}{2\,Ntot}\right) \\ (1-m)\,m\left(1-\frac{3}{2\,Ntot}\right) & m^2 & (-1+m)^2 & (1-m)\,m\left(1-\frac{3}{2\,Ntot}\right) \\ m^2\left(1-\frac{3}{2\,Ntot}\right) & -(-1+m)\,m & -(-1+m)\,m & \frac{(-1+m)^2(-3+2\,Ntot)}{2\,Ntot} \end{pmatrix}$$

$$\left\{1-2m+\frac{3(-1+2m)}{2\,Ntot},\ 1-2m,\ -\frac{3+\sqrt{9+4(-1+m)m\left(9+(-1+m)m(3-4\,Ntot)^2\right)}-4\,Ntot-2(-1+m)m(-3+4\,Ntot)}{4\,Ntot},\ \frac{-3+\sqrt{9+4(-1+m)m\left(9+(-1+m)m(3-4\,Ntot)^2\right)}+4\,Ntot+2(-1+m)m(-3+4\,Ntot)}{4\,Ntot}\right\}$$

$$\left\{\{-1,0,0,1\},\{0,-1,1,0\},\left\{1,\frac{-3-6(-1+m)m+\sqrt{9+4(-1+m)m\left(9+(-1+m)m(3-4\,Ntot)^2\right)}}{8(-1+m)m\,Ntot},\frac{-3-6(-1+m)m+\sqrt{9+4(-1+m)m\left(9+(-1+m)m(3-4\,Ntot)^2\right)}}{8(-1+m)m\,Ntot},1\right\},\left\{1,-\frac{3+6(-1+m)m+\sqrt{9+4(-1+m)m\left(9+(-1+m)m(3-4\,Ntot)^2\right)}}{8(-1+m)m\,Ntot},-\frac{3+6(-1+m)m+\sqrt{9+4(-1+m)m\left(9+(-1+m)m(3-4\,Ntot)^2\right)}}{8(-1+m)m\,Ntot},1\right\}\right\}$$

```
RightVG = RightV[[4]]
RightVG[[2]] == RightVG[[3]]
```

$$\left\{1,-\frac{3+6(-1+m)m+\sqrt{9+4(-1+m)m\left(9+(-1+m)m(3-4\,Ntot)^2\right)}}{8(-1+m)m\,Ntot},-\frac{3+6(-1+m)m+\sqrt{9+4(-1+m)m\left(9+(-1+m)m(3-4\,Ntot)^2\right)}}{8(-1+m)m\,Ntot},1\right\}$$

True

```
CorrHHsym =
  1 - rHH / (Hap^2/(Hap+2*Dip)^2 * rHH + 2*Hap*(2*Dip)/(Hap+2*Dip)^2 * rHD + (2*Dip)^2/(Hap+2*Dip)^2 * rDD) /. rHH → RightVG[[1]] /.
      rHD → RightVG[[2]] /. rDD → RightVG[[4]] /. Hap → Ntot * ρH /.
    Dip → Ntot * (1 - ρH) /. ρH → 2/3 // FullSimplify
CorrHDsym = 1 - rHD / (Hap^2/(Hap+2*Dip)^2 * rHH + 2*Hap*(2*Dip)/(Hap+2*Dip)^2 * rHD + (2*Dip)^2/(Hap+2*Dip)^2 * rDD) /.
       rHH → RightVG[[1]] /. rHD → RightVG[[2]] /. rDD → RightVG[[4]] /.
     Hap → Ntot * ρH /. Dip → Ntot * (1 - ρH) /. ρH → 2/3 // FullSimplify
CorrDDsym = 1 - rDD / (Hap^2/(Hap+2*Dip)^2 * rHH + 2*Hap*(2*Dip)/(Hap+2*Dip)^2 * rHD + (2*Dip)^2/(Hap+2*Dip)^2 * rDD) /.
       rHH → RightVG[[1]] /. rHD → RightVG[[2]] /. rDD → RightVG[[4]] /.
     Hap → Ntot * ρH /. Dip → Ntot * (1 - ρH) /. ρH → 2/3 // FullSimplify
```

$$\frac{1}{3}\left(\sqrt{9+4\,(-1+m)\,m\,\left(9+(-1+m)\,m\,(3-4\,\text{Ntot})^2\right)}+2\,(-1+m)\,m\,(-3+4\,\text{Ntot})\right)$$

$$\frac{1}{3}\left(-\sqrt{9+4\,(-1+m)\,m\,\left(9+(-1+m)\,m\,(3-4\,\text{Ntot})^2\right)}-2\,(-1+m)\,m\,(-3+4\,\text{Ntot})\right)$$

$$\frac{1}{3}\left(\sqrt{9+4\,(-1+m)\,m\,\left(9+(-1+m)\,m\,(3-4\,\text{Ntot})^2\right)}+2\,(-1+m)\,m\,(-3+4\,\text{Ntot})\right)$$

```
EqC4a =
  1/3 * (Sqrt[9 - 4 * m * (1 - m) * (9 - m * (1 - m) * (4 * Ntot - 3)^2)] - 2 * m * (1 - m) * (4 Ntot - 3));
EqC4a - CorrHHsym // Simplify
```

0

```
CorrHHsym == CorrDDsym
```

True

```
Limit[CorrHHsym, m → 0]
Limit[CorrHHsym, m → 1]
```

1

1

```
Limit[CorrHHsym, m → 1/2]
Simplify[%, 1 < Ntot]
```

$\frac{1}{6}\left(3-4\,\text{Ntot}+\sqrt{(-3+4\,\text{Ntot})^2}\right)$

0

```
Series[CorrHHsym /. m → cm * ϵ /. Ntot → cNtot * 1/ϵ, {ϵ, 0, 0}] // Simplify
Normal[%] /. cm → m/ϵ /. cNtot → Ntot * ϵ /. Ntot → 3 * Ndeem // Simplify
```

$\frac{1}{3}\left(-8\,\text{cm}\,\text{cNtot}+\sqrt{9+64\,\text{cm}^2\,\text{cNtot}^2}\right)+O[\epsilon]^1$

$-8\,\text{m}\,\text{Ndeem}+\sqrt{1+64\,\text{m}^2\,\text{Ndeem}^2}$

```
Series[CorrHHsym /. m → cm * ϵ /. Ntot → cNtot * 1/ϵ, {ϵ, 0, 0}] // Simplify
Normal[%] /. cm → m/ϵ /. cNtot → Ntot * ϵ /. Ntot → 3/2 * Nlocal // Simplify
```

$\frac{1}{3}\left(-8\,\text{cm}\,\text{cNtot}+\sqrt{9+64\,\text{cm}^2\,\text{cNtot}^2}\right)+O[\epsilon]^1$

$-4\,\text{m}\,\text{Nlocal}+\sqrt{1+16\,\text{m}^2\,\text{Nlocal}^2}$

This approximation is only half that obtained by Rousset's method ($\frac{1}{1+4\,\theta\text{local}}$, where θlocal=m Nlocal) when θlocal is large:

```
Limit[(-4 θlocal + Sqrt[1 + 16 θlocal^2]) / (1/(1+4 θlocal)), θlocal → Infinity]
```

$\frac{1}{2}$

```
Series[CorrHHsym /. m → cm * ϵ^2 /. Ntot → cNtot * 1/ϵ, {ϵ, 0, 1}] // Simplify
Normal[%] /. cm → m/ϵ^2 /. cNtot → Ntot * ϵ /. Ntot → 3/2 * Nlocal // Simplify
```

$1-\frac{8}{3}(\text{cm}\,\text{cNtot})\,\epsilon+O[\epsilon]^2$

$1-4\,\text{m}\,\text{Nlocal}$

```
Simplify[Series[CorrHHsym /. m → cm * ϵ /. Ntot → cNtot * 1/ϵ^2, {ϵ, 0, 1}],
 0 < cm && 0 < cNtot]
Simplify[Normal[%] /. cm → m/ϵ /. cNtot → Ntot * ϵ^2 /. Ntot → 3/2 * Nlocal, {ϵ > 0}]
```

$$\frac{3\,\epsilon}{16\,\mathrm{cm}\,\mathrm{cNtot}} + O[\epsilon]^2$$

$$\frac{1}{8\,\mathrm{m}\,\mathrm{Nlocal}}$$

Alternatively, we can focus on the case where sexuality is nearly complete (asexuality rare, with mHH and mDD of order ϵ):

```
FullSimplify[Normal[Series[CorrHHsym /. m → 1 - θii/Ntot /. Ntot → cNtot * 1/ϵ, {ϵ, 0, 0}]] /.
  cNtot → Ntot * ϵ, {0 < θii, Ntot > 0}]
```

$$\frac{1}{3}\left(-8\,\theta\mathrm{ii} + \sqrt{9 + 64\,\theta\mathrm{ii}^2}\right)$$

This approaches 1, as it should, when there is very little asexual reproduction (θii approaches 0):

```
Limit[%, θii → 0]
```

1

But note that this is not generally true when there is very rare sexuality and the case is not fully symmetric.

Fst measured relative to HD for the complete symmetry case

If we instead compare sampling within a ploidy population to between ploidy populations (instead of the average) we get:

```
CorrHHsym2 = 1 - rHH/rHD /. rHH → RightVG[[1]] /. rHD → RightVG[[2]] /. rDD → RightVG[[4]] /.
    Hap → Ntot * ρH /. Dip → Ntot * (1 - ρH) // FullSimplify
CorrDDsym2 = 1 - rDD/rHD /. rHH → RightVG[[1]] /. rHD → RightVG[[2]] /. rDD → RightVG[[4]] /.
    Hap → Ntot * ρH /. Dip → Ntot * (1 - ρH) // FullSimplify
```

$$1 + \frac{8\,(-1+m)\,m\,\mathrm{Ntot}}{3 + 6\,(-1+m)\,m + \sqrt{9 + 4\,(-1+m)\,m\,\left(9 + (-1+m)\,m\,(3 - 4\,\mathrm{Ntot})^2\right)}}$$

$$1 + \frac{8\,(-1+m)\,m\,\mathrm{Ntot}}{3 + 6\,(-1+m)\,m + \sqrt{9 + 4\,(-1+m)\,m\,\left(9 + (-1+m)\,m\,(3 - 4\,\mathrm{Ntot})^2\right)}}$$

```
CorrHHsym2 == CorrDDsym2
True
```

This is no longer EqC4a:

$$EqC4a = \frac{1}{3} * \left(\sqrt{9 - 4 * m * (1 - m) * \left(9 - m * (1 - m) * (4 * Ntot - 3)^2\right)} - 2 * m * (1 - m) * (4\,Ntot - 3)\right);$$

```
FullSimplify[EqC4a - CorrHHsym2, {m > 0, Ntot > 0}]
```

$$\frac{8\,(-1 + m)\,m\,Ntot\left(\sqrt{9 + 4\,(-1 + m)\,m\left(9 + (-1 + m)\,m\,(3 - 4\,Ntot)^2\right)} + 2\,(-1 + m)\,m\,(-3 + 4\,Ntot)\right)}{3\left(3 + 6\,(-1 + m)\,m + \sqrt{9 + 4\,(-1 + m)\,m\left(9 + (-1 + m)\,m\,(3 - 4\,Ntot)^2\right)}\right)}$$

By multiplying top and bottom of the fraction in CorrHH2 by $3 + 6\,(-1 + m)\,m - \sqrt{9 + 4\,(-1 + m)\,m\left(9 + (-1 + m)\,m\,(3 - 4\,Ntot)^2\right)}$, we can simplify it to:

$$1 + \frac{8\,(-1 + m)\,m\,Ntot\left(3 + 6\,(-1 + m)\,m - \sqrt{9 + 4\,(-1 + m)\,m\left(9 + (-1 + m)\,m\,(3 - 4\,Ntot)^2\right)}\right)}{(3 + 6\,(-1 + m)\,m)^2 - \left(9 + 4\,(-1 + m)\,m\left(9 + (-1 + m)\,m\,(3 - 4\,Ntot)^2\right)\right)};$$

```
FullSimplify[Factor[%], {m > 0, Ntot > 0}]
```

$$\frac{-3 + \sqrt{9 + 4\,(-1 + m)\,m\left(9 + (-1 + m)\,m\,(3 - 4\,Ntot)^2\right)} + 2\,(-1 + m)\,m\,(-9 + 4\,Ntot)}{4\,(-1 + m)\,m\,(-3 + 2\,Ntot)}$$

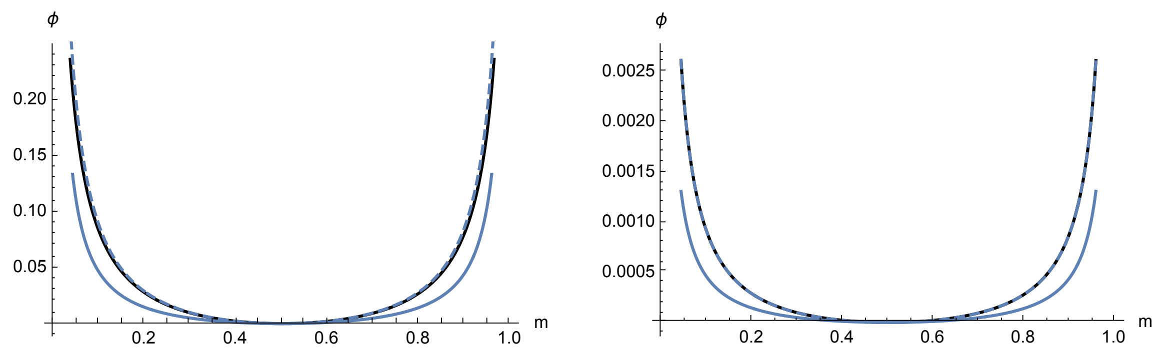
$$EqC4b = \frac{3 + 2 * m * (1 - m) * (4 * Ntot - 9) - \sqrt{9 - 4 * m * (1 - m) * \left(9 - m * (1 - m) * (4 * Ntot - 3)^2\right)}}{4 * m * (1 - m) * (2 * Ntot - 3)};$$

```
FullSimplify[EqC4b - CorrHHsym2, {m > 0, Ntot > 0}]
0
```

The alternative definition (dashed) is nearly twice the Fst value obtained by comparing to the average (solid), especially when the population size is large, but this alternative measure better matches Rousset’s Fst (black):

$$Eq3 = \frac{(1 - 2 * m)^2}{\frac{2}{3} * Ntot - (1 - 2 * m)^2 * \left(\frac{2}{3} * Ntot - 1\right)};$$

```
GraphicsGrid[
 {{Show[
    Plot[Eq3 /. Ntot → 30, {m, 0, 1}, PlotStyle → Black, AxesLabel → {"m", "ϕ"}],
    Plot[EqC4a /. Ntot → 30, {m, 0, 1}],
    Plot[EqC4b /. Ntot → 30, {m, 0, 1}, PlotStyle → Dashed]
   ],
   Show[
    Plot[Eq3 /. Ntot → 3000, {m, 0, 1}, PlotStyle → Black, AxesLabel → {"m", "ϕ"}],
    Plot[EqC4a /. Ntot → 3000, {m, 0, 1}],
    Plot[EqC4b /. Ntot → 3000, {m, 0, 1}, PlotStyle → Dashed]
   ]}}]
```



which reduces to the classic Fst prediction when expressing the total population size in terms of the effective number of diploids:

```
Limit[CorrHHsym2, m → 0]
Limit[CorrHHsym2, m → 1]
```

1

1

$$\text{Limit}\left[\text{CorrHHsym2},\ m \to \frac{1}{2}\right]$$

```
Simplify[%, 1 < Ntot]
```

$$1 - \frac{4\,\text{Ntot}}{3 + \sqrt{(-3 + 4\,\text{Ntot})^2}}$$

0

```
Series[CorrHHsym2 /. m → cm * ϵ /. Ntot → cNtot * 1/ϵ, {ϵ, 0, 0}] // Simplify
Normal[%] /. cm → m/ϵ /. cNtot → Ntot * ϵ /. Ntot → 3 * Ndeem // Simplify
```

$$\left(1-\frac{8\,\text{cm}\,\text{cNtot}}{3+\sqrt{9+64\,\text{cm}^2\,\text{cNtot}^2}}\right)+O[\epsilon]^1$$

$$1-\frac{8\,\text{m}\,\text{Ndeem}}{1+\sqrt{1+64\,\text{m}^2\,\text{Ndeem}^2}}$$

```
Series[CorrHHsym2 /. m → cm * ϵ /. Ntot → cNtot * 1/ϵ, {ϵ, 0, 0}] // Simplify
Normal[%] /. cm → m/ϵ /. cNtot → Ntot * ϵ /. Ntot → 3/2 * Nlocal // Simplify
```

$$\left(1-\frac{8\,\text{cm}\,\text{cNtot}}{3+\sqrt{9+64\,\text{cm}^2\,\text{cNtot}^2}}\right)+O[\epsilon]^1$$

$$1-\frac{4\,\text{m}\,\text{Nlocal}}{1+\sqrt{1+16\,\text{m}^2\,\text{Nlocal}^2}}$$

Multiplying the top and bottom of the first by $3-\sqrt{9+64\,\text{cm}^2\,\text{cNtot}^2}$ and simplifying:

$$\left(1-\frac{8\,\text{cm}\,\text{cNtot}\left(3-\sqrt{9+64\,\text{cm}^2\,\text{cNtot}^2}\right)}{9-\left(9+64\,\text{cm}^2\,\text{cNtot}^2\right)}\right)\ //\ \text{Simplify}$$

$$1-\frac{-3+\sqrt{9+64\,\text{cm}^2\,\text{cNtot}^2}}{8\,\text{cm}\,\text{cNtot}}$$

Multiplying the top and bottom of the second by $1-\sqrt{1+16\,\text{m}^2\,\text{Nlocal}^2}$ and simplifying:

$$1-\frac{4\,\text{m}\,\text{Nlocal}\left(1-\sqrt{1+16\,\text{m}^2\,\text{Nlocal}^2}\right)}{1-\left(1+16\,\text{m}^2\,\text{Nlocal}^2\right)}\ //\ \text{Simplify}$$

$$1-\frac{-1+\sqrt{1+16\,\text{m}^2\,\text{Nlocal}^2}}{4\,\text{m}\,\text{Nlocal}}$$

For large θlocal=m Nlocal, this matches the Rousset result ($\frac{1}{1+4\,\theta\text{local}}$):

$$\text{Limit}\left[\frac{1-\frac{-1+\sqrt{1+16\,\theta\text{local}^2}}{4\,\theta\text{local}}}{\frac{1}{1+4\,\theta\text{local}}},\ \theta\text{local}\to\text{Infinity}\right]$$

1

Very rate sexuality and large population for the complete symmetry case

```
Eq6 = (1 - 2 * m)^2 / (2/3 * Ntot - (1 - 2 * m)^2 * (2/3 * Ntot - 1));

Series[% /. m → cm * ϵ^2 /. Ntot → cNtot * 1/ϵ, {ϵ, 0, 1}] // Simplify

Normal[%] /. cm → m/ϵ^2 /. cNtot → Ntot * ϵ /. Ntot → 3 * Ndeem // Simplify
```

$1 - \frac{8}{3}(\text{cm cNtot})\,\epsilon + O[\epsilon]^2$

$1 - 8\,\text{m Ndeem}$

```
Series[CorrHHsym /. m → cm * ϵ^2 /. Ntot → cNtot * 1/ϵ, {ϵ, 0, 1}] // Simplify

Normal[%] /. cm → m/ϵ^2 /. cNtot → Ntot * ϵ /. Ntot → 3 * Ndeem // Simplify
```

$1 - \frac{8}{3}(\text{cm cNtot})\,\epsilon + O[\epsilon]^2$

$1 - 8\,\text{m Ndeem}$

```
Series[CorrHHsym2 /. m → cm * ϵ^2 /. Ntot → cNtot * 1/ϵ, {ϵ, 0, 1}] // Simplify

Normal[%] /. cm → m/ϵ^2 /. cNtot → Ntot * ϵ /. Ntot → 3 * Ndeem // Simplify
```

$1 - \frac{4}{3}(\text{cm cNtot})\,\epsilon + O[\epsilon]^2$

$1 - 4\,\text{m Ndeem}$

```
Simplify[Series[CorrHHsym2 /. m → cm * ϵ /. Ntot → cNtot * 1/ϵ^2, {ϵ, 0, 1}],
  0 < cm && 0 < cNtot]

Simplify[Normal[%] /. cm → m/ϵ /. cNtot → Ntot * ϵ^2 /. Ntot → 3/2 * Nlocal, {ϵ > 0}]
```

$\frac{3\,\epsilon}{8\,\text{cm cNtot}} + O[\epsilon]^2$

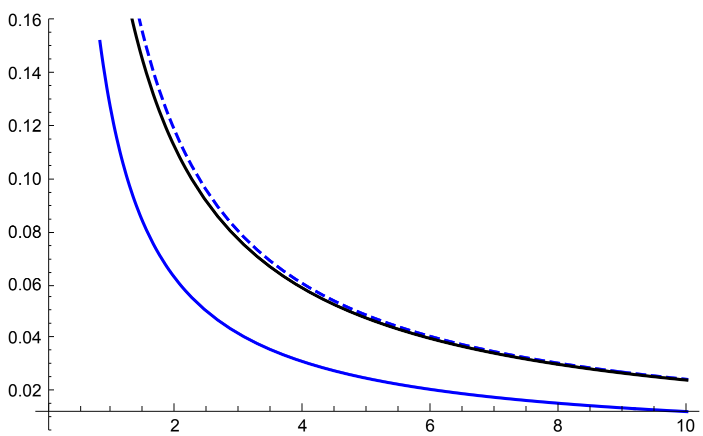
$\frac{1}{4\,\text{m Nlocal}}$

```
FullSimplify[Normal[Series[
    1/3 * (Sqrt[9 - 4 * m * (1 - m) * (9 - m * (1 - m) * (4 * Ntot - 3)^2)] - 2 * m * (1 - m) * (4 Ntot - 3)) /.
      m → θ/Ntot /. Ntot -> Ntot / ϵ, {ϵ, 0, 0}]], {θ > 0, Ntot > 0}]
```

$$\frac{1}{3}\left(-8\,\theta+\sqrt{9+64\,\theta^2}\right)$$

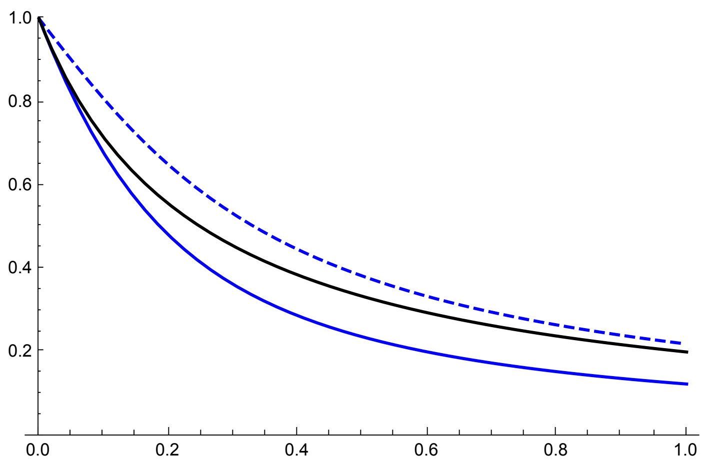
Defining θlocal = m Nlocal = $\frac{2}{3}$ m Ntot, we can compare the three approximations, finding that the alternative definition using HD sampling (dashed) better matches Rousset (black) than does using the average (blue):

```
Show[
 Plot[{-4 θlocal + Sqrt[1 + 16 θlocal^2]}, {θlocal, 0, 10}, PlotStyle → Blue],
 Plot[1 - (-1 + Sqrt[1 + 16 θlocal^2])/(4 θlocal), {θlocal, 0, 10}, PlotStyle → {Blue, Dashed}],
 Plot[1/(1 + 4 θlocal), {θlocal, 0, 10}, PlotStyle → Black]
]
```



unless migration is very rare (θlocal<<1), in which case it is the average and Rousset's method that match (at ~1-4θlocal):

```
Show[
 Plot[{-4 θlocal + Sqrt[1 + 16 θlocal^2]}, {θlocal, 0, 1},
  PlotRange → {Automatic, {0, 1}}, PlotStyle → {Blue}],
 Plot[1 - (4 θlocal)/(1 + Sqrt[1 + 16 θlocal^2]), {θlocal, 0, 1}, PlotStyle → {Blue, Dashed}],
 Plot[1/(1 + 4 θlocal), {θlocal, 0, 1}, PlotStyle → Black]
]
```



Alternatively, we can focus on the case where sexuality is nearly complete (asexuality rare, with mHH and mDD of order ϵ):

```
FullSimplify[
 Normal[Series[CorrHH2 /. m → 1 - θii/Ntot /. Ntot → Ntõt * 1/ϵ, {ϵ, 0, 0}]] /. Ntõt → ϵ Ntot,
 {0 < θii, Ntot > 0}]
```

$$1-\frac{8\,\theta ii}{3+\sqrt{9+64\,\theta ii^2}}$$

This approaches 1, as it should, when there is very little asexual reproduction (θii approaches 0):

```
Limit[%, θii → 0]
```

1

But note that this is not generally true when there is very rare sexuality and the case is not fully symmetric.

Appendix D

Variance effective size in Bessho and Otto (2022)

$$\texttt{varianceNe} = \frac{\rho H * \rho D}{cD^2 * \rho H + 2 * cH^2 * \rho D} * \texttt{Ntot};$$

For the global regulation model, we have

$$\texttt{solH} = \left(aH * wH + aD * wD - 2 * wD + \sqrt{4 * (1 - aH) * (1 - aD) * \frac{f * wH}{2} * wD + (aH * wH - aD * wD)^2}\right) \Big/ \left(2 * \left(aH * wH + \frac{f * wH}{2} * (1 - aH) - wD\right)\right);$$

$$\texttt{NeG} = \texttt{varianceNe} \;/.\; cH \to \frac{(1 - aH) * \frac{f}{2} * wH * \rho H^2}{(1 - aH) * \frac{f}{2} * wH * \rho H^2 + (1 - aD) * wD * \rho D^2} \;/.\; cD \to \frac{(1 - aD) * wD * \rho D^2}{(1 - aH) * \frac{f}{2} * wH * \rho H^2 + (1 - aD) * wD * \rho D^2} \;/.\; \rho D \to 1 - \rho H \;/.\; \rho H \to \texttt{solH} \;//\; \texttt{Simplify}$$

$$\Bigg(4\,\texttt{Ntot}\left(wD - aH\,wH + \frac{1}{2}(-1 + aH)\,f\,wH\right)^4 \Bigg(\left((-1 + aH)\,f\,wH\left(-2\,wD + aD\,wD + aH\,wH + \sqrt{2\,(-1 + aD)\,(-1 + aH)\,f\,wD\,wH + (aD\,wD - aH\,wH)^2}\right)^2 + 2\,(-1 + aD)\,wD\left(aD\,wD - aH\,wH - f\,wH + aH\,f\,wH + \sqrt{2\,(-1 + aD)\,(-1 + aH)\,f\,wD\,wH + (aD\,wD - aH\,wH)^2}\right)^2\right)^2\Bigg)\Bigg) \Big/ \Bigg((2\,wD + (aH\,(-2 + f) - f)\,wH)^4\left(-wD + aH\,wH - \frac{1}{2}(-1 + aH)\,f\,wH\right)\Big((-1 + aH)^2 f^2 wH^2 \left(-2\,wD + aD\,wD + aH\,wH + \sqrt{2\,(-1 + aD)\,(-1 + aH)\,f\,wD\,wH + (aD\,wD - aH\,wH)^2}\right)^3 - 2\,(-1 + aD)^2 wD^2\left(aD\,wD - aH\,wH - f\,wH + aH\,f\,wH + \sqrt{2\,(-1 + aD)\,(-1 + aH)\,f\,wD\,wH + (aD\,wD - aH\,wH)^2}\right)^3\Big)\Bigg)$$

For the local regulation model, we have

$$\texttt{NeL} = \texttt{varianceNe} \;/.\; cH \to \frac{1 + \frac{aH*wH*\rho H}{(1-aD)*wD*\rho D}}{2 + \frac{aH*wH*\rho H}{(1-aD)*wD*\rho D} + \frac{2}{f} * \frac{aD*wD*\rho D}{(1-aH)*wH*\rho H}} \;/.\; cD \to \frac{1 + \frac{2}{f} * \frac{aD*wD*\rho D}{(1-aH)*wH*\rho H}}{2 + \frac{aH*wH*\rho H}{(1-aD)*wD*\rho D} + \frac{2}{f} * \frac{aD*wD*\rho D}{(1-aH)*wH*\rho H}} \;/.\; \rho D \to 1 - \rho H;$$

Equations (from above)

Migration rates are backwards rates so that mHfromH+mHfromD sum to one:

```
constraints = {mHfromH + mHfromD == 1, mDfromH + mDfromD == 1, ρD + ρH == 1};
subconstraints = {mHfromH → 1 - mHfromD, mDfromD → 1 - mDfromH};
```

$$\text{FNlarge} = \left\{\frac{(1-X)*((2-X)*X*(2*\rho D)-\text{mHfromD}\,(\rho H+2*\rho D))}{(2-X)*X^2*\rho H*(2*\rho D)*\text{Ntot}},\ \frac{(1-X)*((2-X)*X*\rho H-\text{mDfromH}*(\rho H+2*\rho D))}{(2-X)*X^2*\rho H*(2*\rho D)*\text{Ntot}}\right\};$$

$$\text{NextQHH} = (1-\mu)^2*\left(\text{mHfromH}^2*\left(\frac{1}{\text{Hap}}+\left(1-\frac{1}{\text{Hap}}\right)*\text{QHH}\right)+\text{mHfromH}*\text{mHfromD}*\text{QHD}+\text{mHfromD}*\text{mHfromH}*\text{QDH}+\text{mHfromD}^2*\left(\frac{1}{2*\text{Dip}}+\left(1-\frac{1}{2*\text{Dip}}\right)*\text{QDD}\right)\right);$$

$$\text{NextQHD} = (1-\mu)^2*\left(\text{mHfromH}*\text{mDfromH}*\left(\frac{1}{\text{Hap}}+\left(1-\frac{1}{\text{Hap}}\right)*\text{QHH}\right)+\text{mHfromH}*\text{mDfromD}*\text{QHD}+\text{mHfromD}*\text{mDfromH}*\text{QDH}+\text{mHfromD}*\text{mDfromD}*\left(\frac{1}{2*\text{Dip}}+\left(1-\frac{1}{2*\text{Dip}}\right)*\text{QDD}\right)\right);$$

$$\text{NextQDH} = (1-\mu)^2*\left(\text{mDfromH}*\text{mHfromH}*\left(\frac{1}{\text{Hap}}+\left(1-\frac{1}{\text{Hap}}\right)*\text{QHH}\right)+\text{mDfromH}*\text{mHfromD}*\text{QHD}+\text{mDfromD}*\text{mHfromH}*\text{QDH}+\text{mDfromD}*\text{mHfromD}*\left(\frac{1}{2*\text{Dip}}+\left(1-\frac{1}{2*\text{Dip}}\right)*\text{QDD}\right)\right);$$

$$\text{NextQDD} = (1-\mu)^2*\left(\text{mDfromD}^2*\left(\frac{1}{2*\text{Dip}}+\left(1-\frac{1}{2*\text{Dip}}\right)*\text{QDD}\right)+\text{mDfromH}*\text{mDfromD}*\text{QHD}+\text{mDfromD}*\text{mDfromH}*\text{QDH}+\text{mDfromH}^2*\left(\frac{1}{\text{Hap}}+\left(1-\frac{1}{\text{Hap}}\right)*\text{QHH}\right)\right);$$

The recursion equations for Q can be described as, $(1-\mu)^2 A\,(Q+c)$;
(this equation corresponds to Eq. (9.30) in Rousset (2004))

$$\text{MatrixA} = \begin{pmatrix} \text{mHfromH}*\text{mHfromH} & \text{mHfromH}*\text{mHfromD} & \text{mHfromD}*\text{mHfromH} & \text{mHfromD}*\text{mHfromD} \\ \text{mHfromH}*\text{mDfromH} & \text{mHfromH}*\text{mDfromD} & \text{mHfromD}*\text{mDfromH} & \text{mHfromD}*\text{mDfromD} \\ \text{mDfromH}*\text{mHfromH} & \text{mDfromH}*\text{mHfromD} & \text{mDfromD}*\text{mHfromH} & \text{mDfromD}*\text{mHfromD} \\ \text{mDfromH}*\text{mDfromH} & \text{mDfromH}*\text{mDfromD} & \text{mDfromD}*\text{mDfromH} & \text{mDfromD}*\text{mDfromD} \end{pmatrix};$$

$$\text{VectC} = \begin{pmatrix} \frac{1}{\text{Hap}}*(1-\text{QHH}) \\ 0 \\ 0 \\ \frac{1}{2*\text{Dip}}*(1-\text{QDD}) \end{pmatrix};$$

$$\begin{pmatrix} \text{NextQHH} \\ \text{NextQHD} \\ \text{NextQDH} \\ \text{NextQDD} \end{pmatrix} - (1-\mu)^2*\text{MatrixA}.\left(\begin{pmatrix} \text{QHH} \\ \text{QHD} \\ \text{QDH} \\ \text{QDD} \end{pmatrix}+\text{VectC}\right) \text{ // Simplify}$$

```
{{0}, {0}, {0}, {0}}
```

Note that, we can write, A = TensorProduct[F, F]

```
MatrixF = (mHfromH  mHfromD
           mDfromH  mDfromD);
TensorProduct[MatrixF, MatrixF] // MatrixForm
MatrixA // MatrixForm
```

$$\begin{pmatrix} \begin{pmatrix} mHfromH^2 & mHfromD\ mHfromH \\ mDfromH\ mHfromH & mDfromD\ mHfromH \end{pmatrix} & \begin{pmatrix} mHfromD\ mHfromH & mHfromD^2 \\ mDfromH\ mHfromD & mDfromD\ mHfromD \end{pmatrix} \\ \begin{pmatrix} mDfromH\ mHfromH & mDfromH\ mHfromD \\ mDfromH^2 & mDfromD\ mDfromH \end{pmatrix} & \begin{pmatrix} mDfromD\ mHfromH & mDfromD\ mHfromD \\ mDfromD\ mDfromH & mDfromD^2 \end{pmatrix} \end{pmatrix}$$

$$\begin{pmatrix} mHfromH^2 & mHfromD\ mHfromH & mHfromD\ mHfromH & mHfromD^2 \\ mDfromH\ mHfromH & mDfromD\ mHfromH & mDfromH\ mHfromD & mDfromD\ mHfromD \\ mDfromH\ mHfromH & mDfromH\ mHfromD & mDfromD\ mHfromH & mDfromD\ mHfromD \\ mDfromH^2 & mDfromD\ mDfromH & mDfromD\ mDfromH & mDfromD^2 \end{pmatrix}$$

Note that, the matrix A is a probaility matrix;

```
MatrixA.(1
         1
         1
         1) /. mHfromD → 1 - mHfromH /. mDfromH → 1 - mDfromD // Simplify
```

```
{{1}, {1}, {1}, {1}}
```

Furthermore, this can be represented as, $(1-\mu)^2$ (GQ + Aδ) and $(1-\mu)^2$ (GQ + ($I-G$) 1);
(this equation corresponds to Eq. (4.4) in Rousset (2004))

```
MatrixG =
 ( mHfromH^2 * (1 - 1/Hap)               mHfromH * mHfromD   mHfromD * mHfromH   mHfromD^2 * (1 - 1/(2*D
   mHfromH * mDfromH * (1 - 1/Hap)       mHfromH * mDfromD   mHfromD * mDfromH   mHfromD * mDfromD * (1
   mDfromH * mHfromH * (1 - 1/Hap)       mDfromH * mHfromD   mDfromD * mHfromH   mDfromD * mHfromD * (1
   mDfromH^2 * (1 - 1/Hap)               mDfromH * mDfromD   mDfromD * mDfromH   mDfromD^2 * (1 - 1/(2*D

 );

Vectδ = ( 1/Hap
          0
          0
          1/(2*Dip) );

(NextQHH, NextQHD, NextQDH, NextQDD) - (1 - μ)^2 * (MatrixG.(QHH, QHD, QDH, QDD) + MatrixA.Vectδ) // Simplify

(NextQHH, NextQHD, NextQDH, NextQDD) - (1 - μ)^2 * (MatrixG.(QHH, QHD, QDH, QDD) +
   (((1 0 0 0), (0 1 0 0), (0 0 1 0), (0 0 0 1)) - MatrixG).(1, 1, 1, 1)) /.
  subconstraints // Simplify

{{0}, {0}, {0}, {0}}

{{0}, {0}, {0}, {0}}
```

Asymptotic inbreeding effective size by Rousset (2004)

At equilibrium, we have
$Q = (1 - \mu)^2 \left(I - (1 - \mu)^2\, G\right)^{-1} (I - G)\, 1.$

We describe (I-G)1 by the linear combination by eigen vector of matrix G (v1, v2, v3, v4),
(I-G)1 = a1 v1 + a2 v2 +a3 v3 + a4 v4.

Using this, we have

$Q = (1-\mu)^2 \left(\frac{1}{1-\lambda 1}\,\text{a1 v1} + \frac{1}{1-\lambda 2}\,\text{a2 v2} + \frac{1}{1-\lambda 3}\,\text{a3v3} + \frac{1}{1-\lambda 4}\,\text{a4v4}\right)$,
where $\lambda 1, \lambda 2, \lambda 3, \lambda 4$ are eigen value of matrix G.

Furthermore, because of $(1-\mu)^2 \lambda^0 + (1-\mu)^4 \lambda^1 + (1-\mu)^6 \lambda^2 + \ldots = \frac{(1-\mu)^2}{1-(1-\mu)^2 \lambda}$, we have

$$Q = \left((1-\mu)^2 \lambda_1^0 \,\text{a1 v1} + (1-\mu)^4 \lambda_1^1 \,\text{a1 v1} + \ldots\right) + \left((1-\mu)^2 \lambda_2^0 \,\text{a2 v2} + (1-\mu)^4 \lambda_2^1 \,\text{a2 v2} + \ldots\right) +.$$
$$\left((1-\mu)^2 \lambda_3^0 \,\text{a3 v3} + (1-\mu)^4 \lambda_3^1 \,\text{a3 v3} + \ldots\right) + \left((1-\mu)^2 \lambda_4^0 \,\text{a4 v4} + (1-\mu)^4 \lambda_4^1 \,\text{a4 v4} + \ldots\right)$$

It becomes

$$Q = (1-\mu)^2 \left(\lambda_1^0 \,\text{a1 v1} + \lambda_2^0 \,\text{a2 v2} + \lambda_3^0 \,\text{a3 v3} + \lambda_4^0 \,\text{a4 v4}\right) + (1-\mu)^4 \left(\lambda_1^1 \,\text{a1 v1} + \lambda_2^1 \,\text{a2 v2} + \lambda_3^1 \,\text{a3 v3} + \lambda_4^1 \,\text{a4 v4}\right) + \ldots.$$

Here the probability of IBD, Q, can be described as
$Q = (1-\mu)^2 C(1) + (1-\mu)^4 C(2) + \ldots$,
where C indicates that the probability of coalecence.

Comparing these equations, we have the probabilty of coalecence using the eigenvalue of matrix G.

Using the leading eigenvalue of the matrix G, we have the inbreeding effective population size,

$$C(t) = \left(\lambda_1^{t-1} \,\text{a1 v1} + \lambda_2^{t-1} \,\text{a2 v2} + \lambda_3^{t-1} \,\text{a3 v3} + \lambda_4^{t-1} \,\text{a4 v4}\right)$$

The inbreeding effective size comparing haploid WF population is defined as,

$$\frac{1}{\text{Ne}} = \text{Limit}\left[\frac{C(t+1)}{1-(C(1)+C(2)+\ldots+C(t))},\ t \to \text{infinity}\right]$$

Using the probability of coalecence, we have

$$\text{Limit}\left[\frac{C(t+1)}{1-(C(1)+C(2)+\ldots+C(t))},\ t \to \text{infinity}\right] = 1 - \lambda 1,$$

where $\lambda 1$ is the leading eigenvalue of matrix G.

Hence, we have the inbreeding effective population size,

$$\text{Ne} = \frac{1}{1-\lambda 1}$$

If we define the effective population size comparing with diploid WF model, it becomes

$$\text{Ne} = \frac{1}{2} \frac{1}{1-\lambda 1}$$

We consider the perturbation, G - A;

```
MatrixG - MatrixA // MatrixForm // Simplify
```

$$\begin{pmatrix} -\frac{\text{mHfromH}^2}{\text{Hap}} & 0 & 0 & -\frac{\text{mHfromD}^2}{2\,\text{Dip}} \\ -\frac{\text{mDfromH mHfromH}}{\text{Hap}} & 0 & 0 & -\frac{\text{mDfromD mHfromD}}{2\,\text{Dip}} \\ -\frac{\text{mDfromH mHfromH}}{\text{Hap}} & 0 & 0 & -\frac{\text{mDfromD mHfromD}}{2\,\text{Dip}} \\ -\frac{\text{mDfromH}^2}{\text{Hap}} & 0 & 0 & -\frac{\text{mDfromD}^2}{2\,\text{Dip}} \end{pmatrix}$$

Because this perturbation is very small when we assume a large population size, we can derive the change in leading eigenvalue, using $\Delta\lambda = \frac{\text{LeftEigenVector}*(G-A)*\text{RightEigenvector}}{\text{LeftEigenVector}*v}$.

Because the matrix A is probability matrix, the leading eigenvalue and right eigenvector is one and unit vector.

```
LeftEigenVectorA = (VHH
                    VHD
                    VDH
                    VDD);

RightEigenVectorA = (1
                     1
                     1
                     1);

DeltaApproximationλG =
  Transpose[LeftEigenVectorA].(MatrixG - MatrixA).RightEigenVectorA
  ----------------------------------------------------------------- // Simplify
          Transpose[LeftEigenVectorA].RightEigenVectorA
```

$$\left\{\left\{-\left(\left(\text{Hap}\left(\text{mDfromD}^2\,\text{VDD}+\text{mDfromD}\,\text{mHfromD}\,(\text{VDH}+\text{VHD})+\text{mHfromD}^2\,\text{VHH}\right)+2\,\text{Dip}\left(\text{mDfromH}^2\,\text{VDD}+\text{mDfromH}\,\text{mHfromH}\,(\text{VDH}+\text{VHD})+\text{mHfromH}^2\,\text{VHH}\right)\right)\Big/\left(2\,\text{Dip}\,\text{Hap}\,(\text{VDD}+\text{VDH}+\text{VHD}+\text{VHH})\right)\right)\right\}\right\}$$

The left eigenvector of matrix A (VHH, VHD, VDH, VDD) can be described as (VH*VH, VH*VD, VH*VD, VD*VD), where the VH and VD are the left eigenvector of the simpler 2x2 matrix F, normalized by their sum $\left(\text{VH} = \frac{\text{mDfromH}}{\text{mHfromD+mDfromH}},\ \text{VD} = \frac{\text{mHfromD}}{\text{mHfromD+mDfromH}}\right)$.

```
Eigenvalues[Simplify[Transpose[MatrixA] /. subconstraints]]
Eigenvectors[Simplify[Transpose[MatrixA] /. subconstraints]]
Eigenvalues[Simplify[Transpose[MatrixF] /. subconstraints]]
Eigenvectors[Simplify[Transpose[MatrixF] /. subconstraints]]
```

$$\left\{1,\ 1-\text{mDfromH}-\text{mHfromD},\ 1-\text{mDfromH}-\text{mHfromD},\ (-1+\text{mDfromH}+\text{mHfromD})^2\right\}$$

$$\left\{\left\{\frac{\text{mDfromH}^2}{\text{mHfromD}^2},\ \frac{\text{mDfromH}}{\text{mHfromD}},\ \frac{\text{mDfromH}}{\text{mHfromD}},\ 1\right\},\ \left\{-\frac{\text{mDfromH}}{\text{mHfromD}},\ -\frac{-\text{mDfromH}+\text{mHfromD}}{\text{mHfromD}},\ 0,\ 1\right\},\ \{0,-1,1,0\},\ \{1,-1,-1,1\}\right\}$$

$$\{1,\ 1-\text{mDfromH}-\text{mHfromD}\}$$

$$\left\{\left\{\frac{\text{mDfromH}}{\text{mHfromD}},\ 1\right\},\ \{-1,1\}\right\}$$

```
{ %[[1, 1]] / (%[[1, 1]] + %[[1, 2]]), %[[1, 2]] / (%[[1, 1]] + %[[1, 2]]) } // Simplify
```

$$\left\{\frac{\text{mDfromH}}{\text{mDfromH}+\text{mHfromD}},\ \frac{\text{mHfromD}}{\text{mDfromH}+\text{mHfromD}}\right\}$$

```
subV = {VH → mDfromH/(mHfromD + mDfromH), VD → mHfromD/(mHfromD + mDfromH)};
```

The leading eigenvalue of the matrix G is approximated as $1 / Ne = \lambda G = 1 - \frac{VH^2}{Hap} - \frac{VD^2}{2*Dip}$.

This means that two gene lineages are in the same ploidy with probaility V and they can coalesce with probability 1/number of chromosomes (Eq.9.32, in Rousset 2004).

```
Part[DeltaApproximationλG[[1]], 1] /. VHH → VH * VH /. VHD → VH * VD /. VDH → VD * VH /.
    VDD → VD * VD /. subconstraints /. subV // Simplify
% - (-VH^2/Hap - VD^2/(2 * Dip)) /. subV // Simplify
```

$$-\frac{2\,Dip\,mDfromH^2 + Hap\,mHfromD^2}{2\,Dip\,Hap\,(mDfromH + mHfromD)^2}$$

0

Then, the leading eigenvalue of the matrix G is approximated as $1 - \frac{VH^2}{Hap} - \frac{VD^2}{2*Dip}$ and we have approximated inbreeding effective size comparing with classical diploid WF model, $Ne = \frac{1}{2}\frac{1}{1-\lambda 1}$;

```
ApproximationλG = 1 - VH^2/Hap - VD^2/(2 * Dip);
InbreedingNe =
  1/2 * 1/(1 - ApproximationλG) /. subV /. mHD → ((1 - aH) * f/2 * wH * ρH)/((1 - aH) * f/2 * wH * ρH + aD * wD * ρD) /.
     mDH → ((1 - aD) * wD * ρD)/(aH * wH * ρH + (1 - aD) * wD * ρD) /. Hap → Ntot * ρH /.
    Dip → Ntot * ρD /. ρD → 1 - ρH // Simplify;
NeG - (InbreedingNe /. ρH → solH) // Simplify
```

0

```
NeL - InbreedingNe // Simplify
```

0

Effective size by Whitlock and Barton (1997)

Using the formulae Eq.(8) and (9) in Whitlock and Barton (1997), we have

```
Hap2 = Hap/2;
Nave = (Hap2 + Dip)/2;
φH = (Hap2 * mHfromH + Dip * mDfromH)/Hap2;
(*Numerator represents number of individuals in the next
 generation that descend from haploids, with mHD being the fraction
 of the next generation of diploids that descend from haploids.*)
φD = (Hap2 * mHfromD + Dip * mDfromD)/Dip;
Eq8inWB = 1/(4 * Nave^2) *
    (((Hap2 * φH^2)/2 * (1 - CorrHHave) + (Dip * φD^2)/2 * (1 - CorrDDave)) + (Hap2^2 * φH^2 * CorrHHave +
        2 * Hap2 * Dip * φH * φD * CorrHDave + Dip^2 * φD^2 * CorrDDave)) // Simplify;
```

$$\text{NeWB} = \frac{1}{2 * \text{Eq8inWB}} \text{ /. subconstraints /. Hap} \to \text{Ntot} * \rho\text{H /. Dip} \to \text{Ntot} * (1 - \rho\text{H}) \text{ // Simplify}$$

$$\Big(\text{Ntot}\,(-2+\rho H)\,(-1+\rho H)\,\rho H\,\Big(\text{mDfromH}^3\,\big(-4+4\,(3+4\,\text{Ntot})\,\rho H-3\,(3+8\,\text{Ntot})\,\rho H^2+8\,\text{Ntot}\,\rho H^3\big)+\text{mDfromH}^2\,\big(24-32\,(2+\text{Ntot})\,\rho H+6\,(7+8\,\text{Ntot})\,\rho H^2-16\,\text{Ntot}\,\rho H^3+3\,\text{mHfromD}\,\big(-4+4\,(3+4\,\text{Ntot})\,\rho H-3\,(3+8\,\text{Ntot})\,\rho H^2+8\,\text{Ntot}\,\rho H^3\big)\big)+\text{mHfromD}\,\big(-4+20\,\rho H-21\,\rho H^2+\text{mHfromD}\,\big(8-32\,(1+\text{Ntot})\,\rho H+6\,(5+8\,\text{Ntot})\,\rho H^2-16\,\text{Ntot}\,\rho H^3\big)+\text{mHfromD}^2\,\big(-4+4\,(3+4\,\text{Ntot})\,\rho H-3\,(3+8\,\text{Ntot})\,\rho H^2+8\,\text{Ntot}\,\rho H^3\big)\big)+\text{mDfromH}\,\big(-20+52\,\rho H-33\,\rho H^2-8\,\text{mHfromD}\,\big(-4+4\,(3+2\,\text{Ntot})\,\rho H-3\,(3+4\,\text{Ntot})\,\rho H^2+4\,\text{Ntot}\,\rho H^3\big)+3\,\text{mHfromD}^2\,\big(-4+4\,(3+4\,\text{Ntot})\,\rho H-3\,(3+8\,\text{Ntot})\,\rho H^2+8\,\text{Ntot}\,\rho H^3\big)\big)\Big)\Big)\Big/$$
$$\Big(4\,\text{mDfromH}^5\,(-1+\rho H)^2\,\big(12-28\,\rho H+19\,\rho H^2\big)+4\,\text{mDfromH}^4\,(-1+\rho H)\,\big(40-152\,\rho H+198\,\rho H^2-86\,\rho H^3+\text{mHfromD}\,\big(-36+132\,\rho H-169\,\rho H^2+76\,\rho H^3\big)\big)+\text{mHfromD}\,\rho H\,\Big(-8+64\,\rho H-114\,\rho H^2+58\,\rho H^3+\text{mHfromD}^4\,\rho H\,\big(12-28\,\rho H+19\,\rho H^2\big)-2\,\text{mHfromD}^3\,\rho H\,\big(28-72\,\rho H+49\,\rho H^2\big)+4\,\text{mHfromD}\,(-1+\rho H)\,\big(-4+16\,(2+\text{Ntot})\,\rho H-(43+16\,\text{Ntot})\,\rho H^2+4\,\text{Ntot}\,\rho H^3\big)+\text{mHfromD}^2\,\big(-8+4\,(31+8\,\text{Ntot})\,\rho H-2\,(151+32\,\text{Ntot})\,\rho H^2+(193+40\,\text{Ntot})\,\rho H^3-8\,\text{Ntot}\,\rho H^4\big)\Big)+\text{mDfromH}\,\rho H\,\Big(-40+160\,\rho H-202\,\rho H^2+82\,\rho H^3-32\,\text{mHfromD}\,\big(-4+22\,\rho H-33\,\rho H^2+15\,\rho H^3\big)-8\,\text{mHfromD}^3\,\big(-20+92\,\rho H-139\,\rho H^2+69\,\rho H^3\big)+\text{mHfromD}^4\,\big(-48+196\,\rho H-272\,\rho H^2+133\,\rho H^3\big)+\text{mHfromD}^2\,\big(-200+4\,(267+8\,\text{Ntot})\,\rho H-2\,(839+32\,\text{Ntot})\,\rho H^2+(813+40\,\text{Ntot})\,\rho H^3-8\,\text{Ntot}\,\rho H^4\big)\Big)+\text{mDfromH}^3\,\Big(-8\,\text{mHfromD}\,\big(32-188\,\rho H+404\,\rho H^2-377\,\rho H^3+129\,\rho H^4\big)+\text{mHfromD}^2\,\big(144-768\,\rho H+1536\,\rho H^2-1384\,\rho H^3+475\,\rho H^4\big)+2\,(-1+\rho H)\,\big(-56-4\,(-81+8\,\text{Ntot})\,\rho H+(-530+64\,\text{Ntot})\,\rho H^2+(263-40\,\text{Ntot})\,\rho H^3+8\,\text{Ntot}\,\rho H^4\big)\Big)+\text{mDfromH}^2\,\Big(-4\,(-1+\rho H)\,\rho H\,\big(60+8\,\text{Ntot}\,(-2+\rho H)^2\,(-1+\rho H)-144\,\rho H+85\,\rho H^2\big)+\text{mHfromD}^3\,\big(48-352\,\rho H+864\,\rho H^2-912\,\rho H^3+361\,\rho H^4\big)-2\,\text{mHfromD}^2\,\big(48-448\,\rho H+1256\,\rho H^2-1424\,\rho H^3+571\,\rho H^4\big)+2\,\text{mHfromD}\,(-1+\rho H)\,\big(-24-4\,(-89+8\,\text{Ntot})\,\rho H+(-874+64\,\text{Ntot})\,\rho H^2+(567-40\,\text{Ntot})\,\rho H^3+8\,\text{Ntot}\,\rho H^4\big)\Big)\Big)$$

$$\text{Series}\Big[\frac{\text{NeWB}}{\text{Ntot}} \text{ /. Ntot} \to \text{cNtot} * \frac{1}{\epsilon}, \{\epsilon, 0, 0\}\Big] \text{ // Simplify}$$

$$\text{NeWBlargeN} = \text{Normal}\Big[\% * \text{Ntot /. mDfromH} \to \frac{(1-\text{aH}) * \frac{f}{2} * \text{wH} * \rho\text{H}}{(1-\text{aH}) * \frac{f}{2} * \text{wH} * \rho\text{H} + \text{aD} * \text{wD} * \rho\text{D}} \text{ /. mHfromD} \to \frac{(1-\text{aD}) * \text{wD} * \rho\text{D}}{\text{aH} * \text{wH} * \rho\text{H} + (1-\text{aD}) * \text{wD} * \rho\text{D}} \text{ /. } \rho\text{D} \to 1-\rho\text{H}\Big] \text{ // Simplify}$$

$$\frac{(\text{mDfromH}+\text{mHfromD})^2\,(-1+\rho H)\,\rho H}{2\,\text{mDfromH}^2\,(-1+\rho H)-\text{mHfromD}^2\,\rho H}+O[\epsilon]^1$$

$$\frac{2\,\text{Ntot}\,(-1+\rho H)\left(\frac{(-1+aD)\,wD\,(-1+\rho H)}{(-1+aD)\,wD\,(-1+\rho H)+aH\,wH\,\rho H}+\frac{(-1+aH)\,f\,wH\,\rho H}{2\,aD\,wD\,(-1+\rho H)+(-1+aH)\,f\,wH\,\rho H}\right)^2}{-\frac{2\,(-1+aD)^2\,wD^2\,(-1+\rho H)^2}{((-1+aD)\,wD\,(-1+\rho H)+aH\,wH\,\rho H)^2}+\frac{4\,(-1+aH)^2\,f^2\,wH^2\,(-1+\rho H)\,\rho H}{(2\,aD\,wD\,(-1+\rho H)+(-1+aH)\,f\,wH\,\rho H)^2}}$$

```
NeG - (NeWBlargeN /. ρH → solH) // Simplify
```

0

```
NeL - NeWBlargeN // Simplify
```

0

Note that even if we measure Fst relative to a sample from haploids and diploids (HD) rather than the average sample across the full population, we must still rephrase the HD-based Fst values in terms of the average-based Fst values in order to use equations (8) and (9) of Barton and Whitlock:

```
(Corrij - fave)/(1 - fave) /. Corrij → (Fij - FHD)/(1 - FHD) /.
   fave → Hap^2/(Hap + 2 * Dip)^2 * (FHH - FHD)/(1 - FHD) + (Hap * (2 * Dip))/(Hap + 2 * Dip)^2 * (FHD - FHD)/(1 - FHD) +
      (Hap * (2 * Dip))/(Hap + 2 * Dip)^2 * (FDH - FHD)/(1 - FHD) + (2 * Dip)^2/(Hap + 2 * Dip)^2 * (FDD - FHD)/(1 - FHD) // Simplify;
(Fij - Fave)/(1 - Fave) /. Fave → Hap^2/(Hap + 2 * Dip)^2 * FHH + (Hap * (2 * Dip))/(Hap + 2 * Dip)^2 * FHD +
      (Hap * (2 * Dip))/(Hap + 2 * Dip)^2 * FDH + (2 * Dip)^2/(Hap + 2 * Dip)^2 * FDD // Simplify;
% -
  %% //
 Simplify
```

0

```
altEq8inWB =
  1/(4 * Nave^2) * (((Hap2 * φH^2)/2 * (1 - ((CorrHHhd - fave)/(1 - fave))) + (Dip * φD^2)/2 * (1 - ((CorrDDhd - fave)/(1 - fave)))) +
       (Hap2^2 * φH^2 * ((CorrHHhd - fave)/(1 - fave)) + 2 * Hap2 * Dip * φH * φD * ((CorrHDhd - fave)/(1 - fave)) +
         Dip^2 * φD^2 * ((CorrDDhd - fave)/(1 - fave)))) /. fave → Hap^2/(Hap + 2 * Dip)^2 * CorrHHhd +
      (2 * Hap * (2 * Dip))/(Hap + 2 * Dip)^2 * CorrHDhd + (2 * Dip)^2/(Hap + 2 * Dip)^2 * CorrDDhd // Simplify;

Eq8inWB = 1/(4 * Nave^2) *
    (((Hap2 * φH^2)/2 * (1 - CorrHHave) + (Dip * φD^2)/2 * (1 - CorrDDave)) + (Hap2^2 * φH^2 * CorrHHave +
         2 * Hap2 * Dip * φH * φD * CorrHDave + Dip^2 * φD^2 * CorrDDave)) // Simplify;
```

(recall that CorrHD2=0).

The above is the same equation as derived above, once put back in the terms used by Whitlock and Barton, and so gives the same Ne:

```
altEq8inWB - Eq8inWB /. subconstraints /. Hap → Ntot * ρH /. Dip → Ntot * (1 - ρH) // Factor
0
```

Figures

Figure 1-4: Fst with different m

Equations

```
subconstraints = {mHfromH → 1 - mHfromD, mDfromD → 1 - mDfromH};

FaiHHstrict = ((1 - X)^3 + Ntot * (1 - X) * ((2 - X) * X * (2 * ρD) - mHfromD * (ρH + 2 * ρD))) /
      ((1 - X)^3 - Ntot * (1 - X) * ((1 - X)^2 * (ρH + 2 * ρD) - mDfromD * ρH - mHfromH * (2 * ρD)) +
        Ntot^2 * X^2 * (2 - X) * (2 * ρD) * ρH) /.
     X → mHfromD + mDfromH /. subconstraints /. ρD → 1 - ρH // Simplify;

FaiDDstrict = ((1 - X)^3 + Ntot * (1 - X) * ((2 - X) * X * ρH - mDfromH * (ρH + 2 * ρD))) /
      ((1 - X)^3 - Ntot * (1 - X) * ((1 - X)^2 * (ρH + 2 ρD) - mDfromD * ρH - mHfromH * (2 * ρD)) +
        Ntot^2 * X^2 * (2 - X) * (2 * ρD) * ρH) /.
     X → mHfromD + mDfromH /. subconstraints /. ρD → 1 - ρH // Simplify;

FaiAverage = ρH/(ρH + 2 * ρD) * FaiHHstrict + (2 * ρD)/(ρH + 2 * ρD) * FaiDDstrict /. ρD → 1 - ρH // Simplify

-(((-(-1 + mDfromH + mHfromD)^3 + (1 - mDfromH - mHfromD) Ntot
        (mHfromD (-2 + ρH) + 2 (-2 + mDfromH + mHfromD) (mDfromH + mHfromD) (-1 + ρH)))
      ρH + 2 (1 - ρH) (-(-1 + mDfromH + mHfromD)^3 + (-1 + mDfromH + mHfromD) Ntot
        (mDfromH^2 ρH + (-2 + mHfromD) mHfromD ρH + mDfromH (2 + (-3 + 2 mHfromD) ρH)))) /
   ((2 - ρH) ((-1 + mDfromH + mHfromD)^3 + (-1 + mDfromH + mHfromD) Ntot
       (mHfromD (2 + mHfromD (-2 + ρH)) +
        mDfromH (4 + 2 mHfromD (-2 + ρH) - 3 ρH) + mDfromH^2 (-2 + ρH)) -
      2 (-2 + mDfromH + mHfromD) (mDfromH + mHfromD)^2 Ntot^2 (-1 + ρH) ρH)))
```

```
FaiHHstrict /. mHfromD → 1 /. mDfromH → 1 // Simplify
FaiHHstrict /. mHfromD → 1 /. mDfromH → 0 // Simplify
FaiHHstrict /. mHfromD → 0 /. mDfromH → 1 // Simplify
FaiHHstrict /. mHfromD → 0 /. mDfromH → 0 // Simplify
```

1

0

0

1

```
FaiDDstrict /. mHfromD → 1 /. mDfromH → 1 // Simplify
FaiDDstrict /. mHfromD → 1 /. mDfromH → 0 // Simplify
FaiDDstrict /. mHfromD → 0 /. mDfromH → 1 // Simplify
FaiDDstrict /. mHfromD → 0 /. mDfromH → 0 // Simplify
```

1

0

0

1

Figure 1: Equal movement, Equal chromosome

```
FaiHHstrict /. mHfromD → m /. mDfromH → m // Simplify
FaiDDstrict /. mHfromD → m /. mDfromH → m // Simplify
```

$$-\left(\left((-1+2\,m)\,\left(1+m\,(-4+Ntot\,(6-7\,\rho H))+m^2\,(4+8\,Ntot\,(-1+\rho H))\right)\right)\Big/\left(1-3\,m\,(2+Ntot\,(-2+\rho H))+8\,m^3\,\left(-1-Ntot\,(-2+\rho H)+2\,Ntot^2\,(-1+\rho H)\,\rho H\right)-2\,m^2\,\left(-6-5\,Ntot\,(-2+\rho H)+8\,Ntot^2\,(-1+\rho H)\,\rho H\right)\right)\right)$$

$$\left((-1+2\,m)\,\left(-1+m\,(4+Ntot\,(2-5\,\rho H))+4\,m^2\,(-1+Ntot\,\rho H)\right)\right)\Big/\left(1-3\,m\,(2+Ntot\,(-2+\rho H))+8\,m^3\,\left(-1-Ntot\,(-2+\rho H)+2\,Ntot^2\,(-1+\rho H)\,\rho H\right)-2\,m^2\,\left(-6-5\,Ntot\,(-2+\rho H)+8\,Ntot^2\,(-1+\rho H)\,\rho H\right)\right)$$

```
FaiHHstrict /. mHfromD → m /. mDfromH → m /. ρH → 2/3 // Simplify
FaiDDstrict /. mHfromD → m /. mDfromH → m /. ρH → 2/3 // Simplify
% - %% // Simplify
```

$$-\frac{3\,(1-2\,m)^2}{-3+m\,(12-8\,\text{Ntot})+4\,m^2\,(-3+2\,\text{Ntot})}$$

$$-\frac{3\,(1-2\,m)^2}{-3+m\,(12-8\,\text{Ntot})+4\,m^2\,(-3+2\,\text{Ntot})}$$

0

$$\text{Eq3} = \frac{(1-2*m)^2}{\frac{2}{3}*\text{Ntot}-(1-2*m)^2*\left(\frac{2}{3}*\text{Ntot}-1\right)};$$

```
Eq3 - FaiHHstrict /. mHfromD → m /. mDfromH → m /. ρH → 2/3 // Simplify
```

0

```
Limit[Eq3, m → 0]
Limit[Eq3, m → 1/2]
Limit[Eq3, m → 1]
```

1

0

1

```
Plot[Eq3 /. Ntot → 10, {m, 0, 1}, PlotRange → {{0, 1}, {0, 1}},
  PlotStyle → {Thickness[0.005], Blue}, AspectRatio → 0.75];
Plot[Eq3 /. Ntot → 100, {m, 0, 1}, PlotRange → {{0, 1}, {0, 1}},
  PlotStyle → {Thickness[0.005], Black}, AspectRatio → 0.75];
Plot[Eq3 /. Ntot → 1000, {m, 0, 1}, PlotRange → {{0, 1}, {0, 1}},
  PlotStyle → {Thickness[0.005], Red}, AspectRatio → 0.75];
Show[%, %%, %%%];

Show[%, AxesOrigin → {0, 0}, AxesStyle → Directive[Black, AbsoluteThickness[0.5]],
 Frame → True, FrameStyle → AbsoluteThickness[0.5], FrameTicksStyle →
  Directive[AbsoluteThickness[0.5], FontFamily → "Times New Roman", FontSize → 18],
 FrameLabel → {Style["", 20, FontFamily → "Times New Roman"],
   Style["", 20, FontFamily → "Times New Roman"]}]
```

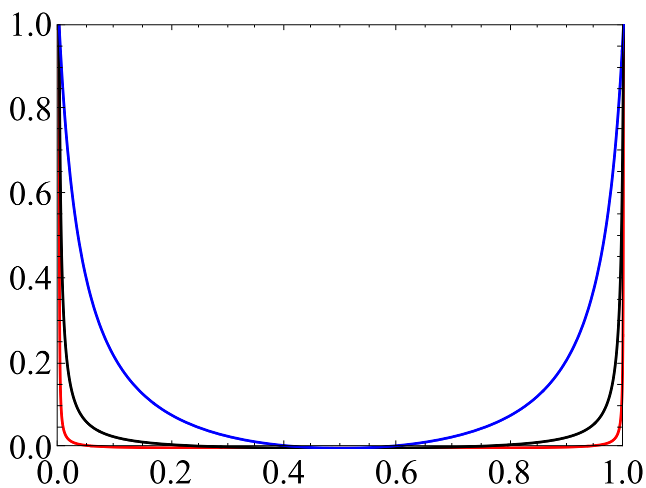


Figure 2: Equal movement

```
FaiHHstrict /. mHfromD → m /. mDfromH → m // Simplify
FaiDDstrict /. mHfromD → m /. mDfromH → m // Simplify
```

$$-\left(\left((-1+2\,m)\left(1+m\,(-4+\text{Ntot}\,(6-7\,\rho H))+m^2\,(4+8\,\text{Ntot}\,(-1+\rho H))\right)\right)\Big/\left(1-3\,m\,(2+\text{Ntot}\,(-2+\rho H))+8\,m^3\left(-1-\text{Ntot}\,(-2+\rho H)+2\,\text{Ntot}^2\,(-1+\rho H)\,\rho H\right)-2\,m^2\left(-6-5\,\text{Ntot}\,(-2+\rho H)+8\,\text{Ntot}^2\,(-1+\rho H)\,\rho H\right)\right)\right)$$

$$\left((-1+2\,m)\left(-1+m\,(4+\text{Ntot}\,(2-5\,\rho H))+4\,m^2\,(-1+\text{Ntot}\,\rho H)\right)\right)\Big/\left(1-3\,m\,(2+\text{Ntot}\,(-2+\rho H))+8\,m^3\left(-1-\text{Ntot}\,(-2+\rho H)+2\,\text{Ntot}^2\,(-1+\rho H)\,\rho H\right)-2\,m^2\left(-6-5\,\text{Ntot}\,(-2+\rho H)+8\,\text{Ntot}^2\,(-1+\rho H)\,\rho H\right)\right)$$

```
FaiHHstrict /. mHfromD → m /. mDfromH → m /. m → 0 // Simplify
FaiHHstrict /. mHfromD → m /. mDfromH → m /. m → 1 // Simplify
FaiDDstrict /. mHfromD → m /. mDfromH → m /. m → 0 // Simplify
FaiDDstrict /. mHfromD → m /. mDfromH → m /. m → 1 // Simplify
```

1

1

1

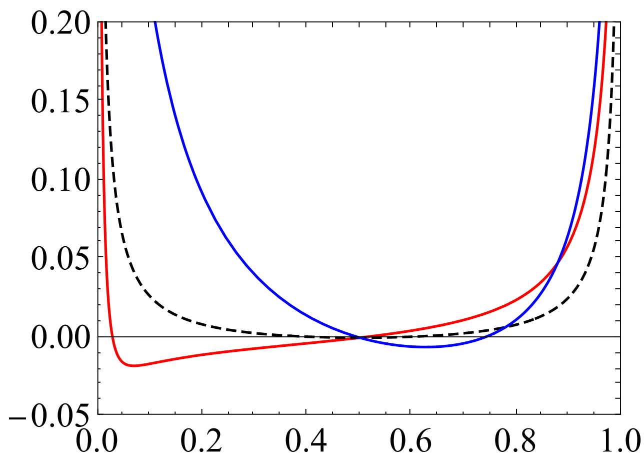
1

```
FaiHHstrict /. mHfromD → m /. mDfromH → m /. m → 1/2 // Simplify
FaiDDstrict /. mHfromD → m /. mDfromH → m /. m → 1/2 // Simplify
```

0

0

```
g1 = Plot[FaiHHstrict /. mHfromD → m /. mDfromH → m /. ρH → 0.9 /. Ntot → 100,
    {m, 0, 1}, PlotRange → {{0, 1}, {-0.1, 0.3}},
    PlotStyle → {Thickness[0.005], Red}, AspectRatio → 0.75];
g2 = Plot[FaiHHstrict /. mHfromD → m /. mDfromH → m /. ρH → 2/3 /. Ntot → 100,
    {m, 0, 1}, PlotRange → {{0, 1}, {-0.1, 0.3}},
    PlotStyle → {Thickness[0.005], Black, Dashed}, AspectRatio → 0.75];
g3 = Plot[FaiHHstrict /. mHfromD → m /. mDfromH → m /. ρH → 0.1 /. Ntot → 100,
    {m, 0, 1}, PlotRange → {{0, 1}, {-0.1, 0.3}},
    PlotStyle → {Thickness[0.005], Blue}, AspectRatio → 0.75];
Show[g1, g2, g3, PlotRange → {{0, 1}, {-0.05, 0.2}}];

Show[%, AxesOrigin → {0, 0}, AxesStyle → Directive[Black, AbsoluteThickness[0.5]],
 Frame → True, FrameStyle → AbsoluteThickness[0.5], FrameTicksStyle →
  Directive[AbsoluteThickness[0.5], FontFamily → "Times New Roman", FontSize → 18],
 FrameLabel → {Style["", 20, FontFamily → "Times New Roman"],
   Style["", 20, FontFamily → "Times New Roman"]}]
```



```
g1 = Plot[FaiDDstrict /. mHfromD → m /. mDfromH → m /. ρH → 0.9 /. Ntot → 100,
    {m, 0, 1}, PlotRange → {{0, 1}, {-0.15, 0.5}},
    PlotStyle → {Thickness[0.005], Red}, AspectRatio → 0.75];
g2 = Plot[FaiDDstrict /. mHfromD → m /. mDfromH → m /. ρH → 2/3 /. Ntot → 100,
    {m, 0, 1}, PlotRange → {{0, 1}, {-0.15, 0.5}},
    PlotStyle → {Thickness[0.005], Black, Dashed}, AspectRatio → 0.75];
g3 = Plot[FaiDDstrict /. mHfromD → m /. mDfromH → m /. ρH → 0.1 /. Ntot → 100,
    {m, 0, 1}, PlotRange → {{0, 1}, {-0.15, 0.5}},
    PlotStyle → {Thickness[0.005], Blue}, AspectRatio → 0.75];
Show[g1, g2, g3, PlotRange → {{0, 1}, {-0.15, 0.2}}];

Show[%, AxesOrigin → {0, 0}, AxesStyle → Directive[Black, AbsoluteThickness[0.5]],
 Frame → True, FrameStyle → AbsoluteThickness[0.5], FrameTicksStyle →
  Directive[AbsoluteThickness[0.5], FontFamily → "Times New Roman", FontSize → 18],
 FrameLabel → {Style["", 20, FontFamily → "Times New Roman"],
   Style["", 20, FontFamily → "Times New Roman"]}]
```

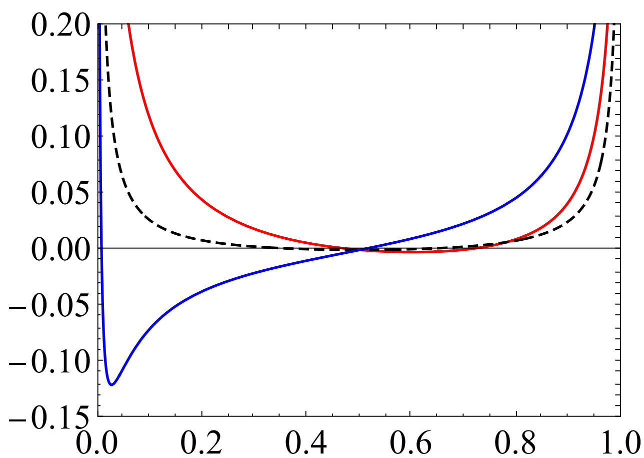
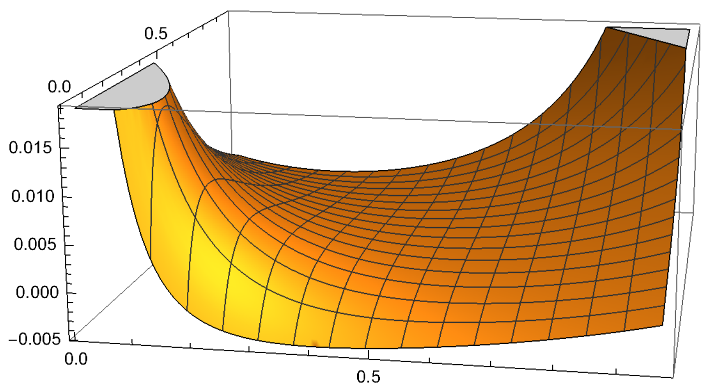
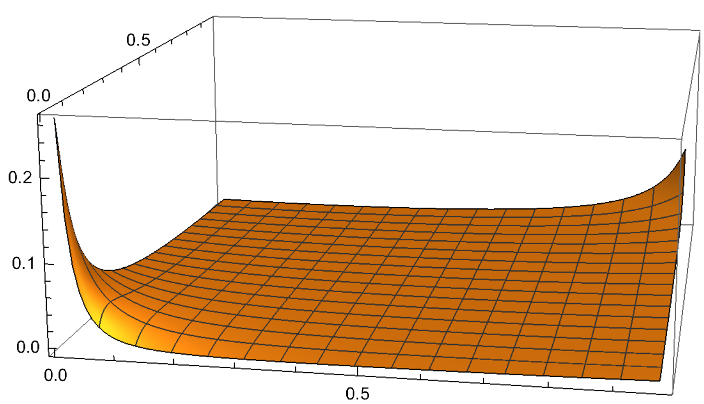


Figure 3: Asymmetry movement, Equal chromosome number

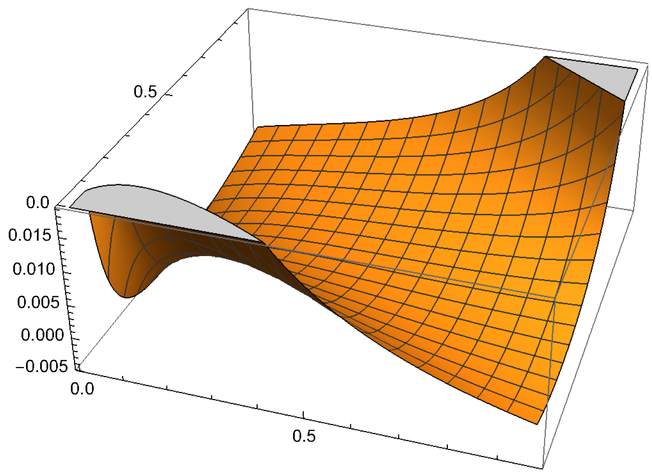
```
MaxV = 0.99;
MinV = 0.01;
RepeatMax = 101;

FQHH = FaiHHstrict /. ρH → 2/3 /. Ntot → 100;
FQDD = FaiDDstrict /. ρH → 2/3 /. Ntot → 100;

OmegaQHH = Table[10, {i, (RepeatMax - 1) * (RepeatMax - 1)}, {j, 3}];
OmegaQDD = Table[10, {i, (RepeatMax - 1) * (RepeatMax - 1)}, {j, 3}];
repeat = 0;
For[repeat1 = 1, repeat1 ≤ RepeatMax - 1, repeat1 = repeat1 + 1,
  For[repeat2 = 1, repeat2 ≤ RepeatMax - 1, repeat2 = repeat2 + 1,
    repeat = repeat + 1;
    x1 = MinV + (MaxV - MinV)/RepeatMax * (repeat1 - 1);
    x2 = MinV + (MaxV - MinV)/RepeatMax * (repeat2 - 1);

    OmegaQHH[[repeat, 1]] = x1;
    OmegaQHH[[repeat, 2]] = x2;
    OmegaQHH[[repeat, 3]] = FQHH /. mHfromD → x1 /. mDfromH → x2;

    OmegaQDD[[repeat, 1]] = x1;
    OmegaQDD[[repeat, 2]] = x2;
    OmegaQDD[[repeat, 3]] = FQDD /. mHfromD → x1 /. mDfromH → x2;
   ];
 ];
```

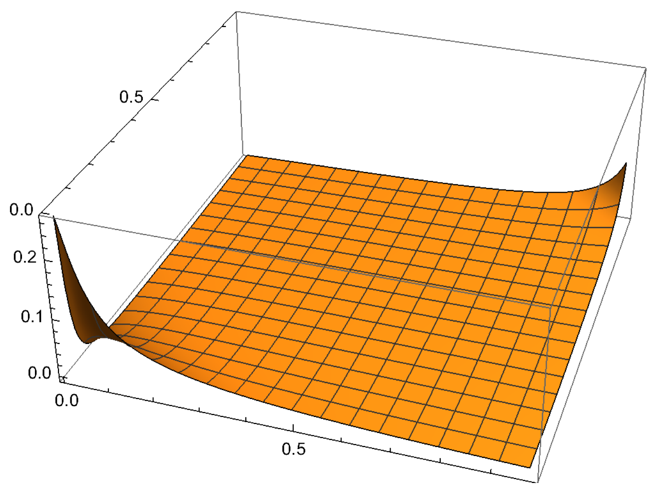
```
ListPlot3D[OmegaQHH]
ListPlot3D[OmegaQHH, PlotRange → All]
```



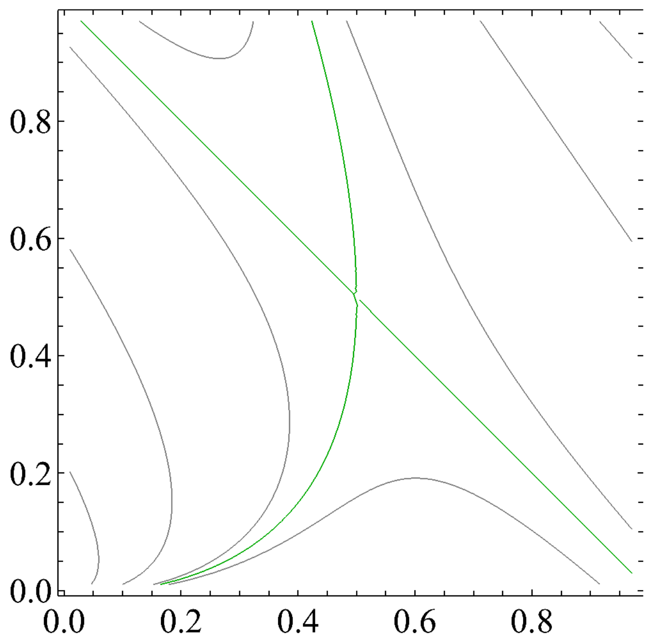


```
ListPlot3D[OmegaQDD]
ListPlot3D[OmegaQDD, PlotRange → All]
```

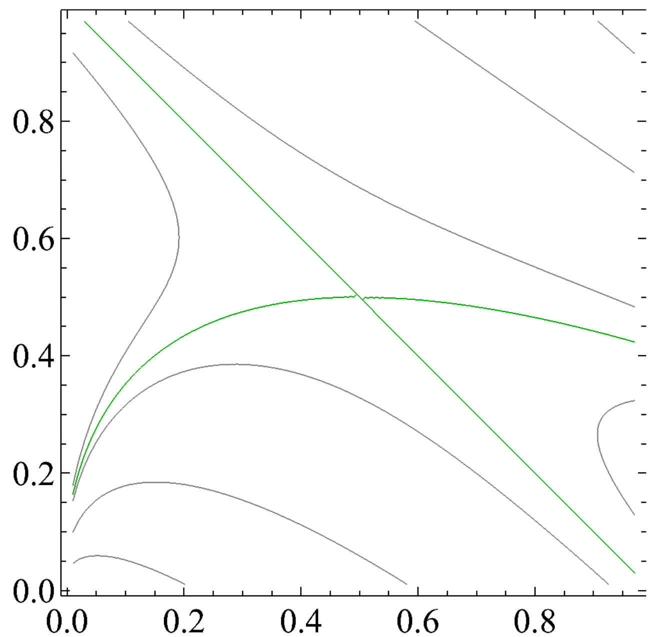




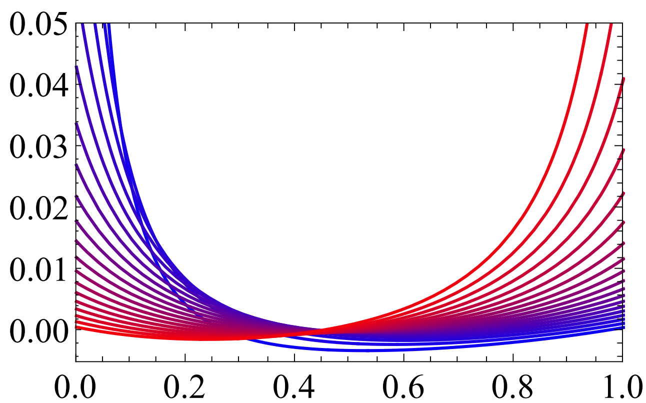
```
ListContourPlot[OmegaQHH,
  Contours → {{-0.001}, {0, Darker[Green]}, {0.001}, {0.01}, {0.05}},
  PlotRange → All, ContourShading → None];

Show[%, AxesOrigin → {0, 0}, AxesStyle → Directive[Black, AbsoluteThickness[0.5]],
 Frame → True, FrameStyle → AbsoluteThickness[0.5], FrameTicksStyle →
  Directive[AbsoluteThickness[0.5], FontFamily → "Times New Roman", FontSize → 18],
 FrameLabel → {Style["", 20, FontFamily → "Times New Roman"],
   Style["", 20, FontFamily → "Times New Roman"]}]
```



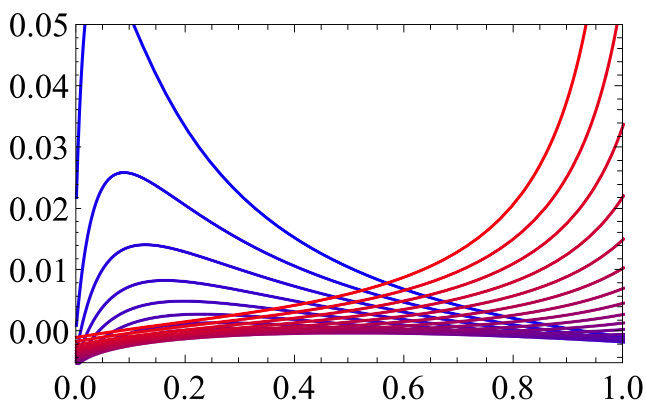
```
ListContourPlot[OmegaQDD,
  Contours → {{-0.001}, {0, Darker[Green]}, {0.001}, {0.01}, {0.05}},
  PlotRange → All, ContourShading → None];

Show[%, AxesOrigin → {0, 0}, AxesStyle → Directive[Black, AbsoluteThickness[0.5]],
 Frame → True, FrameStyle → AbsoluteThickness[0.5], FrameTicksStyle →
  Directive[AbsoluteThickness[0.5], FontFamily → "Times New Roman", FontSize → 18],
 FrameLabel → {Style["", 20, FontFamily → "Times New Roman"],
   Style["", 20, FontFamily → "Times New Roman"]}]
```



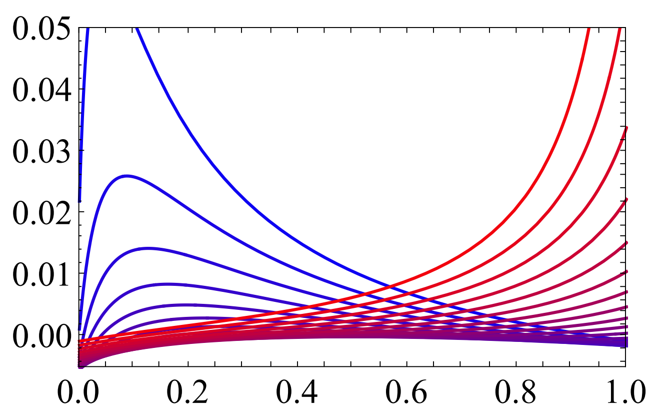
```
Plot[Evaluate[
   FaiHHstrict /. ρH → 2/3 /. Ntot → 100 /. mDfromH → Table[i, {i, 0.05, 0.95, 0.05}]],
  {mHfromD, 0, 1}, PlotStyle → Table[RGBColor[i, 0, 1 - i], {i, 0.05, 0.95, 0.05}],
  PlotRange → {{0, 1}, {-0.005, 0.05}}
 ];

Show[%, AxesOrigin → {0, 0}, AxesStyle → Directive[Black, AbsoluteThickness[0.5]],
 Frame → True, FrameStyle → AbsoluteThickness[0.5], FrameTicksStyle →
  Directive[AbsoluteThickness[0.5], FontFamily → "Times New Roman", FontSize → 18],
 FrameLabel → {Style["", 20, FontFamily → "Times New Roman"],
   Style["", 20, FontFamily → "Times New Roman"]}]
```



```
Plot[Evaluate[
    FaiHHstrict /. ρH → 2/3 /. Ntot → 100 /. mHfromD → Table[i, {i, 0.05, 0.95, 0.05}]],
  {mDfromH, 0, 1}, PlotStyle → Table[RGBColor[i, 0, 1 - i], {i, 0.05, 0.95, 0.05}],
  PlotRange → {{0, 1}, {-0.005, 0.05}}
 ];

Show[%, AxesOrigin → {0, 0}, AxesStyle → Directive[Black, AbsoluteThickness[0.5]],
 Frame → True, FrameStyle → AbsoluteThickness[0.5], FrameTicksStyle →
  Directive[AbsoluteThickness[0.5], FontFamily → "Times New Roman", FontSize → 18],
 FrameLabel → {Style["", 20, FontFamily → "Times New Roman"],
   Style["", 20, FontFamily → "Times New Roman"]}]
```



```
Plot[Evaluate[
   FaiDDstrict /. ρH → 2/3 /. Ntot → 100 /. mDfromH → Table[i, {i, 0.05, 0.95, 0.05}]],
  {mHfromD, 0, 1}, PlotStyle → Table[RGBColor[i, 0, 1 - i], {i, 0.05, 0.95, 0.05}],
  PlotRange → {{0, 1}, {-0.005, 0.05}}
 ];

Show[%, AxesOrigin → {0, 0}, AxesStyle → Directive[Black, AbsoluteThickness[0.5]],
 Frame → True, FrameStyle → AbsoluteThickness[0.5], FrameTicksStyle →
  Directive[AbsoluteThickness[0.5], FontFamily → "Times New Roman", FontSize → 18],
 FrameLabel → {Style["", 20, FontFamily → "Times New Roman"],
   Style["", 20, FontFamily → "Times New Roman"]}]
```



```
Plot[Evaluate[
   FaiDDstrict /. ρH → 2/3 /. Ntot → 100 /. mHfromD → Table[i, {i, 0.05, 0.95, 0.05}]],
  {mDfromH, 0, 1}, PlotStyle → Table[RGBColor[i, 0, 1 - i], {i, 0.05, 0.95, 0.05}],
  PlotRange → {{0, 1}, {-0.005, 0.05}}
 ];

Show[%, AxesOrigin → {0, 0}, AxesStyle → Directive[Black, AbsoluteThickness[0.5]],
 Frame → True, FrameStyle → AbsoluteThickness[0.5], FrameTicksStyle →
  Directive[AbsoluteThickness[0.5], FontFamily → "Times New Roman", FontSize → 18],
 FrameLabel → {Style["", 20, FontFamily → "Times New Roman"],
   Style["", 20, FontFamily → "Times New Roman"]}]
```

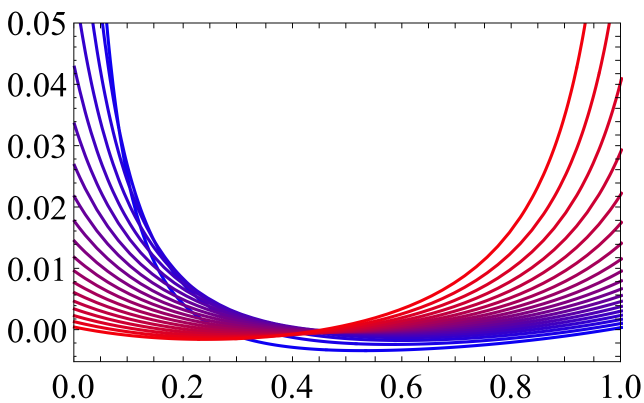
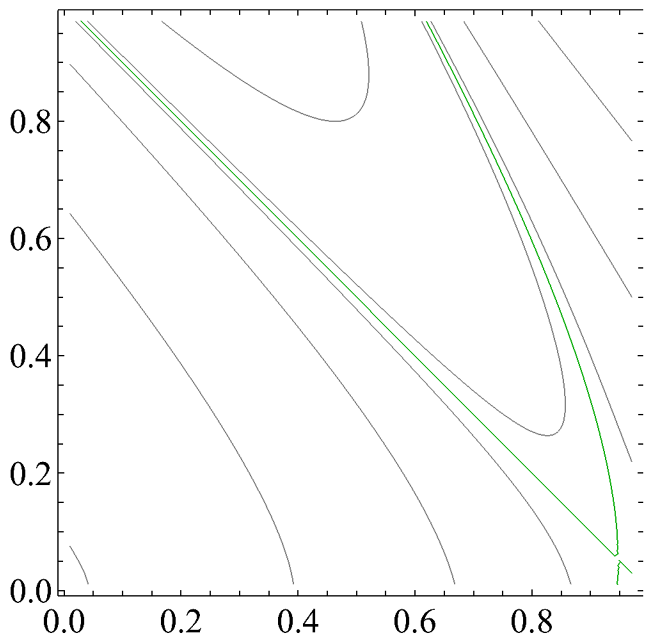


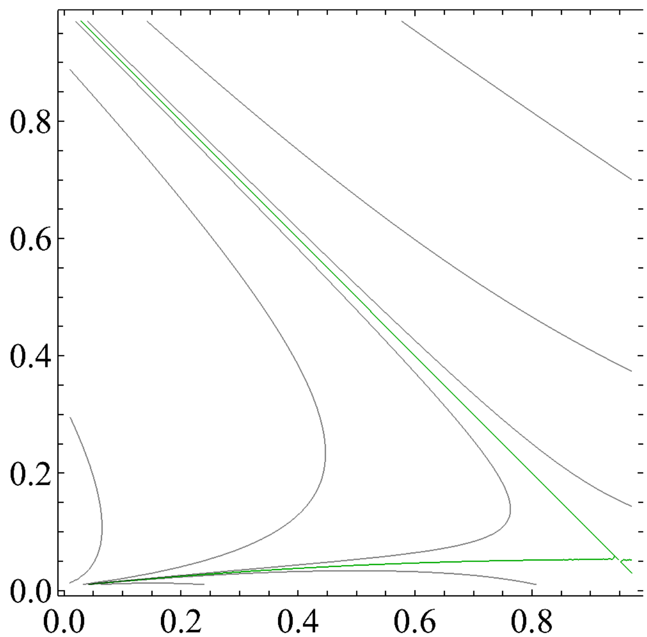
Figure 4: Asymmetry movement

```
MaxV = 0.99;
MinV = 0.01;
RepeatMax = 101;

FQHH = FaiHHstrict /. ρH → 0.1 /. Ntot → 100;
FQDD = FaiDDstrict /. ρH → 0.1 /. Ntot → 100;

OmegaQHH = Table[10, {i, (RepeatMax - 1) * (RepeatMax - 1)}, {j, 3}];
OmegaQDD = Table[10, {i, (RepeatMax - 1) * (RepeatMax - 1)}, {j, 3}];
repeat = 0;
For[repeat1 = 1, repeat1 ≤ RepeatMax - 1, repeat1 = repeat1 + 1,
  For[repeat2 = 1, repeat2 ≤ RepeatMax - 1, repeat2 = repeat2 + 1,
    repeat = repeat + 1;
    x1 = MinV + (MaxV - MinV)/RepeatMax * (repeat1 - 1);
    x2 = MinV + (MaxV - MinV)/RepeatMax * (repeat2 - 1);

    OmegaQHH[[repeat, 1]] = x1;
    OmegaQHH[[repeat, 2]] = x2;
    OmegaQHH[[repeat, 3]] = FQHH /. mHfromD → x1 /. mDfromH → x2;

    OmegaQDD[[repeat, 1]] = x1;
    OmegaQDD[[repeat, 2]] = x2;
    OmegaQDD[[repeat, 3]] = FQDD /. mHfromD → x1 /. mDfromH → x2;
   ];
 ];
```

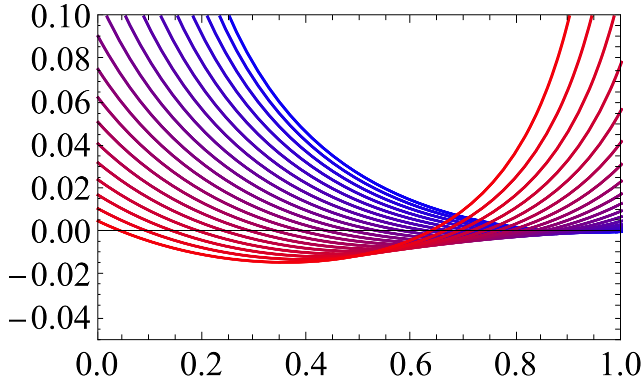
```
ListContourPlot[OmegaQHH,
  Contours → {{-0.01}, {-0.001}, {0, Darker[Green]}, {0.001}, {0.01}, {0.05}, {0.5}},
  PlotRange → All, ContourShading → None];

Show[%, AxesOrigin → {0, 0}, AxesStyle → Directive[Black, AbsoluteThickness[0.5]],
 Frame → True, FrameStyle → AbsoluteThickness[0.5], FrameTicksStyle →
  Directive[AbsoluteThickness[0.5], FontFamily → "Times New Roman", FontSize → 18],
 FrameLabel → {Style["", 20, FontFamily → "Times New Roman"],
   Style["", 20, FontFamily → "Times New Roman"]}]
```



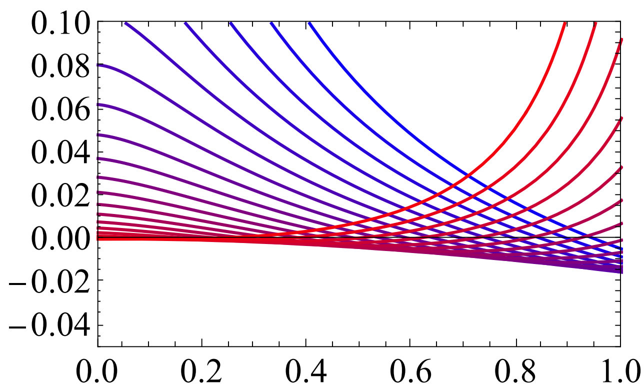
```
ListContourPlot[OmegaQDD, Contours →
   {{-0.1}, {-0.01}, {-0.001}, {0, Darker[Green]}, {0.001}, {0.01}, {0.05}, {0.5}},
  PlotRange → All, ContourShading → None];

Show[%, AxesOrigin → {0, 0}, AxesStyle → Directive[Black, AbsoluteThickness[0.5]],
 Frame → True, FrameStyle → AbsoluteThickness[0.5], FrameTicksStyle →
  Directive[AbsoluteThickness[0.5], FontFamily → "Times New Roman", FontSize → 18],
 FrameLabel → {Style["", 20, FontFamily → "Times New Roman"],
   Style["", 20, FontFamily → "Times New Roman"]}]
```



```
Plot[Evaluate[
    FaiHHstrict /. ρH → 0.1 /. Ntot → 100 /. mDfromH → Table[i, {i, 0.05, 0.95, 0.05}]],
  {mHfromD, 0, 1}, PlotStyle → Table[RGBColor[i, 0, 1 - i], {i, 0.05, 0.95, 0.05}],
  PlotRange → {{0, 1}, {-0.05, 0.1}}
 ];

Show[%, AxesOrigin → {0, 0}, AxesStyle → Directive[Black, AbsoluteThickness[0.5]],
 Frame → True, FrameStyle → AbsoluteThickness[0.5], FrameTicksStyle →
  Directive[AbsoluteThickness[0.5], FontFamily → "Times New Roman", FontSize → 18],
 FrameLabel → {Style["", 20, FontFamily → "Times New Roman"],
   Style["", 20, FontFamily → "Times New Roman"]}]
```

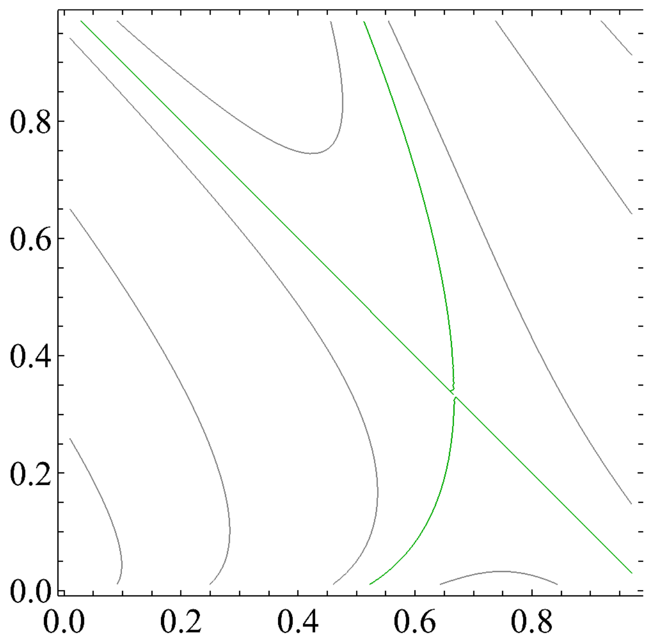


```
Plot[Evaluate[
   FaiHHstrict /. ρH → 0.1 /. Ntot → 100 /. mHfromD → Table[i, {i, 0.05, 0.95, 0.05}]],
  {mDfromH, 0, 1}, PlotStyle → Table[RGBColor[i, 0, 1 - i], {i, 0.05, 0.95, 0.05}],
  PlotRange → {{0, 1}, {-0.05, 0.1}}
 ];

Show[%, AxesOrigin → {0, 0}, AxesStyle → Directive[Black, AbsoluteThickness[0.5]],
 Frame → True, FrameStyle → AbsoluteThickness[0.5], FrameTicksStyle →
  Directive[AbsoluteThickness[0.5], FontFamily → "Times New Roman", FontSize → 18],
 FrameLabel → {Style["", 20, FontFamily → "Times New Roman"],
   Style["", 20, FontFamily → "Times New Roman"]}]
```

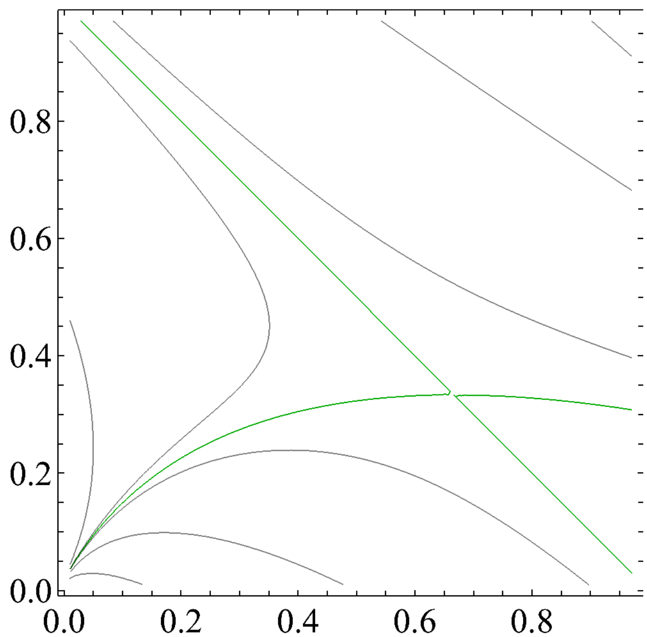


```
MaxV = 0.99;
MinV = 0.01;
RepeatMax = 101;

FQHH = FaiHHstrict /. ρH → 0.5 /. Ntot → 100;
FQDD = FaiDDstrict /. ρH → 0.5 /. Ntot → 100;

OmegaQHH = Table[10, {i, (RepeatMax - 1) * (RepeatMax - 1)}, {j, 3}];
OmegaQDD = Table[10, {i, (RepeatMax - 1) * (RepeatMax - 1)}, {j, 3}];
repeat = 0;
For[repeat1 = 1, repeat1 ≤ RepeatMax - 1, repeat1 = repeat1 + 1,
  For[repeat2 = 1, repeat2 ≤ RepeatMax - 1, repeat2 = repeat2 + 1,
    repeat = repeat + 1;
    x1 = MinV + (MaxV - MinV)/RepeatMax * (repeat1 - 1);
    x2 = MinV + (MaxV - MinV)/RepeatMax * (repeat2 - 1);

    OmegaQHH[[repeat, 1]] = x1;
    OmegaQHH[[repeat, 2]] = x2;
    OmegaQHH[[repeat, 3]] = FQHH /. mHfromD → x1 /. mDfromH → x2;

    OmegaQDD[[repeat, 1]] = x1;
    OmegaQDD[[repeat, 2]] = x2;
    OmegaQDD[[repeat, 3]] = FQDD /. mHfromD → x1 /. mDfromH → x2;
  ];
];
```

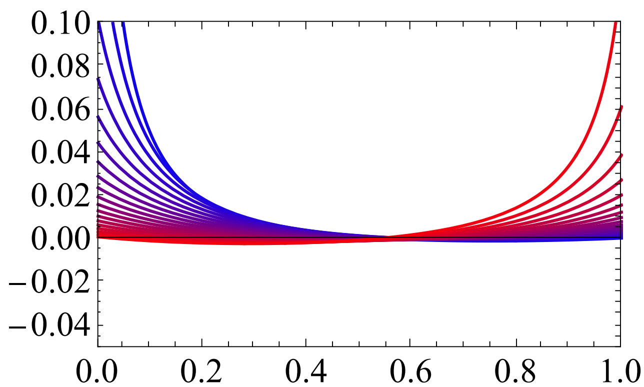
```
ListContourPlot[OmegaQHH,
  Contours → {{-0.001}, {0, Darker[Green]}, {0.001}, {0.01}, {0.05}},
  PlotRange → All, ContourShading → None];

Show[%, AxesOrigin → {0, 0}, AxesStyle → Directive[Black, AbsoluteThickness[0.5]],
 Frame → True, FrameStyle → AbsoluteThickness[0.5], FrameTicksStyle →
  Directive[AbsoluteThickness[0.5], FontFamily → "Times New Roman", FontSize → 18],
 FrameLabel → {Style["", 20, FontFamily → "Times New Roman"],
   Style["", 20, FontFamily → "Times New Roman"]}]
```



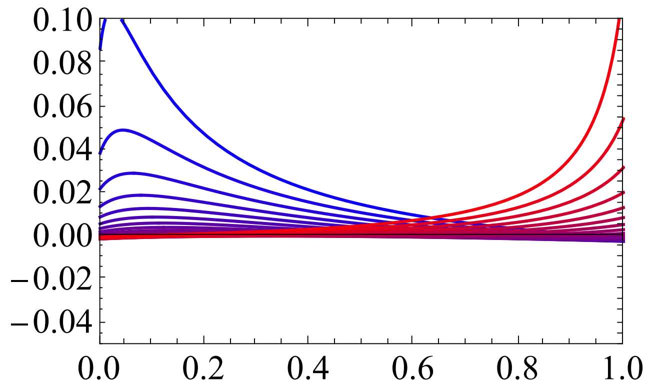
```
ListContourPlot[OmegaQDD,
  Contours → {{-0.01}, {-0.001}, {0, Darker[Green]}, {0.001}, {0.01}, {0.05}},
  PlotRange → All, ContourShading → None];

Show[%, AxesOrigin → {0, 0}, AxesStyle → Directive[Black, AbsoluteThickness[0.5]],
 Frame → True, FrameStyle → AbsoluteThickness[0.5], FrameTicksStyle →
  Directive[AbsoluteThickness[0.5], FontFamily → "Times New Roman", FontSize → 18],
 FrameLabel → {Style["", 20, FontFamily → "Times New Roman"],
   Style["", 20, FontFamily → "Times New Roman"]}]
```



```
Plot[Evaluate[
   FaiHHstrict /. ρH → 0.5 /. Ntot → 100 /. mDfromH → Table[i, {i, 0.05, 0.95, 0.05}]],
  {mHfromD, 0, 1}, PlotStyle → Table[RGBColor[i, 0, 1 - i], {i, 0.05, 0.95, 0.05}],
  PlotRange → {{0, 1}, {-0.05, 0.1}}
 ];

Show[%, AxesOrigin → {0, 0}, AxesStyle → Directive[Black, AbsoluteThickness[0.5]],
 Frame → True, FrameStyle → AbsoluteThickness[0.5], FrameTicksStyle →
  Directive[AbsoluteThickness[0.5], FontFamily → "Times New Roman", FontSize → 18],
 FrameLabel → {Style["", 20, FontFamily → "Times New Roman"],
   Style["", 20, FontFamily → "Times New Roman"]}]
```

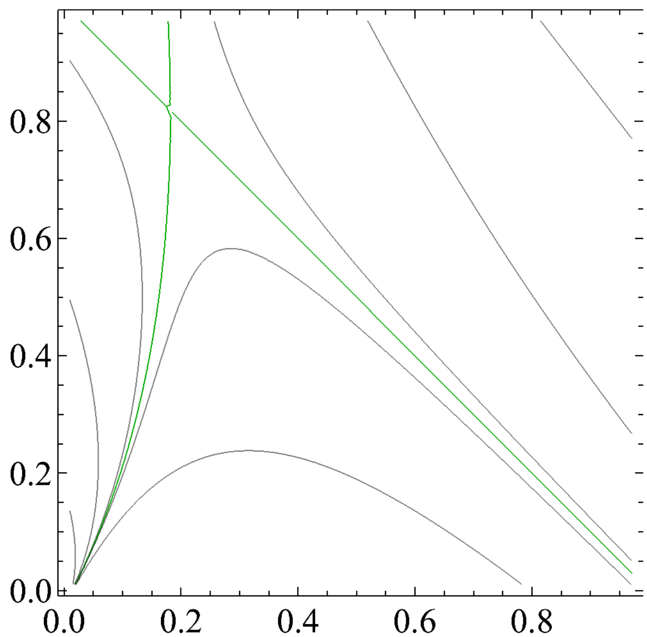


```
Plot[Evaluate[
    FaiHHstrict /. ρH → 0.5 /. Ntot → 100 /. mHfromD → Table[i, {i, 0.05, 0.95, 0.05}]],
  {mDfromH, 0, 1}, PlotStyle → Table[RGBColor[i, 0, 1 - i], {i, 0.05, 0.95, 0.05}],
  PlotRange → {{0, 1}, {-0.05, 0.1}}
 ];

Show[%, AxesOrigin → {0, 0}, AxesStyle → Directive[Black, AbsoluteThickness[0.5]],
 Frame → True, FrameStyle → AbsoluteThickness[0.5], FrameTicksStyle →
  Directive[AbsoluteThickness[0.5], FontFamily → "Times New Roman", FontSize → 18],
 FrameLabel → {Style["", 20, FontFamily → "Times New Roman"],
   Style["", 20, FontFamily → "Times New Roman"]}]
```

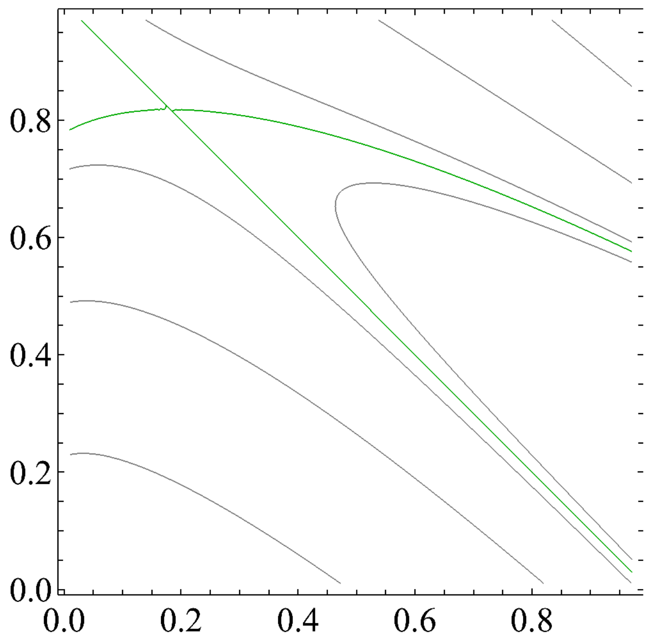


```
MaxV = 0.99;
MinV = 0.01;
RepeatMax = 101;

FQHH = FaiHHstrict /. ρH → 0.9 /. Ntot → 100;
FQDD = FaiDDstrict /. ρH → 0.9 /. Ntot → 100;

OmegaQHH = Table[10, {i, (RepeatMax - 1) * (RepeatMax - 1)}, {j, 3}];
OmegaQDD = Table[10, {i, (RepeatMax - 1) * (RepeatMax - 1)}, {j, 3}];
repeat = 0;
For[repeat1 = 1, repeat1 ≤ RepeatMax - 1, repeat1 = repeat1 + 1,
  For[repeat2 = 1, repeat2 ≤ RepeatMax - 1, repeat2 = repeat2 + 1,
    repeat = repeat + 1;
    x1 = MinV + (MaxV - MinV)/RepeatMax * (repeat1 - 1);
    x2 = MinV + (MaxV - MinV)/RepeatMax * (repeat2 - 1);

    OmegaQHH[[repeat, 1]] = x1;
    OmegaQHH[[repeat, 2]] = x2;
    OmegaQHH[[repeat, 3]] = FQHH /. mHfromD → x1 /. mDfromH → x2;

    OmegaQDD[[repeat, 1]] = x1;
    OmegaQDD[[repeat, 2]] = x2;
    OmegaQDD[[repeat, 3]] = FQDD /. mHfromD → x1 /. mDfromH → x2;
  ];
];
```

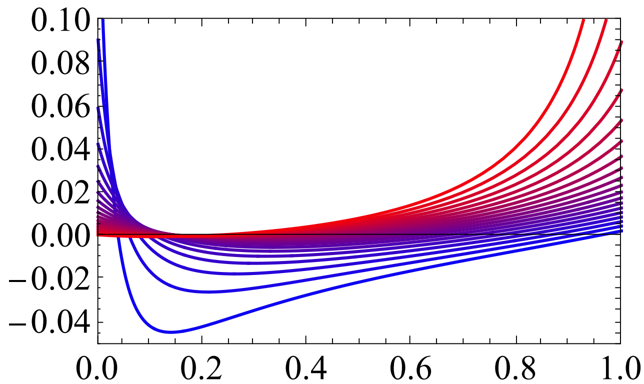
```
ListContourPlot[OmegaQHH,
  Contours → {{-0.01}, {-0.001}, {0, Darker[Green]}, {0.001}, {0.01}, {0.05}},
  PlotRange → All, ContourShading → None];

Show[%, AxesOrigin → {0, 0}, AxesStyle → Directive[Black, AbsoluteThickness[0.5]],
 Frame → True, FrameStyle → AbsoluteThickness[0.5], FrameTicksStyle →
  Directive[AbsoluteThickness[0.5], FontFamily → "Times New Roman", FontSize → 18],
 FrameLabel → {Style["", 20, FontFamily → "Times New Roman"],
   Style["", 20, FontFamily → "Times New Roman"]}]
```



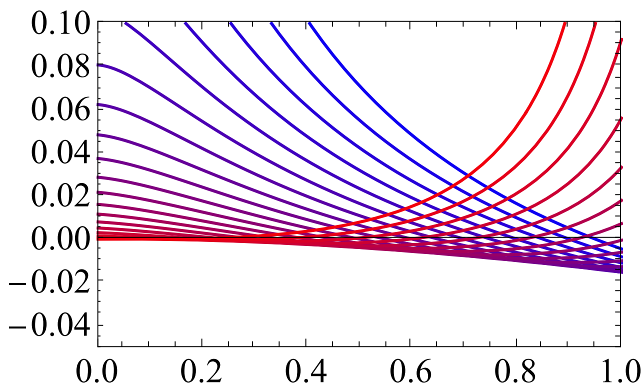
```
ListContourPlot[OmegaQDD,
  Contours → {{-0.01}, {-0.001}, {0, Darker[Green]}, {0.001}, {0.01}, {0.05}},
  PlotRange → All, ContourShading → None];

Show[%, AxesOrigin → {0, 0}, AxesStyle → Directive[Black, AbsoluteThickness[0.5]],
 Frame → True, FrameStyle → AbsoluteThickness[0.5], FrameTicksStyle →
  Directive[AbsoluteThickness[0.5], FontFamily → "Times New Roman", FontSize → 18],
 FrameLabel → {Style["", 20, FontFamily → "Times New Roman"],
   Style["", 20, FontFamily → "Times New Roman"]}]
```



```
Plot[Evaluate[
   FaiHHstrict /. ρH → 0.9 /. Ntot → 100 /. mDfromH → Table[i, {i, 0.05, 0.95, 0.05}]],
  {mHfromD, 0, 1}, PlotStyle → Table[RGBColor[i, 0, 1 - i], {i, 0.05, 0.95, 0.05}],
  PlotRange → {{0, 1}, {-0.05, 0.1}}
 ];

Show[%, AxesOrigin → {0, 0}, AxesStyle → Directive[Black, AbsoluteThickness[0.5]],
 Frame → True, FrameStyle → AbsoluteThickness[0.5], FrameTicksStyle →
  Directive[AbsoluteThickness[0.5], FontFamily → "Times New Roman", FontSize → 18],
 FrameLabel → {Style["", 20, FontFamily → "Times New Roman"],
   Style["", 20, FontFamily → "Times New Roman"]}]
```



```
Plot[Evaluate[
   FaiHHstrict /. ρH → 0.1 /. Ntot → 100 /. mHfromD → Table[i, {i, 0.05, 0.95, 0.05}]],
  {mDfromH, 0, 1}, PlotStyle → Table[RGBColor[i, 0, 1 - i], {i, 0.05, 0.95, 0.05}],
  PlotRange → {{0, 1}, {-0.05, 0.1}}
 ];

Show[%, AxesOrigin → {0, 0}, AxesStyle → Directive[Black, AbsoluteThickness[0.5]],
 Frame → True, FrameStyle → AbsoluteThickness[0.5], FrameTicksStyle →
  Directive[AbsoluteThickness[0.5], FontFamily → "Times New Roman", FontSize → 18],
 FrameLabel → {Style["", 20, FontFamily → "Times New Roman"],
   Style["", 20, FontFamily → "Times New Roman"]}]
```



Supplementary: Average Fst, Equal chromosome number

```
FaiAverage /. ρH → 2/3 // FullSimplify
```

$$\text{Eq8} = \frac{(1-X)^2}{\frac{2}{3} * \text{Ntot} - (1-X)^2 * \left(\frac{2}{3} * \text{Ntot} - 1\right)} \text{ /. } X \rightarrow \text{mHfromD} + \text{mDfromH};$$

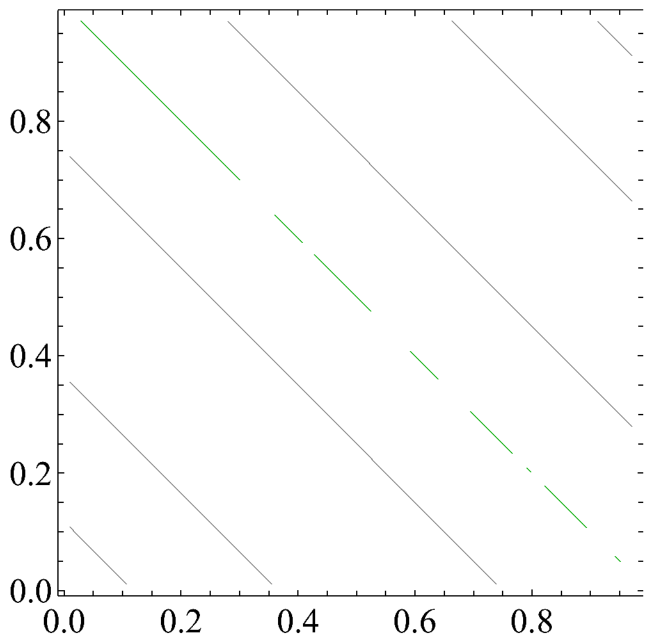
```
% - %% // Simplify
```

$$-\frac{3\,(-1+\text{mDfromH}+\text{mHfromD})^2}{-3\,(-1+\text{mDfromH}+\text{mHfromD})^2+2\,(-2+\text{mDfromH}+\text{mHfromD})\,(\text{mDfromH}+\text{mHfromD})\,\text{Ntot}}$$

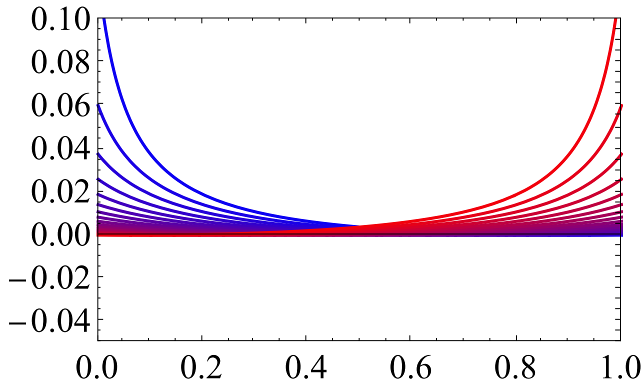
0

```
MaxV = 0.99;
MinV = 0.01;
RepeatMax = 101;

OmegaQave = Table[10, {i, (RepeatMax - 1) * (RepeatMax - 1)}, {j, 3}];

repeat = 0;
For[repeat1 = 1, repeat1 ≤ RepeatMax - 1, repeat1 = repeat1 + 1,
  For[repeat2 = 1, repeat2 ≤ RepeatMax - 1, repeat2 = repeat2 + 1,
    repeat = repeat + 1;
    x1 = MinV + (MaxV - MinV)/RepeatMax * (repeat1 - 1);
    x2 = MinV + (MaxV - MinV)/RepeatMax * (repeat2 - 1);

    OmegaQave[[repeat, 1]] = x1;
    OmegaQave[[repeat, 2]] = x2;
    OmegaQave[[repeat, 3]] =
     FaiAverage /. ρH → 2/3 /. Ntot → 100 /. mHfromD → x1 /. mDfromH → x2;

   ];
  ];
```

```
ListContourPlot[OmegaQave,
  Contours → {{-0.01}, {-0.001}, {0, Darker[Green]}, {0.001}, {0.01}, {0.05}, {0.5}},
  PlotRange → All, ContourShading → None];

Show[%, AxesOrigin → {0, 0}, AxesStyle → Directive[Black, AbsoluteThickness[0.5]],
 Frame → True, FrameStyle → AbsoluteThickness[0.5], FrameTicksStyle →
  Directive[AbsoluteThickness[0.5], FontFamily → "Times New Roman", FontSize → 18],
 FrameLabel → {Style["", 20, FontFamily → "Times New Roman"],
   Style["", 20, FontFamily → "Times New Roman"]}]
```



```
Plot[Evaluate[
    FaiAverage /. ρH → 2/3 /. Ntot → 100 /. mDfromH → Table[i, {i, 0.05, 0.95, 0.05}]],
  {mHfromD, 0, 1}, PlotStyle → Table[RGBColor[i, 0, 1 - i], {i, 0.05, 0.95, 0.05}],
  PlotRange → {{0, 1}, {-0.05, 0.1}}
 ];

Show[%, AxesOrigin → {0, 0}, AxesStyle → Directive[Black, AbsoluteThickness[0.5]],
 Frame → True, FrameStyle → AbsoluteThickness[0.5], FrameTicksStyle →
  Directive[AbsoluteThickness[0.5], FontFamily → "Times New Roman", FontSize → 18],
 FrameLabel → {Style["", 20, FontFamily → "Times New Roman"],
   Style["", 20, FontFamily → "Times New Roman"]}]
```



```
Plot[Evaluate[
   FaiAverage /. ρH → 2/3 /. Ntot → 100 /. mHfromD → Table[i, {i, 0.05, 0.95, 0.05}]],
  {mDfromH, 0, 1}, PlotStyle → Table[RGBColor[i, 0, 1 - i], {i, 0.05, 0.95, 0.05}],
  PlotRange → {{0, 1}, {-0.05, 0.1}}
 ];

Show[%, AxesOrigin → {0, 0}, AxesStyle → Directive[Black, AbsoluteThickness[0.5]],
 Frame → True, FrameStyle → AbsoluteThickness[0.5], FrameTicksStyle →
  Directive[AbsoluteThickness[0.5], FontFamily → "Times New Roman", FontSize → 18],
 FrameLabel → {Style["", 20, FontFamily → "Times New Roman"],
   Style["", 20, FontFamily → "Times New Roman"]}]
```

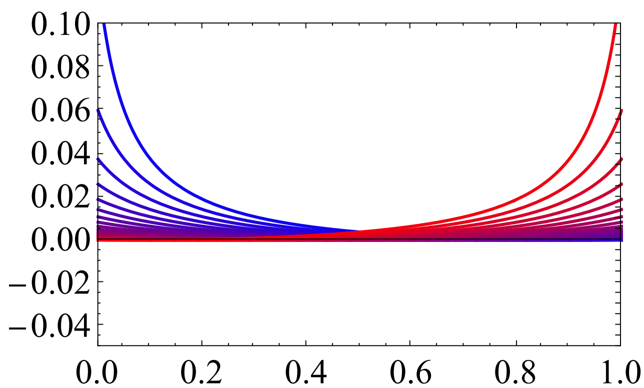
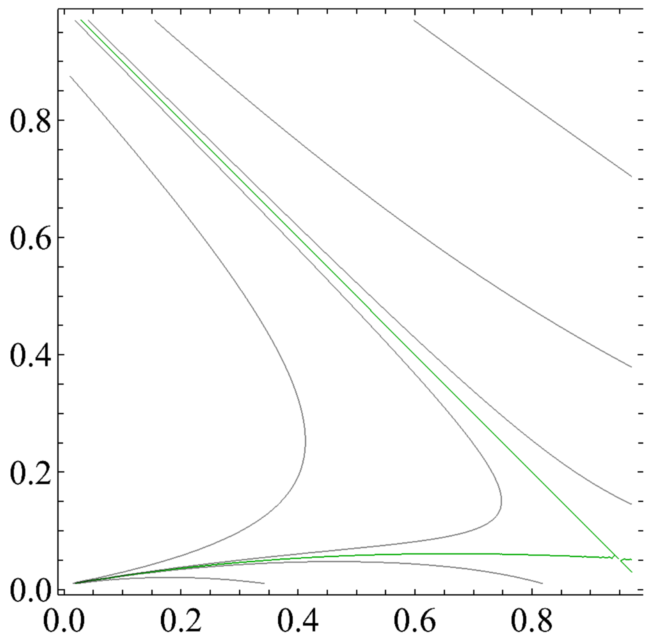


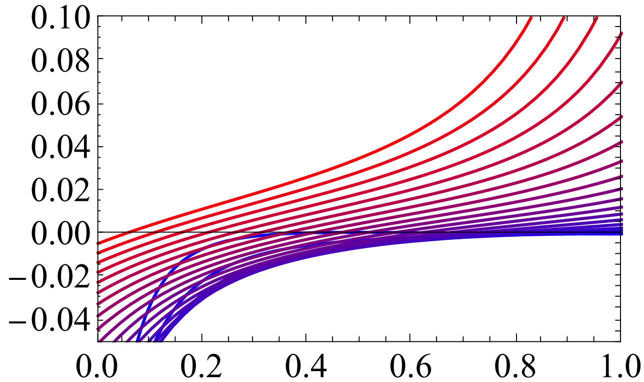
Figure 5: Average Fst

```
MaxV = 0.99;
MinV = 0.01;
RepeatMax = 101;

OmegaQave = Table[10, {i, (RepeatMax - 1) * (RepeatMax - 1)}, {j, 3}];

repeat = 0;
For[repeat1 = 1, repeat1 ≤ RepeatMax - 1, repeat1 = repeat1 + 1,
  For[repeat2 = 1, repeat2 ≤ RepeatMax - 1, repeat2 = repeat2 + 1,
    repeat = repeat + 1;
    x1 = MinV + (MaxV - MinV)/RepeatMax * (repeat1 - 1);
    x2 = MinV + (MaxV - MinV)/RepeatMax * (repeat2 - 1);

    OmegaQave[[repeat, 1]] = x1;
    OmegaQave[[repeat, 2]] = x2;
    OmegaQave[[repeat, 3]] =
     FaiAverage /. ρH → 0.1 /. Ntot → 100 /. mHfromD → x1 /. mDfromH → x2;

   ];
 ];
```

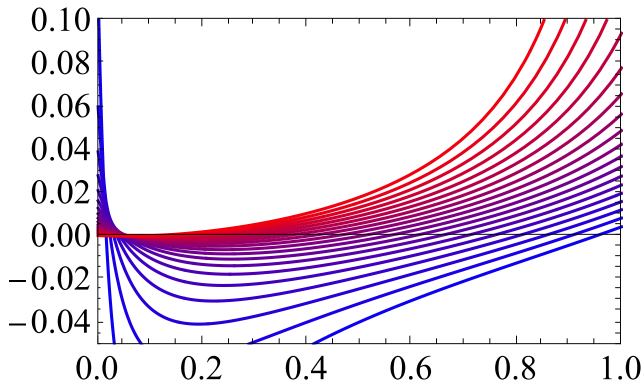
```
ListContourPlot[OmegaQave,
  Contours → {{-0.01}, {-0.001}, {0, Darker[Green]}, {0.001}, {0.01}, {0.05}, {0.5}},
  PlotRange → All, ContourShading → None];

Show[%, AxesOrigin → {0, 0}, AxesStyle → Directive[Black, AbsoluteThickness[0.5]],
 Frame → True, FrameStyle → AbsoluteThickness[0.5], FrameTicksStyle →
  Directive[AbsoluteThickness[0.5], FontFamily → "Times New Roman", FontSize → 18],
 FrameLabel → {Style["", 20, FontFamily → "Times New Roman"],
   Style["", 20, FontFamily → "Times New Roman"]}]
```



```
Plot[Evaluate[
   FaiAverage /. ρH → 0.1 /. Ntot → 100 /. mDfromH → Table[i, {i, 0.05, 0.95, 0.05}]],
  {mHfromD, 0, 1}, PlotStyle → Table[RGBColor[i, 0, 1 - i], {i, 0.05, 0.95, 0.05}],
  PlotRange → {{0, 1}, {-0.05, 0.1}}
 ];

Show[%, AxesOrigin → {0, 0}, AxesStyle → Directive[Black, AbsoluteThickness[0.5]],
 Frame → True, FrameStyle → AbsoluteThickness[0.5], FrameTicksStyle →
  Directive[AbsoluteThickness[0.5], FontFamily → "Times New Roman", FontSize → 18],
 FrameLabel → {Style["", 20, FontFamily → "Times New Roman"],
   Style["", 20, FontFamily → "Times New Roman"]}]
```

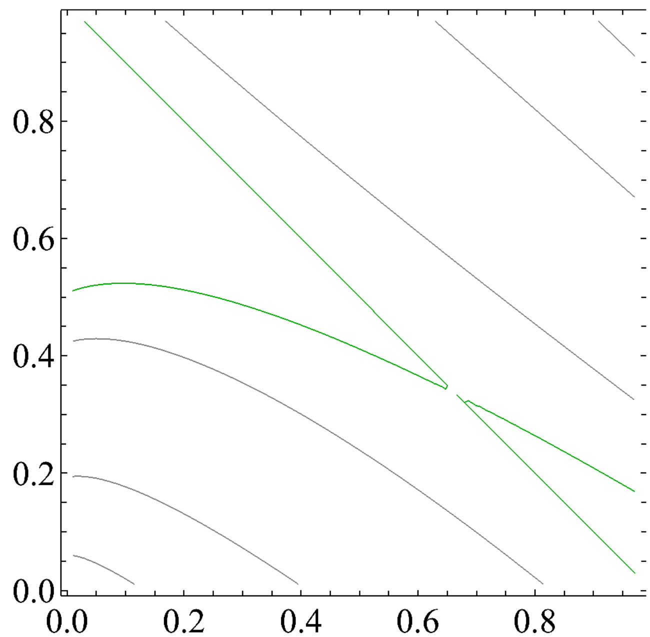


```
Plot[Evaluate[
    FaiAverage /. ρH → 0.1 /. Ntot → 100 /. mHfromD → Table[i, {i, 0.05, 0.95, 0.05}]],
  {mDfromH, 0, 1}, PlotStyle → Table[RGBColor[i, 0, 1 - i], {i, 0.05, 0.95, 0.05}],
  PlotRange → {{0, 1}, {-0.05, 0.1}}
 ];

Show[%, AxesOrigin → {0, 0}, AxesStyle → Directive[Black, AbsoluteThickness[0.5]],
 Frame → True, FrameStyle → AbsoluteThickness[0.5], FrameTicksStyle →
  Directive[AbsoluteThickness[0.5], FontFamily → "Times New Roman", FontSize → 18],
 FrameLabel → {Style["", 20, FontFamily → "Times New Roman"],
   Style["", 20, FontFamily → "Times New Roman"]}]
```

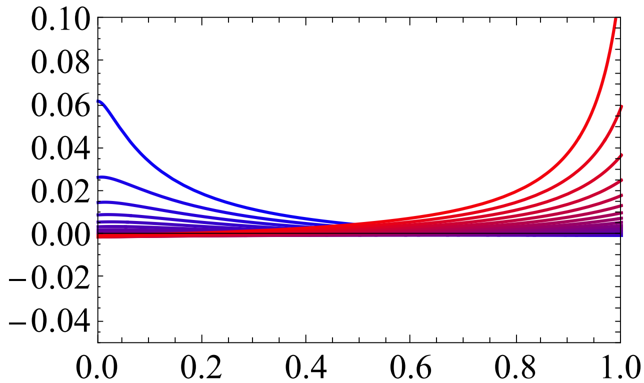


```
MaxV = 0.99;
MinV = 0.01;
RepeatMax = 101;

OmegaQave = Table[10, {i, (RepeatMax - 1) * (RepeatMax - 1)}, {j, 3}];

repeat = 0;
For[repeat1 = 1, repeat1 ≤ RepeatMax - 1, repeat1 = repeat1 + 1,
  For[repeat2 = 1, repeat2 ≤ RepeatMax - 1, repeat2 = repeat2 + 1,
    repeat = repeat + 1;
    x1 = MinV + (MaxV - MinV)/RepeatMax * (repeat1 - 1);
    x2 = MinV + (MaxV - MinV)/RepeatMax * (repeat2 - 1);

    OmegaQave[[repeat, 1]] = x1;
    OmegaQave[[repeat, 2]] = x2;
    OmegaQave[[repeat, 3]] =
     FaiAverage /. ρH → 0.5 /. Ntot → 100 /. mHfromD → x1 /. mDfromH → x2;

  ];
 ];
```

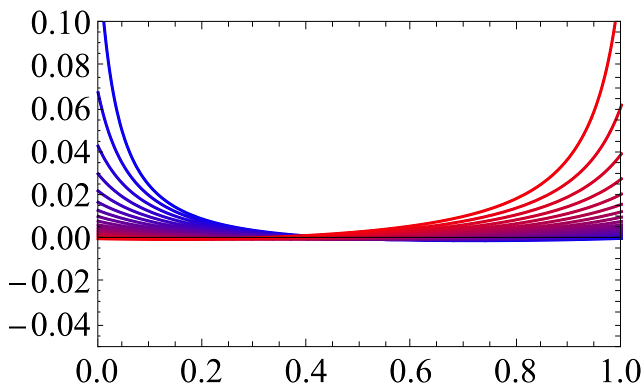
```
ListContourPlot[OmegaQave,
  Contours → {{-0.01}, {-0.001}, {0, Darker[Green]}, {0.001}, {0.01}, {0.05}, {0.5}},
  PlotRange → All, ContourShading → None];

Show[%, AxesOrigin → {0, 0}, AxesStyle → Directive[Black, AbsoluteThickness[0.5]],
 Frame → True, FrameStyle → AbsoluteThickness[0.5], FrameTicksStyle →
  Directive[AbsoluteThickness[0.5], FontFamily → "Times New Roman", FontSize → 18],
 FrameLabel → {Style["", 20, FontFamily → "Times New Roman"],
   Style["", 20, FontFamily → "Times New Roman"]}]
```



```
Plot[Evaluate[
   FaiAverage /. ρH → 0.5 /. Ntot → 100 /. mDfromH → Table[i, {i, 0.05, 0.95, 0.05}]],
  {mHfromD, 0, 1}, PlotStyle → Table[RGBColor[i, 0, 1 - i], {i, 0.05, 0.95, 0.05}],
  PlotRange → {{0, 1}, {-0.05, 0.1}}
 ];

Show[%, AxesOrigin → {0, 0}, AxesStyle → Directive[Black, AbsoluteThickness[0.5]],
 Frame → True, FrameStyle → AbsoluteThickness[0.5], FrameTicksStyle →
  Directive[AbsoluteThickness[0.5], FontFamily → "Times New Roman", FontSize → 18],
 FrameLabel → {Style["", 20, FontFamily → "Times New Roman"],
   Style["", 20, FontFamily → "Times New Roman"]}]
```

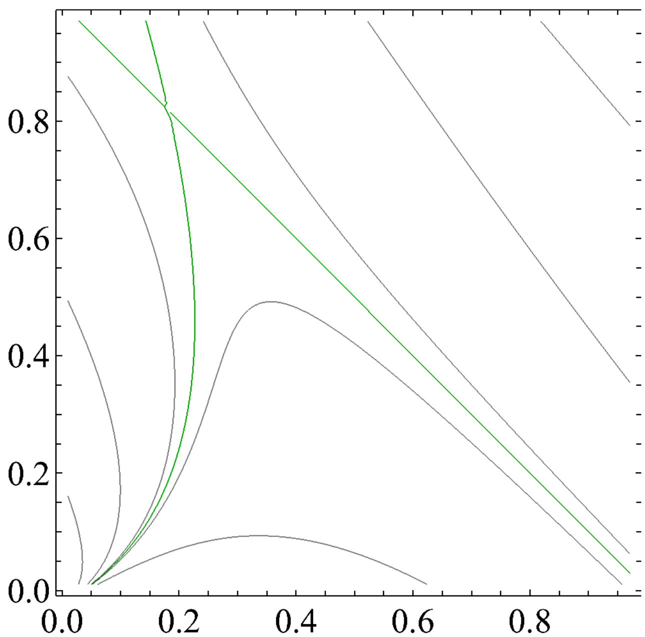


```
Plot[Evaluate[
   FaiAverage /. ρH → 0.5 /. Ntot → 100 /. mHfromD → Table[i, {i, 0.05, 0.95, 0.05}]],
  {mDfromH, 0, 1}, PlotStyle → Table[RGBColor[i, 0, 1 - i], {i, 0.05, 0.95, 0.05}],
  PlotRange → {{0, 1}, {-0.05, 0.1}}
 ];

Show[%, AxesOrigin → {0, 0}, AxesStyle → Directive[Black, AbsoluteThickness[0.5]],
 Frame → True, FrameStyle → AbsoluteThickness[0.5], FrameTicksStyle →
  Directive[AbsoluteThickness[0.5], FontFamily → "Times New Roman", FontSize → 18],
 FrameLabel → {Style["", 20, FontFamily → "Times New Roman"],
   Style["", 20, FontFamily → "Times New Roman"]}]
```

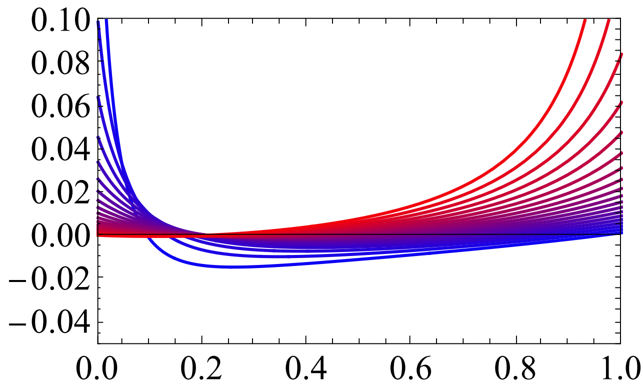


```
MaxV = 0.99;
MinV = 0.01;
RepeatMax = 101;

OmegaQave = Table[10, {i, (RepeatMax - 1) * (RepeatMax - 1)}, {j, 3}];

repeat = 0;
For[repeat1 = 1, repeat1 ≤ RepeatMax - 1, repeat1 = repeat1 + 1,
  For[repeat2 = 1, repeat2 ≤ RepeatMax - 1, repeat2 = repeat2 + 1,
    repeat = repeat + 1;
    x1 = MinV + (MaxV - MinV)/RepeatMax * (repeat1 - 1);
    x2 = MinV + (MaxV - MinV)/RepeatMax * (repeat2 - 1);

    OmegaQave[[repeat, 1]] = x1;
    OmegaQave[[repeat, 2]] = x2;
    OmegaQave[[repeat, 3]] =
     FaiAverage /. ρH → 0.9 /. Ntot → 100 /. mHfromD → x1 /. mDfromH → x2;

   ];
 ];
```

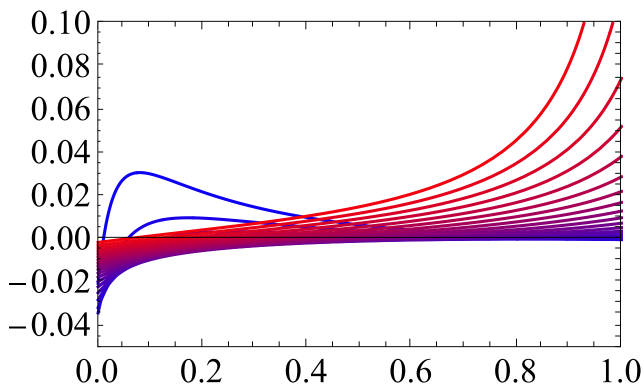
```
ListContourPlot[OmegaQave,
  Contours → {{-0.01}, {-0.001}, {0, Darker[Green]}, {0.001}, {0.01}, {0.05}, {0.5}},
  PlotRange → All, ContourShading → None];

Show[%, AxesOrigin → {0, 0}, AxesStyle → Directive[Black, AbsoluteThickness[0.5]],
 Frame → True, FrameStyle → AbsoluteThickness[0.5], FrameTicksStyle →
  Directive[AbsoluteThickness[0.5], FontFamily → "Times New Roman", FontSize → 18],
 FrameLabel → {Style["", 20, FontFamily → "Times New Roman"],
   Style["", 20, FontFamily → "Times New Roman"]}]
```



```
Plot[Evaluate[
   FaiAverage /. ρH → 0.9 /. Ntot → 100 /. mDfromH → Table[i, {i, 0.05, 0.95, 0.05}]],
  {mHfromD, 0, 1}, PlotStyle → Table[RGBColor[i, 0, 1 - i], {i, 0.05, 0.95, 0.05}],
  PlotRange → {{0, 1}, {-0.05, 0.1}}
 ];

Show[%, AxesOrigin → {0, 0}, AxesStyle → Directive[Black, AbsoluteThickness[0.5]],
 Frame → True, FrameStyle → AbsoluteThickness[0.5], FrameTicksStyle →
  Directive[AbsoluteThickness[0.5], FontFamily → "Times New Roman", FontSize → 18],
 FrameLabel → {Style["", 20, FontFamily → "Times New Roman"],
   Style["", 20, FontFamily → "Times New Roman"]}]
```



```
Plot[Evaluate[
   FaiAverage /. ρH → 0.9 /. Ntot → 100 /. mHfromD → Table[i, {i, 0.05, 0.95, 0.05}]],
  {mDfromH, 0, 1}, PlotStyle → Table[RGBColor[i, 0, 1 - i], {i, 0.05, 0.95, 0.05}],
  PlotRange → {{0, 1}, {-0.05, 0.1}}
 ];

Show[%, AxesOrigin → {0, 0}, AxesStyle → Directive[Black, AbsoluteThickness[0.5]],
 Frame → True, FrameStyle → AbsoluteThickness[0.5], FrameTicksStyle →
  Directive[AbsoluteThickness[0.5], FontFamily → "Times New Roman", FontSize → 18],
 FrameLabel → {Style["", 20, FontFamily → "Times New Roman"],
   Style["", 20, FontFamily → "Times New Roman"]}]
```



Supplementary: Coalescence process considering FIS

Equations

$$\text{NextQHH} = (1-\mu)^2 * \left(\text{mHfromH}^2 * \left(\frac{1}{\text{Hap}} + \left(1 - \frac{1}{\text{Hap}}\right) * \text{QHH}\right) + \text{mHfromH} * \text{mHfromD} * \text{QHD} + \text{mHfromD} * \text{mHfromH} * \text{QDH} + \text{mHfromD}^2 * \left(\frac{1}{2 * \text{Dip}} + \frac{1}{2 * \text{Dip}} * \text{QDDw} + \left(1 - \frac{2}{2 * \text{Dip}}\right) * \text{QDDb}\right)\right);$$

$$\text{NextQHD} = (1-\mu)^2 * \left(\text{mHfromH} * \text{mDfromH} * \left(\frac{1}{\text{Hap}} + \left(1 - \frac{1}{\text{Hap}}\right) * \text{QHH}\right) + \text{mHfromD} * \text{mDfromH} * \text{QDH} + \text{mHfromH} * \text{mDfromD} * \text{QHD} + \text{mHfromD} * \text{mDfromD} * \left(\frac{1}{2 * \text{Dip}} + \frac{1}{2 * \text{Dip}} * \text{QDDw} + \left(1 - \frac{2}{2 * \text{Dip}}\right) * \text{QDDb}\right)\right);$$

$$\text{NextQDH} = (1-\mu)^2 * \left(\text{mDfromH} * \text{mHfromH} * \left(\frac{1}{\text{Hap}} + \left(1 - \frac{1}{\text{Hap}}\right) * \text{QHH}\right) + \text{mDfromD} * \text{mHfromH} * \text{QDH} + \text{mDfromH} * \text{mHfromD} * \text{QHD} + \text{mDfromD} * \text{mHfromD} * \left(\frac{1}{2 * \text{Dip}} + \frac{1}{2 * \text{Dip}} * \text{QDDw} + \left(1 - \frac{2}{2 * \text{Dip}}\right) * \text{QDDb}\right)\right);$$

$$\text{NextQDDb} = (1-\mu)^2 * \left(\text{mDfromD}^2 * \left(\frac{1}{2 * \text{Dip}} + \frac{1}{2 * \text{Dip}} * \text{QDDw} + \left(1 - \frac{2}{2 * \text{Dip}}\right) * \text{QDDb}\right) + \text{mDfromH} * \text{mDfromD} * \text{QHD} + \text{mDfromD} * \text{mDfromH} * \text{QDH} + \text{mDfromH}^2 * \left(\frac{1}{\text{Hap}} + \left(1 - \frac{1}{\text{Hap}}\right) * \text{QHH}\right)\right);$$

$$\text{NextQDDw} = (1-\mu)^2 * \left(\text{mDfromD} * \text{QDDw} + \text{mDfromH} * \left(\frac{1}{\text{Hap}} + \left(1 - \frac{1}{\text{Hap}}\right) * \text{QHH}\right)\right);$$

Recall that these are backwards rates so that mDD+mHD sum to one:

```
constraints = {mHfromH + mHfromD == 1, mDfromH + mDfromD == 1, ρD + ρH == 1};
subconstraints = {mHfromH → 1 - mHfromD, mDfromD → 1 - mDfromH};
```

Exact FST and FIS

At equilibrium, we have

```
sol =
  Simplify[Solve[(NextQHH == QHH && NextQDDb == QDDb && NextQDDw == QDDw && NextQHD == QHD &&
      NextQDH == QDH), {QHH, QHD, QDH, QDDb, QDDw}], constraints];
```

When there is not mutation, because of a finite population size, Q must be 1.

```
sol /. subconstraints /. μ → 0 // Simplify
{{QHH → 1, QHD → 1, QDH → 1, QDDb → 1, QDDw → 1}}
```

```
EqQHH = Simplify[QHH /. sol[[1]], constraints];
EqQHD = Simplify[QHD /. sol[[1]], constraints];
EqQDH = Simplify[QDH /. sol[[1]], constraints];
EqQDDb = Simplify[QDDb /. sol[[1]], constraints];
EqQDDw = Simplify[QDDw /. sol[[1]], constraints];
```

Note that, we can show QHD = QDH,

```
EqQHD == EqQDH
```

```
True
```

Using Q, we define the F-like measures for the haploid-diploid population.

```
FaiHstrict = Simplify[Limit[(EqQHH - EqQHD)/(1 - EqQHD), μ → 0], constraints]
```

```
((mDfromH - mHfromH)
    ((2 - 2 Dip) mDfromH^3 + 4 (-1 + Dip) mDfromH^2 mHfromH - (-1 + mHfromH) mHfromH +
      mDfromH (-1 + Hap (-1 + mHfromH) + mHfromH + 2 Dip mHfromH + (2 - 2 Dip) mHfromH^2))) /
  (- (mDfromH - mHfromH) (mDfromH + 2 (-1 + Dip) mDfromH^3 + (-1 - 2 Dip) mDfromH mHfromH +
        (4 - 4 Dip) mDfromH^2 mHfromH + (-1 + mHfromH) mHfromH +
        2 (-1 + Dip) mDfromH mHfromH^2) + Hap (2 (-1 + Dip) mDfromH^4 -
        (-1 + mHfromH)^2 (1 + mHfromH) - 2 (-1 + Dip) mDfromH^3 (-1 + 3 mHfromH) -
        mDfromH (-1 + mHfromH) (1 - 2 Dip - 4 mHfromH + 2 (-1 + Dip) mHfromH^2) +
        mDfromH^2 (3 - 2 Dip + mHfromH - 4 Dip mHfromH + 6 (-1 + Dip) mHfromH^2)))
```

```
FaiDbstrict = Simplify[Limit[(EqQDDb - EqQHD)/(1 - EqQHD), μ → 0], constraints]
```

```
- ((mDfromH (mDfromH - mHfromH) (2 Dip mDfromH - (mDfromH - mHfromH)^2 +
          Hap (-1 + mDfromH + mDfromH^2 - 2 mDfromH mHfromH + mHfromH^2))) /
     (- (mDfromH - mHfromH) (mDfromH + 2 (-1 + Dip) mDfromH^3 + (-1 - 2 Dip) mDfromH mHfromH +
           (4 - 4 Dip) mDfromH^2 mHfromH + (-1 + mHfromH) mHfromH +
           2 (-1 + Dip) mDfromH mHfromH^2) + Hap (2 (-1 + Dip) mDfromH^4 -
           (-1 + mHfromH)^2 (1 + mHfromH) - 2 (-1 + Dip) mDfromH^3 (-1 + 3 mHfromH) -
           mDfromH (-1 + mHfromH) (1 - 2 Dip - 4 mHfromH + 2 (-1 + Dip) mHfromH^2) +
           mDfromH^2 (3 - 2 Dip + mHfromH - 4 Dip mHfromH + 6 (-1 + Dip) mHfromH^2))))
```

```
FaiDwstrict = Simplify[Limit[(EqQDDw - EqQHD)/(1 - EqQHD), μ → 0], constraints]
```

```
((-1 + mHfromH) (2 Dip mDfromH - (mDfromH - mHfromH)^2 +
     Hap (-1 + mDfromH + mDfromH^2 - 2 mDfromH mHfromH + mHfromH^2))) /
 (-(mDfromH - mHfromH) (mDfromH + 2 (-1 + Dip) mDfromH^3 + (-1 - 2 Dip) mDfromH mHfromH +
       (4 - 4 Dip) mDfromH^2 mHfromH + (-1 + mHfromH) mHfromH +
       2 (-1 + Dip) mDfromH mHfromH^2) + Hap (2 (-1 + Dip) mDfromH^4 -
       (-1 + mHfromH)^2 (1 + mHfromH) - 2 (-1 + Dip) mDfromH^3 (-1 + 3 mHfromH) -
       mDfromH (-1 + mHfromH) (1 - 2 Dip - 4 mHfromH + 2 (-1 + Dip) mHfromH^2) +
       mDfromH^2 (3 - 2 Dip + mHfromH - 4 Dip mHfromH + 6 (-1 + Dip) mHfromH^2)))
```

```
FISstrict = Simplify[Limit[(EqQDDw - EqQDDb)/(1 - EqQDDb) /. subconstraints, μ → 0], constraints]
```

```
((-1 + mDfromH) (1 + mDfromH - mHfromH) (2 Dip mDfromH - (mDfromH - mHfromH)^2 +
     Hap (-1 + mDfromH + mDfromH^2 - 2 mDfromH mHfromH + mHfromH^2))) /
 (-(mDfromH - mHfromH) (mDfromH + (-1 + 2 Dip) mDfromH^3 + (-1 - 2 Dip) mDfromH mHfromH +
       (-1 + mHfromH) mHfromH + (-1 + 2 Dip) mDfromH mHfromH^2 -
       2 mDfromH^2 (Dip - mHfromH + 2 Dip mHfromH)) +
    Hap (1 + mDfromH - mHfromH) (-1 + (-1 + 2 Dip) mDfromH^3 + (2 - 4 Dip) mDfromH^2 mHfromH +
       mHfromH^2 + mDfromH (2 - 2 Dip - 2 mHfromH + (-1 + 2 Dip) mHfromH^2)))
```

we can rewrite FaiHstrict as:

```
numerator =
  (1 - X)^3 + Hap * mHfromD * mDfromH * (1 - X) + 2 * Dip * mDfromH * ((1 - X)^2 - mHfromH) * (1 - X) -
    (1 - X)^2 * (1 + mDfromH * (1 - 2 * X)) // Simplify;
denominator = (1 - X)^3 + Hap * ((1 - X)^2 - mDfromD) * (X + mDfromH * (1 - 2 * X)) +
    2 * Dip * mDfromH * ((1 - X)^2 - mHfromH) * (1 - X) - 2 * Hap * Dip * mDfromH * (2 - X) * X^2 -
    (1 - X)^2 * (1 + mDfromH * (1 - 2 * X)) // Simplify;
numerator/denominator // FullSimplify;
% - FaiHstrict /. X → mHfromD + mDfromH /. subconstraints /. ρD → 1 - ρH // Factor
```

```
0
```

While this doesn’t equal FaiHHstrict obtained without considering between and within diploid sampling, it does when the population size is large (here assuming intermediate migration rates):

```
FaiHstrict /. Hap → Ntot * ρH /. Dip → Ntot * ρD // Simplify
```

```
((mDfromH - mHfromH)
   (-(-1 + mHfromH) mHfromH + mDfromH^3 (2 - 2 Ntot ρD) + 4 mDfromH^2 mHfromH (-1 + Ntot ρD) +
     mDfromH (-1 + mHfromH + 2 mHfromH Ntot ρD + mHfromH^2 (2 - 2 Ntot ρD) +
         (-1 + mHfromH) Ntot ρH))) /
 (-(mDfromH - mHfromH) (mDfromH + (-1 + mHfromH) mHfromH +
      mDfromH^2 mHfromH (4 - 4 Ntot ρD) + 2 mDfromH^3 (-1 + Ntot ρD) +
      2 mDfromH mHfromH^2 (-1 + Ntot ρD) - mDfromH mHfromH (1 + 2 Ntot ρD)) +
   Ntot (-(-1 + mHfromH)^2 (1 + mHfromH) + 2 mDfromH^4 (-1 + Ntot ρD) -
      2 mDfromH^3 (-1 + 3 mHfromH) (-1 + Ntot ρD) -
      mDfromH (-1 + mHfromH) (1 - 4 mHfromH - 2 Ntot ρD + 2 mHfromH^2 (-1 + Ntot ρD)) +
      mDfromH^2 (3 + mHfromH - 2 Ntot ρD - 4 mHfromH Ntot ρD + 6 mHfromH^2 (-1 + Ntot ρD))) ρH)
```

If N is large (total population size) relative to the migration rates (i.e., none of the migration rates is very rare) these reduce to the same FNlarge obtained above without considering sampling within and between diploids:

```
Factor[Normal[Series[{FaiHstrict, FaiDbstrict} /. Hap → Ntot * ρH /. Dip → Ntot * ρD /.
    Ntot → Ntot/ϵ, {ϵ, 0, 1}]]] /. ϵ → 1
```

```
{-(((mDfromH - mHfromH) (2 mDfromH^2 ρD -
        2 mHfromH ρD - 4 mDfromH mHfromH ρD + 2 mHfromH^2 ρD + ρH - mHfromH ρH)) /
    (2 (-1 + mDfromH - mHfromH) (1 + mDfromH - mHfromH)^2 Ntot ρD ρH)),
 -(((mDfromH - mHfromH) (2 mDfromH ρD - ρH + mDfromH ρH +
        mDfromH^2 ρH - 2 mDfromH mHfromH ρH + mHfromH^2 ρH)) /
    (2 (-1 + mDfromH - mHfromH) (1 + mDfromH - mHfromH)^2 Ntot ρD ρH))}
```

From above (ignoring between/within), we derived the following in this case:

```
FNlarge = {(1 - X) * ((2 - X) * X * (2 * ρD) - mHfromD (ρH + 2 * ρD)) / ((2 - X) * X^2 * ρH * (2 * ρD) * Ntot),
    (1 - X) * ((2 - X) * X * ρH - mDfromH * (ρH + 2 * ρD)) / ((2 - X) * X^2 * ρH * (2 * ρD) * Ntot)};
```

As expected this equals the same large N approximation as found without considering within and between sampling:

```
Factor[%% - FNlarge /. X → mDfromH + mHfromD /. ρD → 1 - ρH /. subconstraints]
```

```
{0, 0}
```

```
Factor[Normal[Series[
    FaiDwstrict /. Hap → Ntot * ρH /. Dip → Ntot * ρD /. Ntot → Ntot/ϵ, {ϵ, 0, 1}]]] /. ϵ → 1
Factor[% - (mHfromD * (- (2 - X) * X * ρH + mDfromH * (ρH + 2 * ρD)))/(mDfromH * (2 - X) * X^2 * ρH * (2 * ρD) * Ntot) /. X → mDfromH + mHfromD /.
   ρD → 1 - ρH /. subconstraints]
```

$$\left((-1+\text{mHfromH})\left(2\,\text{mDfromH}\,\rho D-\rho H+\text{mDfromH}\,\rho H+\text{mDfromH}^2\,\rho H-2\,\text{mDfromH}\,\text{mHfromH}\,\rho H+\text{mHfromH}^2\,\rho H\right)\right)\Big/\left(2\,\text{mDfromH}\,(-1+\text{mDfromH}-\text{mHfromH})\,(1+\text{mDfromH}-\text{mHfromH})^2\,\text{Ntot}\,\rho D\,\rho H\right)$$

0

```
Factor[Normal[Series[
    FISstrict /. Hap → Ntot * ρH /. Dip → Ntot * ρD /. Ntot → Ntot/ϵ, {ϵ, 0, 1}]]] /. ϵ → 1
Factor[% - (mDfromD * (- (2 - X) * X * ρH + mDfromH * (ρH + 2 * ρD)))/(mDfromH * (2 - X) * X * ρH * (2 * ρD) * Ntot) /. X → mDfromH + mHfromD /.
   ρD → 1 - ρH /. subconstraints]
```

$$\left((-1+\text{mDfromH})\left(2\,\text{mDfromH}\,\rho D-\rho H+\text{mDfromH}\,\rho H+\text{mDfromH}^2\,\rho H-2\,\text{mDfromH}\,\text{mHfromH}\,\rho H+\text{mHfromH}^2\,\rho H\right)\right)\Big/\left(2\,\text{mDfromH}\,(-1+\text{mDfromH}-\text{mHfromH})\,(1+\text{mDfromH}-\text{mHfromH})\,\text{Ntot}\,\rho D\,\rho H\right)$$

0

Rare sexuality in a large population

We consider the case when there is frequent asexual reproduction (a≒1, and then mHfromD and mDfromH is small), and large population size. We assume;
- mHfromD = O(ϵ)
- mDfromH = O(ϵ)
- Ntot = O(1/ϵ)

These assumptions indicates, θHD = mHfromD Ntot = O(1) and θDH = mDfromH Ntot = O(1).

```
FaiH◆RS = Simplify[
  Normal[Series[FaiHstrict /. subconstraints /. Hap → Ntot * ρH /. Dip → Ntot * ρD /.
      mHfromD → θHD/Ntot /. mDfromH → θDH/Ntot /. Ntot → cNtot * 1/ϵ, {ϵ, 0, 0}]]]
```

$$\left(\theta HD+4\,\theta DH^2\,\rho D+\theta DH\,(2+2\,\theta HD\,\rho D-\theta HD\,\rho H)\right)\Big/\left(4\,\theta DH^3\,\rho D\,\rho H+\theta HD\,(1+2\,\theta HD\,\rho H)+\theta DH\left(2+2\,\theta HD\,\rho D+5\,\theta HD\,\rho H+4\,\theta HD^2\,\rho D\,\rho H\right)+2\,\theta DH^2\,(\rho H+\rho D\,(2+4\,\theta HD\,\rho H))\right)$$

```
FaiDb◆RS = Simplify[
  Normal[Series[FaiDbstrict /. subconstraints /. Hap → Ntot * ρH /. Dip → Ntot * ρD /.
      mHfromD → θHD/Ntot /. mDfromH → θDH/Ntot /. Ntot → cNtot * 1/ϵ, {ϵ, 0, 0}]]]
```

$$(\theta DH\ (1 + 2\ \theta HD\ \rho H + \theta DH\ (-2\ \rho D + \rho H)))\ \Big/\ \Big(4\ \theta DH^3\ \rho D\ \rho H + \theta HD\ (1 + 2\ \theta HD\ \rho H) + \theta DH\ \big(2 + 2\ \theta HD\ \rho D + 5\ \theta HD\ \rho H + 4\ \theta HD^2\ \rho D\ \rho H\big) + 2\ \theta DH^2\ (\rho H + \rho D\ (2 + 4\ \theta HD\ \rho H))\Big)$$

```
FaiDw◆RS = Simplify[
  Normal[Series[FaiDwstrict /. subconstraints /. Hap → Ntot * ρH /. Dip → Ntot * ρD /.
      mHfromD → θHD/Ntot /. mDfromH → θDH/Ntot /. Ntot → cNtot * 1/ϵ, {ϵ, 0, 0}]]]
```

$$-\Big((\theta HD\ (1 + 2\ \theta HD\ \rho H + \theta DH\ (-2\ \rho D + \rho H)))\ \Big/\ \Big(4\ \theta DH^3\ \rho D\ \rho H + \theta HD\ (1 + 2\ \theta HD\ \rho H) + \theta DH\ \big(2 + 2\ \theta HD\ \rho D + 5\ \theta HD\ \rho H + 4\ \theta HD^2\ \rho D\ \rho H\big) + 2\ \theta DH^2\ (\rho H + \rho D\ (2 + 4\ \theta HD\ \rho H))\Big)\Big)$$

```
FIS◆RS = Simplify[
  Normal[Series[FISstrict /. subconstraints /. Hap → Ntot * ρH /. Dip → Ntot * ρD /.
      mHfromD → θHD/Ntot /. mDfromH → θDH/Ntot /. Ntot → cNtot * 1/ϵ, {ϵ, 0, 0}]]]
```

$$((\theta DH + \theta HD)\ (-1 + 2\ \theta DH\ \rho D - \theta DH\ \rho H - 2\ \theta HD\ \rho H))\ \Big/\ \Big(4\ \theta DH^3\ \rho D\ \rho H + \theta HD\ (1 + 2\ \theta HD\ \rho H) + \theta DH\ \big(1 + 2\ \theta HD\ \rho D + 3\ \theta HD\ \rho H + 4\ \theta HD^2\ \rho D\ \rho H\big) + \theta DH^2\ (\rho H + \rho D\ (6 + 8\ \theta HD\ \rho H))\Big)$$

```
FaiH◆RS
```

$$\big(\theta HD + 4\ \theta DH^2\ \rho D + \theta DH\ (2 + 2\ \theta HD\ \rho D - \theta HD\ \rho H)\big)\ \Big/\ \Big(4\ \theta DH^3\ \rho D\ \rho H + \theta HD\ (1 + 2\ \theta HD\ \rho H) + \theta DH\ \big(2 + 2\ \theta HD\ \rho D + 5\ \theta HD\ \rho H + 4\ \theta HD^2\ \rho D\ \rho H\big) + 2\ \theta DH^2\ (\rho H + \rho D\ (2 + 4\ \theta HD\ \rho H))\Big)$$

```
FaiDave◆RS = Simplify[
  Normal[Series[1/(2 * Dip - 1) * FaiDwstrict + (2 * Dip - 2)/(2 * Dip - 1) * FaiDbstrict /. subconstraints /.
        Hap → Ntot * ρH /. Dip → Ntot * ρD /. mHfromD → θHD/Ntot /.
      mDfromH → θDH/Ntot /. Ntot → cNtot * 1/ϵ, {ϵ, 0, 0}]]]
```

$$(\theta DH\ (1 + 2\ \theta HD\ \rho H + \theta DH\ (-2\ \rho D + \rho H)))\ \Big/\ \Big(4\ \theta DH^3\ \rho D\ \rho H + \theta HD\ (1 + 2\ \theta HD\ \rho H) + \theta DH\ \big(2 + 2\ \theta HD\ \rho D + 5\ \theta HD\ \rho H + 4\ \theta HD^2\ \rho D\ \rho H\big) + 2\ \theta DH^2\ (\rho H + \rho D\ (2 + 4\ \theta HD\ \rho H))\Big)$$