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A reassessment of explanations for discordant introgressions of mitochondrial and nuclear genomes

Timothée Bonnet Raphaël Leblois François Rousset Pierre-André Crochet

UMRs CBGP & ISEM & CEFÉ, (INRA - CNRS, Montpellier, France) raphael.leblois@supagro.inra.fr



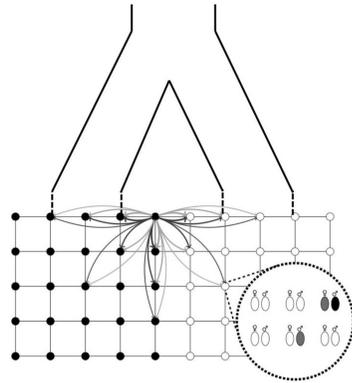
Motivation

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

\mathbf{a} : vector of proportions of introgressed nuclear gene copies

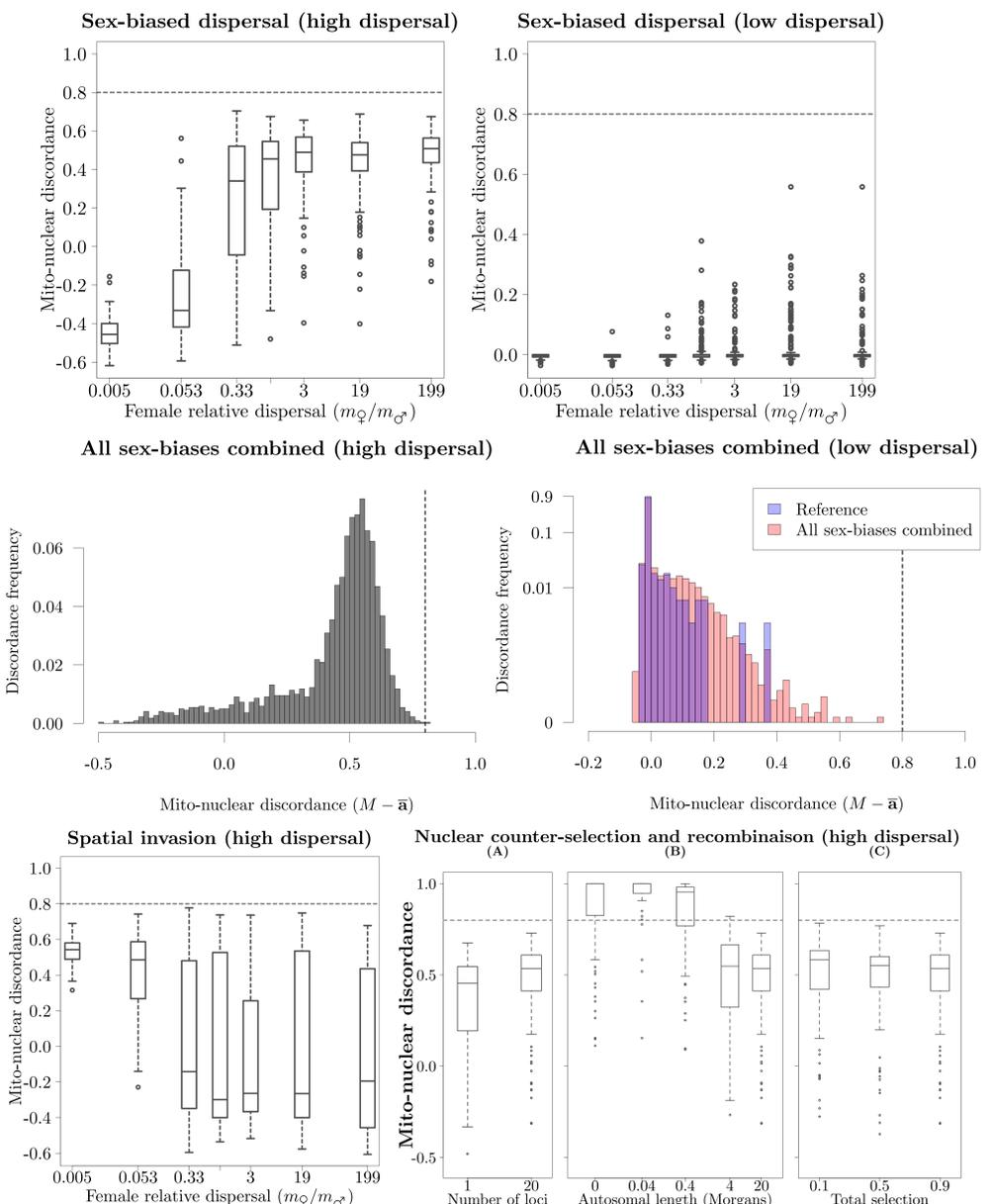
We are mostly interested in the following output:

► $M - \bar{\mathbf{a}}$ the **mito-nuclear introgression discordance**

and we define a Massively Discordant Mitochondrial Introgression (**MDMI**) when $M - \bar{\mathbf{a}} > 0.8$

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Results



Conclusions

Gene flow	Sex-biases	Invasion	Nu Selection	Mt Selection	MDMI
High	-	-	-	-	No
	Yes	-	-	-	No ¹
	-	Yes	-	-	No
	-	-	Yes	-	Yes
Low	-	-	-	-	No
	Yes	-	-	-	No
	-	Yes	-	-	No
	-	-	-	Yes	Yes
Single hybridization	-	-	-	-	No ²

- 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' Fs on Mt polymorphism 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**