Coalescence and linkage disequilibrium in facultatively sexual diploids

Matthew Hartfield[1,2], Stephen I. Wright[1], and Aneil F. Agrawal[1]

1 – Department of Ecology and Evolutionary Biology, University of Toronto, Ontario, Canada.
2 – Bioinformatics Research Centre, University of Aarhus, 8000C Aarhus, Denmark.

Supplementary *Mathematica* File. Comments to matthew.hartfield@birc.au.dk.

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Section A: Analytical Calculations

Here we follow the approach of McVean (2002, *Genetics* 162: 987-991) using a coalescent approach to calculate a metric of linkage disequilibrium between two sites (see also Wakeley 2009, chapter 7). The linkage disequilibrium metric calculated here is

$$r_d^2 = \frac{E[(\mathrm{Dxy})^2]}{E[\mathrm{fx}*(1-\mathrm{fx})*\mathrm{fy}*(1-\mathrm{fy})]}$$

where Dxy is the linkage disequilibrium between sites x and y and fx is the frequency of the minor allele at site x. This metric is similar to, but not the same as, $E[r^2] = E\left[\frac{(\mathrm{Dxy})^2}{\mathrm{fx}*(1-\mathrm{fx})*\mathrm{fy}*(1-\mathrm{fy})}\right]$. The metric calculated here, r_d^2, is an overestimate of the expected value of r^2, though it tends to be a better approximation of r^2 if only sites with intermediate allele frequencies are used in its calculation (McVean 2002).

Possible states

We consider two samples at each of two sites, A and B. The system consists of 17 possible states (including coalescence at both sites). These 17 states (labelled S1-S17) are depicted below. In the state depictions below curly braces "{ }" denote samples in separate individuals and a slash "/" denotes samples on separate homologs within an individual. See Figure S1.

S1: [{AB}, {AB}] (i.e., ancestral material at both sites on each of two homologs but homologs are in separate individuals)
S2: [{AB/AB}] (i.e., ancestral material at both sites on each of two homologs within a single individual)
S3: [{AB}, {A}, {B}] (i.e., ancestral material at both sites on one homolog in one individual, ancestral material at the A site on one homolog in a second individual, and ancestral material at the B site on one homolog in a third individual)
S4: [{AB}, {A/B}] (i.e., ancestral material at both sites on one homolog in one individual and ancestral material at the A site on one homolog and at the B site on the other homolog in a second individual)
S5: [{AB/A}, {B}] (i.e., ancestral material at both sites on one homolog and at the A site on the other homolog in one individual, and ancestral material at the B site on one homolog in a second individual)
S6: [{AB/B}, {A}] (i.e., ancestral material at both sites on one homolog and at the B site on the other homolog in one individual, and ancestral material at the A site on one homolog in a second individual)
S7: [{A}, {A}, {B}, {B}] (i.e., ancestral material comes from one homolog from each of four separate individuals)
S8: [{A/A}, {B}, {B}] (i.e., ancestral material on both homologs for the A site from one individual and ancestral material from a single homolog from each of two other individuals at the B site)
S9: [{A/B}, {A}, {B}] (i.e., ancestral material from one homolog for the A site and from the other homolog for the B site from one individual and ancestral material from a single homolog from each of two other individuals, one for the A site and one for the B site)
S10: [{B/B}, {A}, {A}] (i.e., ancestral material on both homologs for the B site from one individual and ancestral material from a single homolog from each of two other individuals at the A site)
S11: [{A/A}, {B/B}] (i.e., ancestral material on both homologs for the A site from one individual and ancestral material from both homologs from a second individual at the B site)
S12: [{A/B}, {A/B}] (i.e., ancestral material from one homolog for the A site and from the other homolog for the B site from one individual, and the same for a second individual)
S13: [{B}, {B}] (i.e., ancestral material from a single homolog from each of two individuals for site B; site A has already coalesced)
S14: [{B/B}] (i.e., ancestral material from both homologs from a single individual for site B; site A has already coalesced)
S15: [{A}, {A}] (i.e., ancestral material from a single homolog from each of two individuals for site A; site B has already coalesced)
S16: [{A/A}] (i.e., ancestral material from both homologs from a single individual for site A; site B has already coalesced)
S17: [ ] (coalescence at both sites)

We need to calculate the transition probabilities among these different states. We do this in two steps. In the first step, we consider the various types of samples that occur *within* a single individual and we calculate the transition probabilities to the sample states from which they could have descended. We then use these transition probablities to construct the transition probabilities of the 17 state samples depicted above using the fact that the descent of samples into separate individu-

als is independent of other descendent individuals.

Transitions for samples from a single individual

We first consider all of the possible types of samples that occur *within* a single individual. There are 9 types of within-individual samples that we label t1-t9. When an individual was created by sex, a within-individual sample will be split (going back in time) into a sample involving two individuals. These types of samples are labelled t10-t19. Three types of coalescence events can occur; the are labelled t20-t22.

t1: {A} (i.e., there is ancestral material at one copy of site A in the individual)
t2: {B} (i.e., there is ancestral material at one copy of site B in the individual)
t3: {AB} (i.e., there is ancestral material at one copy of both A and B and they are on the same homolog)
t4: {A/B} (i.e., there is ancestral material at one copy of each site on different homologs)
t5: {A/A} (i.e., there is ancestral material at both copies of site A; note this is the same as state S16)
t6: {B/B} (i.e., there is ancestral material at both copies of site B; note this is the same as state S14)
t7: {AB/A} (i.e., there is ancestral material at both copies of site A, but only one of the copies of site B)
t8: {AB/B} (i.e., there is ancestral material at both copies of site B, but only one of the copies of site A)
t9: {AB/AB} (i.e., there is ancestral material at both copies of both sites; note this is the same as state S2)

Within-individual samples can be **split by sex** into the following types:
t10: [{A}, {B}] (i.e., there is ancestral material at a copy of A in one individual and a copy of B in another individual)
t11: [{AB}, {A}] (i.e., there is ancestral material at copies of A and B on a single homolog in one individual and a copy of A in another individual)
t12: [{AB}, {B}] (i.e., there is ancestral material at copies of A and B on a single homolog in one individual and a copy of A in another individual)
t13: [{A/B}, {A}] (i.e., there is ancestral material at copies of A&B on separate homologs in one individual and a copy of A in another individual)
t14: [{A/B}, {B}] (i.e., there is ancestral material at copies of A&B on separate homologs in one individual and a copy of B in another individual)
t15: [{A}, {A}] (i.e., there is ancestral material at a copy of A in one individual and a copy of A in another individual; note this is the same as state S15)
t16: [{B}, {B}] (i.e., there is ancestral material at a copy of B in one individual and a copy of B in another individual; note this is the same as state S13)
t17:[{AB}, {AB}]] (i.e., there is ancestral material at a copy of A and B on a single homolog in one individual in one individual and a copy of A and B on a single homolog in another individual; note this is the same as state S1)
t18: [{A/B}, {A/B}] (i.e., there is ancestral material at a copy of A and B on separate homologs in one individual in one individual and a copy of A and B on separate homologs in another individual; note this is the same as state S12)

t19:[{AB}, {A/B}]] (i.e., there is ancestral material at a copy of A and B on the same homolog in one individual in one individual and a copy of A and B on separate homologs in another individual; note this is the same as state S4)

transitions involving coalescence
t20: coalescence at site A (no information with respect to B)
t21: coalescence at site B (no information with respect to A)
t22: coalescence at both sites A and B

Below is a 9 x 22 matrix, called "SingleIndividualTransMat", that gives the transition probabilities from the 9 types of within-individual samples to each of the 22 possible conditions from which they could have descended. Calculation of these transitions is based on the following:
Let
$\gamma 1$ be the probability that either one of the two sites (but not both) is involved in a *mitotic* gene conversion event
$\gamma 2$ be the probability that both of two sites will be included in a mitotic gene conversion event (note: $\gamma 2 + \gamma 1/2$ is the probability that one specific site (say, site B) is involved in a mitotic gene conversion regardless of whether that gene conversion also includes the other sites)
σ be the probability an individual was created by sexual reproduction (via the random union of gametes).
c be the probability of a meiotic crossover between sites A and B, conditional on sex occurring
$\gamma 1S$ be the probability that either one of the two sites (but not both) is involved in a *meiotic* gene conversion event, conditional on sex occurring
cA be the probability of a mitotic crossover
$1/n$ be the probability two samples in different individuals descend from the same individual in the previous generation (we use "n" rather than "N" to represent in the population size because the latter is a reserved character in *Mathematica)*

A further comment on mitotic gene conversion:
$\gamma 1$ is the probability of a mitotic gene conversion in a diploid at either site but not both. For an individual A1B1/A2B2 it includes 4 different (but equally probable conversion events A1→A2, A2→A1, B1→B2, and B2→B1. Almost always, we are interested in the quantity $\gamma 1/2$. This is the probability of conversion in either direction at only one of the sites (which is important for coalescence when we have ancestral material on both homologs at the site in one individual). $\gamma 1/2$ is also the probability of conversion of either site to the other homolog but only in one direction (which is important for moving ancestral material between homologs when we only have ancestral material on one homolog for each site, though not necessarily the same haplotype for each site).

There is a slightly tricky issue that arises with respect to two separate gametes descending from a single individual that affects the probabilities for state "t9". We assume every haplotype arises from an 'independent' cell lineage within an individual so that if a gene conversion happened in the cell lineage that led to the formation of one gamete, it has no effect on whether or not there as a gene conversion for a second gamete.

We assume that at most one "disruption" event per (i.e., mitotic/meiotic crossover or gene conver-

sion) cell lineage.

```
SingleIndividualTransMat =
 {{1, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0},
  {0, 1, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0},
  {0, 0, σ (1 - (c + γ1S/2 + γ1/2 + cA)) + (1 - σ) (1 - γ1/2 - cA),
   σ (c + γ1S/2 + γ1/2 + cA) + (1 - σ) (γ1/2 + cA), 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0,
   0, 0, 0, 0, 0, 0}, {0, 0, σ/(2 n) + (1 - σ) (γ1/2 + cA), σ/(2 n) + (1 - σ) (1 - γ1/2 - cA),
   0, 0, 0, 0, 0, σ (1 - 1/n), 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0},
  {0, 0, 0, 0, σ/(2 n) (1 - (γ1/2 + γ2)) + (1 - σ) (1 - (γ1/2 + γ2)), 0, 0, 0, 0, 0, 0,
   0, 0, 0, σ (1 - 1/n), 0, 0, 0, 0, σ/(2 n) (1 + (γ1/2 + γ2)) + (1 - σ) (γ1/2 + γ2), 0, 0},
  {0, 0, 0, 0, 0, σ/(2 n) (1 - (γ1/2 + γ2)) + (1 - σ) (1 - (γ1/2 + γ2)), 0, 0, 0, 0, 0,
   0, 0, 0, 0, σ (1 - 1/n), 0, 0, 0, 0, σ/(2 n) (1 + (γ1/2 + γ2)) + (1 - σ) (γ1/2 + γ2), 0},
  {0, σ/(2 n) + (1 - σ) (γ1/2 + γ2), 0, 0, 0, 0, σ/(2 n) + (1 - σ) (1 - (γ1/2 + γ2)), 0, 0,
   0, σ (1 - (c + γ1S/2 + γ1/2 + cA)) (1 - 1/n), 0, σ (c + γ1S/2 + γ1/2 + cA) (1 - 1/n),
   0, 0, 0, 0, 0, 0, 0, 0, 0}, {σ/(2 n) + (1 - σ) (γ1/2 + γ2), 0, 0, 0, 0, 0, 0,
   σ/(2 n) + (1 - σ) (1 - (γ1/2 + γ2)), 0, 0, 0, σ (1 - (c + γ1S/2 + γ1/2 + cA)) (1 - 1/n),
   0, σ (c + γ1S/2 + γ1/2 + cA) (1 - 1/n), 0, 0, 0, 0, 0, 0, 0, 0},
  {0, 0, 0, 0, (1 - σ) (γ1/2) + σ/(2 n) 2 (1 - (c + γ1S/2 + γ1/2 + cA)) (c + γ1S/2 + γ1/2 + cA),
   (1 - σ) (γ1/2) + σ/(2 n) 2 (1 - (c + γ1S/2 + γ1/2 + cA)) (c + γ1S/2 + γ1/2 + cA), 0, 0,
   (1 - σ) (1 - γ1 - γ2) + σ/(2 n) ((1 - (c + γ1S/2 + γ1/2 + cA))^2 + (c + γ1S/2 + γ1/2 + cA)^2), 0, 0,
   0, 0, 0, 0, 0, σ (1 - 1/n) (1 - (c + γ1S/2 + γ1/2 + cA))^2, σ (1 - 1/n) (c + γ1S/2 + γ1/2 + cA)^2,
   σ (1 - 1/n) (2 (1 - (c + γ1S/2 + γ1/2 + cA)) (c + γ1S/2 + γ1/2 + cA)), 0, 0,
   σ/(2 n) ((1 - (c + γ1S/2 + γ1/2 + cA))^2 + (c + γ1S/2 + γ1/2 + cA)^2) + (1 - σ) γ2}};
```

As expected, the rows of this matrix each sum to unity.

```
Table[Simplify[Plus @@ SingleIndividualTransMat[[i]]], {i, 9}]
```

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

Constructing the transition matrix for the 17 states

In the expressions below, we ignore terms that are $O(n^{-2})$.

```
TransMat = Table[Table[0, {17}], {17}];

TransMat[[1, 1]] = (SingleIndividualTransMat[[3, 3]])^2 * (1 - 1/n);

TransMat[[1, 2]] = (SingleIndividualTransMat[[3, 3]])^2 1/(2 n) +
    (SingleIndividualTransMat[[3, 4]])^2 1/(2 n);

TransMat[[1, 4]] = 2 SingleIndividualTransMat[[3, 3]]
    SingleIndividualTransMat[[3, 4]] (1 - 1/n);

TransMat[[1, 12]] = (SingleIndividualTransMat[[3, 4]])^2 (1 - 1/n);

TransMat[[1, 14]] =
  2 SingleIndividualTransMat[[3, 3]] SingleIndividualTransMat[[3, 4]] 1/(2 n);

TransMat[[1, 16]] = 2 SingleIndividualTransMat[[3, 3]]
    SingleIndividualTransMat[[3, 4]] 1/(2 n);

TransMat[[1, 17]] = (SingleIndividualTransMat[[3, 3]])^2 1/(2 n) +
    (SingleIndividualTransMat[[3, 4]])^2 1/(2 n);

TransMat[[2, 1]] = SingleIndividualTransMat[[9, 17]];
TransMat[[2, 2]] = SingleIndividualTransMat[[9, 9]];
TransMat[[2, 4]] = SingleIndividualTransMat[[9, 19]];
TransMat[[2, 12]] = SingleIndividualTransMat[[9, 18]];
TransMat[[2, 13]] = SingleIndividualTransMat[[9, 16]];
TransMat[[2, 14]] = SingleIndividualTransMat[[9, 6]];
TransMat[[2, 15]] = SingleIndividualTransMat[[9, 15]];
TransMat[[2, 16]] = SingleIndividualTransMat[[9, 5]];
TransMat[[2, 17]] = SingleIndividualTransMat[[9, 22]];
```

```
TransMat[[3, 1]] = SingleIndividualTransMat[[3, 3]] * 1/(2 n);

TransMat[[3, 3]] = SingleIndividualTransMat[[3, 3]] * (1 - 3/n);

TransMat[[3, 4]] =
  SingleIndividualTransMat[[3, 3]] * 1/(2 n) + SingleIndividualTransMat[[3, 4]] * 1/(2 n);

TransMat[[3, 5]] = SingleIndividualTransMat[[3, 3]] * 1/(2 n) +
   SingleIndividualTransMat[[3, 4]] * 1/(2 n);

TransMat[[3, 6]] = SingleIndividualTransMat[[3, 3]] * 1/(2 n) +
   SingleIndividualTransMat[[3, 4]] * 1/(2 n);

TransMat[[3, 9]] = SingleIndividualTransMat[[3, 4]] * (1 - 3/n);

TransMat[[3, 12]] = SingleIndividualTransMat[[3, 4]] * 1/(2 n);

TransMat[[3, 13]] =
  SingleIndividualTransMat[[3, 3]] * 1/(2 n) + SingleIndividualTransMat[[3, 4]] * 1/(2 n);

TransMat[[3, 15]] = SingleIndividualTransMat[[3, 3]] * 1/(2 n) +
   SingleIndividualTransMat[[3, 4]] * 1/(2 n);

TransMat[[4, 1]] =
  SingleIndividualTransMat[[3, 3]] SingleIndividualTransMat[[4, 3]] (1 - 1/n);

TransMat[[4, 2]] = SingleIndividualTransMat[[3, 4]]
    SingleIndividualTransMat[[4, 4]] 1/(2 n) +
   SingleIndividualTransMat[[3, 3]] SingleIndividualTransMat[[4, 3]] 1/(2 n);

TransMat[[4, 3]] = SingleIndividualTransMat[[3, 3]]
   SingleIndividualTransMat[[4, 10]] (1 - 2/n);

TransMat[[4, 4]] = SingleIndividualTransMat[[3, 3]]
    SingleIndividualTransMat[[4, 4]] (1 - 1/n) +
   SingleIndividualTransMat[[3, 4]] SingleIndividualTransMat[[4, 3]] (1 - 1/n);

TransMat[[4, 5]] = SingleIndividualTransMat[[3, 3]]
    SingleIndividualTransMat[[4, 10]] * 1/(2 n) +
   SingleIndividualTransMat[[3, 4]] SingleIndividualTransMat[[4, 10]] * 1/(2 n);
```

```
TransMat[[4, 6]] = SingleIndividualTransMat[[3, 3]]
     SingleIndividualTransMat[[4, 10]] * 1/(2 n) +
   SingleIndividualTransMat[[3, 4]] SingleIndividualTransMat[[4, 10]] * 1/(2 n);
TransMat[[4, 9]] = SingleIndividualTransMat[[3, 4]]
   SingleIndividualTransMat[[4, 10]] (1 - 2/n);
TransMat[[4, 12]] = SingleIndividualTransMat[[3, 4]]
   SingleIndividualTransMat[[4, 4]] (1 - 1/n);
TransMat[[4, 13]] = SingleIndividualTransMat[[3, 3]]
     SingleIndividualTransMat[[4, 10]] * 1/(2 n) +
   SingleIndividualTransMat[[3, 4]] SingleIndividualTransMat[[4, 10]] * 1/(2 n);
TransMat[[4, 14]] = SingleIndividualTransMat[[3, 3]]
     SingleIndividualTransMat[[4, 4]] * 1/(2 n) +
   SingleIndividualTransMat[[3, 4]] SingleIndividualTransMat[[4, 3]] * 1/(2 n);
TransMat[[4, 15]] = SingleIndividualTransMat[[3, 3]]
     SingleIndividualTransMat[[4, 10]] * 1/(2 n) +
   SingleIndividualTransMat[[3, 4]] SingleIndividualTransMat[[4, 10]] * 1/(2 n);
TransMat[[4, 16]] = SingleIndividualTransMat[[3, 3]]
     SingleIndividualTransMat[[4, 4]] * 1/(2 n) +
   SingleIndividualTransMat[[3, 4]] SingleIndividualTransMat[[4, 3]] * 1/(2 n);
TransMat[[4, 17]] = SingleIndividualTransMat[[3, 4]]
     SingleIndividualTransMat[[4, 4]] * 1/(2 n) +
   SingleIndividualTransMat[[3, 3]] SingleIndividualTransMat[[4, 3]] * 1/(2 n);
```

$$\text{TransMat}[[5,1]] = \text{SingleIndividualTransMat}[[7,11]] * \frac{1}{2n};$$

$$\text{TransMat}[[5,2]] = \text{SingleIndividualTransMat}[[7,7]] * \frac{1}{2n};$$

$$\text{TransMat}[[5,3]] = \text{SingleIndividualTransMat}[[7,11]] \left(1 - \frac{2}{n}\right);$$

$$\text{TransMat}[[5,4]] = \text{SingleIndividualTransMat}[[7,13]] \frac{1}{2n} + \text{SingleIndividualTransMat}[[7,11]] \frac{1}{2n};$$

$$\text{TransMat}[[5,5]] = \text{SingleIndividualTransMat}[[7,7]] \left(1 - \frac{1}{n}\right);$$

$$\text{TransMat}[[5,6]] = \text{SingleIndividualTransMat}[[7,13]] \frac{1}{2n} + \text{SingleIndividualTransMat}[[7,11]] \frac{1}{2n};$$

$$\text{TransMat}[[5,9]] = \text{SingleIndividualTransMat}[[7,13]] \left(1 - \frac{2}{n}\right);$$

$$\text{TransMat}[[5,12]] = \text{SingleIndividualTransMat}[[7,13]] \frac{1}{2n};$$

$$\text{TransMat}[[5,13]] = \text{SingleIndividualTransMat}[[7,2]] \left(1 - \frac{1}{n}\right);$$

$$\text{TransMat}[[5,14]] = \text{SingleIndividualTransMat}[[7,2]] \frac{1}{2n};$$

$$\text{TransMat}[[5,15]] = \text{SingleIndividualTransMat}[[7,13]] \frac{1}{2n} + \text{SingleIndividualTransMat}[[7,11]] \frac{1}{2n};$$

$$\text{TransMat}[[5,16]] = \text{SingleIndividualTransMat}[[7,7]] \frac{1}{2n};$$

$$\text{TransMat}[[5,17]] = \text{SingleIndividualTransMat}[[7,2]] \frac{1}{2n};$$

$$\text{TransMat}[[6,1]] = \text{SingleIndividualTransMat}[[8,12]]\ \frac{1}{2n};$$

$$\text{TransMat}[[6,2]] = \text{SingleIndividualTransMat}[[8,8]]\ \frac{1}{2n};$$

$$\text{TransMat}[[6,3]] = \text{SingleIndividualTransMat}[[8,12]]\ \left(1-\frac{2}{n}\right);$$

$$\text{TransMat}[[6,4]] = \text{SingleIndividualTransMat}[[8,14]]\ \frac{1}{2n} + \text{SingleIndividualTransMat}[[8,12]]\ \frac{1}{2n};$$

$$\text{TransMat}[[6,5]] = \text{SingleIndividualTransMat}[[8,14]]\ \frac{1}{2n} + \text{SingleIndividualTransMat}[[8,12]]\ \frac{1}{2n};$$

$$\text{TransMat}[[6,6]] = \text{SingleIndividualTransMat}[[8,8]]\ \left(1-\frac{1}{n}\right);$$

$$\text{TransMat}[[6,9]] = \text{SingleIndividualTransMat}[[8,14]]\ \left(1-\frac{2}{n}\right);$$

$$\text{TransMat}[[6,12]] = \text{SingleIndividualTransMat}[[8,14]]\ \frac{1}{2n};$$

$$\text{TransMat}[[6,13]] = \text{SingleIndividualTransMat}[[8,14]]\ \frac{1}{2n} + \text{SingleIndividualTransMat}[[8,12]]\ \frac{1}{2n};$$

$$\text{TransMat}[[6,14]] = \text{SingleIndividualTransMat}[[8,8]]\ \frac{1}{2n};$$

$$\text{TransMat}[[6,15]] = \text{SingleIndividualTransMat}[[8,1]]\ \left(1-\frac{1}{n}\right);$$

$$\text{TransMat}[[6,16]] = \text{SingleIndividualTransMat}[[8,1]]\ \frac{1}{2n};$$

$$\text{TransMat}[[6,17]] = \text{SingleIndividualTransMat}[[8,1]]\ \frac{1}{2n};$$

$$\text{TransMat}[[7,3]] = \frac{4}{2n};$$

$$\text{TransMat}[[7,7]] = \left(1-\frac{6}{n}\right);$$

$$\text{TransMat}[[7,8]] = \frac{1}{2n};$$

$$\text{TransMat}[[7,9]] = \frac{4}{2n};$$

$$\text{TransMat}[[7,10]] = \frac{1}{2n};$$

$$\text{TransMat}[[7,13]] = \frac{1}{2n};$$

$$\text{TransMat}[[7,15]] = \frac{1}{2n};$$

$$\text{TransMat}[[8, 3]] = \text{SingleIndividualTransMat}[[5, 15]] \frac{4}{2n};$$

$$\text{TransMat}[[8, 5]] = \text{SingleIndividualTransMat}[[5, 5]] \frac{2}{n};$$

$$\text{TransMat}[[8, 7]] = \text{SingleIndividualTransMat}[[5, 15]] \left(1 - \frac{5}{n}\right);$$

$$\text{TransMat}[[8, 8]] = \text{SingleIndividualTransMat}[[5, 5]] \left(1 - \frac{3}{n}\right);$$

$$\text{TransMat}[[8, 9]] = \text{SingleIndividualTransMat}[[5, 15]] \frac{4}{2n};$$

$$\text{TransMat}[[8, 10]] = \text{SingleIndividualTransMat}[[5, 15]] \frac{1}{2n};$$

$$\text{TransMat}[[8, 11]] = \text{SingleIndividualTransMat}[[5, 5]] \frac{1}{2n};$$

$$\text{TransMat}[[8, 13]] = \text{SingleIndividualTransMat}[[5, 20]] \left(1 - \frac{1}{n}\right);$$

$$\text{TransMat}[[8, 14]] = \text{SingleIndividualTransMat}[[5, 20]] \frac{1}{2n};$$

$$\text{TransMat}[[8, 15]] = \text{SingleIndividualTransMat}[[5, 15]] \frac{1}{2n};$$

$$\text{TransMat}[[8, 16]] = \text{SingleIndividualTransMat}[[5, 5]] \frac{1}{2n};$$

$$\text{TransMat}[[8, 17]] = \text{SingleIndividualTransMat}[[5, 20]] \frac{1}{2n};$$

$$\text{TransMat}[[9,1]] = \text{SingleIndividualTransMat}[[4,3]]\,\frac{1}{2n};$$

$$\text{TransMat}[[9,3]] = \text{SingleIndividualTransMat}[[4,3]]\left(1-\frac{3}{n}\right)+ \text{SingleIndividualTransMat}[[4,10]]\,\frac{3}{2n};$$

$$\text{TransMat}[[9,4]] = \text{SingleIndividualTransMat}[[4,4]]\,\frac{1}{2n}+ \text{SingleIndividualTransMat}[[4,3]]\,\frac{1}{2n};$$

$$\text{TransMat}[[9,5]] = \text{SingleIndividualTransMat}[[4,4]]\,\frac{1}{2n}+ \text{SingleIndividualTransMat}[[4,3]]\,\frac{1}{2n};$$

$$\text{TransMat}[[9,6]] = \text{SingleIndividualTransMat}[[4,4]]\,\frac{1}{2n}+ \text{SingleIndividualTransMat}[[4,3]]\,\frac{1}{2n};$$

$$\text{TransMat}[[9,7]] = \text{SingleIndividualTransMat}[[4,10]]\left(1-\frac{5}{n}\right);$$

$$\text{TransMat}[[9,8]] = \text{SingleIndividualTransMat}[[4,10]]\,\frac{1}{2n};$$

$$\text{TransMat}[[9,9]] = \text{SingleIndividualTransMat}[[4,4]]\left(1-\frac{3}{n}\right)+ \text{SingleIndividualTransMat}[[4,10]]\,\frac{3}{2n};$$

$$\text{TransMat}[[9,10]] = \text{SingleIndividualTransMat}[[4,10]]\,\frac{1}{2n};$$

$$\text{TransMat}[[9,12]] = \text{SingleIndividualTransMat}[[4,4]]\,\frac{1}{2n};$$

$$\text{TransMat}[[9,13]] = \text{SingleIndividualTransMat}[[4,4]]\,\frac{1}{2n}+ \text{SingleIndividualTransMat}[[4,3]]\,\frac{1}{2n}+\text{SingleIndividualTransMat}[[4,10]]\,\frac{1}{2n};$$

$$\text{TransMat}[[9,15]] = \text{SingleIndividualTransMat}[[4,4]]\,\frac{1}{2n}+ \text{SingleIndividualTransMat}[[4,3]]\,\frac{1}{2n}+\text{SingleIndividualTransMat}[[4,10]]\,\frac{1}{2n};$$

$$\text{TransMat}[[10, 3]] = \text{SingleIndividualTransMat}[[6, 16]] \frac{4}{2n};$$

$$\text{TransMat}[[10, 6]] = \text{SingleIndividualTransMat}[[6, 6]] \frac{2}{n};$$

$$\text{TransMat}[[10, 7]] = \text{SingleIndividualTransMat}[[6, 16]] \left(1 - \frac{5}{n}\right);$$

$$\text{TransMat}[[10, 8]] = \text{SingleIndividualTransMat}[[6, 16]] \frac{1}{2n};$$

$$\text{TransMat}[[10, 9]] = \text{SingleIndividualTransMat}[[6, 16]] \frac{4}{2n};$$

$$\text{TransMat}[[10, 10]] = \text{SingleIndividualTransMat}[[6, 6]] \left(1 - \frac{3}{n}\right);$$

$$\text{TransMat}[[10, 11]] = \text{SingleIndividualTransMat}[[6, 6]] \frac{1}{2n};$$

$$\text{TransMat}[[10, 13]] = \text{SingleIndividualTransMat}[[6, 16]] \frac{1}{2n};$$

$$\text{TransMat}[[10, 14]] = \text{SingleIndividualTransMat}[[6, 6]] \frac{1}{2n};$$

$$\text{TransMat}[[10, 15]] = \text{SingleIndividualTransMat}[[6, 21]] \left(1 - \frac{1}{n}\right);$$

$$\text{TransMat}[[10, 16]] = \text{SingleIndividualTransMat}[[6, 21]] \frac{1}{2n};$$

$$\text{TransMat}[[10, 17]] = \text{SingleIndividualTransMat}[[6, 21]] \frac{1}{2n};$$

```
TransMat[[11, 2]] =
  SingleIndividualTransMat[[5, 5]] SingleIndividualTransMat[[6, 6]] 1/n;
TransMat[[11, 3]] = SingleIndividualTransMat[[5, 15]]
   SingleIndividualTransMat[[6, 16]] 4/(2 n);
TransMat[[11, 5]] = SingleIndividualTransMat[[5, 5]]
   SingleIndividualTransMat[[6, 16]] 2/n;
TransMat[[11, 6]] = SingleIndividualTransMat[[5, 15]]
   SingleIndividualTransMat[[6, 6]] 2/n;
TransMat[[11, 7]] = SingleIndividualTransMat[[5, 15]]
   SingleIndividualTransMat[[6, 16]] (1 - 4/n);
TransMat[[11, 8]] = SingleIndividualTransMat[[5, 5]]
   SingleIndividualTransMat[[6, 16]] (1 - 2/n);
TransMat[[11, 9]] = SingleIndividualTransMat[[5, 15]]
   SingleIndividualTransMat[[6, 16]] 4/(2 n);
TransMat[[11, 10]] = SingleIndividualTransMat[[5, 15]]
   SingleIndividualTransMat[[6, 6]] (1 - 2/n);
TransMat[[11, 11]] = SingleIndividualTransMat[[5, 5]]
   SingleIndividualTransMat[[6, 6]] (1 - 1/n);
TransMat[[11, 13]] = SingleIndividualTransMat[[5, 20]]
   SingleIndividualTransMat[[6, 16]];
TransMat[[11, 14]] = SingleIndividualTransMat[[5, 20]]
   SingleIndividualTransMat[[6, 6]];
TransMat[[11, 15]] = SingleIndividualTransMat[[5, 15]]
   SingleIndividualTransMat[[6, 21]];
TransMat[[11, 16]] = SingleIndividualTransMat[[5, 5]]
   SingleIndividualTransMat[[6, 21]];
TransMat[[11, 17]] = SingleIndividualTransMat[[5, 20]]
   SingleIndividualTransMat[[6, 21]];

TransMat[[12, 1]] = (SingleIndividualTransMat[[4, 3]])^2 (1 - 1/n);
TransMat[[12, 2]] = (SingleIndividualTransMat[[4, 4]])^2 1/(2 n) +
   (SingleIndividualTransMat[[4, 3]])^2 1/(2 n);
TransMat[[12, 3]] = 2 SingleIndividualTransMat[[4, 3]]
    SingleIndividualTransMat[[4, 10]] (1 - 2/n) +
```

$$(\text{SingleIndividualTransMat}[[4, 10]])^2 \frac{2}{2n};$$

$$\text{TransMat}[[12, 4]] = 2\,\text{SingleIndividualTransMat}[[4, 4]]$$
$$\text{SingleIndividualTransMat}[[4, 3]] \left(1 - \frac{1}{n}\right);$$

$$\text{TransMat}[[12, 5]] = 2\,\text{SingleIndividualTransMat}[[4, 4]]$$
$$\text{SingleIndividualTransMat}[[4, 10]] \frac{1}{2n} +$$
$$2\,\text{SingleIndividualTransMat}[[4, 3]]\,\text{SingleIndividualTransMat}[[4, 10]] \frac{1}{2n};$$

$$\text{TransMat}[[12, 6]] = 2\,\text{SingleIndividualTransMat}[[4, 4]]$$
$$\text{SingleIndividualTransMat}[[4, 10]] \frac{1}{2n} +$$
$$2\,\text{SingleIndividualTransMat}[[4, 3]]\,\text{SingleIndividualTransMat}[[4, 10]] \frac{1}{2n};$$

$$\text{TransMat}[[12, 7]] = (\text{SingleIndividualTransMat}[[4, 10]])^2 \left(1 - \frac{4}{n}\right);$$

$$\text{TransMat}[[12, 8]] = (\text{SingleIndividualTransMat}[[4, 10]])^2 \frac{1}{2n};$$

$$\text{TransMat}[[12, 9]] =$$
$$2\,\text{SingleIndividualTransMat}[[4, 4]]\,\text{SingleIndividualTransMat}[[4, 10]] \left(1 - \frac{2}{n}\right) +$$
$$(\text{SingleIndividualTransMat}[[4, 10]])^2 \frac{2}{2n};$$

$$\text{TransMat}[[12, 10]] = (\text{SingleIndividualTransMat}[[4, 10]])^2 \frac{1}{2n};$$

$$\text{TransMat}[[12, 12]] = (\text{SingleIndividualTransMat}[[4, 4]])^2 \left(1 - \frac{1}{n}\right);$$

$$\text{TransMat}[[12, 13]] =$$
$$2\,\text{SingleIndividualTransMat}[[4, 4]]\,\text{SingleIndividualTransMat}[[4, 10]] \frac{1}{2n} +$$
$$2\,\text{SingleIndividualTransMat}[[4, 3]]\,\text{SingleIndividualTransMat}[[4, 10]] \frac{1}{2n} +$$
$$(\text{SingleIndividualTransMat}[[4, 10]])^2 \frac{1}{2n};$$

$$\text{TransMat}[[12, 14]] = 2\,\text{SingleIndividualTransMat}[[4, 4]]$$
$$\text{SingleIndividualTransMat}[[4, 3]] \frac{1}{2n};$$

$$\text{TransMat}[[12, 15]] = 2\,\text{SingleIndividualTransMat}[[4, 4]]$$
$$\text{SingleIndividualTransMat}[[4, 10]] \frac{1}{2n} +$$
$$2\,\text{SingleIndividualTransMat}[[4, 3]]\,\text{SingleIndividualTransMat}[[4, 10]] \frac{1}{2n} +$$
$$(\text{SingleIndividualTransMat}[[4, 10]])^2 \frac{1}{2n};$$

$$\text{TransMat}[[12, 16]] = 2\,\text{SingleIndividualTransMat}[[4, 4]]$$
$$\text{SingleIndividualTransMat}[[4, 3]] \frac{1}{2n};$$

```
TransMat[[12, 17]] = (SingleIndividualTransMat[[4, 4]])^2 1/(2 n) +
    (SingleIndividualTransMat[[4, 3]])^2 1/(2 n);

TransMat[[13, 13]] = (1 - 1/n);
TransMat[[13, 14]] = 1/(2 n) (1 - (γ1/2 + γ2));
TransMat[[13, 17]] = 1/(2 n) (1 + (γ1/2 + γ2));

TransMat[[15, 15]] = (1 - 1/n);
TransMat[[15, 16]] = 1/(2 n) (1 - (γ1/2 + γ2));
TransMat[[15, 17]] = 1/(2 n) (1 + (γ1/2 + γ2));

TransMat[[14, 13]] = SingleIndividualTransMat[[6, 16]];
TransMat[[14, 14]] = SingleIndividualTransMat[[6, 6]];
TransMat[[14, 17]] = SingleIndividualTransMat[[6, 21]];

TransMat[[16, 15]] = SingleIndividualTransMat[[5, 15]];
TransMat[[16, 16]] = SingleIndividualTransMat[[5, 5]];
TransMat[[16, 17]] = SingleIndividualTransMat[[5, 20]];

TransMat[[17, 17]] = 1;
```

As expected the rows of the matrix each sum to unity.

```
Table[Plus @@ TransMat[[i]] /. subTwoIndividualsSources // FullSimplify, {i, 17}]
```

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

Other needed substitutions and useful functions

Following the method of McVean (2002), we need to calculate the expected value of the product of the coalescence times for site A and site B (labelled *tx* and *ty* here) from each of the first 16 states. (For the states S13-S17, one or both sites have already coalesced so E[*tx*ty*] = 0.)

```
ExpectedValueOfProductOfCoalescentTimesForSitesAandBGivenStateDummyList =
  {EtxtyS1, EtxtyS2, EtxtyS3, EtxtyS4, EtxtyS5, EtxtyS6, EtxtyS7,
   EtxtyS8, EtxtyS9, EtxtyS10, EtxtyS11, EtxtyS12, 0, 0, 0, 0};
```

We will need to use results from single-site coalescence (provided in a later section). *E[tb]* and E[*tw*] are the expected times to coalescence for a single site where the two copies come from different individuals ("between-individual sample") or from the same individual ("within-individual sample"), respectively. Considering the 17 states of the two site model, the expected coalescence time for each site individually is as follows.

```
ExpectedCoalescentTimeForSiteAGivenState =
  {Etb, Etw, Etb, Etb, Etw, Etb, Etb, Etw, Etb, Etb, Etw, Etb, 0, 0, Etb, Etw, 0};
ExpectedCoalescentTimeForSiteBGivenState =
  {Etb, Etw, Etb, Etb, Etb, Etw, Etb, Etb, Etb, Etw, Etw, Etb, Etb, Etw, 0, 0, 0};
```

We use "first-step" analysis (Wakeley 2007, chapters 5 and 7) to calculate the values of E[*tx*ty*] for each state. The function below creates the equations, we need to solve. These equations have the form

$E[t_x\, t_y \mid Z = z] = E[\tau_z^2] + E[\tau_z]\sum_{k \neq z} P_{zk}\, E[t_x \mid Z = k] + E[\tau_z]\sum_{k \neq z} P_{zk}\, E[t_y \mid Z = k] + \sum_{k \neq z} P_{zk}\, E[t_x\, t_y \mid Z = k]$

where τ_z is the time to leave state *z and* P_{zk} is the probability of going from state *z* to state *k* conditional on leaving state z. In discrete time, τ_z follows a geometric distribution with parameter 1 - $T_{ii}$where T_{ii} is the *i*th diagonal element of the transition matrix.

```
ExpectedValueOfProductOfCoalescentTimesForSitesAandBGivenState[state_] :=
 (2 - (1 - TransMat[[state, state]]))/(1 - TransMat[[state, state]])^2 + 1/(1 - TransMat[[state, state]])
  Sum[If[j == state, 0, (TransMat[[state, j]] / (1 - TransMat[[state, state]]))
     ExpectedCoalescentTimeForSiteAGivenState[[j]]], {j, 16}] +
 1/(1 - TransMat[[state, state]]) Sum[If[j == state, 0,
    (TransMat[[state, j]] / (1 - TransMat[[state, state]]))
     ExpectedCoalescentTimeForSiteBGivenState[[j]]], {j, 16}] +
 Sum[If[j == state, 0, TransMat[[state, j]]/(1 - TransMat[[state, state]])
    ExpectedValueOfProductOfCoalescentTimesForSitesAandBGivenStateDummyList[[
     j]]], {j, 16}]
```

We will use the function below to perform Taylor series approximations with respect to the dummy variable ξ (where $0 < \xi << 1$), given set of assumptions about the order magnitude of different parameters in terms of ξ.

```
TS[x_, toorder_, assumptions_] := Normal[Series[x /. assumptions, {ξ, 0, toorder}]]
```

We will use the function below to create a set of equations for the E[*tx*ty*] to a given order.

```
eqnsToOrder[toorder_, assumptions_] := Block[{subThisEtxtyList = Table[
      ExpectedValueOfProductOfCoalescentTimesForSitesAandBGivenStateDummyList[[
        i]] → TS[
        ExpectedValueOfProductOfCoalescentTimesForSitesAandBGivenStateDummyList
          [[i]] /. subEtxtyInParts, toorder + 1, {}], {i, 12}]},
  eqns = Flatten[Table[TS[
      (ExpectedValueOfProductOfCoalescentTimesForSitesAandBGivenStateDummyList
          [[i]] /. subThisEtxtyList) ==
       (ExpectedValueOfProductOfCoalescentTimesForSitesAandBGivenState[i] /.
         subThisEtxtyList), toorder, assumptions], {i, 1, 12}]]
 ]
```

Further comments on gene conversion probabilities

In this section, we relate the gene conversion parameters used in the coalescent simulation to the gene conversion parameters used in the two-site analysis of linkage disequilibrium.

Our two sites are assumed to be separated by L gaps between base pairs (i.e., the two focal sites are separated by L - 1 intervening base pairs). We have assumed that $\gamma 1$ is the probability that either one of focal two sites (but NOT both) will be included in a mitotic gene conversion event; $\gamma 2$ is the probability that both of focal sites separated by L gaps will be included in a mitotic gene conversion event.

Following Hein and Wuif (2000 *Genetics* 155: 451-462), let $Q = L/\lambda$ where λ is the mean tract length in base pairs (bp). Gene conversion tract lengths are assume to follow an exponential distribution. We will use Q to be the parameter of the exponential distribution to describe the length distribution of conversion tracts (on the L scale). Thus $1/Q$ is the mean tract length, as measured on a scale of L bp.

```
ExponentialDistribution[Q] // Mean
```

$$\frac{1}{Q}$$

For a gene conversion event that starts a distance x (on the L scale) from the focal sequence, then the probability that the gene conversion event completely covers the focal sequence is

```
Simplify[1 - CDF[ExponentialDistribution[Q], x + 1], Assumptions → {x > 0}]
```

$$e^{-Q\,(1+x)}$$

We now have to consider all the possible positions where the gene conversion could start to find the total probability of a gene conversion that could cover the entire focal sequence, i.e., we are trying to find $\gamma 2$.
Let g be the probability that a gene conversion starts at particular gap. We can think of all tracts as "starting" on the left end and moving right. Note that the density of conversion sites is gL (not g) on the L scale.

This is $\gamma 2$ (assuming g and λ apply to mitotic gene conversion events):

```
Simplify[Integrate[g L e^-Q (1+x), {x, 0, ∞}], Assumptions → {Q > 0}] /. L → Q λ
```

$$e^{-Q}\, g\, \lambda$$

If tract lengths are very short ($\lambda \to 0$), then there is no chance of a conversion tract covering the focal sequence.

If tracts are very long ($\lambda \to \infty$), then this expression behaves strangely due to the integration occurring over an infinite number of sites (i.e., even a site that is an infinite distance away can cover the focal tract because the tract length is infinite). This is not a problem as we are not interested in the limit as $\lambda \to \infty$. If we were to hold the genome-wide rate of gene conversion constant, then the per-

base rate *g* would have to decline as we made the genome longer, i.e., g ∝ 1/*B* where *B* is total number of bases on the chromosome. As *B*→ ∞, then *g*→ 0 and the probability would remain finite.

We now calculate the probability that a conversion tract that starts a distance *x* inside the focal sequence will terminate within the focal sequence

```
Simplify[CDF[ExponentialDistribution[Q], 1 - x], Assumptions → {1 - x > 0}]
```

$$1 - e^{Q\,(-1+x)}$$

We use the result above to calculate the probability that a conversion tract that starts inside the focal sequence does *not* affect either of the focal sites at its termini by integrating over all possible starting locations within the focal sequence

```
ProbBothEndsAreWithFocalSeqGivenItStartsInFocalSeq =
 Simplify[ Integrate[Simplify[CDF[ExponentialDistribution[Q], 1 - x],
    Assumptions → {1 - x > 0}], {x, 0, 1}], Assumptions → {Q > 0}]
```

$$1 + \frac{-1 + e^{-Q}}{Q}$$

From the result above, we can calculate the probability that a gene conversion event that starts within the focal sequence does extend far enough to cover one (but not both) of the focal sites at the termini.

```
ProbItStartsWithinFocalSeqAndEndsOutsideGivenItStartsInFocalSeq =
 1 - ProbBothEndsAreWithFocalSeqGivenItStartsInFocalSeq
```

$$-\frac{-1 + e^{-Q}}{Q}$$

The probabilities above are conditional on the tract starting within the focal sequence. The probability of starting within the tract is *gL*. By symmetry, the (unconditional) probability that a tract starts outside and ends within the tract is also
*gL** ProbItStartsWithinFocalSeqAndEndsOutsideGivenItStartsInFocalSeq.

So considering that $\gamma 1$ is the probability that either (but not both) sites are converted (and assuming g and λ apply to asexual gene conversion events), then $\gamma 1$ is equal to

```
2 g L * ProbItStartsWithinFocalSeqAndEndsOutsideGivenItStartsInFocalSeq /.
 Q → L / λ
```

$$-2\left(-1 + e^{-\frac{L}{\lambda}}\right) g\,\lambda$$

It may be useful to use the substitution:

```
subGeneConversionProbabilitiesAsAFunctionOfLength =
 {γ1 → 2 g L * ProbItStartsWithinFocalSeqAndEndsOutsideGivenItStartsInFocalSeq /.
   Q → L / λ, γ2 →
    Simplify[Integrate[g L e^(-Q (1+x)), {x, 0, ∞}], Assumptions → {Q > 0}] /. Q → L / λ}
```

$$\left\{\gamma 1 \to -2\left(-1 + e^{-\frac{L}{\lambda}}\right) g\,\lambda,\ \gamma 2 \to e^{-\frac{L}{\lambda}}\, g\,\lambda\right\}$$

$$\left\{\gamma 1 \to -2\left(-1+e^{-\frac{L}{\lambda}}\right) g\lambda,\ \gamma 2 \to e^{-\frac{L}{\lambda}} g\lambda\right\}$$

$$\left\{\gamma 1 \to -2\left(-1+e^{-\frac{L}{\lambda}}\right) g\lambda,\ \gamma 2 \to e^{-\frac{L}{\lambda}} g\lambda\right\}$$

The probability that one specific site is covered by a mitotic gene conversion event (regardless of whether the other is or not) is $\frac{\gamma 1}{2} + \gamma 2$

```
γ1/2 + γ2 /. subGeneConversionProbabilitiesAsAFunctionOfLength // Simplify
```

$$g\lambda$$

Single site coalescence

We will need to use results from single-site coalescence (Hartfield et al. 2016 *Genetics* 202: 297-312). For the single-site case, there are three states: (i) the two copies are in different individuals; (i) both copies are in the same individual; and (iii) coalesced.

From eq. 10 in Hartfield et al. 2016, the transition matrix for the single site case is:

```
SingleSiteTransMat =
  {{1 - 1/n, (1 - γ)/(2 n), (1 + γ)/(2 n)}, {σ (1 - 1/n), (1 - γ) (1 - σ) + σ (1 - γ)/(2 n), (1 - σ) γ + σ (1 + γ)/(2 n)},
   {0, 0, 1}} /. γ → γ1/2 + γ2;
```

Using first-step analysis (Wakeley 2009, chapter 5), we can write equations for the expected values of coalescent times from two copies from different individuals (E[*tb*]) and two copies from the same individual (E[*tw*]) as

$E[T_i] = E[\tau_i] + P_{ij} E[T_j]$

where $E[\tau_i]$ is the expected time to leave state *i* and $P_{ij}$is the probability of moving from state *i* to state *j* conditional on leaving state *i*. In discrete time, the time to leave state *i* follows a geometric distribution with parameter 1 - M_{ii} from the transition matrix **M**, so $E[\tau_i] = 1/(1\text{-}M_{ii})$

```
SingleSiteEqns = {Etb == 1/(1 - SingleSiteTransMat[[1, 1]]) +
      (SingleSiteTransMat[[1, 2]] / (1 - SingleSiteTransMat[[1, 1]])) Etw,
   Etw == 1/(1 - SingleSiteTransMat[[2, 2]]) +
      (SingleSiteTransMat[[2, 1]] / (1 - SingleSiteTransMat[[2, 2]])) Etb};

SingleSiteCoalescentTimesExact =
 Solve[SingleSiteEqns, {Etb, Etw}][[1]] // Simplify
```

$$\left\{Etb \to ((-1+2n)\gamma 1(-1+\sigma) + 2(-1+(-1+2n)\gamma 2(-1+\sigma)+\sigma-2n\sigma))/(\gamma 1(-2+\sigma)+2\gamma 2(-2+\sigma)-2\sigma),\ Etw \to \frac{-4-4(-1+n)\sigma}{\gamma 1(-2+\sigma)+2\gamma 2(-2+\sigma)-2\sigma}\right\}$$

Below we confirm this is the same as eq. (11) of Hartfield et al. 2016 (noting that the results pre-

sented there are on the coalescent time scale so differs by a factor of 2n)

```
TS[{Etb, Etw} /. SingleSiteCoalescentTimesExact, -2, {n → n/ξ^3, γ1 → γ1 ξ^2, γ2 → γ2 ξ^2,
    σ → ξ^2 σ}] /. ξ → 1 /. σ → ϕ γ /. γ → γ1/2 + γ2 // FullSimplify;
Collect[Expand[% /. γ1 + 2 γ2 → Hartfieldγ / n /. γ1 n ϕ + 2 γ2 n ϕ → Hartfieldγ ϕ] /.
    Hartfieldγ → 1 / InvHartfieldγ,
  InvHartfieldγ, Simplify] /. InvHartfieldγ → 1 / Hartfieldγ
{2 n/(Hartfieldγ (2 + ϕ)) + 2 n (1 + ϕ)/(2 + ϕ), 4 n/(Hartfieldγ (2 + ϕ)) + 2 n ϕ/(2 + ϕ)}
```

Results under different assumptions

Here we derived r_d^2 under various assumptions. We consider two main cases: where sex is **not** rare at the population level ($n\sigma >> 1$) and where it is. For the former case, we analyze the model both in discrete time and in continuous time. For discrete time, we examine several different versions (making slightly different assumptions) but we always obtain the same result. We also obtain the same result for the continuous time analysis. The result is very different if sex is rare at the population level.

Discrete time analysis:
When sex is not rare at the individual level $\sigma \sim O(1)$
LD is $\frac{10+\Psi}{(2+\Psi)\ (11+\Psi)}$ where $\Psi = \rho A + \rho\ \sigma + \frac{\Gamma_1}{2} + \frac{\sigma\ \Gamma_{S1}}{2}$
which simplifies to $\frac{10+\rho\ \sigma}{(2+\rho\ \sigma)\ (11+\rho\ \sigma)}$ if there is no gene conversion

Here we assume sex is not too rare. Specifically, we assume $\sigma \sim O(1)$. Other assumptions: c, $\gamma 1$, $\gamma 2$, $\gamma 1S$, $cA \sim O(1/n)$

```
OrderOfN = -1;
subAssumptionsForSexRareAtIndividualLevelButCommonAtPopLevel =
 {n → n ξ^OrderOfN, σ → σ ξ^0, c → c ξ^-OrderOfN, γ1S → γ1S ξ^-OrderOfN, γ1 → γ1 ξ^-OrderOfN,
  γ2 → γ2 ξ^-OrderOfN, cA → cA ξ^-OrderOfN, Etb → EtbOn ξ^OrderOfN + EtbOnplus1 ξ^OrderOfN+1,
  Etw → EtwOn ξ^OrderOfN + EtwOnplus1 ξ^OrderOfN+1}
{n → n/ξ, σ → σ, c → c ξ, γ1S → γ1S ξ, γ1 → γ1 ξ, γ2 → γ2 ξ,
 cA → cA ξ, Etb → EtbOnplus1 + EtbOn/ξ, Etw → EtwOnplus1 + EtwOn/ξ}
```

We first calculate the single-site coalescent times under these assumptions

```
SingleSiteCoalescentTimesApprox =
  TS[{Etb, Etw} /. SingleSiteCoalescentTimesExact, OrderOfN + 2,
   subAssumptionsForSexRareAtIndividualLevelButCommonAtPopLevel];

subAppropriateValuesForPartsOfSingleSiteCoalescentTimes =
 {EtbOn → Coefficient[SingleSiteCoalescentTimesApprox[[1]], ξ, OrderOfN],
  EtbOnplus1 →
   Coefficient[SingleSiteCoalescentTimesApprox[[1]], ξ, OrderOfN + 1], EtwOn →
   Coefficient[SingleSiteCoalescentTimesApprox[[2]], ξ, OrderOfN], EtwOnplus1 →
   Coefficient[SingleSiteCoalescentTimesApprox[[2]], ξ, OrderOfN + 1]}
```

$$\left\{\text{EtbOn} \to 2\,n,\ \text{EtbOnplus1} \to \frac{1 - n\,\gamma 1 - 2\,n\,\gamma 2 - \sigma}{\sigma},\ \text{EtwOn} \to 2\,n,\right.$$
$$\left.\text{EtwOnplus1} \to \frac{1}{\sigma}(2 - 2\,n\,\gamma 1 - 4\,n\,\gamma 2 - 2\,\sigma + n\,\gamma 1\,\sigma + 2\,n\,\gamma 2\,\sigma)\right\}$$

We will use a Taylor series approximation to obtain expressions for the E[*tx*ty*]; in doing so, it is useful to decompose the E[*tx*ty*] into parts of different magnitude.

```
subEtxtyInParts = {EtxtyS1 → EtxtyS1On2 ξ^-2 + EtxtyS1On1 ξ^-1,
    EtxtyS2 → EtxtyS2On2 ξ^-2 + EtxtyS2On1 ξ^-1,
    EtxtyS3 → EtxtyS3On2 ξ^-2 + EtxtyS3On1 ξ^-1, EtxtyS4 →
     EtxtyS4On2 ξ^-2 + EtxtyS4On1 ξ^-1, EtxtyS5 → EtxtyS5On2 ξ^-2 + EtxtyS5On1 ξ^-1,
    EtxtyS6 → EtxtyS6On2 ξ^-2 + EtxtyS6On1 ξ^-1, EtxtyS7 →
     EtxtyS7On2 ξ^-2 + EtxtyS7On1 ξ^-1, EtxtyS8 → EtxtyS8On2 ξ^-2 + EtxtyS8On1 ξ^-1,
    EtxtyS9 → EtxtyS9On2 ξ^-2 + EtxtyS9On1 ξ^-1, EtxtyS10 →
     EtxtyS10On2 ξ^-2 + EtxtyS10On1 ξ^-1, EtxtyS11 → EtxtyS11On2 ξ^-2 + EtxtyS11On1 ξ^-1,
    EtxtyS12 → EtxtyS12On2 ξ^-2 + EtxtyS12On1 ξ^-1};
```

We next solve expressions for the leading order parts of the E[*tx*ty*]

```
subSolnsForLeadingOrderEtxty = Simplify[Solve[eqnsToOrder[-2,
       subAssumptionsForSexRareAtIndividualLevelButCommonAtPopLevel],
      {EtxtyS1On2, EtxtyS2On2, EtxtyS3On2, EtxtyS4On2, EtxtyS5On2,
       EtxtyS6On2, EtxtyS7On2, EtxtyS8On2, EtxtyS9On2,
       EtxtyS10On2, EtxtyS11On2, EtxtyS12On2}][[1]]];

DummyListOfNamesOfLeadingOrderPartsOfEtxty =
  (ExpectedValueOfProductOfCoalescentTimesForSitesAandBGivenStateDummyList[[
      1 ;; 12]] /. Table[
      ExpectedValueOfProductOfCoalescentTimesForSitesAandBGivenStateDummyList[
        [i]] → TS[
        ExpectedValueOfProductOfCoalescentTimesForSitesAandBGivenStateDummyLi
          st[[i]] /. subEtxtyInParts, -2, {}], {i, 12}] /. ξ → 1);

LeadingOrderPartsOfEtxty =
  DummyListOfNamesOfLeadingOrderPartsOfEtxty /. subSolnsForLeadingOrderEtxty /.
   subAppropriateValuesForPartsOfSingleSiteCoalescentTimes;
```

Now calculate the disequilibrium following McVean (2002). For simplicity (and in analogy with the

haploid case), we assume only single homolog is taken from each individual sampled.

```
LDmetric = (LeadingOrderPartsOfEtxty[[1]] -
      2 (LeadingOrderPartsOfEtxty[[3]]) + LeadingOrderPartsOfEtxty[[7]]) /
    (LeadingOrderPartsOfEtxty[[7]]) // FullSimplify
```

$$\frac{1}{9}\left(\frac{4}{1+n\ (2\ cA+\gamma 1+(2\ c+\gamma 1S)\ \sigma)}+\frac{1}{11+2\ n\ (2\ cA+\gamma 1+(2\ c+\gamma 1S)\ \sigma)}\right)$$

We can expressed this in terms of population-scaled parameters as

```
LDmetric /. c → ρ / (4 n) /. γ1 → Γ1 / (4 n) /. γ1S → ΓS1 / (4 n) /. cA → ρA / (4 n) //
 FullSimplify
% /. (2 ρA + 2 ρ σ + Γ1 + σ ΓS1) → 2 Ψ // Simplify // Factor
```

$$\frac{2}{9}\left(\frac{8}{4+2\ \rho A+2\ \rho\ \sigma+\Gamma_1+\sigma\ \Gamma_{S1}}+\frac{1}{22+2\ \rho A+2\ \rho\ \sigma+\Gamma_1+\sigma\ \Gamma_{S1}}\right)$$

$$\frac{10+\Psi}{(2+\Psi)\ (11+\Psi)}$$

Ignoring mitotic and meiotic gene conversion (and mitotic crossovers), this is simply

```
LDmetric /. c → ρ / (4 n) /. γ1 → 0 /. γ1S → 0 /. cA → 0 // FullSimplify
```

$$\frac{10+\rho\ \sigma}{(2+\rho\ \sigma)\ (11+\rho\ \sigma)}$$

Discrete time analysis:
When sex is rare at the individual level ($\sigma << 1$) but not too rare at the population level $n\sigma >> 1$
LD is $\frac{10+\Psi}{(2+\Psi)\ (11+\Psi)}$ where $\Psi = \rho A + \rho\ \sigma + \frac{\Gamma_1}{2} + \frac{\sigma\ \Gamma_{S1}}{2}$
which simplifies to $\frac{10+\rho\ \sigma}{(2+\rho\ \sigma)\ (11+\rho\ \sigma)}$ if there is no gene conversion

Here we assume that population size is large and sex can be rare but not too rare, i.e., $1/n << \sigma << 1$. This means that sex occurs regularly at the population level, $n\sigma >> 1$, even if it is rare at an individual level. Specifically, we assume $n \sim O(\xi^{-2})$ and $\sigma \sim O(\xi)$ for $0 < \xi << 1$. Other assumptions: c , $\gamma 1S \sim O(\xi)$, and cA, $\gamma 1$, $\gamma 2 \sim O(\xi^2)$

```
OrderOfN = -2;
subAssumptionsForSexRareAtIndividualLevelButCommonAtPopLevel =
 {n → n ξ^OrderOfN, σ → σ ξ^-OrderOfN-1, c → c ξ^-OrderOfN-1,
  γ1S → γ1S ξ^-OrderOfN-1, γ1 → γ1 ξ^-OrderOfN, γ2 → γ2 ξ^-OrderOfN,
  cA → cA ξ^-OrderOfN, Etb → EtbOn ξ^OrderOfN + EtbOnplus1 ξ^OrderOfN+1,
  Etw → EtwOn ξ^OrderOfN + EtwOnplus1 ξ^OrderOfN+1}
```

$$\left\{n \to \frac{n}{\xi^2},\ \sigma \to \xi\ \sigma,\ c \to c\ \xi,\ \gamma 1S \to \gamma 1S\ \xi,\ \gamma 1 \to \gamma 1\ \xi^2,\ \gamma 2 \to \gamma 2\ \xi^2,\right.$$

$$\left.cA \to cA\ \xi^2,\ Etb \to \frac{EtbOn}{\xi^2}+\frac{EtbOnplus1}{\xi},\ Etw \to \frac{EtwOn}{\xi^2}+\frac{EtwOnplus1}{\xi}\right\}$$

We first calculate the single-site coalescent times under these assumptions

```
SingleSiteCoalescentTimesApprox =
  TS[{Etb, Etw} /. SingleSiteCoalescentTimesExact, OrderOfN + 2,
   subAssumptionsForSexRareAtIndividualLevelButCommonAtPopLevel];

subAppropriateValuesForPartsOfSingleSiteCoalescentTimes =
 {EtbOn → Coefficient[SingleSiteCoalescentTimesApprox[[1]], ξ, OrderOfN],
  EtbOnplus1 →
   Coefficient[SingleSiteCoalescentTimesApprox[[1]], ξ, OrderOfN + 1], EtwOn →
   Coefficient[SingleSiteCoalescentTimesApprox[[2]], ξ, OrderOfN], EtwOnplus1 →
   Coefficient[SingleSiteCoalescentTimesApprox[[2]], ξ, OrderOfN + 1]}
```

$$\left\{\text{EtbOn} \to 2\,\text{n},\ \text{EtbOnplus1} \to \frac{1 - \text{n}\,\gamma 1 - 2\,\text{n}\,\gamma 2}{\sigma},\right.$$
$$\left.\text{EtwOn} \to 2\,\text{n},\ \text{EtwOnplus1} \to -\frac{2\,(-1 + \text{n}\,\gamma 1 + 2\,\text{n}\,\gamma 2)}{\sigma}\right\}$$

In a later section, we will use a Taylor series approximation to obtain expressions for the E[*tx*ty*]; in doing so, it is useful to decompose the E[*tx*ty*] into parts of different magnitude.

```
subEtxtyInParts =
  {EtxtyS1 → EtxtyS1On4 ξ^-4 + EtxtyS1On3 ξ^-3 + EtxtyS1On2 ξ^-2 + EtxtyS1On1 ξ^-1,
   EtxtyS2 → EtxtyS2On4 ξ^-4 + EtxtyS2On3 ξ^-3 + EtxtyS2On2 ξ^-2 + EtxtyS2On1 ξ^-1,
   EtxtyS3 → EtxtyS3On4 ξ^-4 + EtxtyS3On3 ξ^-3 + EtxtyS3On2 ξ^-2 + EtxtyS3On1 ξ^-1,
   EtxtyS4 → EtxtyS4On4 ξ^-4 + EtxtyS4On3 ξ^-3 + EtxtyS4On2 ξ^-2 + EtxtyS4On1 ξ^-1,
   EtxtyS5 → EtxtyS5On4 ξ^-4 + EtxtyS5On3 ξ^-3 + EtxtyS5On2 ξ^-2 + EtxtyS5On1 ξ^-1,
   EtxtyS6 → EtxtyS6On4 ξ^-4 + EtxtyS6On3 ξ^-3 + EtxtyS6On2 ξ^-2 + EtxtyS6On1 ξ^-1,
   EtxtyS7 → EtxtyS7On4 ξ^-4 + EtxtyS7On3 ξ^-3 + EtxtyS7On2 ξ^-2 + EtxtyS7On1 ξ^-1,
   EtxtyS8 → EtxtyS8On4 ξ^-4 + EtxtyS8On3 ξ^-3 + EtxtyS8On2 ξ^-2 + EtxtyS8On1 ξ^-1,
   EtxtyS9 → EtxtyS9On4 ξ^-4 + EtxtyS9On3 ξ^-3 + EtxtyS9On2 ξ^-2 + EtxtyS9On1 ξ^-1,
   EtxtyS10 → EtxtyS10On4 ξ^-4 + EtxtyS10On3 ξ^-3 + EtxtyS10On2 ξ^-2 + EtxtyS10On1 ξ^-1,
   EtxtyS11 → EtxtyS11On4 ξ^-4 + EtxtyS11On3 ξ^-3 + EtxtyS11On2 ξ^-2 + EtxtyS11On1 ξ^-1,
   EtxtyS12 → EtxtyS12On4 ξ^-4 + EtxtyS12On3 ξ^-3 + EtxtyS12On2 ξ^-2 + EtxtyS12On1 ξ^-1};
```

We next solve expressions for the leading order parts of the E[*tx*ty*]

```
subSolnsForLeadingOrderEtxty = Simplify[Solve[eqnsToOrder[-4,
       subAssumptionsForSexRareAtIndividualLevelButCommonAtPopLevel],
      {EtxtyS1On4, EtxtyS2On4, EtxtyS3On4, EtxtyS4On4, EtxtyS5On4,
       EtxtyS6On4, EtxtyS7On4, EtxtyS8On4, EtxtyS9On4,
       EtxtyS10On4, EtxtyS11On4, EtxtyS12On4}][[1]]];

DummyListOfNamesOfLeadingOrderPartsOfEtxty =
  (ExpectedValueOfProductOfCoalescentTimesForSitesAandBGivenStateDummyList[[
      1 ;; 12]] /. Table[
      ExpectedValueOfProductOfCoalescentTimesForSitesAandBGivenStateDummyList[
        [i]] → TS[
        ExpectedValueOfProductOfCoalescentTimesForSitesAandBGivenStateDummyLi
          st[[i]] /. subEtxtyInParts, -4, {}], {i, 12}] /. ξ → 1);

LeadingOrderPartsOfEtxty =
  DummyListOfNamesOfLeadingOrderPartsOfEtxty /. subSolnsForLeadingOrderEtxty /.
   subAppropriateValuesForPartsOfSingleSiteCoalescentTimes;
```

Now calculate the disequilibrium following McVean (2002). For simplicity (and in analogy with the haploid case), we assume only single homolog is taken from each individual sampled.

```
LDmetric = (LeadingOrderPartsOfEtxty[[1]] -
     2 (LeadingOrderPartsOfEtxty[[3]]) + LeadingOrderPartsOfEtxty[[7]]) /
   (LeadingOrderPartsOfEtxty[[7]]) // FullSimplify
```

$$\frac{1}{9}\left(\frac{4}{1+n\,(2\,cA+\gamma 1+(2\,c+\gamma 1S)\,\sigma)}+\frac{1}{11+2\,n\,(2\,cA+\gamma 1+(2\,c+\gamma 1S)\,\sigma)}\right)$$

We can expressed this in terms of population-scaled parameters as

```
LDmetric /. c → ρ / (4 n) /. γ1 → Γ1 / (4 n) /. γ1S → ΓS1 / (4 n) /. cA → ρA / (4 n) //
 FullSimplify

% /. (2 ρA + 2 ρ σ + Γ1 + σ ΓS1) → 2 Ψ // Simplify // Factor
```

$$\frac{2}{9}\left(\frac{8}{4+2\,\rho A+2\,\rho\,\sigma+\Gamma_1+\sigma\,\Gamma_{S1}}+\frac{1}{22+2\,\rho A+2\,\rho\,\sigma+\Gamma_1+\sigma\,\Gamma_{S1}}\right)$$

$$\frac{10+\Psi}{(2+\Psi)\,(11+\Psi)}$$

Ignoring mitotic and meiotic gene conversion, this is simply

```
LDmetric /. c → ρ / (4 n) /. γ1 → 0 /. γ1S → 0 /. cA → 0 // FullSimplify
```

$$\frac{10+\rho\,\sigma}{(2+\rho\,\sigma)\,(11+\rho\,\sigma)}$$

Continuous time analysis:

When sex is not rare at the individual level $\sigma >> n^{-1}$

LD is $\frac{10+\Psi}{(2+\Psi)\,(11+\Psi)}$ where $\Psi = \rho A + \rho\,\sigma + \frac{\Gamma_1}{2} + \frac{\sigma\,\Gamma_{S1}}{2}$

which simplifies to $\frac{10+\rho\,\sigma}{(2+\rho\,\sigma)\,(11+\rho\,\sigma)}$ if there is no gene conversion

Here we assume the rate of sex is not very low at the population level, i.e., $\sigma >> 1/n$. We now analyze this case,using the continuous time approximation where we measure time on a coalescent time scale where 1 time unit is 2*n* generations.

We will as assume that as $n \to \infty$,
$4\,n\,\gamma 1 \to \Gamma_1$, $4\,n\,\gamma 2 \to \Gamma_2$, $4\,n\,\gamma 1S \to \Gamma_{S1}$, 4 n c $\to \rho$, 4 n cA $\to \rho$A

We use the method of Mohle (1998, *Advances in Applied Probability* 30: 493-512) as described in Wakeley (2009, chapter 6) to change the discrete time transition matrix into one for the continuous time approximation. This can be applied to a transition matrix that has transitions operating at different time scales. However, under the assumptions used here, all the transitions are slow.

First we redo the single-site coalescence in this framework.

```
SingleSiteTransMatV2 =
 SingleSiteTransMat /. {γ1 → Γ1 / (4 n), γ2 → Γ2 / (4 n)} // Simplify
```

$$\left\{\left\{\frac{-1+n}{n}, -\frac{-8\,n+\Gamma 1+2\,\Gamma 2}{16\,n^2}, \frac{8\,n+\Gamma 1+2\,\Gamma 2}{16\,n^2}\right\},\right.$$
$$\left\{\frac{(-1+n)\,\sigma}{n}, -\frac{(8\,n-\Gamma 1-2\,\Gamma 2)\,(2\,n\,(-1+\sigma)-\sigma)}{16\,n^2}, \frac{1}{16\,n^2}\right.$$
$$\left.\left.((\Gamma 1+2\,\Gamma 2)\,\sigma+n\,(4\,\Gamma 2-2\,\Gamma 1\,(-1+\sigma)+8\,\sigma-4\,\Gamma 2\,\sigma))\right\}, \{0, 0, 1\}\right\}$$

```
SingleSiteTransMatFastPart = Limit[SingleSiteTransMatV2, n → ∞]
% // MatrixForm
```

```
{{1, 0, 0}, {σ, 1 - σ, 0}, {0, 0, 1}}
```

$$\begin{pmatrix} 1 & 0 & 0 \\ \sigma & 1-\sigma & 0 \\ 0 & 0 & 1 \end{pmatrix}$$

```
SingleSiteFastPartStationaryDist = Limit[
   MatrixPower[SingleSiteTransMatFastPart, x], x → ∞, Assumptions → {σ > 0, σ < 1}]
```

```
{{1, 0, 0}, {1, 0, 0}, {0, 0, 1}}
```

Note the result above indicates that the samples in the second state “instantaneously” (on the coalescent time scale) go to the first state.

```
SingleSiteTransMatSlowPart =
 Limit[2 n (SingleSiteTransMatV2 - SingleSiteTransMatFastPart), n → ∞]
```

$$\left\{\{-2, 1, 1\},\right.$$
$$\left.\left\{-2\,\sigma, \frac{1}{4}(\Gamma 1\,(-1+\sigma)+2\,\Gamma 2\,(-1+\sigma)+4\,\sigma), \frac{1}{4}(\Gamma 1-2\,\Gamma 2\,(-1+\sigma)+4\,\sigma-\Gamma 1\,\sigma)\right\}, \{0, 0, 0\}\right\}$$

The rate matrix for the slow processes is given by:

```
SingleSiteGMat = SingleSiteFastPartStationaryDist.
    SingleSiteTransMatSlowPart.SingleSiteFastPartStationaryDist // Simplify;
% // MatrixForm
```

$$\begin{pmatrix} -1 & 0 & 1 \\ -1 & 0 & 1 \\ 0 & 0 & 0 \end{pmatrix}$$

From the results above, we see that we can collapse to a simpler system where we ignore the “both samples within an individual” state. This is just the classic coalescence case where the expected time to coalescence is 1 (on the coalescent time scale measured in 2N generations).

Next we consider the two site model

```
FastPartOfTransMat =
 Limit[(TransMat) /. {c → ρ / (4 n), γ1S → Γ1S / (4 n), γ1 → Γ1 / (4 n),
    γ2 → Γ2 / (4 n), cA → ρA / (4 n)}, n → ∞]
```

```
{{1, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0},
 {σ, 1 - σ, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0},
 {0, 0, 1, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0},
 {0, 0, σ, 1 - σ, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0},
 {0, 0, σ, 0, 1 - σ, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0},
 {0, 0, σ, 0, 0, 1 - σ, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0},
 {0, 0, 0, 0, 0, 0, 1, 0, 0, 0, 0, 0, 0, 0, 0, 0},
 {0, 0, 0, 0, 0, 0, σ, 1 - σ, 0, 0, 0, 0, 0, 0, 0, 0},
 {0, 0, 0, 0, 0, 0, σ, 0, 1 - σ, 0, 0, 0, 0, 0, 0, 0},
 {0, 0, 0, 0, 0, 0, σ, 0, 0, 1 - σ, 0, 0, 0, 0, 0, 0},
 {0, 0, 0, 0, 0, 0, σ^2, -(-1 + σ) σ, 0, -(-1 + σ) σ, (-1 + σ)^2, 0, 0, 0, 0, 0},
 {0, 0, 0, 0, 0, 0, σ^2, 0, -2 (-1 + σ) σ, 0, 0, (-1 + σ)^2, 0, 0, 0, 0, 0},
 {0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 1, 0, 0, 0, 0},
 {0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, σ, 1 - σ, 0, 0, 0},
 {0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 1, 0, 0},
 {0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, σ, 1 - σ, 0},
 {0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 1}}
```

```
StationaryFast =
  Limit[MatrixPower[FastPartOfTransMat, x], x → ∞, Assumptions → {σ > 0, σ < 1}];
% // MatrixForm
```

$$\begin{pmatrix}
1&0&0&0&0&0&0&0&0&0&0&0&0&0&0&0&0\\
1&0&0&0&0&0&0&0&0&0&0&0&0&0&0&0&0\\
0&0&1&0&0&0&0&0&0&0&0&0&0&0&0&0&0\\
0&0&1&0&0&0&0&0&0&0&0&0&0&0&0&0&0\\
0&0&1&0&0&0&0&0&0&0&0&0&0&0&0&0&0\\
0&0&1&0&0&0&0&0&0&0&0&0&0&0&0&0&0\\
0&0&0&0&0&0&1&0&0&0&0&0&0&0&0&0&0\\
0&0&0&0&0&0&1&0&0&0&0&0&0&0&0&0&0\\
0&0&0&0&0&0&1&0&0&0&0&0&0&0&0&0&0\\
0&0&0&0&0&0&1&0&0&0&0&0&0&0&0&0&0\\
0&0&0&0&0&0&1&0&0&0&0&0&0&0&0&0&0\\
0&0&0&0&0&0&1&0&0&0&0&0&0&0&0&0&0\\
0&0&0&0&0&0&0&0&0&0&0&0&1&0&0&0&0\\
0&0&0&0&0&0&0&0&0&0&0&0&1&0&0&0&0\\
0&0&0&0&0&0&0&0&0&0&0&0&0&0&1&0&0\\
0&0&0&0&0&0&0&0&0&0&0&0&0&0&1&0&0\\
0&0&0&0&0&0&0&0&0&0&0&0&0&0&0&0&1
\end{pmatrix}$$

```
SlowPartOfTransMat =
 Limit[2 n (TransMat - FastPartOfTransMat) /. {c → ρ / (4 n), γ1S → Γ1S / (4 n),
    γ1 → Γ1 / (4 n), γ2 →  Γ2 / (4 n), cA → ρA / (4 n)}, n → ∞]
```

$$\Big\{\Big\{\frac{1}{2}(-4-\Gamma1-2\rho A-\Gamma1S\,\sigma-2\rho\sigma),1,0,$$
$$\frac{1}{2}(\Gamma1+2\rho A+(\Gamma1S+2\rho)\sigma),0,0,0,0,0,0,0,0,0,0,0,0,1\Big\},$$
$$\Big\{-\frac{1}{2}(\Gamma1+\Gamma1S+2(2+\rho+\rho A))\sigma,\ \frac{1}{2}(\Gamma1(-1+\sigma)+\Gamma2(-1+\sigma)+2\sigma),0,$$
$$\frac{1}{2}(\Gamma1+\Gamma1S+2(\rho+\rho A))\sigma,0,0,0,0,0,0,0,0,0,\ \frac{1}{4}(\Gamma1-\Gamma1\sigma),0,$$
$$\frac{1}{4}(\Gamma1-\Gamma1\sigma),\ \frac{1}{2}(\Gamma2+2\sigma-\Gamma2\sigma)\Big\},\ \Big\{1,0,\ \frac{1}{4}(-24-\Gamma1-2\rho A-\Gamma1S\,\sigma-2\rho\sigma),$$
$$1,1,1,0,0,\ \frac{1}{4}(\Gamma1+2\rho A+(\Gamma1S+2\rho)\sigma),0,0,0,1,0,1,0,0\Big\},$$
$$\Big\{\frac{1}{4}(\Gamma1-2\rho A(-1+\sigma)+4\sigma-\Gamma1\sigma),0,-\frac{1}{4}\sigma(24+\Gamma1+2\rho A+\Gamma1S\,\sigma+2\rho\sigma),$$
$$\frac{1}{4}\left(-8+2\Gamma1(-1+\sigma)+4\rho A(-1+\sigma)+12\sigma-\Gamma1S\,\sigma-2\rho\sigma+\Gamma1S\,\sigma^2+2\rho\sigma^2\right),$$
$$\sigma,\sigma,0,0,\ \frac{1}{4}\sigma(\Gamma1+2\rho A+(\Gamma1S+2\rho)\sigma),0,0,$$
$$-\frac{1}{4}(-1+\sigma)(\Gamma1+2\rho A+(\Gamma1S+2\rho)\sigma),\sigma,1-\sigma,\sigma,1-\sigma,0\Big\},$$
$$\Big\{\sigma,1-\sigma,-\frac{1}{4}(\Gamma1+\Gamma1S+2(12+\rho+\rho A))\sigma,\sigma,\ \frac{1}{4}(\Gamma1(-1+\sigma)+2(-4+\Gamma2(-1+\sigma)+6\sigma)),$$
$$\sigma,0,0,\ \frac{1}{4}(\Gamma1+\Gamma1S+2(\rho+\rho A))\sigma,0,0,0,\ \frac{1}{4}(\Gamma1-2\Gamma2(-1+\sigma)+4\sigma-\Gamma1\sigma),$$

$$\left\{0, \sigma, 1-\sigma, 0\right\}, \left\{\sigma, 1-\sigma, -\frac{1}{4}(\Gamma 1+\Gamma 1 S+2(12+\rho+\rho A))\sigma, \sigma, \sigma,\right.$$
$$\frac{1}{4}(\Gamma 1(-1+\sigma)+2(-4+\Gamma 2(-1+\sigma)+6\sigma)), 0, 0, \frac{1}{4}(\Gamma 1+\Gamma 1 S+2(\rho+\rho A))\sigma,$$
$$\left.0, 0, 0, \sigma, 1-\sigma, \frac{1}{4}(\Gamma 1-2\Gamma 2(-1+\sigma)+4\sigma-\Gamma 1\sigma), 0, 0\right\},$$
$$\{0, 0, 4, 0, 0, 0, -12, 1, 4, 1, 0, 0, 1, 0, 1, 0, 0\},$$
$$\left\{0, 0, 4\sigma, 0, 4-4\sigma, 0, -12\sigma, \frac{1}{4}(\Gamma 1(-1+\sigma)+2\Gamma 2(-1+\sigma)+4(-6+7\sigma)),\right.$$
$$\left.4\sigma, \sigma, 1-\sigma, 0, \frac{1}{4}(\Gamma 1-2\Gamma 2(-1+\sigma)+4\sigma-\Gamma 1\sigma), 0, \sigma, 1-\sigma, 0\right\},$$
$$\left\{0, 0, \frac{1}{4}(\Gamma 1-\Gamma 1\sigma+2(\rho A+8\sigma-\rho A\sigma)), 1-\sigma, 1-\sigma, 1-\sigma, -12\sigma, \sigma,\right.$$
$$\left.\frac{1}{4}(\Gamma 1(-1+\sigma)+2\rho A(-1+\sigma)+8(-3+5\sigma)), \sigma, 0, 1-\sigma, 1, 0, 1, 0, 0\right\},$$
$$\left\{0, 0, 4\sigma, 0, 0, 4-4\sigma, -12\sigma, \sigma, 4\sigma, \frac{1}{4}(\Gamma 1(-1+\sigma)+2\Gamma 2(-1+\sigma)+4(-6+7\sigma)),\right.$$
$$\left.1-\sigma, 0, \sigma, 1-\sigma, \frac{1}{4}(\Gamma 1-2\Gamma 2(-1+\sigma)+4\sigma-\Gamma 1\sigma), 0, 0\right\}, \left\{0, 2(-1+\sigma)^2, 4\sigma^2, 0,\right.$$
$$-4(-1+\sigma)\sigma, -4(-1+\sigma)\sigma, -12\sigma^2, \frac{1}{4}\sigma(\Gamma 1(-1+\sigma)+2\Gamma 2(-1+\sigma)+4(-6+7\sigma)),$$
$$4\sigma^2, \frac{1}{4}\sigma(\Gamma 1(-1+\sigma)+2\Gamma 2(-1+\sigma)+4(-6+7\sigma)),$$
$$-\frac{1}{2}(-1+\sigma)(-4+\Gamma 1(-1+\sigma)+2\Gamma 2(-1+\sigma)+8\sigma), 0,$$
$$-\frac{1}{4}(\Gamma 1(-1+\sigma)+2\Gamma 2(-1+\sigma)-4\sigma)\sigma, \frac{1}{4}(\Gamma 1(-1+\sigma)+2\Gamma 2(-1+\sigma)-4\sigma)(-1+\sigma),$$
$$\left.-\frac{1}{4}(\Gamma 1(-1+\sigma)+2\Gamma 2(-1+\sigma)-4\sigma)\sigma, \frac{1}{4}(\Gamma 1(-1+\sigma)+2\Gamma 2(-1+\sigma)-4\sigma)(-1+\sigma), 0\right\},$$
$$\left\{0, (-1+\sigma)^2, -\frac{1}{2}(\Gamma 1(-1+\sigma)+2\rho A(-1+\sigma)-8\sigma)\sigma,\right.$$
$$\frac{1}{2}(\Gamma 1(-1+\sigma)+2\rho A(-1+\sigma)-4\sigma)(-1+\sigma), -2(-1+\sigma)\sigma, -2(-1+\sigma)\sigma,$$
$$-12\sigma^2, \sigma^2, \frac{1}{2}\sigma(\Gamma 1(-1+\sigma)+2\rho A(-1+\sigma)+8(-3+4\sigma)), \sigma^2, 0,$$
$$-\frac{1}{2}(-1+\sigma)(-4+\Gamma 1(-1+\sigma)+2\rho A(-1+\sigma)+8\sigma), -(-2+\sigma)\sigma, 0, -(-2+\sigma)\sigma,$$
$$\left.0, (-1+\sigma)^2\right\}, \{0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, -2, 1, 0, 0, 1\},$$
$$\left\{0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, -2\sigma, \frac{1}{4}(\Gamma 1(-1+\sigma)+2\Gamma 2(-1+\sigma)+4\sigma), 0, 0,\right.$$
$$\left.\frac{1}{4}(\Gamma 1-2\Gamma 2(-1+\sigma)+4\sigma-\Gamma 1\sigma)\right\}, \{0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, -2, 1, 1\},$$
$$\left\{0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, -2\sigma, \frac{1}{4}(\Gamma 1(-1+\sigma)+2\Gamma 2(-1+\sigma)+4\sigma),\right.$$
$$\left.\frac{1}{4}(\Gamma 1-2\Gamma 2(-1+\sigma)+4\sigma-\Gamma 1\sigma)\right\}, \{0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0\}\Big\}$$

We can calculate the infinitesimal generator or rate matrix of the slow processes as

```
Gmat = StationaryFast.SlowPartOfTransMat.StationaryFast // Simplify;
% // MatrixForm
```

$\frac{1}{2}(-2-\Gamma1-2\,\rho A-\Gamma1S\,\sigma-2\,\rho\,\sigma)$	0	$\frac{1}{2}(\Gamma1+2\,\rho A+(\Gamma1S+2\,\rho)\,\sigma)$	0	0	0	0
$\frac{1}{2}(-2-\Gamma1-2\,\rho A-\Gamma1S\,\sigma-2\,\rho\,\sigma)$	0	$\frac{1}{2}(\Gamma1+2\,\rho A+(\Gamma1S+2\,\rho)\,\sigma)$	0	0	0	0
1	0	$\frac{1}{4}(-12-\Gamma1-2\,\rho A-\Gamma1S\,\sigma-2\,\rho\,\sigma)$	0	0	0	$\frac{1}{4}(\Gamma1+2\,\rho A+($I
1	0	$\frac{1}{4}(-12-\Gamma1-2\,\rho A-\Gamma1S\,\sigma-2\,\rho\,\sigma)$	0	0	0	$\frac{1}{4}(\Gamma1+2\,\rho A+($I
1	0	$\frac{1}{4}(-12-\Gamma1-2\,\rho A-\Gamma1S\,\sigma-2\,\rho\,\sigma)$	0	0	0	$\frac{1}{4}(\Gamma1+2\,\rho A+($I
1	0	$\frac{1}{4}(-12-\Gamma1-2\,\rho A-\Gamma1S\,\sigma-2\,\rho\,\sigma)$	0	0	0	$\frac{1}{4}(\Gamma1+2\,\rho A+($I
0	0	4	0	0	0	-6
0	0	4	0	0	0	-6
0	0	4	0	0	0	-6
0	0	4	0	0	0	-6
0	0	4	0	0	0	-6
0	0	4	0	0	0	-6
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0

Considering the form of the stationary distribution from the fast part of the matrix and the form of the generator matrix, it is clear that we can simplify the system by ignoring states that move "instantaneously" (on the coalescent time scale) into other states. We retain only States 1, 3, 7, 13, 15, and 17. (We have dropped all the states where there is ancestral material on more than one homolog per individual (i.e., no "paired" samples) because pair samples are split instantaneously by sex on the coalescent time scale if σ >> 1/N.)

For this simplified system, the generator matrix is

```
GmatSimplifiedSystem = Gmat[[{1, 3, 7, 13, 15, 17}, {1, 3, 7, 13, 15, 17}]];
% // MatrixForm
```

$\frac{1}{2}(-2-\Gamma1-2\,\rho A-\Gamma1S\,\sigma-2\,\rho\,\sigma)$	$\frac{1}{2}(\Gamma1+2\,\rho A+(\Gamma1S+2\,\rho)\,\sigma)$	0
1	$\frac{1}{4}(-12-\Gamma1-2\,\rho A-\Gamma1S\,\sigma-2\,\rho\,\sigma)$	$\frac{1}{4}(\Gamma1+2\,\rho A+(\Gamma1S+2\,\rho)\,\sigma$
0	4	-6
0	0	0
0	0	0
0	0	0

The i^{th} element of the vector below gives the rate of leaving state *i*.

```
LeavingRateVec = Simplify[
  Table[Sum[If[j == i, 0, GmatSimplifiedSystem[[i, j]]], {j, 1, 6}], {i, 5}]]
```

$$\left\{\frac{1}{2}(2+\Gamma1+2\,\rho A+\Gamma1S\,\sigma+2\,\rho\,\sigma),\ \frac{1}{4}(12+\Gamma1+2\,\rho A+\Gamma1S\,\sigma+2\,\rho\,\sigma),\ 6,\ 1,\ 1\right\}$$

For this simplified system (and using the results from the section above on single site coalescence),

here are the expected coalescence times for each single site from each state.

```
ExpectedCoalescentTimeForSiteAGivenStateSimplifiedSystem = {1, 1, 1, 0, 1, 0};
ExpectedCoalescentTimeForSiteBGivenStateSimplifiedSystem = {1, 1, 1, 1, 0, 0};

ExpectedValueOfProductOfCoalescentTimesForSitesAandBGivenStateDummyListSimplif
  iedSystem = {EtxtyS1, EtxtyS3, EtxtyS7, 0, 0, 0};
```

Using first-step analysis, the function below gives the expected value of the product of the coalescent times for sites A and B given that they start in a given state (i.e., what we have called the E[*tx*ty*] above).

We use "first-step" analysis (Wakeley 2007, chapters 5 and 7) to calculate the values of E[*tx*ty*] for each state. The function below creates the equations, we need to solve. These equations have the form

$E[t_x\, t_y \mid Z = z] = E[\tau_z^2] + E[\tau_z] \sum_{k \neq z} P_{zk}\, E[t_x \mid Z = k] + E[\tau_z] \sum_{k \neq z} P_{zk}\, E[t_y \mid Z = k] + \sum_{k \neq z} P_{zk}\, E[t_x\, t_y \mid Z = k]$

where τ_z is the time to leave state *z and* P_{zk} is the probability of going from state *z* to state *k* conditional on leaving state z. In discrete time, τ_z follows an exponential distribution with parameter v_i where v_i is the *i*th element of the leaving rate vector.

```
ExpectedValueOfProductOfCoalescentTimesForSitesAandBGivenStateVSimplifiedSystem
  [state_] := 2/LeavingRateVec[[state]]^2 + 1/LeavingRateVec[[state]] Sum[
    If[j == state, 0, (GmatSimplifiedSystem[[state, j]] / LeavingRateVec[[state]])
      ExpectedCoalescentTimeForSiteAGivenStateSimplifiedSystem[[j]]], {j, 5}] +
  1/LeavingRateVec[[state]] Sum[If[j == state, 0,
     (GmatSimplifiedSystem[[state, j]] / LeavingRateVec[[state]])
      ExpectedCoalescentTimeForSiteBGivenStateSimplifiedSystem[[j]]], {j, 5}] +
  Sum[If[j == state, 0, (GmatSimplifiedSystem[[state, j]] /
       LeavingRateVec[[state]])
     ExpectedValueOfProductOfCoalescentTimesForSitesAandBGivenStateDummyListS
       implifiedSystem[[j]]], {j, 5}]
```

We next solve expressions for the E[*tx*ty*]

```
SetOfEquationsForEtxty = Table[Simplify[
    ExpectedValueOfProductOfCoalescentTimesForSitesAandBGivenStateVSimplified\
System[i]] ==
   ExpectedValueOfProductOfCoalescentTimesForSitesAandBGivenStateDummyListSimp\
lifiedSystem[[i]], {i, 3}]

SolnsForEtxty = Solve[SetOfEquationsForEtxty,
   ExpectedValueOfProductOfCoalescentTimesForSitesAandBGivenStateDummyListSimp\
lifiedSystem[[1 ;; 3]]] // FullSimplify
Date[]
```

$$\left\{\frac{4+\text{EtxtyS3}\ (\Gamma 1+2\,\rho A+\Gamma 1S\,\sigma+2\,\rho\,\sigma)}{2+\Gamma 1+2\,\rho A+\Gamma 1S\,\sigma+2\,\rho\,\sigma}==\text{EtxtyS1},\right.$$

$$(8+4\,\text{EtxtyS1}+\text{EtxtyS7}\ (\Gamma 1+2\,\rho A+\Gamma 1S\,\sigma+2\,\rho\,\sigma))\ /\ (12+\Gamma 1+2\,\rho A+\Gamma 1S\,\sigma+2\,\rho\,\sigma)==$$

$$\left.\text{EtxtyS3},\ \frac{1}{3}\ (1+2\,\text{EtxtyS3})==\text{EtxtyS7}\right\}$$

$$\left\{\left\{\text{EtxtyS1}\to 1+(2\ (36+\Gamma 1+2\,\rho A+\Gamma 1S\,\sigma+2\,\rho\,\sigma))\ /\ \left(72+26\,\Gamma 1+\Gamma 1^2+\right.\right.\right.$$

$$\left.52\,\rho A+4\,\Gamma 1\,\rho A+4\,\rho A^2+2\ (\Gamma 1S+2\,\rho)\ (13+\Gamma 1+2\,\rho A)\,\sigma+(\Gamma 1S+2\,\rho)^2\,\sigma^2\right),$$

$$\text{EtxtyS3}\to 1+24\ /\ \left(72+26\,\Gamma 1+\Gamma 1^2+52\,\rho A+4\,\Gamma 1\,\rho A+4\,\rho A^2+\right.$$

$$\left.2\ (\Gamma 1S+2\,\rho)\ (13+\Gamma 1+2\,\rho A)\,\sigma+(\Gamma 1S+2\,\rho)^2\,\sigma^2\right),$$

$$\text{EtxtyS7}\to((4+\Gamma 1+2\,\rho A+\Gamma 1S\,\sigma+2\,\rho\,\sigma)\ (22+\Gamma 1+2\,\rho A+\Gamma 1S\,\sigma+2\,\rho\,\sigma))\ /\ \left(72+\right.$$

$$\left.\left.\left.26\,\Gamma 1+\Gamma 1^2+52\,\rho A+4\,\Gamma 1\,\rho A+4\,\rho A^2+2\ (\Gamma 1S+2\,\rho)\ (13+\Gamma 1+2\,\rho A)\,\sigma+(\Gamma 1S+2\,\rho)^2\,\sigma^2\right)\right\}\right\}$$

```
{2018, 5, 22, 16, 47, 37.158321}

LDmetric = (1 /
      ExpectedValueOfProductOfCoalescentTimesForSitesAandBGivenStateDummyList\
SimplifiedSystem[[3]])
    (ExpectedValueOfProductOfCoalescentTimesForSitesAandBGivenStateDummyListS\
implifiedSystem[[1]] - 2
     ExpectedValueOfProductOfCoalescentTimesForSitesAandBGivenStateDummyLis\
tSimplifiedSystem[[2]] +
      ExpectedValueOfProductOfCoalescentTimesForSitesAandBGivenStateDummyList\
SimplifiedSystem[[3]]) /. SolnsForEtxty[[1]] // Simplify

% /. Γ1 + 2 ρA + Γ1S σ + 2 ρ σ → 2 Ψ // Simplify
```

$$(2\ (20+\Gamma 1+2\,\rho A+\Gamma 1S\,\sigma+2\,\rho\,\sigma))\ /\ ((4+\Gamma 1+2\,\rho A+\Gamma 1S\,\sigma+2\,\rho\,\sigma)\ (22+\Gamma 1+2\,\rho A+\Gamma 1S\,\sigma+2\,\rho\,\sigma))$$

$$\frac{10+\Psi}{22+13\,\Psi+\Psi^2}$$

Continuous time analysis:
When sex is rare at the population level, $n\sigma \sim O(1)$
LD is result is complicated when there is gene conversion but the leading

order term when there is no gene conversion is (for $\Omega = n\sigma$)

$$\left(216 + 990\,\Omega + 1935\,\Omega^2 + 2091\,\Omega^3 + 1268\,\Omega^4 + 380\,\Omega^5 + 40\,\Omega^6\right) / \left(216 + 1206\,\Omega + 2979\,\Omega^2 + 3927\,\Omega^3 + 2684\,\Omega^4 + 836\,\Omega^5 + 88\,\Omega^6\right)$$

Here we assume the rate of sex is very low, $\sigma \sim O(1/n)$. As known from previous single-site models, coalescence is qualitatively different when the rate of sex is this low. To analyze this case, we use the continuous time approximation where we measure time on a coalescent time scale where 1 time unit is $2n$ generations.

We will as assume that as $n \to \infty$,
$n^*\sigma \to \Omega$, $4\,n\,\gamma 1 \to \Gamma_1$, $4\,n\,\gamma 2 \to \Gamma_2$, $4\,n\,\gamma 1S \to \Gamma_{S1}$, 4 n cA $\to \rho$A

We use the method of Mohle (1998, *Advances in Applied Probability* 30: 493-512) as described in Wakeley (2009, chapter 6) to change the discrete time transition matrix into one for the continuous time approximation. This can be applied to a transition matrix that has transitions operating at different time scales. However, under the assumptions used here, all the transitions are slow.

First we redo the single-site coalescence in this framework.

```
SingleSiteTransMatV2 =
 SingleSiteTransMat /. {σ → Ω / n, γ1 → Γ1 / (4 n), γ2 → Γ2 / (4 n)} // Simplify
```

$$\left\{\left\{\frac{-1+n}{n}, -\frac{-8\,n+\Gamma 1+2\,\Gamma 2}{16\,n^2}, \frac{8\,n+\Gamma 1+2\,\Gamma 2}{16\,n^2}\right\},\right.$$
$$\left\{\frac{(-1+n)\,\Omega}{n^2}, \frac{(8\,n-\Gamma 1-2\,\Gamma 2)\left(2\,n^2+\Omega-2\,n\,\Omega\right)}{16\,n^3}, \frac{1}{16\,n^3}\right.$$
$$\left.\left.\left(2\,n^2\,(\Gamma 1+2\,\Gamma 2)-2\,n\,(-4+\Gamma 1+2\,\Gamma 2)\,\Omega+(\Gamma 1+2\,\Gamma 2)\,\Omega\right)\right\}, \{0, 0, 1\}\right\}$$

```
SingleSiteTransMatFastPart = Limit[SingleSiteTransMatV2, n → ∞]
```

```
{{1, 0, 0}, {0, 1, 0}, {0, 0, 1}}
```

Note the result above is just the identity matrix (i.e., there are no fast transitions).

```
SingleSiteTransMatSlowPart =
 Limit[2 n (SingleSiteTransMatV2 - SingleSiteTransMatFastPart), n → ∞]
```

$$\left\{\{-2, 1, 1\}, \left\{2\,\Omega, \frac{1}{4}\,(-\Gamma 1-2\,(\Gamma 2+4\,\Omega)), \frac{1}{4}\,(\Gamma 1+2\,\Gamma 2)\right\}, \{0, 0, 0\}\right\}$$

```
LeavingRateSingleSite = {Plus @@ SingleSiteTransMatSlowPart[[1, 2 ;; 3]],
  SingleSiteTransMatSlowPart[[2, 1]] + SingleSiteTransMatSlowPart[[2, 3]]}
```

$$\left\{2, \frac{1}{4}\,(\Gamma 1+2\,\Gamma 2)+2\,\Omega\right\}$$

```
SingleSiteEqnsV2 = {Etb == 1/LeavingRateSingleSite[[1]] +
      (SingleSiteTransMatSlowPart[[1, 2]] / LeavingRateSingleSite[[1]]) Etw,
    Etw == 1/LeavingRateSingleSite[[2]] +
      (SingleSiteTransMatSlowPart[[2, 1]] / LeavingRateSingleSite[[2]]) Etb};

SingleSiteCoalescentTimesV2 =
 Solve[SingleSiteEqnsV2, {Etb, Etw}][[1]] // Simplify
```

$$\left\{\text{Etb} \to \frac{4+\Gamma 1+2\,\Gamma 2+8\,\Omega}{2\,\Gamma 1+4\,\Gamma 2+8\,\Omega},\ \text{Etw} \to \frac{4\,(1+\Omega)}{\Gamma 1+2\,\Gamma 2+4\,\Omega}\right\}$$

Next we consider the two site model

```
FastPartOfTransMat = Limit[
   (TransMat) /. {σ → Ω / n, γ1 → Γ1 / (4 n), γ2 → Γ2 / (4 n), cA → ρA / (4 n)}, n → ∞]
```

```
{{1, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0},
 {0, 1, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0},
 {0, 0, 1, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0},
 {0, 0, 0, 1, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0},
 {0, 0, 0, 0, 1, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0},
 {0, 0, 0, 0, 0, 1, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0},
 {0, 0, 0, 0, 0, 0, 1, 0, 0, 0, 0, 0, 0, 0, 0, 0},
 {0, 0, 0, 0, 0, 0, 0, 1, 0, 0, 0, 0, 0, 0, 0, 0},
 {0, 0, 0, 0, 0, 0, 0, 0, 1, 0, 0, 0, 0, 0, 0, 0},
 {0, 0, 0, 0, 0, 0, 0, 0, 0, 1, 0, 0, 0, 0, 0, 0},
 {0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 1, 0, 0, 0, 0, 0},
 {0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 1, 0, 0, 0, 0},
 {0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 1, 0, 0, 0},
 {0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 1, 0, 0},
 {0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 1, 0},
 {0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 1}}
```

Note the matrix above is the identity matrix.

```
SlowPartOfTransMat = Limit[2 n (TransMat - FastPartOfTransMat) /.
    {σ → Ω / n, γ1 → Γ1 / (4 n), γ2 → Γ2 / (4 n), cA → ρA / (4 n)}, n → ∞]
```

$$\left\{\left\{-\frac{\Gamma 1}{2}-\rho A-2\,(1+2\,c\,\Omega+\gamma 1S\,\Omega),\ 1,\ 0,\right.\right.$$
$$\left.\frac{\Gamma 1}{2}+\rho A+2\,(2\,c+\gamma 1S)\,\Omega,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 1\right\},$$
$$\left\{\frac{1}{2}\,(-2+2\,c+\gamma 1S)^2\,\Omega,\ \frac{1}{2}\,(-\Gamma 1-\Gamma 2-4\,\Omega),\ 0,\ -\left(4\,c^2+4\,c\,(-1+\gamma 1S)+(-2+\gamma 1S)\,\gamma 1S\right)\Omega,\right.$$
$$\left.0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ \frac{1}{2}\,(2\,c+\gamma 1S)^2\,\Omega,\ 0,\ \frac{\Gamma 1}{4},\ 0,\ \frac{\Gamma 1}{4},\ \frac{\Gamma 2}{2}\right\},$$
$$\left\{1,\ 0,\ -6-\frac{\Gamma 1}{4}-\frac{\rho A}{2}-2\,c\,\Omega-\gamma 1S\,\Omega,\ 1,\ 1,\ 1,\ 0,\ 0,\ \frac{1}{4}\,(\Gamma 1+2\,\rho A+8\,c\,\Omega+4\,\gamma 1S\,\Omega),\right.$$
$$\left.0,\ 0,\ 0,\ 1,\ 0,\ 1,\ 0,\ 0\right\},\ \left\{\frac{1}{4}\,(\Gamma 1+2\,\rho A),\ 0,\ 2\,\Omega,\ -2-\frac{\Gamma 1}{2}-\rho A-2\,\Omega-2\,c\,\Omega-\gamma 1S\,\Omega,\right.$$
$$\left.0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ \frac{1}{4}\,(\Gamma 1+2\,\rho A+8\,c\,\Omega+4\,\gamma 1S\,\Omega),\ 0,\ 1,\ 0,\ 1,\ 0\right\},$$
$$\left\{0,\ 1,\ -(-2+2\,c+\gamma 1S)\,\Omega,\ 0,\ \frac{1}{4}\,(-\Gamma 1-2\,(4+\Gamma 2+4\,\Omega)),\ 0,\ 0,\ 0,\ (2\,c+\gamma 1S)\,\Omega,\right.$$
$$\left.0,\ 0,\ 0,\ \frac{1}{4}\,(\Gamma 1+2\,\Gamma 2),\ 0,\ 0,\ 1,\ 0\right\},\ \left\{0,\ 1,\ -(-2+2\,c+\gamma 1S)\,\Omega,\ 0,\ 0,\right.$$
$$\left.\frac{1}{4}\,(-\Gamma 1-2\,(4+\Gamma 2+4\,\Omega)),\ 0,\ 0,\ (2\,c+\gamma 1S)\,\Omega,\ 0,\ 0,\ 0,\ 0,\ 1,\ \frac{1}{4}\,(\Gamma 1+2\,\Gamma 2),\ 0,\ 0\right\},$$
$$\{0,\ 0,\ 4,\ 0,\ 0,\ 0,\ -12,\ 1,\ 4,\ 1,\ 0,\ 0,\ 1,\ 0,\ 1,\ 0,\ 0\},$$
$$\left\{0,\ 0,\ 0,\ 0,\ 4,\ 0,\ 2\,\Omega,\ -\frac{\Gamma 1}{4}-\frac{\Gamma 2}{2}-2\,(3+\Omega),\ 0,\ 0,\ 1,\ 0,\ \frac{1}{4}\,(\Gamma 1+2\,\Gamma 2),\ 0,\ 0,\ 1,\ 0\right\},$$
$$\left\{0,\ 0,\ \frac{1}{4}\,(\Gamma 1+2\,\rho A),\ 1,\ 1,\ 1,\ 2\,\Omega,\ 0,\ -\frac{\Gamma 1}{4}-\frac{\rho A}{2}-2\,(3+\Omega),\ 0,\ 0,\ 1,\ 1,\ 0,\ 1,\ 0,\ 0\right\},$$
$$\left\{0,\ 0,\ 0,\ 0,\ 0,\ 4,\ 2\,\Omega,\ 0,\ 0,\ -\frac{\Gamma 1}{4}-\frac{\Gamma 2}{2}-2\,(3+\Omega),\ 1,\ 0,\ 0,\ 1,\ \frac{1}{4}\,(\Gamma 1+2\,\Gamma 2),\ 0,\ 0\right\},$$
$$\left\{0,\ 2,\ 0,\ 0,\ 0,\ 0,\ 0,\ 2\,\Omega,\ 0,\ 2\,\Omega,\ -2-\frac{\Gamma 1}{2}-\Gamma 2-4\,\Omega,\ 0,\ 0,\ \frac{1}{4}\,(\Gamma 1+2\,\Gamma 2),\ 0,\ \frac{1}{4}\,(\Gamma 1+2\,\Gamma 2),\right.$$
$$\left.0\right\},\ \left\{0,\ 1,\ 0,\ \frac{\Gamma 1}{2}+\rho A,\ 0,\ 0,\ 0,\ 0,\ 4\,\Omega,\ 0,\ 0,\ -2-\frac{\Gamma 1}{2}-\rho A-4\,\Omega,\ 0,\ 0,\ 0,\ 0,\ 1\right\},$$
$$\{0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ -2,\ 1,\ 0,\ 0,\ 1\},$$
$$\left\{0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 2\,\Omega,\ \frac{1}{4}\,(-\Gamma 1-2\,(\Gamma 2+4\,\Omega)),\ 0,\ 0,\ \frac{1}{4}\,(\Gamma 1+2\,\Gamma 2)\right\},$$
$$\{0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ -2,\ 1,\ 1\},$$
$$\left\{0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 2\,\Omega,\ \frac{1}{4}\,(-\Gamma 1-2\,(\Gamma 2+4\,\Omega)),\ \frac{1}{4}\,(\Gamma 1+2\,\Gamma 2)\right\},$$
$$\{0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0,\ 0\}\Big\}$$

The i^{th} element of the vector below gives the rate of leaving state *i*.

```
LeavingRateVec = Simplify[
  Table[Sum[If[j == i, 0, SlowPartOfTransMat[[i, j]]], {j, 1, 17}], {i, 16}]]
```

$$\left\{2+\frac{\Gamma 1}{2}+\rho A+4\,c\,\Omega+2\,\gamma 1S\,\Omega,\ \frac{1}{2}(\Gamma 1+\Gamma 2+4\,\Omega),\ \frac{1}{4}(24+\Gamma 1+2\,\rho A+8\,c\,\Omega+4\,\gamma 1S\,\Omega),\right.$$
$$2+\frac{\Gamma 1}{2}+\rho A+2\,\Omega+2\,c\,\Omega+\gamma 1S\,\Omega,\ \frac{1}{4}(8+\Gamma 1+2\,\Gamma 2+8\,\Omega),\ \frac{1}{4}(8+\Gamma 1+2\,\Gamma 2+8\,\Omega),$$
$$12,\ \frac{1}{4}(24+\Gamma 1+2\,\Gamma 2+8\,\Omega),\ \frac{1}{4}(24+\Gamma 1+2\,\rho A+8\,\Omega),\ \frac{1}{4}(24+\Gamma 1+2\,\Gamma 2+8\,\Omega),$$
$$\left.2+\frac{\Gamma 1}{2}+\Gamma 2+4\,\Omega,\ 2+\frac{\Gamma 1}{2}+\rho A+4\,\Omega,\ 2,\ \frac{1}{4}(\Gamma 1+2\,\Gamma 2+8\,\Omega),\ 2,\ \frac{1}{4}(\Gamma 1+2\,\Gamma 2+8\,\Omega)\right\}$$

Using first-step analysis, the function below gives the expected value of the product of the coalescent times for sites A and B given that they start in a given state (i.e., what we have called the E[*tx*ty*] above).

We use "first-step" analysis (Wakeley 2007, chapters 5 and 7) to calculate the values of E[*tx*ty*] for each state. The function below creates the equations, we need to solve. These equations have the form

$E\left[t_x\,t_y \mid Z=z\right] = E\left[\tau_z^2\right] + E[\tau_z]\sum_{k\neq z}P_{zk}\,E[t_x \mid Z=k] + E[\tau_z]\sum_{k\neq z}P_{zk}\,E\left[t_y \mid Z=k\right] + \sum_{k\neq z}P_{zk}\,E\left[t_x\,t_y \mid Z=k\right]$

where τ_z is the time to leave state *z and* P_{zk} is the probability of going from state *z* to state *k* conditional on leaving state z. In discrete time, τ_z follows an exponential distribution with parameter v_i where v_i is the *i*th element of the leaving rate vector.

```
ExpectedValueOfProductOfCoalescentTimesForSitesAandBGivenStateV2[state_] :=
  2/LeavingRateVec[[state]]^2 + 1/LeavingRateVec[[state]] Sum[
     If[j == state, 0, (SlowPartOfTransMat[[state, j]] / LeavingRateVec[[state]])
       ExpectedCoalescentTimeForSiteAGivenState[[j]]], {j, 16}] +
   1/LeavingRateVec[[state]] Sum[If[j == state, 0,
     (SlowPartOfTransMat[[state, j]] / LeavingRateVec[[state]])
      ExpectedCoalescentTimeForSiteBGivenState[[j]]], {j, 16}] +
  Sum[If[j == state, 0, (SlowPartOfTransMat[[state, j]] / LeavingRateVec[[state]])
     ExpectedValueOfProductOfCoalescentTimesForSitesAandBGivenStateDummyList[[
      j]]], {j, 16}]
```

We next solve expressions for the E[*tx*ty*]

```
SetOfEquationsForEtxty = Table[
   Simplify[ExpectedValueOfProductOfCoalescentTimesForSitesAandBGivenStateV2[
       i] /. SingleSiteCoalescentTimesV2] ==
    ExpectedValueOfProductOfCoalescentTimesForSitesAandBGivenStateDummyList[[
     i]], {i, 12}];

SolnsForEtxty = Solve[SetOfEquationsForEtxty,
   ExpectedValueOfProductOfCoalescentTimesForSitesAandBGivenStateDummyList[[
    1 ;; 12]]];
Date[]
```

```
{2018, 3, 23, 13, 24, 57.439799}
```

```
LDmetric =
  (1 / ExpectedValueOfProductOfCoalescentTimesForSitesAandBGivenStateDummyList[[
       7]])
    (ExpectedValueOfProductOfCoalescentTimesForSitesAandBGivenStateDummyList[[
       1]] - 2
       ExpectedValueOfProductOfCoalescentTimesForSitesAandBGivenStateDummyList
        [[3]] +
      ExpectedValueOfProductOfCoalescentTimesForSitesAandBGivenStateDummyList[
       [7]]) /. SolnsForEtxty[[1]];
```

Below we assume no mitotic gene conversion or mitotic crossing over and then obtain an approximate solution to leading order in c and $\gamma 1S$.

```
LDmetricOnlyMeioticDisruptionNoMitotic = Normal[
   Series[LDmetric /. {Γ1 → 0, Γ2 → 0, ρA → 0, c → c ξ, γ1S → γ1S ξ}, {ξ, 0, 1}]];
Collect[%, ξ, Simplify] /. ξ → 1
```

$$\left(216 + 990\,\Omega + 1935\,\Omega^2 + 2091\,\Omega^3 + 1268\,\Omega^4 + 380\,\Omega^5 + 40\,\Omega^6\right) \Big/ \left(216 + 1206\,\Omega + 2979\,\Omega^2 + 3927\,\Omega^3 + 2684\,\Omega^4 + 836\,\Omega^5 + 88\,\Omega^6\right) - \left(4\,(2\,c + \gamma 1S)\,\Omega\left(104\,976 + 1\,211\,112\,\Omega + 6\,466\,068\,\Omega^2 + 21\,128\,958\,\Omega^3 + 47\,076\,534\,\Omega^4 + 75\,433\,482\,\Omega^5 + 89\,388\,390\,\Omega^6 + 79\,350\,143\,\Omega^7 + 52\,856\,023\,\Omega^8 + 26\,191\,784\,\Omega^9 + 9\,461\,280\,\Omega^{10} + 2\,402\,944\,\Omega^{11} + 403\,152\,\Omega^{12} + 39\,744\,\Omega^{13} + 1728\,\Omega^{14}\right)\right) \Big/ \left(\left(3 + 6\,\Omega + 2\,\Omega^2\right)\left(216 + 1206\,\Omega + 2979\,\Omega^2 + 3927\,\Omega^3 + 2684\,\Omega^4 + 836\,\Omega^5 + 88\,\Omega^6\right)^2\right)$$

This can also be written as follows, if sex is scaled by 2N instead (i.e. $\Omega = 2N\sigma$):

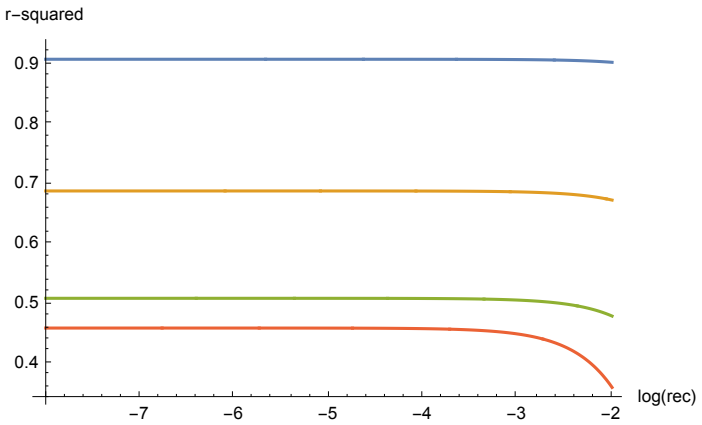
```
LDmetricOnlyMeioticDisruptionNoMitoticV2 =
 (216 + 990 Ω + 1935 Ω^2 + 2091 Ω^3 + 1268 Ω^4 + 380 Ω^5 + 40 Ω^6) /
     (216 + 1206 Ω + 2979 Ω^2 + 3927 Ω^3 + 2684 Ω^4 + 836 Ω^5 + 88 Ω^6) -
    (4 (2 c + γ1S) Ω (104 976 + 1 211 112 Ω + 6 466 068 Ω^2 + 21 128 958 Ω^3 + 47 076 534 Ω^4 +
          75 433 482 Ω^5 + 89 388 390 Ω^6 + 79 350 143 Ω^7 + 52 856 023 Ω^8 + 26 191 784 Ω^9 +
          9 461 280 Ω^10 + 2 402 944 Ω^11 + 403 152 Ω^12 + 39 744 Ω^13 + 1728 Ω^14)) /
     ((3 + 6 Ω + 2 Ω^2) (216 + 1206 Ω + 2979 Ω^2 + 3927 Ω^3 + 2684 Ω^4 + 836 Ω^5 + 88 Ω^6)^2) /. {Ω → Ω/2}
```

$$\left(216+495\,\Omega+\frac{1935\,\Omega^2}{4}+\frac{2091\,\Omega^3}{8}+\frac{317\,\Omega^4}{4}+\frac{95\,\Omega^5}{8}+\frac{5\,\Omega^6}{8}\right)\Big/\left(216+603\,\Omega+\frac{2979\,\Omega^2}{4}+\frac{3927\,\Omega^3}{8}+\frac{671\,\Omega^4}{4}+\frac{209\,\Omega^5}{8}+\frac{11\,\Omega^6}{8}\right)-\left(2\,(2\,c+\gamma 1S)\,\Omega\left(104\,976+605\,556\,\Omega+1\,616\,517\,\Omega^2+\frac{10\,564\,479\,\Omega^3}{4}+\frac{23\,538\,267\,\Omega^4}{8}+\frac{37\,716\,741\,\Omega^5}{16}+\frac{44\,694\,195\,\Omega^6}{32}+\frac{79\,350\,143\,\Omega^7}{128}+\frac{52\,856\,023\,\Omega^8}{256}+\frac{3\,273\,973\,\Omega^9}{64}+\frac{295\,665\,\Omega^{10}}{32}+\frac{18\,773\,\Omega^{11}}{16}+\frac{25\,197\,\Omega^{12}}{256}+\frac{621\,\Omega^{13}}{128}+\frac{27\,\Omega^{14}}{256}\right)\right)\Big/\left(\left(3+3\,\Omega+\frac{\Omega^2}{2}\right)\left(216+603\,\Omega+\frac{2979\,\Omega^2}{4}+\frac{3927\,\Omega^3}{8}+\frac{671\,\Omega^4}{4}+\frac{209\,\Omega^5}{8}+\frac{11\,\Omega^6}{8}\right)^2\right)$$

```
(216 + 495 Ω + 1935 Ω^2/4 + 2091 Ω^3/8 + 317 Ω^4/4 + 95 Ω^5/8 + 5 Ω^6/8) /
   (216 + 603 Ω + 2979 Ω^2/4 + 3927 Ω^3/8 + 671 Ω^4/4 + 209 Ω^5/8 + 11 Ω^6/8) // Simplify
(1728 + 3960 Ω + 3870 Ω^2 + 2091 Ω^3 + 634 Ω^4 + 95 Ω^5 + 5 Ω^6) /
 (1728 + 4824 Ω + 5958 Ω^2 + 3927 Ω^3 + 1342 Ω^4 + 209 Ω^5 + 11 Ω^6)

(1728 + 3960 Ω + 3870 Ω^2 + 2091 Ω^3 + 634 Ω^4 + 95 Ω^5 + 5 Ω^6) /
    (1728 + 4824 Ω + 5958 Ω^2 + 3927 Ω^3 + 1342 Ω^4 + 209 Ω^5 + 11 Ω^6) -
   {(216 + 495 Ω + 1935 Ω^2/4 + 2091 Ω^3/8 + 317 Ω^4/4 + 95 Ω^5/8 + 5 Ω^6/8) /
      (216 + 603 Ω + 2979 Ω^2/4 + 3927 Ω^3/8 + 671 Ω^4/4 + 209 Ω^5/8 + 11 Ω^6/8)} // Simplify
{0}
```

Note the following results in this section use $\Omega = n\sigma$.

```
LDmetricOnlyMeioticDisruptionNoMitoticVb =
  Normal[LDmetricOnlyMeioticDisruptionNoMitotic] /. ξ → 1 /. γ1S → 0;
Plot[{LDmetricOnlyMeioticDisruptionNoMitoticVb /. c → 10^x /. γ1S → 0 /. Ω → 0.1,
  LDmetricOnlyMeioticDisruptionNoMitoticVb /. c → 10^x /. γ1S → 0 /. Ω → 0.5,
  LDmetricOnlyMeioticDisruptionNoMitoticVb /. c → 10^x /. γ1S → 0 /. Ω → 2,
  LDmetricOnlyMeioticDisruptionNoMitoticVb /. c → 10^x /. γ1S → 0 /. Ω → 10},
 {x, -8, -2}, AxesLabel → {"log(rec)", "r-squared"}]
```



Next we examine the case where we assume no meiotic crossing over and no meiotic gene conversion.

```
LDmetricNoMeioticGCandNoMeioticCO = LDmetric /. {c → 0, γ1S → 0} // Simplify
```

$$
\begin{aligned}
&\left(\Gamma 1^8\ (10+\Omega) + \Gamma 1^7\left(540+448\,\Omega+39\,\Omega^2+9\,\Gamma 2\ (10+\Omega)+6\,\rho A\ (10+\Omega)\right)+\right.\\
&\quad 2\,\Gamma 1^6\left(5240+9368\,\Omega+4108\,\Omega^2+314\,\Omega^3+16\,\Gamma 2^2\ (10+\Omega)+6\,\rho A^2\ (10+\Omega)+\right.\\
&\qquad \rho A\left(1440+1206\,\Omega+107\,\Omega^2\right)+\Gamma 2\left(2070+1731\,\Omega+149\,\Omega^2+27\,\rho A\ (10+\Omega)\right)\Big)+\\
&\quad 4\,\Gamma 1^5\left(14\,\Gamma 2^3\ (10+\Omega)+2\,\rho A^3\ (10+\Omega)+\rho A^2\left(1260+1068\,\Omega+97\,\Omega^2\right)+\right.\\
&\qquad 2\,\rho A\left(5840+10\,848\,\Omega+4885\,\Omega^2+390\,\Omega^3\right)+\\
&\qquad 4\left(5976+18\,264\,\Omega+16\,667\,\Omega^2+5058\,\Omega^3+338\,\Omega^4\right)+\\
&\qquad \Gamma 2^2\left(3060+2574\,\Omega+218\,\Omega^2+48\,\rho A\ (10+\Omega)\right)+\Gamma 2\left(27\,\rho A^2\ (10+\Omega)+\right.\\
&\qquad\quad \left.\left.6\,\rho A\left(900+762\,\Omega+67\,\Omega^2\right)+2\left(8590+15\,258\,\Omega+6673\,\Omega^2+496\,\Omega^3\right)\right)\Big)+\\
&\quad 8\,\Gamma 1^4\left(6\,\Gamma 2^4\ (10+\Omega)+\rho A^3\left(360+310\,\Omega+29\,\Omega^2\right)+2\,\rho A^2\left(4020+8002\,\Omega+3726\,\Omega^2+313\,\Omega^3\right)+\right.\\
&\qquad 4\,\rho A\left(10\,512+34\,126\,\Omega+32\,784\,\Omega^2+10\,413\,\Omega^3+750\,\Omega^4\right)+\\
&\qquad 16\left(3584+16\,929\,\Omega+26\,097\,\Omega^2+16\,005\,\Omega^3+3699\,\Omega^4+212\,\Omega^5\right)+\\
&\qquad 2\,\Gamma 2^3\left(1080+908\,\Omega+75\,\Omega^2+21\,\rho A\ (10+\Omega)\right)+2\,\Gamma 2^2\\
&\qquad\quad \left(10\,530+18\,543\,\Omega+8030\,\Omega^2+572\,\Omega^3+24\,\rho A^2\ (10+\Omega)+\rho A\left(3870+3309\,\Omega+287\,\Omega^2\right)\right)+\\
&\qquad \Gamma 2\left(9\,\rho A^3\ (10+\Omega)+\rho A^2\left(4590+3951\,\Omega+357\,\Omega^2\right)+\rho A\left(36\,600+67\,450\,\Omega+\right.\right.\\
&\qquad\quad \left.\left.\left.30\,448\,\Omega^2+2380\,\Omega^3\right)+4\left(16\,604+49\,973\,\Omega+44\,947\,\Omega^2+13\,433\,\Omega^3+852\,\Omega^4\right)\right)\Big)+\\
&\quad 16\,\Gamma 1^3\left(\Gamma 2^5\ (10+\Omega)+\Gamma 2^4\left(720+594\,\Omega+47\,\Omega^2+18\,\rho A\ (10+\Omega)\right)+2\,\Gamma 2^3\right.\\
&\qquad \left(5870+10\,227\,\Omega+4316\,\Omega^2+286\,\Omega^3+21\,\rho A^2\ (10+\Omega)+\rho A\left(2610+2241\,\Omega+190\,\Omega^2\right)\right)+\\
&\qquad 2\,\Gamma 2^2\left(32\,848+97\,338\,\Omega+85\,842\,\Omega^2+24\,914\,\Omega^3+1448\,\Omega^4+8\,\rho A^3\ (10+\Omega)+\right.\\
&\qquad\quad \left.\rho A^2\left(3150+2757\,\Omega+247\,\Omega^2\right)+\rho A\left(21\,100+38\,348\,\Omega+17\,249\,\Omega^2+1304\,\Omega^3\right)\right)+\\
&\qquad 2\,\Gamma 2\left(\rho A^3\left(630+555\,\Omega+52\,\Omega^2\right)+\rho A^2\left(11\,730+23\,287\,\Omega+10\,960\,\Omega^2+910\,\Omega^3\right)+\right.\\
&\qquad\quad \left.2\,\rho A\left(27\,204+86\,473\,\Omega+81\,781\,\Omega^2+25\,758\,\Omega^3+1788\,\Omega^4\right)+\right.
\end{aligned}
$$

$$
\begin{aligned}
&4\left(16\,904+76\,601\,\Omega+115\,100\,\Omega^2+68\,883\,\Omega^3+15\,430\,\Omega^4+808\,\Omega^5\right)\Big)+\\
&2\left(\rho A^3\left(800+1838\,\Omega+895\,\Omega^2+80\,\Omega^3\right)+2\,\rho A^2\left(5076+18\,614\,\Omega+19\,552\,\Omega^2+6589\,\Omega^3+\right.\right.\\
&\left.\left.516\,\Omega^4\right)+4\,\rho A\left(9112+47\,754\,\Omega+79\,118\,\Omega^2+51\,743\,\Omega^3+12\,786\,\Omega^4+824\,\Omega^5\right)+\right.\\
&\left.8\left(5724+35\,802\,\Omega+80\,877\,\Omega^2+81\,328\,\Omega^3+36\,912\,\Omega^4+6744\,\Omega^5+320\,\Omega^6\right)\right)\Big)+\\
&32\,\Gamma1^2\left(\Gamma2^5\left(90+69\,\Omega+5\,\Omega^2+3\,\rho A\,(10+\Omega)\right)+\right.\\
&\Gamma2^4\left(18\,\rho A^2\,(10+\Omega)+3\,\rho A\left(540+456\,\Omega+37\,\Omega^2\right)+2\left(1410+2437\,\Omega+964\,\Omega^2+55\,\Omega^3\right)\right)+\\
&2\,\Gamma2^3\left(13\,692+39\,716\,\Omega+34\,054\,\Omega^2+9322\,\Omega^3+456\,\Omega^4+7\,\rho A^3\,(10+\Omega)+\right.\\
&\left.\rho A^2\left(1980+1758\,\Omega+155\,\Omega^2\right)+\rho A\left(10\,760+19\,092\,\Omega+8425\,\Omega^2+600\,\Omega^3\right)\right)+\\
&2\,\Gamma2^2\left(\rho A^3\left(810+735\,\Omega+69\,\Omega^2\right)+3\,\rho A^2\left(4070+7977\,\Omega+3784\,\Omega^2+308\,\Omega^3\right)+\right.\\
&2\,\rho A\left(24\,144+75\,147\,\Omega+69\,382\,\Omega^2+21\,386\,\Omega^3+1392\,\Omega^4\right)+\\
&\left.4\left(12\,988+56\,896\,\Omega+83\,269\,\Omega^2+48\,210\,\Omega^3+10\,208\,\Omega^4+448\,\Omega^5\right)\right)+\\
&2\,\Gamma2\left(\rho A^3\left(2020+4820\,\Omega+2409\,\Omega^2+216\,\Omega^3\right)+\right.\\
&\rho A^2\left(23\,412+83\,454\,\Omega+86\,684\,\Omega^2+29\,326\,\Omega^3+2256\,\Omega^4\right)+\\
&4\,\rho A\left(19\,568+96\,319\,\Omega+154\,117\,\Omega^2+98\,103\,\Omega^3+23\,698\,\Omega^4+1440\,\Omega^5\right)+\\
&\left.8\left(11\,170+65\,212\,\Omega+140\,257\,\Omega^2+136\,055\,\Omega^3+59\,544\,\Omega^4+10\,316\,\Omega^5+416\,\Omega^6\right)\right)+\\
&4\left(\rho A^3\left(480+2582\,\Omega+3295\,\Omega^2+1206\,\Omega^3+104\,\Omega^4\right)+\right.\\
&2\,\rho A^2\left(2484+16\,702\,\Omega+32\,104\,\Omega^2+23\,505\,\Omega^3+6354\,\Omega^4+464\,\Omega^5\right)+4\,\rho A\\
&\left(5136+35\,588\,\Omega+87\,869\,\Omega^2+95\,227\,\Omega^3+46\,548\,\Omega^4+9308\,\Omega^5+528\,\Omega^6\right)+8\left(5004+\right.\\
&\left.\left.30\,374\,\Omega+79\,612\,\Omega^2+107\,869\,\Omega^3+76\,336\,\Omega^4+26\,556\,\Omega^5+3872\,\Omega^6+144\,\Omega^7\right)\right)\Big)+\\
&64\,\Gamma1\left(\Gamma2^5\left(200+358\,\Omega+118\,\Omega^2+4\,\Omega^3+3\,\rho A^2\,(10+\Omega)+2\,\rho A\left(90+69\,\Omega+5\,\Omega^2\right)\right)+\right.\\
&\Gamma2^4\left(6\,\rho A^3\,(10+\Omega)+9\,\rho A^2\left(120+106\,\Omega+9\,\Omega^2\right)+4\,\rho A\left(1110+1900\,\Omega+787\,\Omega^2+49\,\Omega^3\right)+\right.\\
&\left.4\left(1080+2983\,\Omega+2456\,\Omega^2+593\,\Omega^3+18\,\Omega^4\right)\right)+\\
&2\,\Gamma2^3\left(5\,\rho A^3\left(90+85\,\Omega+8\,\Omega^2\right)+\rho A^2\left(5310+10\,009\,\Omega+4728\,\Omega^2+370\,\Omega^3\right)+\right.\\
&2\,\rho A\left(8352+25\,273\,\Omega+22\,421\,\Omega^2+6550\,\Omega^3+372\,\Omega^4\right)+\\
&\left.4\left(3594+15\,268\,\Omega+21\,626\,\Omega^2+11\,953\,\Omega^3+2278\,\Omega^4+64\,\Omega^5\right)\right)+\\
&2\,\Gamma2^2\left(\rho A^3\left(1640+4126\,\Omega+2133\,\Omega^2+192\,\Omega^3\right)+\right.\\
&2\,\rho A^2\left(8556+29\,718\,\Omega+30\,164\,\Omega^2+10\,159\,\Omega^3+756\,\Omega^4\right)+\\
&4\,\rho A\left(12\,484+58\,508\,\Omega+90\,329\,\Omega^2+55\,215\,\Omega^3+12\,690\,\Omega^4+680\,\Omega^5\right)+\\
&\left.8\left(5860+33\,133\,\Omega+68\,787\,\Omega^2+64\,303\,\Omega^3+26\,766\,\Omega^4+4204\,\Omega^5+112\,\Omega^6\right)\right)+\\
&8\,\Gamma2\left(\rho A^3\left(418+2231\,\Omega+2939\,\Omega^2+1106\,\Omega^3+96\,\Omega^4\right)+\right.\\
&\rho A^2\left(4626+27\,599\,\Omega+50\,474\,\Omega^2+36\,108\,\Omega^3+9724\,\Omega^4+696\,\Omega^5\right)+\\
&2\,\rho A\left(8860+54\,431\,\Omega+124\,443\,\Omega^2+128\,338\,\Omega^3+60\,168\,\Omega^4+11\,520\,\Omega^5+592\,\Omega^6\right)+\\
&4\left(6438+38\,521\,\Omega+97\,079\,\Omega^2+125\,749\,\Omega^3+85\,148\,\Omega^4+28\,104\,\Omega^5+\right.\\
&\left.\left.3736\,\Omega^6+96\,\Omega^7\right)\right)+8\left(\rho A^3\,\Omega\left(826+2673\,\Omega+2522\,\Omega^2+772\,\Omega^3+64\,\Omega^4\right)+\right.\\
&2\,\rho A^2\left(720+6630\,\Omega+20\,391\,\Omega^2+25\,939\,\Omega^3+14\,514\,\Omega^4+3292\,\Omega^5+224\,\Omega^6\right)+4\,\rho A\\
&\left(3744+21\,686\,\Omega+58\,143\,\Omega^2+83\,393\,\Omega^3+63\,204\,\Omega^4+23\,848\,\Omega^5+3912\,\Omega^6+192\,\Omega^7\right)+\\
&\left.8\left(3888+22\,938\,\Omega+60\,311\,\Omega^2+90\,608\,\Omega^3+81\,144\,\Omega^4+\right.\right.\\
&\left.\left.41\,720\,\Omega^5+11\,200\,\Omega^6+1280\,\Omega^7+32\,\Omega^8\right)\right)\Big)+\\
&128\left(\Gamma2^5\left(\rho A^3\,(10+\Omega)+\rho A^2\left(90+69\,\Omega+5\,\Omega^2\right)+2\,\rho A\left(100+179\,\Omega+59\,\Omega^2+2\,\Omega^3\right)+\right.\right.\\
&\left.4\left(30+85\,\Omega+70\,\Omega^2+14\,\Omega^3\right)\right)+\\
&\Gamma2^4\left(\rho A^3\left(180+180\,\Omega+17\,\Omega^2\right)+2\,\rho A^2\left(810+1363\,\Omega+610\,\Omega^2+43\,\Omega^3\right)+\right.\\
&\left.4\,\rho A\left(900+2473\,\Omega+2036\,\Omega^2+509\,\Omega^3+18\,\Omega^4\right)+\right.
\end{aligned}
$$

$$
\begin{aligned}
&8\left(270+1047\,\Omega+1403\,\Omega^2+736\,\Omega^3+118\,\Omega^4\right)\Big)+\\
&2\,\Gamma 2^3\left(\rho A^3\left(420+1144\,\Omega+619\,\Omega^2+56\,\Omega^3\right)+2\,\rho A^2\left(1926+6605\,\Omega+6374\,\Omega^2+2085\,\Omega^3+\right.\right.\\
&\quad\left.144\,\Omega^4\right)+4\,\rho A\left(2244+10\,147\,\Omega+14\,910\,\Omega^2+8495\,\Omega^3+1730\,\Omega^4+64\,\Omega^5\right)+\\
&\quad\left.8\left(738+4209\,\Omega+8533\,\Omega^2+7632\,\Omega^3+2970\,\Omega^4+392\,\Omega^5\right)\right)+\\
&4\,\Gamma 2^2\left(\rho A^3\left(356+1880\,\Omega+2583\,\Omega^2+1006\,\Omega^3+88\,\Omega^4\right)+\right.\\
&\quad\rho A^2\left(3852+21\,386\,\Omega+37\,580\,\Omega^2+25\,926\,\Omega^3+6836\,\Omega^4+464\,\Omega^5\right)+\\
&\quad4\,\rho A\left(3076+17\,907\,\Omega+38\,764\,\Omega^2+37\,981\,\Omega^3+16\,692\,\Omega^4+2892\,\Omega^5+112\,\Omega^6\right)+\\
&\quad\left.8\left(1506+9409\,\Omega+23\,541\,\Omega^2+29\,482\,\Omega^3+18\,966\,\Omega^4+5788\,\Omega^5+640\,\Omega^6\right)\right)+\\
&8\,\Gamma 2\left(\rho A^3\left(72+894\,\Omega+2533\,\Omega^2+2402\,\Omega^3+756\,\Omega^4+64\,\Omega^5\right)+\right.\\
&\quad2\,\rho A^2\left(1044+7044\,\Omega+18\,633\,\Omega^2+22\,031\,\Omega^3+11\,862\,\Omega^4+2652\,\Omega^5+176\,\Omega^6\right)+4\,\rho A\\
&\quad\left(3240+18\,156\,\Omega+45\,739\,\Omega^2+61\,491\,\Omega^3+44\,048\,\Omega^4+15\,672\,\Omega^5+2376\,\Omega^6+96\,\Omega^7\right)+\\
&\quad8\left(2268+13\,680\,\Omega+36\,075\,\Omega^2+53\,072\,\Omega^3+45\,642\,\Omega^4+22\,180\,\Omega^5+5464\,\Omega^6+\right.\\
&\quad\left.\left.512\,\Omega^7\right)\right)+32\left(\rho A^3\,\Omega\left(18+221\,\Omega+491\,\Omega^2+372\,\Omega^3+100\,\Omega^4+8\,\Omega^5\right)+\right.\\
&\quad2\,\rho A^2\left(216+1134\,\Omega+3165\,\Omega^2+5150\,\Omega^3+4501\,\Omega^4+1968\,\Omega^5+380\,\Omega^6+24\,\Omega^7\right)+\\
&\quad4\,\rho A\left(864+4842\,\Omega+12\,343\,\Omega^2+18\,682\,\Omega^3+17\,473\,\Omega^4+9622\,\Omega^5+\right.\\
&\quad2844\,\Omega^6+384\,\Omega^7+16\,\Omega^8\Big)+8\left(648+4266\,\Omega+12\,177\,\Omega^2+\right.\\
&\quad\left.\left.\left.19\,863\,\Omega^3+20\,220\,\Omega^4+12\,930\,\Omega^5+4936\,\Omega^6+1000\,\Omega^7+80\,\Omega^8\right)\right)\right)\Big/\\
&\left(\Gamma 1^8\left(22+13\,\Omega+\Omega^2\right)+\Gamma 1^7\left(1332+1744\,\Omega+591\,\Omega^2+40\,\Omega^3+9\,\Gamma 2\left(22+13\,\Omega+\Omega^2\right)+\right.\right.\\
&\quad\left.6\,\rho A\left(22+13\,\Omega+\Omega^2\right)\right)+\\
&2\,\Gamma 1^6\left(15\,560+34\,048\,\Omega+23\,140\,\Omega^2+5522\,\Omega^3+328\,\Omega^4+16\,\Gamma 2^2\left(22+13\,\Omega+\Omega^2\right)+\right.\\
&\quad6\,\rho A^2\left(22+13\,\Omega+\Omega^2\right)+\rho A\left(3600+4822\,\Omega+1677\,\Omega^2+116\,\Omega^3\right)+\\
&\quad\left.\Gamma 2\left(5058+6551\,\Omega+2190\,\Omega^2+146\,\Omega^3+27\,\rho A\left(22+13\,\Omega+\Omega^2\right)\right)\right)+\\
&4\,\Gamma 1^5\left(14\,\Gamma 2^3\left(22+13\,\Omega+\Omega^2\right)+2\,\rho A^3\left(22+13\,\Omega+\Omega^2\right)+\right.\\
&\quad\rho A^2\left(3204+4412\,\Omega+1581\,\Omega^2+112\,\Omega^3\right)+\\
&\quad2\,\rho A\left(18\,248+41\,676\,\Omega+29\,467\,\Omega^2+7338\,\Omega^3+456\,\Omega^4\right)+\\
&\quad4\left(23\,472+75\,352\,\Omega+82\,349\,\Omega^2+37\,466\,\Omega^3+6830\,\Omega^4+352\,\Omega^5\right)+\\
&\quad2\,\Gamma 2^2\left(3690+4697\,\Omega+1536\,\Omega^2+100\,\Omega^3+24\,\rho A\left(22+13\,\Omega+\Omega^2\right)\right)+\\
&\quad\Gamma 2\left(27\,\rho A^2\left(22+13\,\Omega+\Omega^2\right)+6\,\rho A\left(2232+2968\,\Omega+1023\,\Omega^2+70\,\Omega^3\right)+\right.\\
&\quad\left.\left.4\left(12\,275+26\,266\,\Omega+17\,457\,\Omega^2+4056\,\Omega^3+232\,\Omega^4\right)\right)\right)+\\
&8\,\Gamma 1^4\left(6\,\Gamma 2^4\left(22+13\,\Omega+\Omega^2\right)+\rho A^3\left(936+1334\,\Omega+495\,\Omega^2+36\,\Omega^3\right)+\right.\\
&\quad2\,\rho A^2\left(13\,596+33\,046\,\Omega+24\,554\,\Omega^2+6429\,\Omega^3+420\,\Omega^4\right)+\\
&\quad4\,\rho A\left(46\,584+157\,102\,\Omega+180\,536\,\Omega^2+86\,569\,\Omega^3+16\,746\,\Omega^4+928\,\Omega^5\right)+\\
&\quad16\left(20\,420+88\,111\,\Omega+138\,502\,\Omega^2+99\,013\,\Omega^3+33\,219\,\Omega^4+4784\,\Omega^5+208\,\Omega^6\right)+\\
&\quad2\,\Gamma 2^3\left(2556+3158\,\Omega+993\,\Omega^2+62\,\Omega^3+21\,\rho A\left(22+13\,\Omega+\Omega^2\right)\right)+\\
&\quad2\,\Gamma 2^2\left(28\,746+59\,617\,\Omega+38\,249\,\Omega^2+8496\,\Omega^3+456\,\Omega^4+\right.\\
&\quad\left.24\,\rho A^2\left(22+13\,\Omega+\Omega^2\right)+\rho A\left(9486+12\,451\,\Omega+4224\,\Omega^2+284\,\Omega^3\right)\right)+\\
&\quad\Gamma 2\left(9\,\rho A^3\left(22+13\,\Omega+\Omega^2\right)+3\,\rho A^2\left(3870+5321\,\Omega+1902\,\Omega^2+134\,\Omega^3\right)+\right.\\
&\quad2\,\rho A\left(54\,948+123\,017\,\Omega+85\,552\,\Omega^2+20\,910\,\Omega^3+1264\,\Omega^4\right)+\\
&\quad\left.4\left(59\,180+185\,625\,\Omega+197\,062\,\Omega^2+86\,607\,\Omega^3+15\,080\,\Omega^4+720\,\Omega^5\right)\right)+\\
&16\,\Gamma 1^3\left(\Gamma 2^5\left(22+13\,\Omega+\Omega^2\right)+\Gamma 2^4\left(1656+1934\,\Omega+561\,\Omega^2+32\,\Omega^3+18\,\rho A\left(22+13\,\Omega+\Omega^2\right)\right)+\right.\\
&\quad2\,\Gamma 2^3\left(15\,182+30\,117\,\Omega+18\,201\,\Omega^2+3718\,\Omega^3+176\,\Omega^4+\right.\\
&\quad\left.21\,\rho A^2\left(22+13\,\Omega+\Omega^2\right)+\rho A\left(6282+8039\,\Omega+2643\,\Omega^2+172\,\Omega^3\right)\right)+
\end{aligned}
$$

$$
\begin{aligned}
&2\,\Gamma 2^2\,\left(8\,\rho A^3\,\left(22+13\,\Omega+\Omega^2\right)+\rho A^2\,\left(7902+10\,811\,\Omega+3840\,\Omega^2+268\,\Omega^3\right)+\right.\\
&\quad\rho A\,\left(60\,244+130\,724\,\Omega+88\,305\,\Omega^2+20\,844\,\Omega^3+1200\,\Omega^4\right)+\\
&\quad\left.2\,\left(52\,736+159\,935\,\Omega+162\,687\,\Omega^2+67\,559\,\Omega^3+10\,840\,\Omega^4+448\,\Omega^5\right)\right)+\\
&2\,\Gamma 2\,\left(\rho A^3\,\left(1638+2353\,\Omega+879\,\Omega^2+64\,\Omega^3\right)+\right.\\
&\quad\rho A^2\,\left(38\,226+91\,885\,\Omega+67\,847\,\Omega^2+17\,646\,\Omega^3+1136\,\Omega^4\right)+\\
&\quad\rho A\,\left(215\,544+712\,542\,\Omega+798\,622\,\Omega^2+372\,816\,\Omega^3+69\,712\,\Omega^4+3648\,\Omega^5\right)+\\
&\quad\left.4\,\left(77\,552+328\,839\,\Omega+502\,585\,\Omega^2+345\,469\,\Omega^3+109\,894\,\Omega^4+14\,616\,\Omega^5+544\,\Omega^6\right)\right)+\\
&2\,\left(\rho A^3\,\left(3128+8394\,\Omega+6657\,\Omega^2+1852\,\Omega^3+128\,\Omega^4\right)+\right.\\
&\quad 2\,\rho A^2\,\left(27\,828+101\,182\,\Omega+124\,904\,\Omega^2+64\,077\,\Omega^3+13\,308\,\Omega^4+800\,\Omega^5\right)+4\,\rho A\\
&\quad\left(66\,400+300\,678\,\Omega+498\,498\,\Omega^2+378\,007\,\Omega^3+135\,538\,\Omega^4+21\,136\,\Omega^5+1024\,\Omega^6\right)+\\
&\quad\left.8\,\left(42\,732+230\,762\,\Omega+482\,579\,\Omega^2+490\,472\,\Omega^3+254\,420\,\Omega^4+\right.\right.\\
&\quad\left.\left.65\,632\,\Omega^5+7472\,\Omega^6+256\,\Omega^7\right)\right)\right)+\\
&32\,\Gamma 1^2\,\left(\Gamma 2^5\,\left(198+205\,\Omega+48\,\Omega^2+2\,\Omega^3+3\,\rho A\,\left(22+13\,\Omega+\Omega^2\right)\right)+\right.\\
&\quad\Gamma 2^4\,\left(18\,\rho A^2\,\left(22+13\,\Omega+\Omega^2\right)+3\,\rho A\,\left(1260+1524\,\Omega+465\,\Omega^2+28\,\Omega^3\right)+\right.\\
&\quad\left.2\,\left(3426+6391\,\Omega+3461\,\Omega^2+591\,\Omega^3+20\,\Omega^4\right)\right)+\\
&\quad 2\,\Gamma 2^3\,\left(7\,\rho A^3\,\left(22+13\,\Omega+\Omega^2\right)+\rho A^2\,\left(4896+6604\,\Omega+2307\,\Omega^2+158\,\Omega^3\right)+\right.\\
&\quad\rho A\,\left(28\,856+59\,484\,\Omega+37\,987\,\Omega^2+8328\,\Omega^3+432\,\Omega^4\right)+\\
&\quad\left.2\,\left(19\,698+56\,684\,\Omega+53\,946\,\Omega^2+20\,267\,\Omega^3+2760\,\Omega^4+80\,\Omega^5\right)\right)+\\
&\quad 2\,\Gamma 2^2\,\left(3\,\rho A^3\,\left(702+1019\,\Omega+384\,\Omega^2+28\,\Omega^3\right)+\right.\\
&\quad 3\,\rho A^2\,\left(12\,590+29\,575\,\Omega+21\,501\,\Omega^2+5496\,\Omega^3+344\,\Omega^4\right)+\\
&\quad 2\,\rho A\,\left(84\,696+271\,073\,\Omega+291\,660\,\Omega^2+129\,596\,\Omega^3+22\,644\,\Omega^4+1056\,\Omega^5\right)+\\
&\quad\left.8\,\left(24\,230+99\,581\,\Omega+145\,660\,\Omega^2+94\,128\,\Omega^3+27\,294\,\Omega^4+3108\,\Omega^5+80\,\Omega^6\right)\right)+\\
&\quad 2\,\Gamma 2\,\left(\rho A^3\,\left(7828+21\,400\,\Omega+17\,209\,\Omega^2+4848\,\Omega^3+336\,\Omega^4\right)+\right.\\
&\quad 2\,\rho A^2\,\left(56\,166+202\,475\,\Omega+246\,525\,\Omega^2+124\,943\,\Omega^3+25\,560\,\Omega^4+1488\,\Omega^5\right)+4\,\rho A\\
&\quad\left(108\,224+485\,551\,\Omega+786\,801\,\Omega^2+576\,991\,\Omega^3+198\,174\,\Omega^4+29\,040\,\Omega^5+1248\,\Omega^6\right)+\\
&\quad\left.8\,\left(56\,038+300\,588\,\Omega+614\,119\,\Omega^2+600\,275\,\Omega^3+293\,976\,\Omega^4+\right.\right.\\
&\quad\left.\left.69\,524\,\Omega^5+6816\,\Omega^6+160\,\Omega^7\right)\right)+\\
&\quad 4\,\left(\rho A^3\,\left(4584+19\,090\,\Omega+26\,477\,\Omega^2+14\,930\,\Omega^3+3392\,\Omega^4+224\,\Omega^5\right)+\right.\\
&\quad 2\,\rho A^2\,\left(30\,132+146\,506\,\Omega+263\,104\,\Omega^2+217\,025\,\Omega^3+84\,906\,\Omega^4+14\,592\,\Omega^5+800\,\Omega^6\right)+\\
&\quad 4\,\rho A\,\left(54\,024+303\,388\,\Omega+668\,975\,\Omega^2+723\,087\,\Omega^3+402\,532\,\Omega^4+\right.\\
&\quad\left.112\,932\,\Omega^5+14\,304\,\Omega^6+576\,\Omega^7\right)+8\,\left(26\,604+169\,214\,\Omega+440\,886\,\Omega^2+\right.\\
&\quad\left.\left.592\,381\,\Omega^3+432\,932\,\Omega^4+170\,500\,\Omega^5+34\,016\,\Omega^6+2928\,\Omega^7+64\,\Omega^8\right)\right)\right)+\\
&128\,\left(\Gamma 2^5\,\left(264+684\,\Omega+480\,\Omega^2+88\,\Omega^3+\rho A^3\,\left(22+13\,\Omega+\Omega^2\right)+\right.\right.\\
&\quad\left.\rho A^2\,\left(198+205\,\Omega+48\,\Omega^2+2\,\Omega^3\right)+\rho A\,\left(440+766\,\Omega+330\,\Omega^2+36\,\Omega^3\right)\right)+\\
&\quad\Gamma 2^4\,\left(\rho A^3\,\left(468+704\,\Omega+273\,\Omega^2+20\,\Omega^3\right)+\rho A^2\,\left(4212+8186\,\Omega+4942\,\Omega^2+966\,\Omega^3+40\,\Omega^4\right)+\right.\\
&\quad 4\,\rho A\,\left(2340+6167\,\Omega+5372\,\Omega^2+1739\,\Omega^3+170\,\Omega^4\right)+\\
&\quad\left.8\,\left(702+2427\,\Omega+2833\,\Omega^2+1312\,\Omega^3+194\,\Omega^4\right)\right)+\\
&\quad 2\,\Gamma 2^3\,\left(\rho A^3\,\left(1572+4612\,\Omega+3895\,\Omega^2+1144\,\Omega^3+80\,\Omega^4\right)+\right.\\
&\quad 2\,\rho A^2\,\left(7074+23\,781\,\Omega+25\,991\,\Omega^2+11\,537\,\Omega^3+1944\,\Omega^4+80\,\Omega^5\right)+\\
&\quad 4\,\rho A\,\left(7860+31\,631\,\Omega+44\,962\,\Omega^2+27\,627\,\Omega^3+7262\,\Omega^4+640\,\Omega^5\right)+\\
&\quad\left.8\,\left(2358+11\,283\,\Omega+19\,791\,\Omega^2+15\,656\,\Omega^3+5522\,\Omega^4+680\,\Omega^5\right)\right)+\\
&\quad 4\,\Gamma 2^2\,\left(\rho A^3\,\left(2396+11\,200\,\Omega+16\,719\,\Omega^2+10\,014\,\Omega^3+2392\,\Omega^4+160\,\Omega^5\right)+\right.
\end{aligned}
$$

$$
\begin{aligned}
&2\,\rho A^2\,\left(10\,782+54\,803\,\Omega+95\,777\,\Omega^2+73\,977\,\Omega^3+26\,338\,\Omega^4+3912\,\Omega^5+160\,\Omega^6\right)+\\
&8\,\left(3594+22\,821\,\Omega+55\,607\,\Omega^2+65\,814\,\Omega^3+39\,490\,\Omega^4+11\,284\,\Omega^5+1184\,\Omega^6\right)+\\
&4\,\rho A\,\left(11\,980+68\,221\,\Omega+143\,156\,\Omega^2+140\,607\,\Omega^3+67\,592\,\Omega^4+15\,036\,\Omega^5+1200\,\Omega^6\right)\Big)+\\
&8\,\Gamma 2\,\Big(\rho A^3\,\left(2088+11\,990\,\Omega+26\,499\,\Omega^2+26\,482\,\Omega^3+12\,324\,\Omega^4+2496\,\Omega^5+160\,\Omega^6\right)+\\
&2\,\rho A^2\,\left(9396+57\,584\,\Omega+140\,439\,\Omega^2+165\,465\,\Omega^3+99\,058\,\Omega^4+29\,580\,\Omega^5+\right.\\
&\left.3936\,\Omega^6+160\,\Omega^7\right)+8\,\left(3132+22\,608\,\Omega+68\,559\,\Omega^2+109\,676\,\Omega^3+\right.\\
&\left.97\,274\,\Omega^4+46\,908\,\Omega^5+11\,256\,\Omega^6+1024\,\Omega^7\right)+4\,\rho A\,\left(10\,440+69\,768\,\Omega+\right.\\
&\left.192\,081\,\Omega^2+269\,551\,\Omega^3+202\,144\,\Omega^4+80\,040\,\Omega^5+15\,448\,\Omega^6+1120\,\Omega^7\right)\Big)+\\
&32\,\Big(\rho A^3\,\left(432+2682\,\Omega+7275\,\Omega^2+10\,345\,\Omega^3+7748\,\Omega^4+2948\,\Omega^5+520\,\Omega^6+32\,\Omega^7\right)+\\
&2\,\rho A^2\,\left(1944+12\,798\,\Omega+37\,249\,\Omega^2+58\,882\,\Omega^3+52\,137\,\Omega^4+25\,492\,\Omega^5+6564\,\Omega^6+\right.\\
&\left.792\,\Omega^7+32\,\Omega^8\right)+8\,\left(648+4914\,\Omega+16\,605\,\Omega^2+32\,067\,\Omega^3+37\,572\,\Omega^4+\right.\\
&\left.26\,466\,\Omega^5+10\,648\,\Omega^6+2200\,\Omega^7+176\,\Omega^8\right)+4\,\rho A\,\left(2160+15\,354\,\Omega+48\,733\,\Omega^2+\right.\\
&\left.86\,808\,\Omega^3+90\,753\,\Omega^4+54\,978\,\Omega^5+18\,516\,\Omega^6+3152\,\Omega^7+208\,\Omega^8\right)\Big)+64\,\Gamma 1\\
&\left(\Gamma 2^5\,\left(440+766\,\Omega+330\,\Omega^2+36\,\Omega^3+3\,\rho A^2\,\left(22+13\,\Omega+\Omega^2\right)+\rho A\,\left(396+410\,\Omega+96\,\Omega^2+4\,\Omega^3\right)\right)+\right.\\
&\Gamma 2^4\,\Big(6\,\rho A^3\,\left(22+13\,\Omega+\Omega^2\right)+3\,\rho A^2\,\left(864+1114\,\Omega+369\,\Omega^2+24\,\Omega^3\right)+\\
&4\,\rho A\,\left(2766+5242\,\Omega+2966\,\Omega^2+537\,\Omega^3+20\,\Omega^4\right)+\\
&4\,\left(2736+7193\,\Omega+6092\,\Omega^2+1871\,\Omega^3+170\,\Omega^4\right)\Big)+\\
&2\,\Gamma 2^3\,\Big(\rho A^3\,\left(1170+1723\,\Omega+657\,\Omega^2+48\,\Omega^3\right)+\\
&\rho A^2\,\left(15\,246+33\,979\,\Omega+23\,681\,\Omega^2+5754\,\Omega^3+336\,\Omega^4\right)+\\
&2\,\rho A\,\left(25\,848+78\,071\,\Omega+78\,257\,\Omega^2+31\,496\,\Omega^3+4704\,\Omega^4+160\,\Omega^5\right)+\\
&4\,\left(11\,370+43\,688\,\Omega+58\,932\,\Omega^2+34\,049\,\Omega^3+8206\,\Omega^4+640\,\Omega^5\right)\Big)+\\
&2\,\Gamma 2^2\,\Big(\rho A^3\,\left(6272+17\,618\,\Omega+14\,447\,\Omega^2+4140\,\Omega^3+288\,\Omega^4\right)+\\
&2\,\rho A^2\,\left(35\,412+125\,074\,\Omega+147\,612\,\Omega^2+72\,403\,\Omega^3+14\,196\,\Omega^4+768\,\Omega^5\right)+\\
&4\,\rho A\,\left(52\,924+232\,356\,\Omega+362\,185\,\Omega^2+250\,839\,\Omega^3+79\,258\,\Omega^4+10\,128\,\Omega^5+320\,\Omega^6\right)+\\
&8\,\left(21\,388+112\,411\,\Omega+219\,407\,\Omega^2+200\,057\,\Omega^3+88\,290\,\Omega^4+17\,556\,\Omega^5+1200\,\Omega^6\right)\Big)+\\
&8\,\Gamma 2\,\Big(\rho A^3\,\left(3490+15\,145\,\Omega+21\,598\,\Omega^2+12\,472\,\Omega^3+2892\,\Omega^4+192\,\Omega^5\right)+\\
&\rho A^2\,\left(37\,674+185\,457\,\Omega+329\,961\,\Omega^2+266\,774\,\Omega^3+101\,884\,\Omega^4+16\,920\,\Omega^5+864\,\Omega^6\right)+\\
&2\,\rho A\,\left(53\,692+303\,641\,\Omega+661\,429\,\Omega^2+693\,808\,\Omega^3+368\,204\,\Omega^4+\right.\\
&\left.96\,104\,\Omega^5+10\,752\,\Omega^6+320\,\Omega^7\right)+4\,\left(20\,910+133\,809\,\Omega+343\,479\,\Omega^2+\right.\\
&\left.444\,409\,\Omega^3+304\,936\,\Omega^4+108\,888\,\Omega^5+18\,424\,\Omega^6+1120\,\Omega^7\right)\Big)+\\
&8\,\Big(\rho A^3\,\left(3168+17\,274\,\Omega+36\,139\,\Omega^2+34\,558\,\Omega^3+15\,444\,\Omega^4+3024\,\Omega^5+192\,\Omega^6\right)+\\
&2\,\rho A^2\,\left(16\,848+99\,614\,\Omega+237\,615\,\Omega^2+281\,443\,\Omega^3+173\,262\,\Omega^4+54\,356\,\Omega^5+7872\,\Omega^6+\right.\\
&\left.384\,\Omega^7\right)+4\,\rho A\,\left(23\,616+153\,590\,\Omega+419\,593\,\Omega^2+601\,101\,\Omega^3+473\,904\,\Omega^4+\right.\\
&\left.203\,920\,\Omega^5+45\,352\,\Omega^6+4512\,\Omega^7+128\,\Omega^8\right)+8\,\left(9072+64\,482\,\Omega+197\,219\,\Omega^2+\right.\\
&\left.328\,596\,\Omega^3+315\,240\,\Omega^4+172\,880\,\Omega^5+51\,792\,\Omega^6+7616\,\Omega^7+416\,\Omega^8\right)\Big)\Big)\Big)
\end{aligned}
$$

If we assume no mitotic gene conversion in addition to no meiotic crossing over and no meiotic gene conversion, then we get the simplified result below.

```
LDmetricNoMeioticGCandNoMeioticCO /. {Γ1 → 0, Γ2 → 0} // Simplify
```

$$\Big(\rho A^3\,\Omega\,\left(18+221\,\Omega+491\,\Omega^2+372\,\Omega^3+100\,\Omega^4+8\,\Omega^5\right)+2\,\rho A^2\,\left(216+1134\,\Omega+3165\,\Omega^2+5150\,\Omega^3+4501\,\Omega^4+1968\,\Omega^5+380\,\Omega^6+24\,\Omega^7\right)+4\,\rho A\,\left(864+4842\,\Omega+12\,343\,\Omega^2+18\,682\,\Omega^3+17\,473\,\Omega^4+9622\,\Omega^5+2844\,\Omega^6+384\,\Omega^7+16\,\Omega^8\right)+8\,\left(648+4266\,\Omega+12\,177\,\Omega^2+19\,863\,\Omega^3+20\,220\,\Omega^4+12\,930\,\Omega^5+4936\,\Omega^6+1000\,\Omega^7+80\,\Omega^8\right)\Big)\Big/\Big(\rho A^3\,\left(432+2682\,\Omega+7275\,\Omega^2+10\,345\,\Omega^3+7748\,\Omega^4+2948\,\Omega^5+520\,\Omega^6+32\,\Omega^7\right)+2\,\rho A^2\,\left(1944+12\,798\,\Omega+37\,249\,\Omega^2+58\,882\,\Omega^3+52\,137\,\Omega^4+25\,492\,\Omega^5+6564\,\Omega^6+792\,\Omega^7+32\,\Omega^8\right)+8\,\left(648+4914\,\Omega+16\,605\,\Omega^2+32\,067\,\Omega^3+37\,572\,\Omega^4+26\,466\,\Omega^5+10\,648\,\Omega^6+2200\,\Omega^7+176\,\Omega^8\right)+4\,\rho A\,\left(2160+15\,354\,\Omega+48\,733\,\Omega^2+86\,808\,\Omega^3+90\,753\,\Omega^4+54\,978\,\Omega^5+18\,516\,\Omega^6+3152\,\Omega^7+208\,\Omega^8\right)\Big)$$

Returning to the result assuming no meiotic crossing over and no meiotic gene conversion, we can re-write this as a function of distance *d* using the relationships:

$$\left\{\gamma 2 \to g\, e^{-\frac{d}{\lambda}}\ \lambda,\ \gamma 1 \to\ g\ 2\ \left(1-e^{-\frac{d}{\lambda}}\right)\ \lambda,\ \ cA \to cA0\ d\right\}$$

where *g* and λ are defined above and cA0 is the per base pair crossover rate.

We introduce here new scaled parameters:

G = 4 n g

A = 4 n cA0

```
LDmetricNoMeioticGCandNoMeioticCOvB =
  LDmetricNoMeioticGCandNoMeioticCO /. {Γ1 → 4 n γ1, Γ2 → 4 n γ2, ρA → 4 n cA} /.
    {γ2 → e^(-d/λ) λ g, γ1 →  2 (1 - e^(-d/λ)) λ g,  cA → cA0 d} /. {g → G / (4 n), cA0 → A / (4 n)};
```

Below we will make some plots of LD under low rates of sex but allowing for mitotic gene conversion and, in some cases, mitotic crossing over. We will assume no meiotic crossing over or meiotic gene conversion (though these have little affect anyways when rates of sex are so low).

The plot below gives LD as a function of distance in base pairs assuming no meiotic recombination or meiotic gene conversion, with low sex (Ω = 1/2).

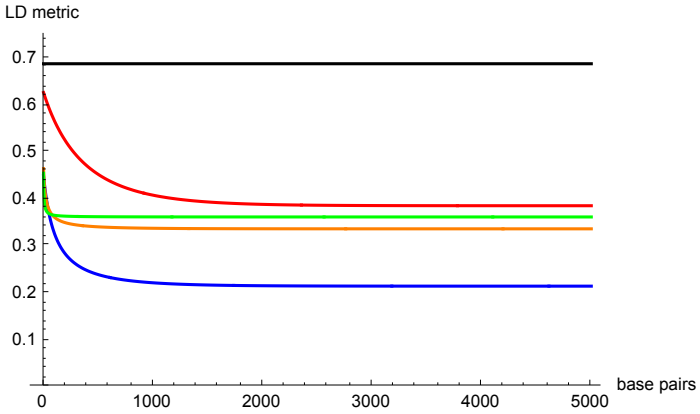
We assume here that there is no mitotic gene conversion (A = 0).

Mitotic gene conversion, average tract length, λ = 500 bp

G = 0 (black), 0.001 (red), 0.01 (blue), 0.1 (orange), or 10 (green)

```
thisλ = 500;
thisSex = 1 / 2;
thisA = 0;
subTheseValues = {λ → thisλ, A → thisA, Ω → thisSex}
Plot[{LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. G → 0,
  LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. G → 0.001,
  LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. G → 0.01,
  LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. G → 0.1,
  LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. G → 1},
 {d, 1, 5000}, AxesLabel → {"base pairs", "LD metric"},
 PlotStyle → {Black, Red, Blue, Orange, Green},
 PlotRange → {Automatic, {0, 0.75}}]
```

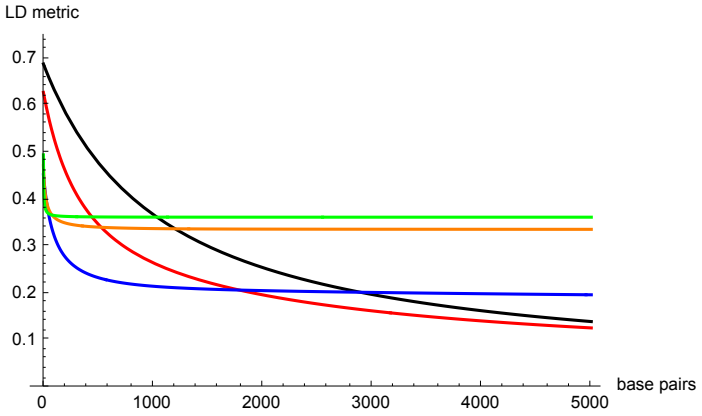
$$\left\{\lambda \to 500,\ A \to 0,\ \Omega \to \frac{1}{2}\right\}$$



The plot below gives LD as a function of distance in base pairs assuming no meiotic recombination or meiotic gene conversion, with low sex (Ω = 1/2).
We assume here that there is a low rate of mitotic gene conversion (A = 0.001).
Mitotic gene conversion, average tract length, λ = 500 bp
G = 0 (black), 0.001 (red), 0.01 (blue), 0.1 (orange), or 10 (green)

```
thisλ = 500;
thisSex = 1 / 2;
thisA = 0.001;
subTheseValues = {λ → thisλ, A → thisA, Ω → thisSex}
Plot[{LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. G → 0,
  LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. G → 0.001,
  LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. G → 0.01,
  LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. G → 0.1,
  LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. G → 1},
 {d, 0, 5000}, AxesLabel → {"base pairs", "LD metric"},
 PlotStyle → {Black, Red, Blue, Orange, Green},
 PlotRange → {Automatic, {0, 0.75}}]
```

$$\left\{\lambda \to 500,\ A \to 0.001,\ \Omega \to \frac{1}{2}\right\}$$



Below is the long distance limit for the LD metric in the absence of meiotic crossing over or meiotic gene conversion. This is minimum value of the LD metric given that LD declines with distance. Note we have to consider the cases with and without mitotic crossovers separately.

With no mitotic crossovers (A = 0), the long distance limit is given below.

```
LongDistanceLimitWithForLDmetricNoMeioticGCandNoMeioticCOvBNoMitCO = Simplify[
  Assuming[{λ > 0}, Limit[LDmetricNoMeioticGCandNoMeioticCOvB /. A → 0, d → ∞]]]
```

$$\left(2\,G^8\,\lambda^8\,(10+\Omega)+G^7\,\lambda^7\left(540+448\,\Omega+39\,\Omega^2\right)+2\,G^6\,\lambda^6\left(2620+4684\,\Omega+2054\,\Omega^2+157\,\Omega^3\right)+\right.$$
$$4\,G^5\,\lambda^5\left(5976+18\,264\,\Omega+16\,667\,\Omega^2+5058\,\Omega^3+338\,\Omega^4\right)+$$
$$16\,G^4\,\lambda^4\left(3584+16\,929\,\Omega+26\,097\,\Omega^2+16\,005\,\Omega^3+3699\,\Omega^4+212\,\Omega^5\right)+$$
$$16\,G^3\,\lambda^3\left(5724+35\,802\,\Omega+80\,877\,\Omega^2+81\,328\,\Omega^3+36\,912\,\Omega^4+6744\,\Omega^5+320\,\Omega^6\right)+$$
$$32\,G^2\,\lambda^2\left(5004+30\,374\,\Omega+79\,612\,\Omega^2+107\,869\,\Omega^3+76\,336\,\Omega^4+26\,556\,\Omega^5+3872\,\Omega^6+144\,\Omega^7\right)+$$
$$64\,G\,\lambda\left(3888+22\,938\,\Omega+60\,311\,\Omega^2+90\,608\,\Omega^3+\right.$$
$$\left.\left.81\,144\,\Omega^4+41\,720\,\Omega^5+11\,200\,\Omega^6+1280\,\Omega^7+32\,\Omega^8\right)+256\right.$$
$$\left.\left(648+4266\,\Omega+12\,177\,\Omega^2+19\,863\,\Omega^3+20\,220\,\Omega^4+12\,930\,\Omega^5+4936\,\Omega^6+1000\,\Omega^7+80\,\Omega^8\right)\right)\Big/$$
$$\left(2\,G^8\,\lambda^8\left(22+13\,\Omega+\Omega^2\right)+G^7\,\lambda^7\left(1332+1744\,\Omega+591\,\Omega^2+40\,\Omega^3\right)+\right.$$
$$2\,G^6\,\lambda^6\left(7780+17\,024\,\Omega+11\,570\,\Omega^2+2761\,\Omega^3+164\,\Omega^4\right)+$$
$$4\,G^5\,\lambda^5\left(23\,472+75\,352\,\Omega+82\,349\,\Omega^2+37\,466\,\Omega^3+6830\,\Omega^4+352\,\Omega^5\right)+$$
$$16\,G^4\,\lambda^4\left(20\,420+88\,111\,\Omega+138\,502\,\Omega^2+99\,013\,\Omega^3+33\,219\,\Omega^4+4784\,\Omega^5+208\,\Omega^6\right)+16\,G^3\,\lambda^3$$
$$\left(42\,732+230\,762\,\Omega+482\,579\,\Omega^2+490\,472\,\Omega^3+254\,420\,\Omega^4+65\,632\,\Omega^5+7472\,\Omega^6+256\,\Omega^7\right)+$$
$$32\,G^2\,\lambda^2\left(26\,604+169\,214\,\Omega+440\,886\,\Omega^2+592\,381\,\Omega^3+432\,932\,\Omega^4+\right.$$
$$\left.\left.170\,500\,\Omega^5+34\,016\,\Omega^6+2928\,\Omega^7+64\,\Omega^8\right)+256\right.$$
$$\left(648+4914\,\Omega+16\,605\,\Omega^2+32\,067\,\Omega^3+37\,572\,\Omega^4+26\,466\,\Omega^5+10\,648\,\Omega^6+2200\,\Omega^7+176\,\Omega^8\right)+$$
$$64\,G\,\lambda\left(9072+64\,482\,\Omega+197\,219\,\Omega^2+328\,596\,\Omega^3+315\,240\,\Omega^4+\right.$$
$$\left.\left.172\,880\,\Omega^5+51\,792\,\Omega^6+7616\,\Omega^7+416\,\Omega^8\right)\right)$$

With mitotic crossovers (A > 0), the long distance limit is given below. (Note this is different than the expression above for A = 0.)

```
LongDistanceLimitForLDmetricNoMeioticGCandNoMeioticCOvB =
 Assuming[{λ > 0}, Limit[LDmetricNoMeioticGCandNoMeioticCOvB, d → ∞]] // Simplify
```

$$\left(2\,G^5\,\lambda^5\,(10+\Omega)+G^4\,\lambda^4\left(360+310\,\Omega+29\,\Omega^2\right)+\right.$$
$$2\,G^3\,\lambda^3\left(800+1838\,\Omega+895\,\Omega^2+80\,\Omega^3\right)+8\,G\,\lambda\,\Omega\left(826+2673\,\Omega+2522\,\Omega^2+772\,\Omega^3+64\,\Omega^4\right)+$$
$$4\,G^2\,\lambda^2\left(480+2582\,\Omega+3295\,\Omega^2+1206\,\Omega^3+104\,\Omega^4\right)+$$
$$\left.32\,\Omega\left(18+221\,\Omega+491\,\Omega^2+372\,\Omega^3+100\,\Omega^4+8\,\Omega^5\right)\right)\Big/$$
$$\left(2\,G^5\,\lambda^5\left(22+13\,\Omega+\Omega^2\right)+G^4\,\lambda^4\left(936+1334\,\Omega+495\,\Omega^2+36\,\Omega^3\right)+\right.$$
$$2\,G^3\,\lambda^3\left(3128+8394\,\Omega+6657\,\Omega^2+1852\,\Omega^3+128\,\Omega^4\right)+$$
$$4\,G^2\,\lambda^2\left(4584+19\,090\,\Omega+26\,477\,\Omega^2+14\,930\,\Omega^3+3392\,\Omega^4+224\,\Omega^5\right)+$$
$$8\,G\,\lambda\left(3168+17\,274\,\Omega+36\,139\,\Omega^2+34\,558\,\Omega^3+15\,444\,\Omega^4+3024\,\Omega^5+192\,\Omega^6\right)+$$
$$\left.32\left(432+2682\,\Omega+7275\,\Omega^2+10\,345\,\Omega^3+7748\,\Omega^4+2948\,\Omega^5+520\,\Omega^6+32\,\Omega^7\right)\right)$$

The long distance limit for the LD metric is unaffected by the rate of mitotic crossing over, provided that A > 0.

```
D[LongDistanceLimitForLDmetricNoMeioticGCandNoMeioticCOvB, A]
```

```
0
```

The long distance limit for the LD metric is an increasing function of the frequency of gene conversion initation. (The expression below is positive as all the terms are positive.)

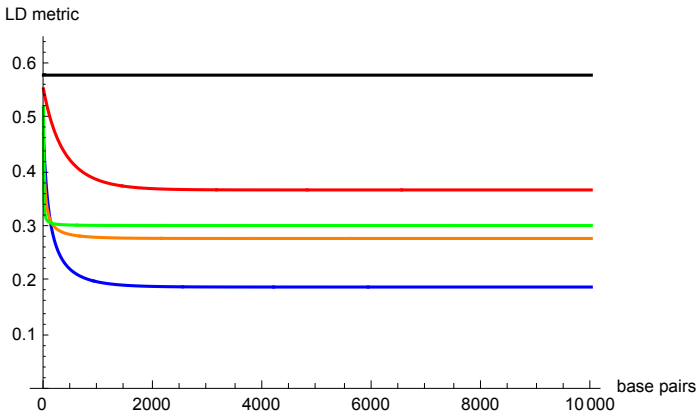
```
D[LongDistanceLimitForLDmetricNoMeioticGCandNoMeioticCOvB, G] // Simplify
```

$$
\begin{aligned}
&\Big(2\lambda\Big(G^8\lambda^8\left(1440+2776\,\Omega+1256\,\Omega^2+168\,\Omega^3+7\,\Omega^4\right)+\\
&\quad 4\,G^7\lambda^7\left(13\,680+36\,232\,\Omega+30\,580\,\Omega^2+9944\,\Omega^3+1197\,\Omega^4+48\,\Omega^5\right)+\\
&\quad 4\,G^6\lambda^6\left(200\,160+698\,308\,\Omega+882\,912\,\Omega^2+503\,083\,\Omega^3+132\,102\,\Omega^4+14\,614\,\Omega^5+568\,\Omega^6\right)+\\
&\quad 16\,G^5\lambda^5\left(363\,600+1\,624\,564\,\Omega+2\,822\,352\,\Omega^2+2\,410\,461\,\Omega^3+1\,069\,892\,\Omega^4+241\,137\,\Omega^5+\right.\\
&\qquad \left.24\,908\,\Omega^6+944\,\Omega^7\right)+16\,G^4\lambda^4\left(1\,440\,000+7\,987\,192\,\Omega+18\,142\,208\,\Omega^2+\right.\\
&\qquad \left.21\,465\,840\,\Omega^3+14\,179\,265\,\Omega^4+5\,270\,092\,\Omega^5+1\,058\,684\,\Omega^6+103\,384\,\Omega^7+3840\,\Omega^8\right)+\\
&\quad 64\,G^3\lambda^3\left(789\,120+5\,347\,156\,\Omega+15\,282\,476\,\Omega^2+23\,783\,651\,\Omega^3+21\,766\,659\,\Omega^4+\right.\\
&\qquad \left.11\,947\,407\,\Omega^5+3\,885\,424\,\Omega^6+713\,720\,\Omega^7+66\,544\,\Omega^8+2432\,\Omega^9\right)+\\
&\quad 64\,G^2\lambda^2\left(898\,560+7\,496\,196\,\Omega+26\,532\,008\,\Omega^2+52\,402\,167\,\Omega^3+63\,246\,080\,\Omega^4+\right.\\
&\qquad \left.48\,001\,956\,\Omega^5+22\,891\,106\,\Omega^6+6\,708\,888\,\Omega^7+1\,147\,648\,\Omega^8+102\,944\,\Omega^9+3712\,\Omega^{10}\right)+\\
&\quad 1024\,\Omega\left(37\,476+294\,876\,\Omega+1\,030\,512\,\Omega^2+2\,102\,470\,\Omega^3+2\,761\,931\,\Omega^4+2\,423\,938\,\Omega^5+\right.\\
&\qquad \left.1\,429\,936\,\Omega^6+559\,686\,\Omega^7+141\,080\,\Omega^8+21\,680\,\Omega^9+1824\,\Omega^{10}+64\,\Omega^{11}\right)+\\
&\quad 512\,G\lambda\left(51\,840+580\,068\,\Omega+2\,620\,920\,\Omega^2+6\,540\,403\,\Omega^3+10\,120\,445\,\Omega^4+10\,159\,764\,\Omega^5+\right.\\
&\qquad \left.6\,686\,064\,\Omega^6+2\,855\,568\,\Omega^7+770\,120\,\Omega^8+124\,296\,\Omega^9+10\,784\,\Omega^{10}+384\,\Omega^{11}\right)\Big)\Big)\Big/\\
&\Big(2\,G^5\lambda^5\left(22+13\,\Omega+\Omega^2\right)+G^4\lambda^4\left(936+1334\,\Omega+495\,\Omega^2+36\,\Omega^3\right)+\\
&\quad 2\,G^3\lambda^3\left(3128+8394\,\Omega+6657\,\Omega^2+1852\,\Omega^3+128\,\Omega^4\right)+\\
&\quad 4\,G^2\lambda^2\left(4584+19\,090\,\Omega+26\,477\,\Omega^2+14\,930\,\Omega^3+3392\,\Omega^4+224\,\Omega^5\right)+\\
&\quad 8\,G\lambda\left(3168+17\,274\,\Omega+36\,139\,\Omega^2+34\,558\,\Omega^3+15\,444\,\Omega^4+3024\,\Omega^5+192\,\Omega^6\right)+\\
&\quad 32\left(432+2682\,\Omega+7275\,\Omega^2+10\,345\,\Omega^3+7748\,\Omega^4+2948\,\Omega^5+520\,\Omega^6+32\,\Omega^7\right)\Big)^2
\end{aligned}
$$

Plots for figures

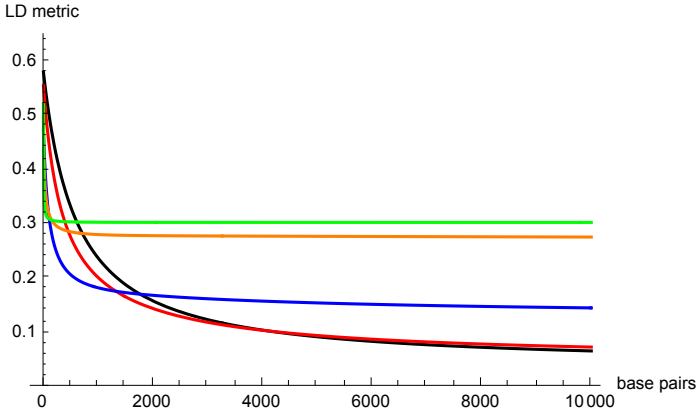
```
thisλ = 500;
thisSex = 1;
thisA = 0;
subTheseValues = {λ → thisλ, A → thisA, Ω → thisSex}
Plot[{LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. G → 0,
  LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. G → 0.001,
  LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. G → 0.01,
  LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. G → 0.1,
  LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. G → 1},
 {d, 0, 10000}, AxesLabel → {"base pairs", "LD metric"},
 PlotStyle → {Black, Red, Blue, Orange, Green},
 PlotRange → {Automatic, {0, 0.65}}]
```

```
{λ → 500, A → 0, Ω → 1}
```



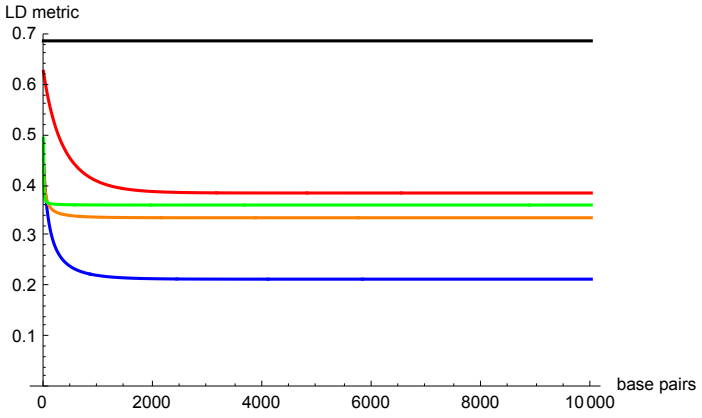
```
thisλ = 500;
thisSex = 1;
thisA = 0.002;
subTheseValues = {λ → thisλ, A → thisA, Ω → thisSex}
Plot[{LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. G → 0,
  LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. G → 0.001,
  LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. G → 0.01,
  LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. G → 0.1,
  LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. G → 1},
 {d, 0, 10000}, AxesLabel → {"base pairs", "LD metric"},
 PlotStyle → {Black, Red, Blue, Orange, Green},
 PlotRange → {Automatic, {0, 0.65}}]
```

$\{\lambda \to 500, A \to 0.002, \Omega \to 1\}$



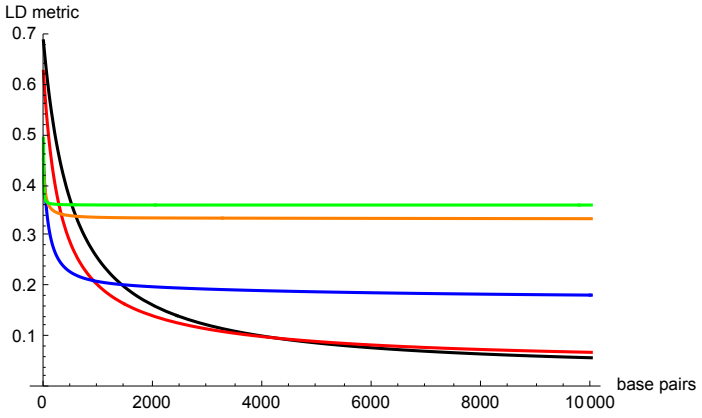
```
thisλ = 500;
thisSex = 1 / 2;
thisA = 0;
subTheseValues = {λ → thisλ, A → thisA, Ω → thisSex}
Plot[{LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. G → 0,
  LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. G → 0.001,
  LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. G → 0.01,
  LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. G → 0.1,
  LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. G → 1},
 {d, 0, 10000}, AxesLabel → {"base pairs", "LD metric"},
 PlotStyle → {Black, Red, Blue, Orange, Green},
 PlotRange → {Automatic, {0, 0.7}}]
```

$$\left\{\lambda \to 500,\ A \to 0,\ \Omega \to \frac{1}{2}\right\}$$



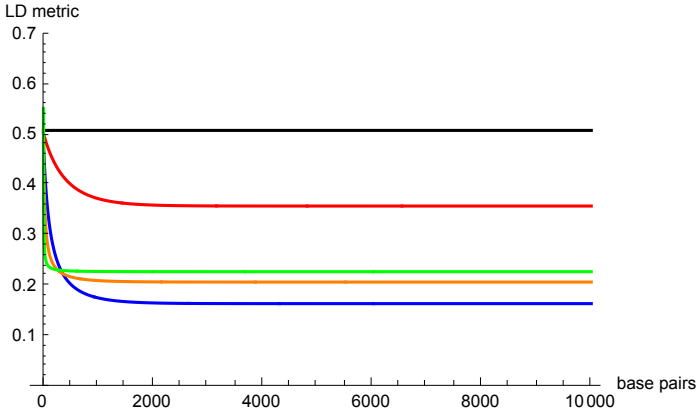
```
thisλ = 500;
thisSex = 1 / 2;
thisA = 0.002;
subTheseValues = {λ → thisλ, A → thisA, Ω → thisSex}
Plot[{LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. G → 0,
  LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. G → 0.001,
  LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. G → 0.01,
  LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. G → 0.1,
  LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. G → 1},
 {d, 0, 10000}, AxesLabel → {"base pairs", "LD metric"},
 PlotStyle → {Black, Red, Blue, Orange, Green},
 PlotRange → {Automatic, {0, 0.7}}]
```

$$\left\{\lambda \to 500,\ A \to 0.002,\ \Omega \to \frac{1}{2}\right\}$$



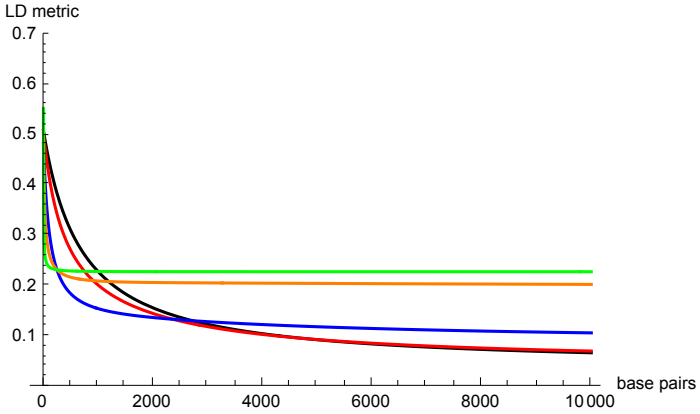
```
thisλ = 500;
thisSex = 2;
thisA = 0;
subTheseValues = {λ → thisλ, A → thisA, Ω → thisSex}
Plot[{LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. G → 0,
  LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. G → 0.001,
  LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. G → 0.01,
  LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. G → 0.1,
  LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. G → 1},
 {d, 0, 10000}, AxesLabel → {"base pairs", "LD metric"},
 PlotStyle → {Black, Red, Blue, Orange, Green},
 PlotRange → {Automatic, {0, 0.7}}]
```

$\{\lambda \to 500, A \to 0, \Omega \to 2\}$



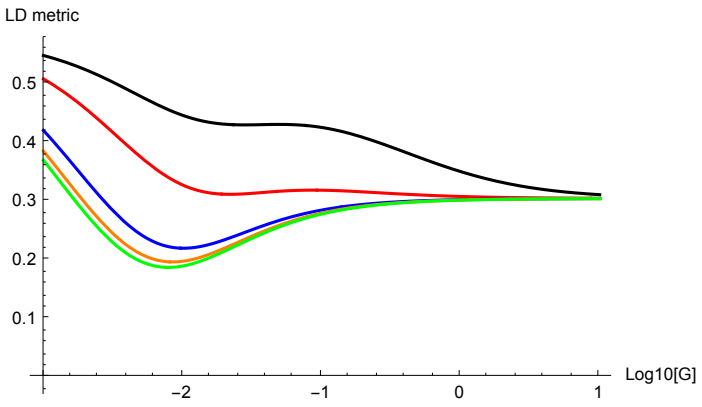
```
thisλ = 500;
thisSex = 2;
thisA = 0.002;
subTheseValues = {λ → thisλ, A → thisA, Ω → thisSex}
Plot[{LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. G → 0,
  LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. G → 0.001,
  LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. G → 0.01,
  LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. G → 0.1,
  LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. G → 1},
 {d, 0, 10000}, AxesLabel → {"base pairs", "LD metric"},
 PlotStyle → {Black, Red, Blue, Orange, Green},
 PlotRange → {Automatic, {0, 0.7}}]
```

$\{\lambda \to 500, A \to 0.002, \Omega \to 2\}$



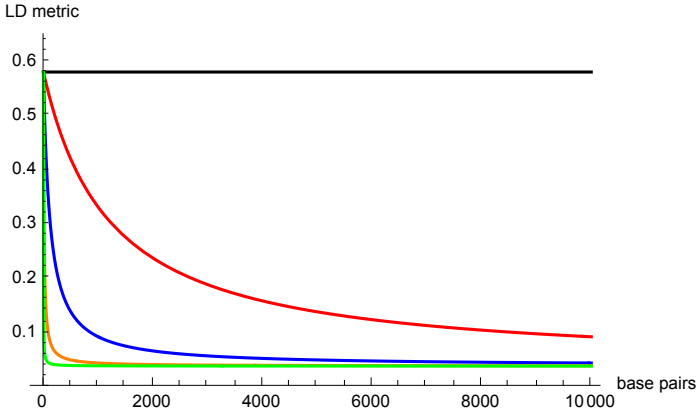
```
thisλ = 500;
thisSex = 1;
thisA = 0;
subTheseValues = {λ → thisλ, A → thisA, Ω → thisSex}

Plot[
 {LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. d → 10 /. G → 10^gexp,
  LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. d → 100 /.
   G → 10^gexp, LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /.
    d → 500 /. G → 10^gexp,
  LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. d → 1000 /.
   G → 10^gexp, LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /.
    d → 2000 /. G → 10^gexp},
 {gexp, -3, 1}, AxesLabel → {"Log10[G]", "LD metric"},
 PlotStyle → {Black, Red, Blue, Orange, Green},
 AxesOrigin → {-3, 0}]
```

```
{λ → 500, A → 0, Ω → 1}
```



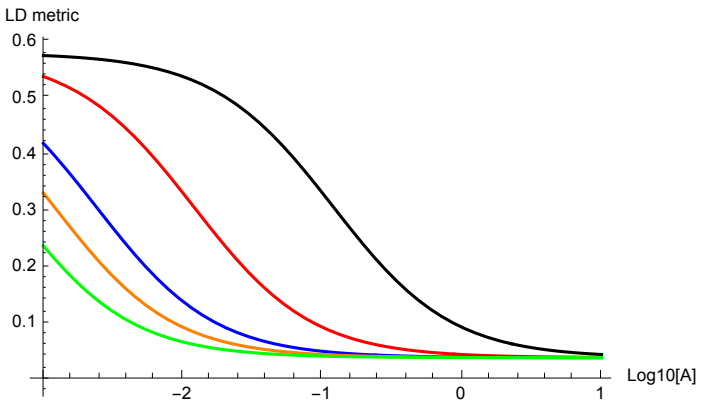
```
thisλ = 500;
thisSex = 1;
thisG = 0;
subTheseValues = {λ → thisλ, G → thisG, Ω → thisSex}
Plot[{LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. A → 0,
  LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. A → 0.001,
  LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. A → 0.01,
  LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. A → 0.1,
  LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. A → 1},
 {d, 0, 10000}, AxesLabel → {"base pairs", "LD metric"},
 PlotStyle → {Black, Red, Blue, Orange, Green},
 PlotRange → {Automatic, {0, 0.65}}]
```

$\{\lambda \to 500, G \to 0, \Omega \to 1\}$



```
thisλ = 500;
thisSex = 1;
thisG = 0;
subTheseValues = {λ → thisλ, G → thisG, Ω → thisSex}

Plot[
 {LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. d → 10 /. A → 10^aexp,
  LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. d → 100 /.
   A → 10^aexp, LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /.
    d → 500 /. A → 10^aexp,
  LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /. d → 1000 /.
   A → 10^aexp, LDmetricNoMeioticGCandNoMeioticCOvB /. subTheseValues /.
    d → 2000 /. A → 10^aexp},
 {aexp, -3, 1}, AxesLabel → {"Log10[A]", "LD metric"},
 PlotStyle → {Black, Red, Blue, Orange, Green},
 AxesOrigin → {-3, 0}]
```

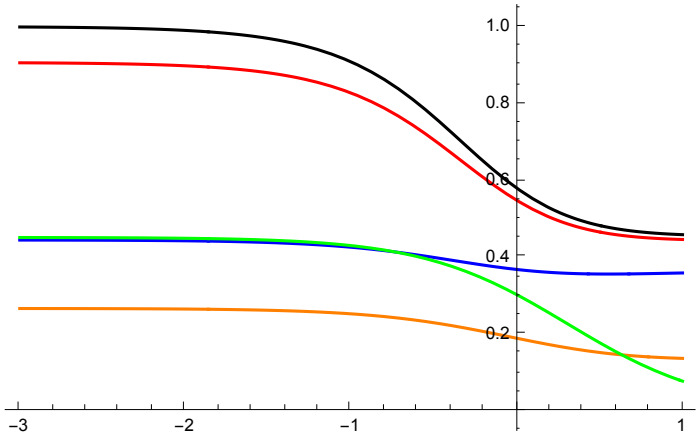
```
{λ → 500, G → 0, Ω → 1}
```



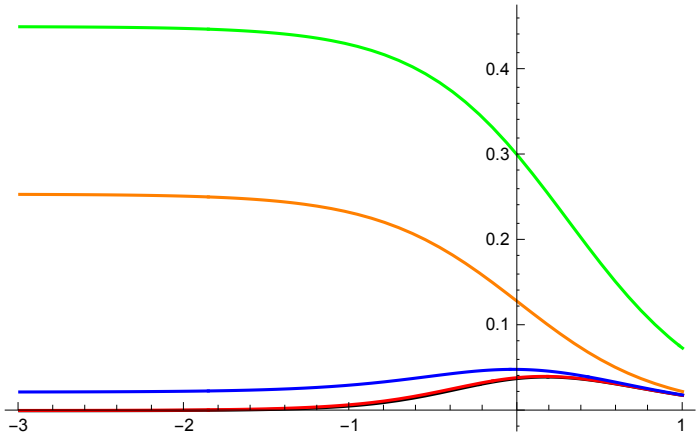
The plots below look at the minimum value of the LD metric (i.e., the long distance limit), as a function of the rate of sex for different values of G, either with or without mitotic gene conversion.

```
bob =
  LongDistanceLimitWithForLDmetricNoMeioticGCandNoMeioticCOvBNoMitCO /. λ → 500;
rob = LongDistanceLimitForLDmetricNoMeioticGCandNoMeioticCOvB /. λ → 500;
```

```
Plot[{bob /. Ω → 10^q /. G → 0, bob /. Ω → 10^q /. G → 0.0001,
  bob /. Ω → 10^q /. G → 0.001, bob /. Ω → 10^q /. G → 0.01, bob /. Ω → 10^q /. G → 1},
 {q, -3, 1}, PlotStyle → {Black, Red, Blue, Orange, Green},
 AxesOrigin → Automatic]
```




```
Plot[{rob /. Ω → 10^q /. G → 0, rob /. Ω → 10^q /. G → 0.0001,
  rob /. Ω → 10^q /. G → 0.001, rob /. Ω → 10^q /. G → 0.01, rob /. Ω → 10^q /. G → 1},
 {q, -3, 1}, PlotStyle → {Black, Red, Blue, Orange, Green},
 AxesOrigin → Automatic]
```



Section B: Drawing start and end breakpoints following gene conversion

Drawing two breakpoints

The joint probability density function (hereafter PDF) of start points *s* and end points *t* is given by (Wiuf and Hein 2000, Eq. 4):

$$\text{Ke}[Q\_] := 1 - \frac{1}{Q}\,(1 - \text{Exp}[-Q])$$

$$\frac{Q\,\text{Exp}[-Q\,(t-s)]}{\text{Ke}[Q]}$$

Where Ke is the probability that both breakpoints lie in the genome sample (K is a protected variable in Mathematica).

If gene conversion occurs where both breakpoints lie in the sample, then we need to jointly draw *s*, *t* from the PDF. This requires draws from two marginal PDFs:
1) f(s), density of start points
2) f(t | s), density of end points *given start point s*.

f(s) is given by integrating the joint PDF over the range (t,1), and is given in the caption of Figure 4 in Wiuf and Hein 2000. Below we only integrate over the numerator Q Exp[-Q(t - s)] for clarity; the main result is obtained by dividing by K(Q):

```
Integrate[Q Exp[-Q (t - s)], {t, s, 1}]
```

$$1 - e^{Q\,(-1+s)}$$

The cumulative density function (hereafter CDF) is simply the integral of this solution from 0 to dummy variable S:

```
Integrate[(1 - Exp[-Q (1 - s)])/(Ke[Q]), {s, 0, S}] // FullSimplify
```

$$\frac{1 - e^{Q\,S} + e^{Q}\,Q\,S}{1 + e^{Q}\,(-1+Q)}$$

Reversing s, S and solving for S, we can obtain F^{-1}, the inverse CDF that is used to convert random uniform numbers between 0 and 1 to actual startpoints (Equation A2 in the main text):

```
Solve[(1 - e^(Q s) + e^Q Q s)/(1 + e^Q (-1 + Q)) == S, s] // FullSimplify
```

Solve: Inverse functions are being used by Solve, so some solutions may not be found; use Reduce for complete solution information.

$$\left\{\left\{s \to \frac{1}{Q} e^{-Q}\left(-1 + S + e^{Q}\left((-1+Q)\,S - \text{ProductLog}\left[-e^{-Q+e^{-Q}\,(-1+S)+(-1+Q)\,S}\right]\right)\right)\right\}\right\}$$

To obtain f(t | s), note that the joint PDF can be written as f(s,t) = f(s) f(t|s).
Hence $\frac{f(s,t)}{f(s)}$ = f(t|s). So we can find the second marginal PDF using this definition:

```
(Q Exp[-Q (t-s)]/Ke[Q])/((1-e^(-Q (1-s)))/Ke[Q]) // FullSimplify
```

$$\frac{e^{Q-Q\,t}\,Q}{-1 + e^{Q-Q\,s}}$$

Checking that it integrates to 1:

```
Integrate[ Q Exp[-Q (t - s)] / (1 - e^(-Q (1-s))), {t, s, 1}]
```

```
1
```

To draw the appropriate end point, first find the cumulative density function (hereafter CDF) of this distribution using dummy variable T in the CDF function:

```
Integrate[ Q Exp[-Q (T - s)] / (1 - e^(-Q (1-s))), {T, s, t}] // FullSimplify
```

$$\frac{e^{Q}\left(-1+e^{Q\,(s-t)}\right)}{-e^{Q}+e^{Q\,s}}$$

Rewriting it as follows:

```
(1 - e^(-Q (t-s)))/(1 - e^(-Q (1-s))) - {(e^Q (-1 + e^(Q (s-t))))/(-e^Q + e^(Q s))} // FullSimplify
```

```
{0}
```

Then we can inverse this function to find the output end point for a given random draw T:

```
Solve[(1 - e^(-Q (t-s)))/(1 - e^(-Q (1-s))) == T, t] // FullSimplify
```

$$\left\{\left\{t \to \text{ConditionalExpression}\left[\frac{1}{Q}\left(Q\,s-2\,i\,\pi\,C[1]-\text{Log}\left[1+\left(-1+e^{Q\,(-1+s)}\right)\,T\right]\right),\ C[1]\in\mathbb{Z}\right]\right\}\right\}$$

We can obtain a simpler expression by assuming C[1] = 0, since it can be equal to any integer:

```
1/Q (Q s - 2 i π C[1] - Log[1 + (-1 + e^(Q (-1+s))) T]) /. C[1] → 0 // FullSimplify
```

$$s-\frac{\text{Log}\left[1+\left(-1+e^{Q\,(-1+s)}\right)\,T\right]}{Q}$$

Rewriting to give Equation A4 in the main text:

```
s - Log[1 - T (1 - e^(-Q (1-s)))]/Q - {s - Log[1 + (-1 + e^(Q (-1+s))) T]/Q} // FullSimplify
```

```
{0}
```

Drawing end-point if gene conversion initiates outside the tract

The PDF of endpoints, given gene conversion initiated outside the tract, equals (Wiuf and Hein 2000, Eq. 8):

```
Exp[-Q t]/(1 - Ke[Q])
```

The CDF is:

```
Integrate[Exp[-Q t]/(1 - Ke[Q]), {t, 0, T}]
```

$$\frac{e^{Q} - e^{Q-Q\,T}}{-1 + e^{Q}}$$

Inverting to give the required transformation:

```
Normal[Solve[(e^Q - e^(Q-Q t))/(-1 + e^Q) == T, t, Reals]] // FullSimplify
```

$$\left\{\left\{t \to \frac{\text{Log}\left[\frac{1}{1+\left(-1+e^{-Q}\right)T}\right]}{Q}\right\}\right\}$$

The *Mathematica* output is:

```
(Q + Log[1/(e^Q + T - e^Q T)])/Q // FullSimplify
```

$$\frac{Q + \text{Log}\left[\frac{1}{e^{Q}+T-e^{Q}T}\right]}{Q}$$

We can rewrite this as:

$$\frac{Q + \text{Log}[1] - \text{Log}\left[e^{Q} + T - e^{Q}T\right]}{Q}$$

Or, given Log[1] = 0 (Equation A6 in the main text):

$$1 - \frac{\text{Log}\left[e^{Q} + T - e^{Q}T\right]}{Q}$$

Comparing this term to the original expression shows they are equal.

```
{1 - Log[e^Q + T - e^Q T]/Q, (Q + Log[1] - Log[e^Q + T - e^Q T])/Q} /. {Q → 0.1, T → 0.5}
```

```
{0.487505, 0.487505}
```

Drawing start-point if gene conversion will end outside the tract

PDF of start points:

```
Exp[-Q (1 - s)]/(1 - Ke[Q])
```

The CDF equals:

```
Integrate[Exp[-Q (1 - s)]/(1 - Ke[Q]), {s, 0, S}]
```

$$\frac{-1 + e^{Q\,S}}{-1 + e^{Q}}$$

Finding the inverse to find how to convert uniform draws to actual startpoints:

```
Normal[Solve[(-1 + e^(Q s))/(-1 + e^Q) == S, s, Reals]] // FullSimplify
```

$$\left\{\left\{s \to \frac{\text{Log}\left[1 + \left(-1 + e^{Q}\right) S\right]}{Q}\right\}\right\}$$

So the inverse function is (Equation A8 in the main text):

$$\frac{\text{Log}\left[1 + \left(-1 + e^{Q}\right) S\right]}{Q}$$

Section C: Probability of 'complete' gene conversion

Let's measure distances in units of (L – 1) where L is the length of the focal sequence (i.e., L-1 is the number of gaps).

Following Wuif and Hein (2000) we will use Q to be the parameter of exponential distribution to describe the length distribution of conversion tracts (on the L-1 scale). $Q = (L\text{-}1)/\lambda$ where λ is the mean tract length in basepairs so $1/Q$ is the mean tract length on the L-1 scale.

```
ExponentialDistribution[Q] // Mean
```

$$\frac{1}{Q}$$

For a gene conversion event that starts a distance x (on the L-1 scale) from the focal sequence, then the probability that the gene conversion event completely covers the focal sequence is:

```
Simplify[1 - CDF[ExponentialDistribution[Q], x + 1], Assumptions → {x > 0}]
```

$$e^{-Q\,(1+x)}$$

We now have to consider all the possible positions where the gene conversion could start to get the total probability of a gene conversion that could cover the entire focal sequence. Note that the density of conversion sites is $g(L\text{-}1)$ (not g) on the (L-1) scale, hence this factor is included in the integrand:

```
Simplify[Integrate[g (L - 1) e^(-Q (1+x)), {x, 0, ∞}], Assumptions → {Q > 0}]
```

$$\frac{e^{-Q}\, g\, (-1 + L)}{Q}$$

Multiplying this result by 2(x–k) gives the probability of 'complete' gene conversion, as given in the manuscript.

We can also write this result as a function of L, λ instead of Q:

```
Simplify[Integrate[g (L - 1) e^(-Q (1+x)), {x, 0, ∞}], Assumptions → {Q > 0}] /.
  Q → ((L - 1) / λ) // FullSimplify
```

$$e^{\frac{1-L}{\lambda}}\, g\, \lambda$$

If tract lengths are very short ($\lambda \to 0$ from above, since λ is always positive), then there is no chance

of a conversion tract covering the focal sequence.

```
Limit[e^((1-L)/λ) g λ, λ → 0, Assumptions → {L > 1}, Direction → "FromAbove"]
```

```
0
```

If tracts are very long ($\lambda \to \infty$), then the solution behaves weirdly due to the integration occurring over an infinite number of sites (i.e., even a site that is an infinite distance away can cover the focal tract because the tract length is infinite). However, If we were to hold the genome-wide rate of gene conversion constant, then the per-base rate g would have to decline as we made the genome longer, i.e., $g \propto 1/B$ where B is total number of bases on the chromosome. As $B \to \infty$, then $g \to 0$ and the probability below would remain finite.

```
Limit[e^((1-L)/λ) g λ, λ → Infinity, Assumptions → L > 1, Direction → "FromAbove"]
```

```
g ∞
```

Section D: Investigating the ratio $E^2[\tau]/\mathrm{Var}[\tau]$

Single population result (Figure 5(c) in the main text)

Mean Coalescent Time (Hartfield et al. 2016):

```
MTB[Ω_, Γ_] := (1 + Γ + Ω)/(2 Γ + Ω)
```

```
MTW[Ω_, Γ_] := (2 + Ω)/(2 Γ + Ω)
```

Variance in Coalescent Time (Hartfield et al. 2016):

```
VarTB[Ω_, Γ_] := (3 + 2 Ω + (Γ + Ω)^2)/(2 Γ + Ω)^2
```

```
VarTW[Ω_, Γ_] := (4 + Ω (2 + 2 Γ + Ω))/(2 Γ + Ω)^2
```

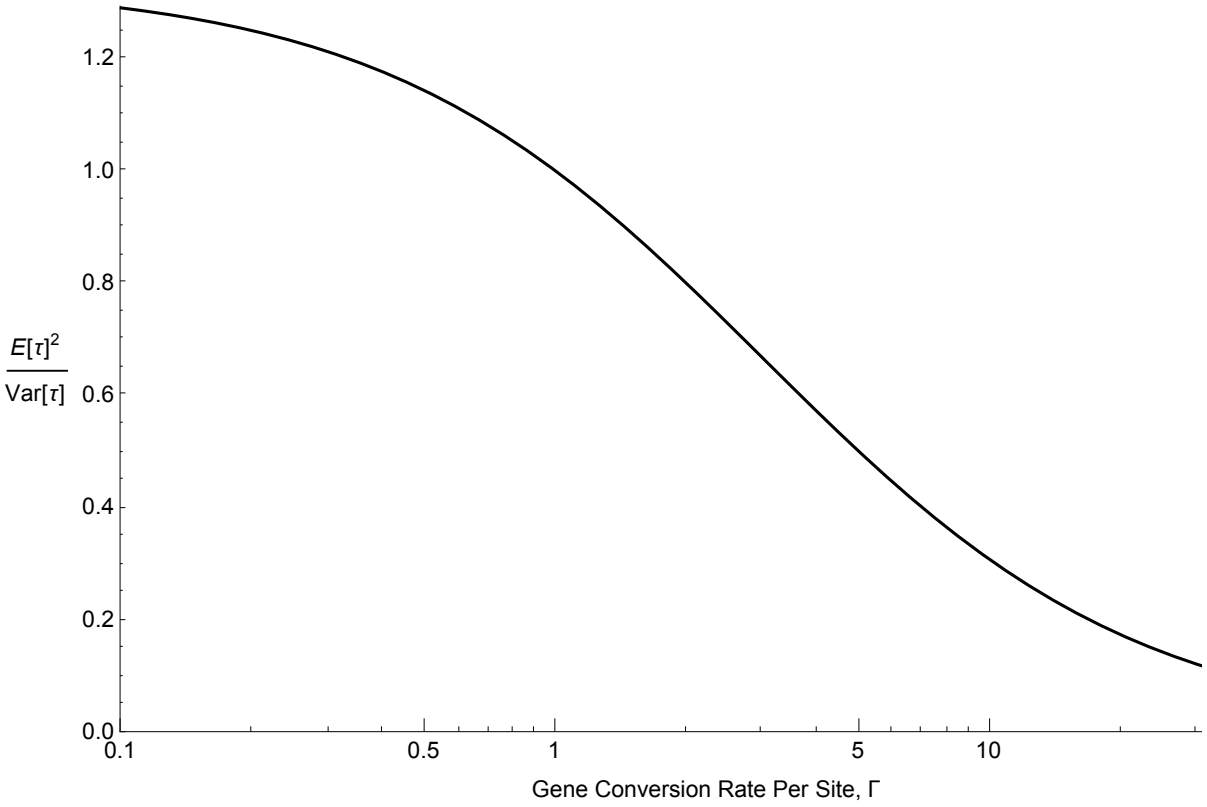
Ratio of E^2/V:

```
RTB[Ω_, Γ_] := (MTB[Ω, Γ])^2/VarTB[Ω, Γ]
```

```
RTW[Ω_, Γ_] := (MTW[Ω, Γ])^2/VarTW[Ω, Γ]
```

Figure 6(d) in the text:

```
LogLinearPlot[{RTW[2, Γ]}, {Γ, 0.1, 50}, PlotRangePadding → 0,
 PlotStyle → Black, Frame → {{True, False}, {True, False}},
 FrameLabel → {{"E[τ]^2 / Var[τ]", None}, {"Gene Conversion Rate Per Site, Γ", None}},
 RotateLabel → False, BaseStyle → {FontSize → 12}]
```



Derivation of results for island model

For the facultative sex coalescent with migration, there are four states:
(1) Two samples reside in different subpopulations
(2) Two samples reside in the same subpopulation, in different individuals
(3) Two samples reside in the same individual, on different chromosomes
(4) Coalescence

The transition matrix can be given as (for m the probabiity of migration; σ the probability of sex; γ the probability of gene conversion; n the within-deme population size; and d the number of demes):

```
MMatFGC = {{1 - 2 m/(d - 1), 2 m/(d - 1), 0, 0}, {2 m, 1 - 1/n - 2 m, (1 - γ)/(2 * n), (1 + γ)/(2 n)},
  {σ * 2 m, σ (1 - 1/n) (1 - 2 m), 1 - σ (1 - 1/n) (1 - 2 m) - σ * 2 m - σ (1 + γ)/(2 * n) - (1 - σ) γ,
  σ (1 + γ)/(2 * n) + (1 - σ) γ}, {0, 0, 0, 1}} // FullSimplify
```

$$\left\{\left\{1-\frac{2\,m}{-1+d},\ \frac{2\,m}{-1+d},\ 0,\ 0\right\},\ \left\{2\,m,\ 1-2\,m-\frac{1}{n},\ -\frac{-1+\gamma}{2\,n},\ \frac{1+\gamma}{2\,n}\right\},\ \left\{2\,m\,\sigma,\ \frac{(1-2\,m)\ (-1+n)\ \sigma}{n},\right.\right.$$
$$\left.\left.(-1+\gamma)\ (-1+\sigma)-\frac{(-1+4\,m+\gamma)\ \sigma}{2\,n},\ \gamma-\gamma\,\sigma+\frac{(1+\gamma)\ \sigma}{2\,n}\right\},\ \{0,\ 0,\ 0,\ 1\}\right\}$$

```
MatrixForm[MMatFGC]
```

$$\begin{pmatrix} 1-\frac{2\,m}{-1+d} & \frac{2\,m}{-1+d} & 0 & 0 \\ 2\,m & 1-2\,m-\frac{1}{n} & -\frac{-1+\gamma}{2\,n} & \frac{1+\gamma}{2\,n} \\ 2\,m\,\sigma & \frac{(1-2\,m)\ (-1+n)\ \sigma}{n} & (-1+\gamma)\ (-1+\sigma)-\frac{(-1+4\,m+\gamma)\ \sigma}{2\,n} & \gamma-\gamma\,\sigma+\frac{(1+\gamma)\ \sigma}{2\,n} \\ 0 & 0 & 0 & 1 \end{pmatrix}$$

In the continuous time limit (assuming σ, γ, m << 1 and n >> 1) we assume that no more than one action occurs per generation. In this case we obtain the simplified transition matrix.

```
MMatFGC2 = {{1 - 2 m/(-1 + d), 2 m/(-1 + d), 0, 0},
  {2 m, 1 - 2 m - 1/n, 1/(2 n), 1/(2 n)}, {0, σ, 1 - σ - γ, γ}, {0, 0, 0, 1}}
```

$$\left\{\left\{1-\frac{2\,m}{-1+d},\ \frac{2\,m}{-1+d},\ 0,\ 0\right\},\ \left\{2\,m,\ 1-2\,m-\frac{1}{n},\ \frac{1}{2\,n},\ \frac{1}{2\,n}\right\},\ \{0,\ \sigma,\ 1-\gamma-\sigma,\ \gamma\},\ \{0,\ 0,\ 0,\ 1\}\right\}$$

This simplified transition matrix provides intuition into how to form the system of Laplace transforms. Working in time units of (2 n d) we see that two samples in different demes leave that state at rate 2M/(d-1) (for M = 2 m n d) with the only outcome being that they are now in the same deme. Two samples in the same deme in different individuals leave that state at rate 2(M+d); if they do leave the state then they go into distinct demes with probability $\frac{2\,M}{2\,(M+d)}$, and they either enter the same individual or coalesce, both with probability $\frac{d}{2\,(M+d)}$. The transition probabilities for two samples in the same individual are as for the single-deme case.

Hence the system of equations for the Laplace transform $\mathbb{E}\left[e^{-sX}\right]$ are given as follows, and can be solved to produce:

```
Solve[V1 == (2 M / (d - 1)) / (2 M / (d - 1) + s) V2 &&
    V2 == (2 (M + d)) / (2 (M + d) + s) ((2 M) / (2 (M + d)) V1 + d / (2 (M + d)) (V3 + 1)) &&
    V3 == (Ω + Γ) / (Ω + Γ + s) ((Ω) / (Ω + Γ) V2 + (Γ) / (Ω + Γ)), {V1, V2, V3}] // FullSimplify
```

$$\left\{\left\{V1 \to (2\,d\,M\,(s+2\,\Gamma+\Omega)) \Big/ \left(\left(4\,d\,M+2\,d\,(-1+d+M)\,s+(-1+d)\,s^2\right)(s+\Gamma)+\left(2\,d\,M+d\,(-1+d+2\,M)\,s+(-1+d)\,s^2\right)\Omega\right),\right.\right.$$
$$V2 \to (d\,(2\,M+(-1+d)\,s)\,(s+2\,\Gamma+\Omega)) \Big/ \left(\left(4\,d\,M+2\,d\,(-1+d+M)\,s+(-1+d)\,s^2\right)(s+\Gamma)+\left(2\,d\,M+d\,(-1+d+2\,M)\,s+(-1+d)\,s^2\right)\Omega\right),$$
$$\left.\left.V3 \to \left(\left(4\,d\,M+2\,d\,(-1+d+M)\,s+(-1+d)\,s^2\right)\Gamma+d\,(2\,M+(-1+d)\,s)\,\Omega\right) \Big/ \left(\left(4\,d\,M+2\,d\,(-1+d+M)\,s+(-1+d)\,s^2\right)(s+\Gamma)+\left(2\,d\,M+d\,(-1+d+2\,M)\,s+(-1+d)\,s^2\right)\Omega\right)\right\}\right\}$$

We check if we can recover the mean coalescent times by taking the derivative of each result and evaluating at s = 0:

```
D[(2 d M (s + 2 Γ + Ω)) / ((4 d M + 2 d (-1 + d + M) s + (-1 + d) s^2) (s + Γ) +
        (2 d M + d (-1 + d + 2 M) s + (-1 + d) s^2) Ω) /.
    {s → (-s)}, s] /. s → 0 // FullSimplify
D[(d (2 M + (-1 + d) s) (s + 2 Γ + Ω)) / ((4 d M + 2 d (-1 + d + M) s + (-1 + d) s^2) (s + Γ) +
        (2 d M + d (-1 + d + 2 M) s + (-1 + d) s^2) Ω) /.
    {s → (-s)}, s] /. s → 0 // FullSimplify
D[((4 d M + 2 d (-1 + d + M) s + (-1 + d) s^2) Γ + d (2 M + (-1 + d) s) Ω) /
      ((4 d M + 2 d (-1 + d + M) s + (-1 + d) s^2) (s + Γ) +
        (2 d M + d (-1 + d + 2 M) s + (-1 + d) s^2) Ω) /.
    {s → (-s)}, s] /. s → 0 // FullSimplify
```

$$\frac{-1+d}{2\,M}+\frac{1+\Gamma+\Omega}{2\,\Gamma+\Omega}$$

$$\frac{1+\Gamma+\Omega}{2\,\Gamma+\Omega}$$

$$\frac{2+\Omega}{2\,\Gamma+\Omega}$$

We can calculate $E[X^2]$ by taking the double derivative of each solution, evaluated at s = 0:

```
D[(2 d M (s + 2 Γ + Ω)) / ((4 d M + 2 d (-1 + d + M) s + (-1 + d) s^2) (s + Γ) +
        (2 d M + d (-1 + d + 2 M) s + (-1 + d) s^2) Ω) /.
    {s → (-s)}, s, s] /. s → 0 // FullSimplify
D[(d (2 M + (-1 + d) s) (s + 2 Γ + Ω)) / ((4 d M + 2 d (-1 + d + M) s + (-1 + d) s^2) (s + Γ) +
        (2 d M + d (-1 + d + 2 M) s + (-1 + d) s^2) Ω) /.
    {s → (-s)}, s, s] /. s → 0 // FullSimplify
D[((4 d M + 2 d (-1 + d + M) s + (-1 + d) s^2) Γ + d (2 M + (-1 + d) s) Ω) /
      ((4 d M + 2 d (-1 + d + M) s + (-1 + d) s^2) (s + Γ) +
        (2 d M + d (-1 + d + 2 M) s + (-1 + d) s^2) Ω) /.
    {s → (-s)}, s, s] /. s → 0 // FullSimplify
```

$$\frac{(-1+d)^2}{2M^2}+\frac{(-1+d)\ (d-\Gamma+2d\Gamma-\Omega+2d\Omega)}{dM\ (2\Gamma+\Omega)}+\frac{2\left(2+\Gamma+\Gamma^2+2\Gamma\Omega+\Omega\ (2+\Omega)\right)}{(2\Gamma+\Omega)^2}$$

$$\left((\Gamma+\Omega)\ (2\Gamma+\Omega)-2d\ (\Gamma+\Omega)\ (2\Gamma+\Omega)+ d^2\ (\Gamma+\Omega)\ (2\Gamma+\Omega)+2dM\left(2+\Gamma+\Gamma^2+2\Gamma\Omega+\Omega\ (2+\Omega)\right)\right)\Big/\left(dM\ (2\Gamma+\Omega)^2\right)$$

$$\left(8dM+2\ (3dM+\Gamma+d\ (-2+d+M)\ \Gamma)\ \Omega+\left((-1+d)^2+2dM\right)\Omega^2\right)\Big/\left(dM\ (2\Gamma+\Omega)^2\right)$$

The variance is calculated as $E\left[X^2\right]-(E[X])^2$:

```
((-1 + d)^2/(2 M^2) + ((-1 + d) (d - Γ + 2 d Γ - Ω + 2 d Ω))/(d M (2 Γ + Ω)) +
    (2 (2 + Γ + Γ^2 + 2 Γ Ω + Ω (2 + Ω)))/(2 Γ + Ω)^2) -
  ((-1 + d)/(2 M) + (1 + Γ + Ω)/(2 Γ + Ω))^2 // FullSimplify
```

$$\frac{(-1+d)^2}{4M^2}+\frac{(-1+d)^2\ (\Gamma+\Omega)}{dM\ (2\Gamma+\Omega)}+\frac{3+2\Omega+(\Gamma+\Omega)^2}{(2\Gamma+\Omega)^2}$$

```
((Γ + Ω) (2 Γ + Ω) - 2 d (Γ + Ω) (2 Γ + Ω) + d^2 (Γ + Ω) (2 Γ + Ω) +
      2 d M (2 + Γ + Γ^2 + 2 Γ Ω + Ω (2 + Ω)))/(d M (2 Γ + Ω)^2) - ((1 + Γ + Ω)/(2 Γ + Ω))^2 // Apart
```

$$\frac{1-2d+d^2+dM}{dM}+\frac{3-4\Gamma+\Gamma^2}{(2\Gamma+\Omega)^2}+\frac{2dM-\Gamma+2d\Gamma-d^2\Gamma-2dM\Gamma}{dM\ (2\Gamma+\Omega)}$$

```
(8 d M + 2 (3 d M + Γ + d (-2 + d + M) Γ) Ω + ((-1 + d)^2 + 2 d M) Ω^2)/(d M (2 Γ + Ω)^2) -
  ((2 + Ω)/(2 Γ + Ω))^2 // Apart
```

$$\frac{1-2d+d^2+dM}{dM}-\frac{4\ (-1+\Gamma)}{(2\Gamma+\Omega)^2}-\frac{2\left(-dM+\Gamma-2d\Gamma+d^2\Gamma+dM\Gamma\right)}{dM\ (2\Gamma+\Omega)}$$

Below are definitions of the mean and variance of coalescent times:

```
MTW[Ω_, Γ_] := (2 + Ω)/(2 Γ + Ω)
MTB[Ω_, Γ_] := (1 + Γ + Ω)/(2 Γ + Ω)
MTD[M_, d_, Ω_, Γ_] := (1 + Γ + Ω)/(2 Γ + Ω) + 2 M/(d - 1)
VarTWM[M_, d_, Ω_, Γ_] := (1 - 2 d + d^2 + d M)/(d M) - 4 (-1 + Γ)/(2 Γ + Ω)^2 - 2 (-d M + Γ - 2 d Γ + d^2 Γ + d M Γ)/(d M (2 Γ + Ω))
VarTBM[M_, d_, Ω_, Γ_] := (1 - 2 d + d^2 + d M)/(d M) + (3 - 4 Γ + Γ^2)/(2 Γ + Ω)^2 + (2 d M - Γ + 2 d Γ - d^2 Γ - 2 d M Γ)/(d M (2 Γ + Ω))
VarTDM[M_, d_, Ω_, Γ_] := (-1 + d)^2/(4 M^2) + (-1 + d)^2 (Γ + Ω)/(d M (2 Γ + Ω)) + (3 + 2 Ω + (Γ + Ω)^2)/(2 Γ + Ω)^2
```

The variance terms evaluated at d = 1 gives the single-deme results:

```
VarTWM[M, 1, Ω, Γ] // FullSimplify
```

$$\frac{4 + \Omega\ (2 + 2\ \Gamma + \Omega)}{(2\ \Gamma + \Omega)^2}$$

```
VarTBM[M, 1, Ω, Γ] // FullSimplify
```

$$\frac{3 + 2\ \Omega + (\Gamma + \Omega)^2}{(2\ \Gamma + \Omega)^2}$$

```
VarTDM[M, 1, Ω, Γ]
```

$$\frac{3 + 2\ \Omega + (\Gamma + \Omega)^2}{(2\ \Gamma + \Omega)^2}$$

The derivative of the variance, with respect to the migration rate, is negative for all cases:

```
D[VarTWM[M, d, Ω, Γ], M] // FullSimplify
```

$$-\frac{(-1 + d)^2\ \Omega}{d\ M^2\ (2\ \Gamma + \Omega)}$$

```
D[VarTBM[M, d, Ω, Γ], M] // FullSimplify
```

$$-\frac{(-1 + d)^2\ (\Gamma + \Omega)}{d\ M^2\ (2\ \Gamma + \Omega)}$$

```
D[VarTDM[M, d, Ω, Γ], M] // FullSimplify
```

$$-\left(\left((-1 + d)^2\ (2\ M\ (\Gamma + \Omega) + d\ (2\ \Gamma + \Omega))\right) \Big/ \left(2\ d\ M^3\ (2\ \Gamma + \Omega)\right)\right)$$

Plot of the ratio $\mathbb{E}^2/\mathrm{Var}$ within individuals as a function of the gene conversion rate Γ, for the single-deme case (black); M = 10 (red) or M = 1 (blue). See also Figure J in the Supplementary Material File.

```
RTWM[M_, d_, Ω_, Γ_] := (MTW[Ω, Γ])^2/VarTWM[M, d, Ω, Γ]
```

```
LogLinearPlot[{RTW[2, Γ], RTWM[10, 4, 2, Γ], RTWM[1, 4, 2, Γ]},
 {Γ, 0.1, 50}, PlotRangePadding → 0, PlotStyle → {Black, Red, Blue},
 Frame → {{True, False}, {True, False}},
 FrameLabel → {{"E[τ]^2 / Var[τ]", None}, {"Gene Conversion Rate Per Site, Γ", None}},
 RotateLabel → False, BaseStyle → {FontSize → 12}]
```