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

Timothée Bonnet Raphaël Leblois François Rousset Pierre-André Crochet

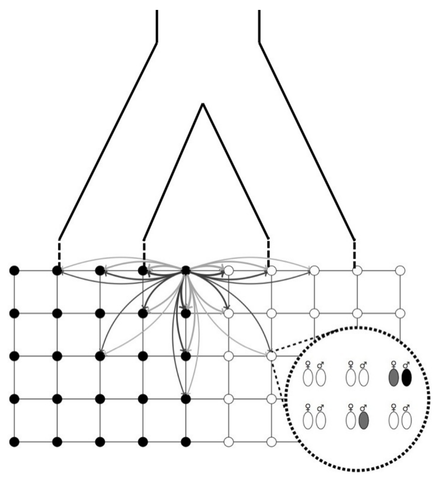
UMRs **CBGP** & **ISEM** & **CEFE**, (**INRA** - **CNRS**, Montpellier, France) raphael.leblois@supagro.inra.fr

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

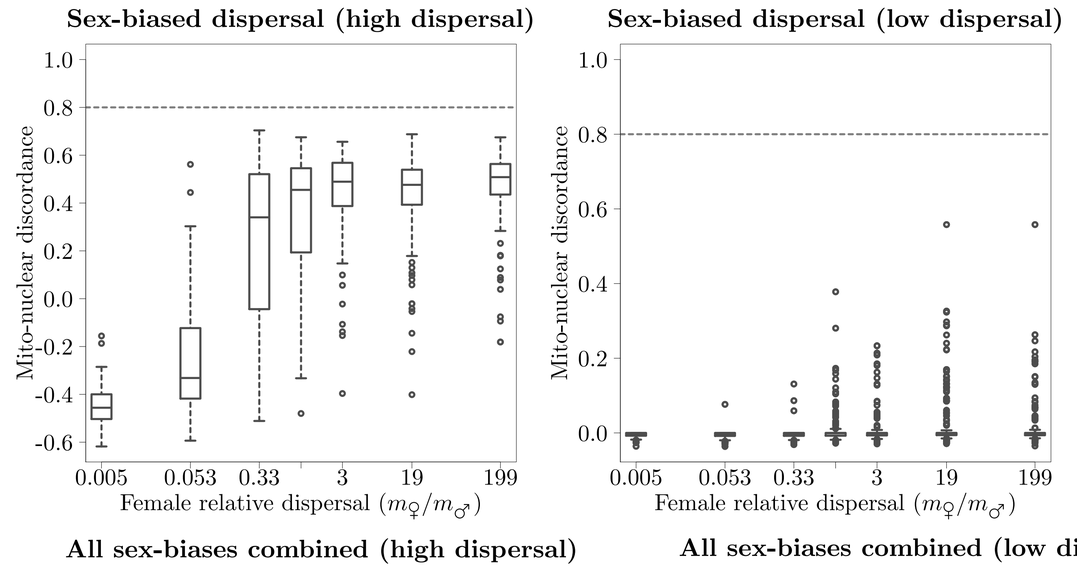
$\mathbf{a}$: vector of proportions of introgressed nuclear gene copies

We are mostly interested in the following output:

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

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

Results



Conclusions

Gene flow	Sex-biases	Invasion	Nu Selection	Mt Selection	MDMI
High	-	-	-	-	No
	Yes	-	-	-	No[1]
	-	Yes	-	-	No
	-	-	Yes	-	**Yes**
	-	-	-	Yes	No
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**

Acknowledgements: This work was partly funded by the Institut de Biologie Computationelle (IBC), and recurrent funds from INRA and CNRS.

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