# **Supplementary Information**

Genetic incompatibilities between mitochondria and nuclear genes: effect on gene flow and speciation

# Authors

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## S1 Recursion equations used for numerical analysis

Below, we give for all four models a formal description of the recursion equations that are used for the numerical analysis of the effective migration rate (Fig. S4). The recursion equations describe the change in allele frequency over time. For a given parameter set, the effective migration rate is calculated by substituting the allele frequencies at the marker locus in formula (1). We assume that the neutral marker locus has two alleles,  $M_1$  and  $M_2$ , and denote the frequency of allele  $M_2$  in the island population in generation t by p(t). The frequency q of  $M_2$  in the mainland population does not affect the effective migration rate as far as it is constant and the limit is taken as  $t \to \infty$  (Kobayashi et al., 2008). Therefore, we assume that the mainland population is fixed for allele  $M_2$  (q=1).

#### Model A: The haploid model with mito-nuclear incompatibility

Let  $F_t(mt_iN_jM_k)$  and  $G_t(mt_iN_jM_k)$  be the frequencies females and males, respectively, of genotype  $mt_iN_jM_k$  in the island population at the beginning of generation *t*. Note that the frequencies are here defined as fractions relative to the entire island population. It holds that

(A.1) 
$$\sum_{i=1}^{2} \sum_{j=1}^{2} \sum_{k=1}^{2} F_t(mt_i N_j M_k) = \sum_{i=1}^{2} \sum_{j=1}^{2} \sum_{k=1}^{2} G_t(mt_i N_j M_k) = \frac{1}{2}.$$

The even sex ratio is maintained because the primary sex ratio is even and both sexes suffer equally from genetic incompatibilities. In the following, we derive recursion equations that describe the allele frequency change between subsequent generations.

Let *K* and *L* be the size of the island population and the number of immigrants per generation, respectively. Let also  $e_f$  and  $e_m$  be the emigration rates of females and males, respectively, from the island population. By definition, the immigration rate *m* is given by

(A.2) 
$$m = \frac{L}{\left(\frac{K}{2}\right)(1-e_f) + \left(\frac{K}{2}\right)(1-e_m) + L} = \frac{L}{K\left(1-\frac{e_f+e_m}{2}\right) + L}$$

We assume that the total number of emigrants is equal to the number of immigrants, so that

(A.3) 
$$K\left(\frac{e_f+e_m}{2}\right) = L.$$

Substituting (A.3) into (A.2) yields

$$(A.4) mtextbf{m} = \frac{e_f + e_m}{2}.$$

Further, we assume that the number of emigrating females (males) is equal to the number of immigrating females (males), so that

(A.5) 
$$\left(\frac{K}{2}\right)e_f = Lm_f,$$

(A.6) 
$$\left(\frac{\kappa}{2}\right)e_m = L(1-m_f)$$

Combining equations (A.3)-(A.6) yields

(A.7)  $e_f = 2mm_f,$ (A.8)  $e_m = 2m(1 - m_f).$ 

Let  $F_t^+(mt_iN_iM_i)$  and  $G_t^+(mt_iN_iM_i)$  be the frequencies of females and males, respectively, of genotype  $mt_iN_iM_i$  in the island population immediately after migration in generation *t*. It holds that

(A.9) 
$$F_t^+(mt_iN_jM_k) = \frac{(1-e_f)KF_t(mt_iN_iM_k) + Lm_f\delta_{2i}\delta_{2j}\delta_{2k}}{K\left(1-\frac{e_f+e_m}{2}\right) + L},$$

(A.10) 
$$G_t^+(mt_iN_jM_k) = \frac{(1-e_m)KG_t(mt_iN_jM_k) + L(1-m_f)\delta_{2i}\delta_{2j}\delta_{2k}}{K\left(1-\frac{e_f+e_m}{2}\right) + L}$$

where  $\delta_{ij}$  is the Kronecker's delta. Substituting (A.3) and (A.4) into (A.9)-(A.10) yields

(A.11) 
$$F_t^+(mt_iN_jM_k) = (1-2mm_f)F_t(mt_iN_jM_k) + mm_f\delta_{2i}\delta_{2j}\delta_{2k},$$

(A.12) 
$$G_{t}^{+}(mt_{i}N_{j}M_{k}) = (1 - 2m(1 - m_{f}))G_{t}(mt_{i}N_{j}M_{k}) + m(1 - m_{f})\delta_{2i}\delta_{2j}\delta_{2k}.$$

Summing up (A.11) and (A.12) over all genotypes shows that migration does not affect the sex ratio. Note that the frequency of  $mt_iN_jM_k$  among females (males) after migration is given by  $\frac{F_t^+(mt_iN_jM_k)}{\frac{1}{2}} = 2F_t^+(mt_iN_jM_k) (2G_t^+(mt_iN_jM_k))$ . Therefore, the frequency of matings between  $mt_iN_jM_k$  females and  $mt_uN_vM_w$  males is given by  $4F_t^+(mt_iN_jM_k)G_t^+(mt_uN_vM_w)$ . Therefore, from Table 1, genotype frequencies in the next generations are given by

$$(A.13) F_{t+1}(mt_aN_bM_c) = G_{t+1}(mt_aN_bM_c) = \frac{1}{2T}\sum_{j=1}^2 \sum_{k=1}^2 \sum_{u=1}^2 \sum_{\nu=1}^2 \sum_{w=1}^2 4F_t^+(mt_aN_jM_k)G_t^+(mt_uN_\nu M_w)\left(\frac{\delta_{bj}+\delta_{b\nu}}{2}\right)\left(\frac{\delta_{ck}+\delta_{cw}}{2}\right)\left(1-s_a(1-\delta_{ab})\right),$$

where

$$T = \sum_{a=1}^{2} \sum_{b=1}^{2} \sum_{c=1}^{2} \sum_{j=1}^{2} \sum_{k=1}^{2} \sum_{u=1}^{2} \sum_{v=1}^{2} \sum_{w=1}^{2} 4F_{t}^{+}(mt_{a}N_{j}M_{k})G_{t}^{+}(mt_{u}N_{v}M_{w})\left(\frac{\delta_{bj}+\delta_{bv}}{2}\right)\left(\frac{\delta_{ck}+\delta_{cw}}{2}\right)\left(1-s_{a}(1-\delta_{ab})\right).$$

We can compute genotype frequencies in any generation by iterating (A.11)-(A.13). In particular, the frequency of allele  $M_2$  at generation t is given by

(A.14) 
$$p(t) = \sum_{i=1}^{2} \sum_{j=1}^{2} \left( F_t(mt_i N_j M_2) + G_t(mt_i N_j M_2) \right).$$

For the numerical analysis, we used the initial condition that  $M_2$  is absent in the island population,  $F_0(mt_iN_jM_k) = G_0(mt_iN_jM_k) = \frac{\delta_{1i}\delta_{1j}\delta_{1k}}{2}$ , iterated equations (A.11)-(A.13) a fixed number of times, and calculated p(t). The effective migration rate was calculated by substituting p(t) in formulae (1). As a result, we found that the numerical estimates of the effective migration rate converge to the analytical formula shown in equation (14) if the limit is taken for  $t \to \infty$  (Fig. S4).

#### Model B: The haploid model with nuclear-nuclear incompatibility

For *Model B*, we do not have to distinguish males and females, and assume that the organisms are hermaphrodites. Let  $H_t(A_iB_jM_k)$  be the frequency of genotype  $A_iB_jM_k$  in the island population at the beginning of generation *t*, where  $M_i$  denotes the alleles at the marker locus. The allele frequencies after migration are given by

(A.15) 
$$H_t^+(A_i B_j M_k) = (1-m)H_t(A_i B_j M_k) + m\delta_{2i}\delta_{2j}\delta_{2k},$$

given that the emigration rate is equal to the immigration rate m. From Table 2, genotype frequencies in the next generation are given by

$$(A.16) \qquad H_{t+1}(A_{a}B_{b}M_{c}) = \\ \frac{1}{T}\sum_{i=1}^{2}\sum_{j=1}^{2}\sum_{k=1}^{2}\sum_{u=1}^{2}\sum_{v=1}^{2}\sum_{w=1}^{2}H_{t}^{+}(A_{i}B_{j}M_{k})H_{t}^{+}(A_{u}B_{v}M_{w})\left(\frac{\delta_{ai}+\delta_{au}}{2}\right)\left(\frac{\delta_{bj}+\delta_{bv}}{2}\right)\left(\frac{\delta_{ck}+\delta_{cw}}{2}\right)\left(1-s_{a}(1-\delta_{ab})\right),$$

where  $s_1 = s_B$ ,  $s_2 = s_A$  and

$$T =$$

$$\sum_{a=1}^{2} \sum_{b=1}^{2} \sum_{i=1}^{2} \sum_{j=1}^{2} \sum_{k=1}^{2} \sum_{u=1}^{2} \sum_{v=1}^{2} \sum_{w=1}^{2} H_{t}^{+} (A_{i}B_{j}M_{k}) H_{t}^{+} (A_{u}B_{v}M_{w}) \left(\frac{\delta_{ai}+\delta_{au}}{2}\right) \left(\frac{\delta_{bj}+\delta_{bv}}{2}\right) \left(1-s_{a}(1-\delta_{ab})\right).$$

The initial condition is given by  $H_0(A_i B_j M_k) = \delta_{1i} \delta_{1j} \delta_{1k}$  and the frequency of allele  $M_2$  by

(A.17) 
$$p(t) = \sum_{i=1}^{2} \sum_{j=1}^{2} H_t (A_i B_j M_2).$$

As above, the effective migration rate was calculated by substituting p(t) in formulae (1). As a result, we found that the numerical estimates of the effective migration rate converge to the analytical formula shown in equation (22) in the limit  $t \to \infty$  (Fig. S4).

## Model C: The diploid model with mito-nuclear incompatibility

For convenience, we let  $N_j N_k (M_l M_n)$  denote the genotype of an individual who inherited  $N_j$  $(M_l)$  from its mother and  $N_k (M_n)$  from its father. Let  $F_t(mt_iN_jN_kM_lM_n)$  and  $G_t(mt_iN_jN_kM_lM_n)$  be the frequencies of females and males, respectively, of genotype  $mt_iN_jN_kM_lM_n$  in the island population in generation *t*. Following the same arguments as for *Model A*, we find that the genotype frequencies after migration are given by

(A.18) 
$$F_t^+(mt_iN_jN_kM_lM_n) = (1 - 2mm_f)F_t(mt_iN_jN_kM_lM_n) + mm_f\delta_{2i}\delta_{2j}\delta_{2k}\delta_{2l}\delta_{2n},$$
  
(A.19) 
$$G_t^+(mt_iN_jN_kM_lM_n) = (1 - 2m(1 - m_f))G_t(mt_iN_jN_kM_lM_n)$$

 $+m(1-m_f)\delta_{2i}\delta_{2j}\delta_{2k}\delta_{2l}\delta_{2n}.$ 

From Table 3, genotype frequencies in the next generation are given by

$$(A.20) F_{t+1}(mt_aN_bN_cM_dM_e) = G_{t+1}(mt_aN_bN_cM_dM_e) = \frac{1}{2T}\sum_{j=1}^2\sum_{k=1}^2\sum_{l=1}^2\sum_{n=1}^2\sum_{u=1}^2\sum_{v=1}^2\sum_{w=1}^2\sum_{x=1}^2\sum_{y=1}^24F_t^+(mt_aN_jN_kM_lM_n)G_t^+(mt_uN_vN_wM_xM_y) \cdot \left(\frac{\delta_{bj} + \delta_{bk}}{2}\right)\left(\frac{\delta_{cv} + \delta_{cw}}{2}\right)\left(\frac{\delta_{dl} + \delta_{dn}}{2}\right)\left(\frac{\delta_{ex} + \delta_{ey}}{2}\right)[1 - h_as_a\{(1 - \delta_{ab})\delta_{ac} + (1 - \delta_{ac})\delta_{ab}\}],$$

where T =

$$\sum_{a=1}^{2} \sum_{b=1}^{2} \sum_{c=1}^{2} \sum_{d=1}^{2} \sum_{e=1}^{2} \sum_{j=1}^{2} \sum_{k=1}^{2} \sum_{l=1}^{2} \sum_{n=1}^{2} \sum_{u=1}^{2} \sum_{v=1}^{2} \sum_{w=1}^{2} \sum_{x=1}^{2} \sum_{y=1}^{2} 4F_{t}^{+} (mt_{a}N_{j}N_{k}M_{l}M_{n})G_{t}^{+} (mt_{u}N_{v}N_{w}M_{x}M_{y}) \\ \left(\frac{\delta_{bj}+\delta_{bk}}{2}\right) \left(\frac{\delta_{cv}+\delta_{cw}}{2}\right) \left(\frac{\delta_{dl}+\delta_{dn}}{2}\right) \left(\frac{\delta_{ex}+\delta_{ey}}{2}\right) [1 - h_{a}s_{a}\{(1 - \delta_{ab})\delta_{ac} + (1 - \delta_{ac})\delta_{ab}\}] (1 - s_{a}(1 - \delta_{ab})(1 - \delta_{ac})).$$

The initial condition is given by  $F_0(mt_iN_jN_kM_lM_n) = G_0(mt_iN_jN_kM_lM_n) = \frac{\delta_{1i}\delta_{1j}\delta_{1k}\delta_{1l}\delta_{1n}}{2}$ and the frequency of the allele  $M_2$  by

(A.21) 
$$p(t) = \sum_{i=1}^{2} \sum_{j=1}^{2} \sum_{k=1}^{2} \sum_{l=1}^{2} \sum_{n=1}^{2} \left( F_t(mt_i N_j N_k M_l M_n) + G_t(mt_i N_j N_k M_l M_n) \right) \left( \frac{\delta_{2l} + \delta_{2n}}{2} \right).$$

As above, the effective migration rate was calculated by substituting p(t) in formulae (1). As a result, we found that the numerical estimates of the effective migration rate converge to the analytical formula shown in equation (35) in the limit  $t \to \infty$  (Fig. S4).

#### Model D-1: The diploid model with asymmetric nuclear-nuclear

# incompatibility

As in *Model B*, we assume that the organisms under consideration are hermaphrodites. As in *Model C*, we let  $A_iA_j$  denote the genotype of an individual who inherited  $A_i$  from its "mother" (e.g., the individual who contributed an ovule) and  $A_j$  from its "father" (e.g., the individual who contributed pollen). The same notation applies to the second incompatibility locus and the neutral marker locus. Let  $H_t(A_iA_jB_kB_lM_nM_r)$  denote the frequency of genotype  $A_iA_jB_kB_lM_nM_r$  at the beginning of generation *t*. Then, the genotype frequencies after migration are given by

(A.22) 
$$H_t^+(A_iA_jB_kB_lM_nM_r) = (1-m)H_t(A_iA_jB_kB_lM_nM_r) + m\delta_{2i}\delta_{2j}\delta_{2k}\delta_{2l}\delta_{2n}\delta_{2r}.$$

From Table 4, genotype frequencies in the next generation are given by

$$(A.23) \qquad H_{t+1}(A_{a}A_{b}B_{c}B_{d}M_{e}M_{f}) = \frac{1}{T}\sum_{i=1}^{2}\sum_{j=1}^{2}\sum_{k=1}^{2}\sum_{l=1}^{2}\sum_{n=1}^{2}\sum_{r=1}^{2}\sum_{x=1}^{2}\sum_{v=1}^{2}\sum_{w=1}^{2}\sum_{x=1}^{2}\sum_{x=1}^{2}\sum_{y=1}^{2}\sum_{z=1}^{2}H_{t}^{+}(A_{i}A_{j}B_{k}B_{l}M_{n}M_{r})$$

$$H_{t}^{+}(A_{u}A_{v}B_{w}B_{x}M_{y}M_{z})\left(\frac{\delta_{ai}+\delta_{aj}}{2}\right)\left(\frac{\delta_{bu}+\delta_{bv}}{2}\right)\left(\frac{\delta_{ck}+\delta_{cl}}{2}\right)\left(\frac{\delta_{dw}+\delta_{dx}}{2}\right)\left(\frac{\delta_{en}+\delta_{er}}{2}\right)\left(\frac{\delta_{fy}+\delta_{fz}}{2}\right)$$

$$(1-s_{A}\delta_{2a}\delta_{2b}\delta_{1c}\delta_{1d})(1-h_{A}s_{A}(1-\delta_{ab}\delta_{cd})(1-\delta_{1a}\delta_{1b})(1-\delta_{2c}\delta_{2d})).$$

where

$$T = \sum_{a=1}^{2} \sum_{b=1}^{2} \sum_{c=1}^{2} \sum_{d=1}^{2} \sum_{e=1}^{2} \sum_{f=1}^{2} \sum_{i=1}^{2} \sum_{j=1}^{2} \sum_{k=1}^{2} \sum_{l=1}^{2} \sum_{n=1}^{2} \sum_{r=1}^{2} \sum_{u=1}^{2} \sum_{v=1}^{2} \sum_{x=1}^{2} \sum_{y=1}^{2} \sum_{z=1}^{2} \sum_{r=1}^{2} \sum_{u=1}^{2} \sum_{v=1}^{2} \sum_{x=1}^{2} \sum_{y=1}^{2} \sum_{z=1}^{2} \sum_{r=1}^{2} \sum_{u=1}^{2} \sum_{v=1}^{2} \sum_{x=1}^{2} \sum_{y=1}^{2} \sum_{z=1}^{2} \sum_{r=1}^{2} \sum_{u=1}^{2} \sum_{v=1}^{2} \sum_{x=1}^{2} \sum_{v=1}^{2} \sum_{v=1}^{2} \sum_{x=1}^{2} \sum_{v=1}^{2} \sum_{v=1}^{2} \sum_{x=1}^{2} \sum_{v=1}^{2} \sum_{v=1}^{2} \sum_{x=1}^{2} \sum_{v=1}^{2} \sum_{v=1}^{2}$$

The initial condition is given by  $H_0(A_iA_jB_kB_lM_nM_r) = \delta_{1i}\delta_{1j}\delta_{1k}\delta_{1l}\delta_{1n}\delta_{1r}$  and the frequency of allele  $M_2$  at generation *t* by

(A.24) 
$$p(t) = \sum_{i=1}^{2} \sum_{j=1}^{2} \sum_{k=1}^{2} \sum_{l=1}^{2} \sum_{n=1}^{2} \sum_{r=1}^{2} H_t \left( A_i A_j B_k B_l M_n M_r \right) \left( \frac{\delta_{2n} + \delta_{2r}}{2} \right).$$

The convergence of equation (1) to equation (36) can be confirmed as we did for *Model A*.

## Model D-2: The diploid model with symmetric nuclear-nuclear

# incompatibility

In the case of symmetric nuclear-nuclear incompatibility, eq. (A.21) still holds for the migration phase. For the mating phase, from Table 5, we have

$$(A.25) \qquad H_{t+1}(A_{a}A_{b}B_{c}B_{d}M_{e}M_{f}) = \frac{1}{T}\sum_{i=1}^{2}\sum_{j=1}^{2}\sum_{k=1}^{2}\sum_{l=1}^{2}\sum_{n=1}^{2}\sum_{r=1}^{2}\sum_{u=1}^{2}\sum_{v=1}^{2}\sum_{w=1}^{2}\sum_{x=1}^{2}\sum_{y=1}^{2}\sum_{z=1}^{2}H_{t}^{+}(A_{i}A_{j}B_{k}B_{l}M_{n}M_{r}) \\ H_{t}^{+}(A_{u}A_{v}B_{w}B_{x}M_{y}M_{z})\left(\frac{\delta_{ai}+\delta_{aj}}{2}\right)\left(\frac{\delta_{bu}+\delta_{bv}}{2}\right)\left(\frac{\delta_{ck}+\delta_{cl}}{2}\right)\left(\frac{\delta_{dw}+\delta_{dx}}{2}\right)\left(\frac{\delta_{en}+\delta_{er}}{2}\right)\left(\frac{\delta_{fy}+\delta_{fz}}{2}\right) \\ (1-s\delta_{ab}\delta_{cd}(1-\delta_{ac}))(1-hs(1-\delta_{ab}\delta_{cd})),$$

where

$$T = \sum_{a=1}^{2} \sum_{b=1}^{2} \sum_{c=1}^{2} \sum_{d=1}^{2} \sum_{e=1}^{2} \sum_{f=1}^{2} \sum_{i=1}^{2} \sum_{j=1}^{2} \sum_{k=1}^{2} \sum_{l=1}^{2} \sum_{n=1}^{2} \sum_{r=1}^{2} \sum_{u=1}^{2} \sum_{v=1}^{2} \sum_{w=1}^{2} \sum_{x=1}^{2} \sum_{y=1}^{2} \sum_{z=1}^{2} \sum_{r=1}^{2} \sum_{w=1}^{2} \sum_{w=1}^{2}$$

 $hs(1-\delta_{ab}\delta_{cd})).$ 

The initial condition is given by  $H_0(A_iA_jB_kB_lM_nM_r) = \delta_{1i}\delta_{1j}\delta_{1k}\delta_{1l}\delta_{1n}\delta_{1r}$  and the frequency of allele  $M_2$  by equation (A.24). The convergence of equation (1) can be checked in the same way as we did for *Model A*.

# **S2** Supplementary Figures



**Figure S1. Fitness graph for haploid NNI.** Shown is the fitness graph for *Model B* (nuclear-nuclear incompatibilities, haploid genetics). There are four genetic classes. Class transitions are indicated by black arrows and attached weighting factors. The graph describes gene flow of rare male and female migrants of genotype  $A_2B_2$  in an island population consisting of mostly  $A_1B_1$  individuals. Blue indicates the migrant genotypes, gray the hybrid genotypes, and white the resident genotypes. Gene flow is measured at a neutrally selected nuclear marker locus, which is not shown in the graph (Methods).



**Figure S2. Fitness graph for diploid MtNI.** Shown is the fitness graph for *Model C* (mito-nuclear incompatibilities, diploid genetics). There are ten genetic classes. Class transitions are indicated by black arrows and attached weighting factors. The graph describes gene flow of rare male and female migrants of genotype  $m_2N_2N_2$  in an island population consisting of mostly  $m_1N_1N_1$  individuals. Blue indicates the migrant genotypes, gray the hybrid genotypes, and white the resident genotypes. Gene flow is measured at a neutrally selected nuclear marker locus, which is not shown in the graph (Methods).



**Figure S3. Gene flow reduction for models with diploid genetics.** Shown is the gene flow factor for an unlinked neutral locus as a function of the level of incompatibility. **(A)** *Model C* with dominant symmetric MtNI and varying incompatibility level  $s_1=s_2$ . **(B)** *Model C* with dominant asymmetric MtNI of type I ( $s_1=0$ ) and varying incompatibility level  $s_2$ . **(C)** *Model C* with dominant asymmetric MtNI of type I ( $s_2=0$ ) and varying incompatibility level  $s_1$ . **(D)** *Model D* with dominant symmetric ( $s_A=s_B$ ) and asymmetric ( $s_B=0$ ) NNI and varying incompatibility level  $s_A$ . Parameters:  $h_1=h_2=h_A=h_B=1$ .



**Figure S4. Gene flow factor: numerical calculations versus analytical formulae.** The figure shows that the numerical estimates of the gene flow factor approximate the derived analytical formula well. Numerical estimates were calculated by numerical iteration of recursion equations (see SI), and subsequent substitution of the marker allele frequencies in formula (1). Solid lines indicate numerical estimates of the gene flow factor as a function of the generation, *t*, and dashed lines the results of the corresponding analytical formulae. **(A)** Model A with  $s_1=0.2$ ,  $s_2=0.8$ , m=0.001,  $m_f=0.9$  (open squares),  $m_f=0.5$  (filled squares),  $m_f=0.1$  (open triangles). **(B)** Model B with m=0.001,  $s_A=s_B=0.8$  (open squares),  $s_A=0.8$ ,  $s_B=0.2$  (filled squares). **(C)** Model C with m=0.001,  $m_f=0.7$ ,  $s_1=s_2=0.5$ ,  $h_1=h_2=0$  (open squares),  $s_1=0.5$ ,  $s_2=0.2$ ,  $h_1=h_2=1$  (filled squares),  $s_1=0.5$ ,  $s_2=0.2$ ,  $h_1=0.3$ ,  $h_2=0.8$  (open triangles). **(D)** Model D with m=0.001,  $s_A=s_B=0.5$  (open squares),  $h_A=h_B=1$  (filled squares).