A reassessment of explanations for discordant introgressions of mitochondrial and nuclear genomes
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Examples of massive mitochondrial introgressions combined with no or very limited nuclear introgressions (i.e., *mito-nuclear discordance*) are accumulating, stimulating the development of various hypotheses to explain this pattern. On the one hand, *selective hypotheses* propose a selective advantage of the introgressing mitochondrial variants, or counter-selection of the nuclear genome; on the other hand, *neutral hypotheses* invoke sex-biased processes and/or drift and/or spatial invasions. The neutral hypotheses however are mostly verbal and have not been quantitatively evaluated. Here we reassess all these hypotheses using simulations under a wide range of demographic and genetic scenarios.

### General simulation settings

- **Spatially explicit simulations of a secondary contact:**
  - 2 habitats, each with 15 x 10 demes of \( N=10 \) diploid adult pairs (\( N_1=N_2=3,000 \))
  - Forward individuals-based simulations of 6,000 generations of secondary contact considering *spatially limited dispersal* (IBD), sex-biased processes, spatial invasion, and selection
  - Standard coalescent to simulate 80,000 generations of divergence between the ancestral populations

- **Multi-locus nuclear genome:**
  - One chromosome with 20 pairs of loci (1 neutral & 1 selected)
  - Recombination within and between pairs of loci

- **Mitochondrial genome:**
  - One chromosome with one pair of linked loci (1 neutral + 1 selected)

- **Local adaptation** is modeled with one nuclear "speciation" locus (proxy for many co-adapted loci in LD):
  - Lower fitness in the non-original habitat
  - Lower fitness for hybrids in both habitats

### Additional demographic and genetic processes explored

- **Sex-biased processes:**
  - Asymmetric crosses: one sex is preferred by both taxa e.g. the female cow in the Bison/Cow example
  - Sex-specific dispersal: one sex disperses more than the other
  - Sex-specific survival: one sex has higher mortality than the other

- **Spatial invasion combined with sex-biased dispersal:**
  - One habitat expands over the other after secondary contact, gradually but completely.
  - Direction and strength of sex-biased dispersal varies among different scenarios

- **Strong drift** (single hybridization event in small populations):
  - Only 3 x 10 demes in each habitat (\( N_1=N_2=600 \))
  - Single inter-taxa mating event allowed between two pure individuals
  - Then no restrictions on matings between hybrids
  - No sex-biased processes

For all scenarios, we considered both high (0.1) and low migration rates (0.001)

### Outputs of the simulation study: introgression measures

\( M \): proportion of introgressed Mt copies in the most introgressed taxon
\( a \): vector of proportions of introgressed nuclear gene copies

We are mostly interested in the following output:

- **\( M – a \) the mito-nuclear introgression discordance**
  - and we define a Massively Discordant Mitochondrial Introgression (MDMI) when \( M – a > 0.8 \)

### Conclusions

- **Neutral processes (sex-biases, strong drift and spatial invasion) fail to explain MDMI**
- **Only positive selection on Mt with low migration rates or counter selection on the whole nuclear genome can create MDMI**
- **but no detection of positive selection using Tajima’s D or Fu’s Fs on Mt polymorphisms observed in the introgressed taxon**

**Take home message**

- **Neutral processes can’t dissociate nuclear and mitochondrial introgression** … because females too have nuclear genes!
- **Our results are in line with recent and increasing evidence that selection on Mt DNA may be common**
- **Beware of verbal models, do not trust but test them using models**

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