Mitonuclear speciation

Species concepts – archaic constructs

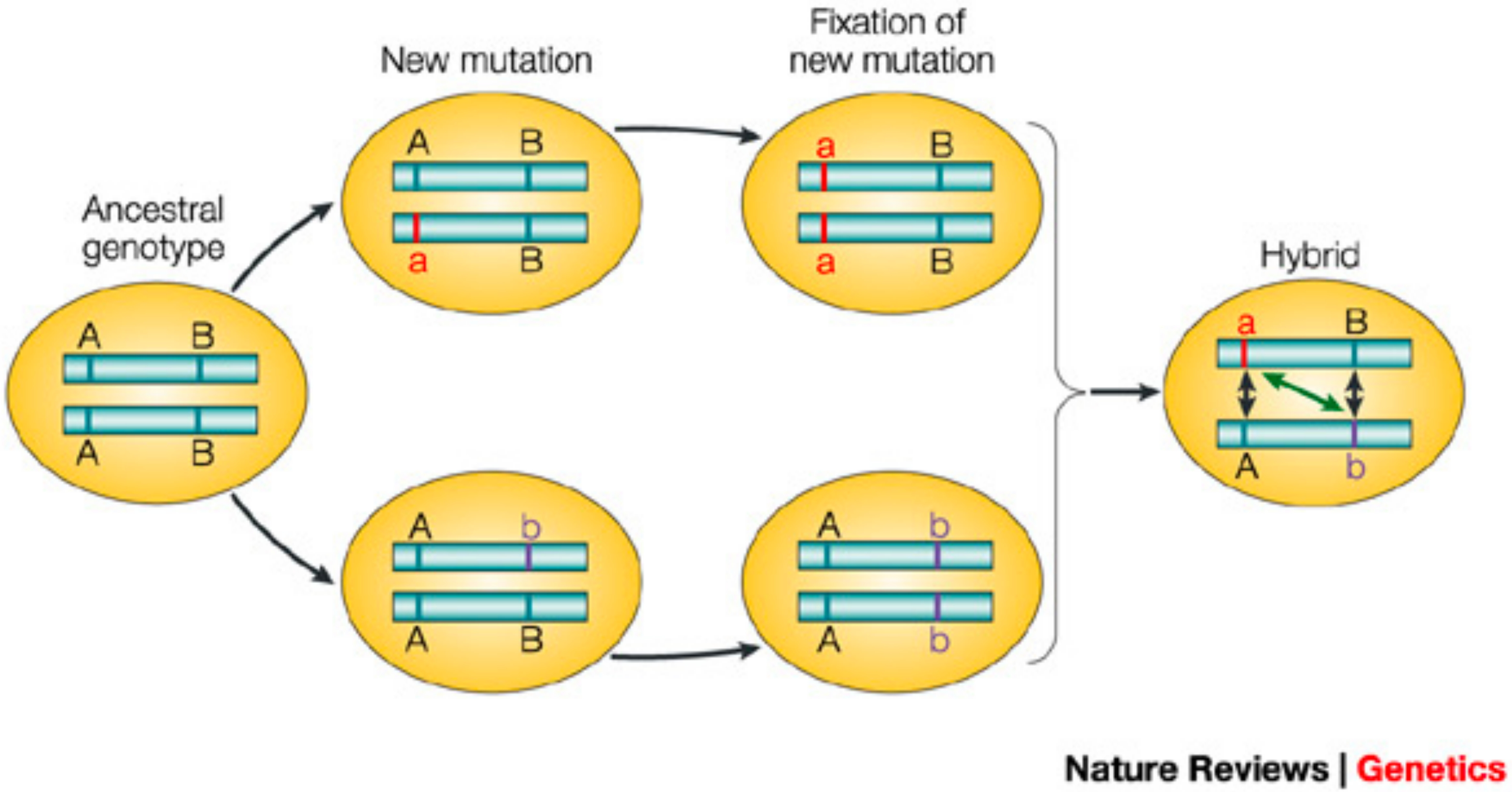
Species concept	Property(ies)	Advocates/references
Biological	Interbreeding (natural reproduction resulting in viable and fertile offspring)	Wright (1940); Mayr (1942); Dobzhansky (1950)
Isolation	*Intrinsic reproductive isolation (absence of interbreeding between heterospecific organisms based on intrinsic properties, as opposed to extrinsic [geographic] barriers)	Mayr (1942); Dobzhansky (1970)
Recognition	*Shared specific mate recognition or fertilization system (mechanisms by which conspecific organisms, or their gametes, recognize one another for mating and fertilization)	Paterson (1985); Masters et al. (1987); Lambert and Spencer (1995)
Ecological	*Same niche or adaptive zone (all components of the environment with which conspecific organisms interact)	Van Valen (1976); Andersson (1990)
Evolutionary	Unique evolutionary role, tendencies, and historical fate	Simpson (1951); Wiley (1978); Mayden (1997)
(some interpretations)	*Diagnosability (qualitative, fixed difference)	Grismer (1999, 2001)
Cohesion	Phenotypic cohesion (genetic or demographic exchangeability)	Templeton (1989, 1998a)
Phylogenetic	Heterogeneous (see next four entries)	(see next four entries)
Hennigian	Ancestor becomes extinct when lineage splits	Hennig (1966); Ridley (1989); Meier and Willmann (2000)
Monophyletic	*Monophyly (consisting of an ancestor and all of its descendants; commonly inferred from possession of shared derived character states)	Rosen (1979); Donoghue (1985); Mishler (1985)
Genealogical	*Exclusive coalescence of alleles (all alleles of a given gene are descended from a common ancestral allele not shared with those of other species)	Baum and Shaw (1995); see also Avise and Ball (1990)
Diagnosable	*Diagnosability (qualitative, fixed difference)	Nelson and Platnick (1981); Cracraft (1983); Nixon and Wheeler (1990)
Phenetic	*Form a phenetic cluster (quantitative difference)	Michener (1970); Sokal and Crovello (1970); Sneath and Sokal (1973)
Genotypic cluster (definition)	*Form a genotypic cluster (deficits of genetic intermediates; e.g., heterozygotes)	Mallet (1995)

De Quieroz 2007

Mitonuclear speciation

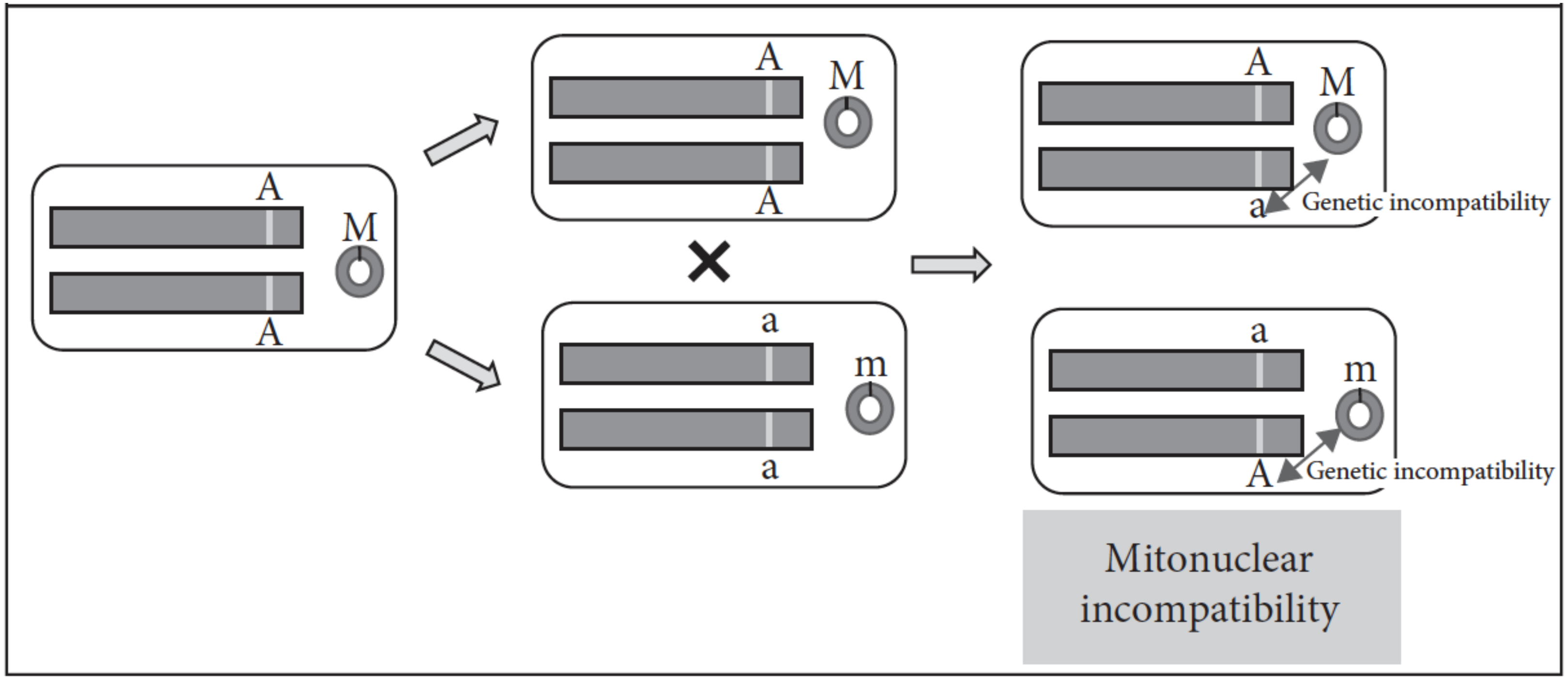
Mt mutational erosion → Nuclear compensation → Coadapted mt and nuc genotypes → BDMIs → Reproductive isolation → Species

DMIs

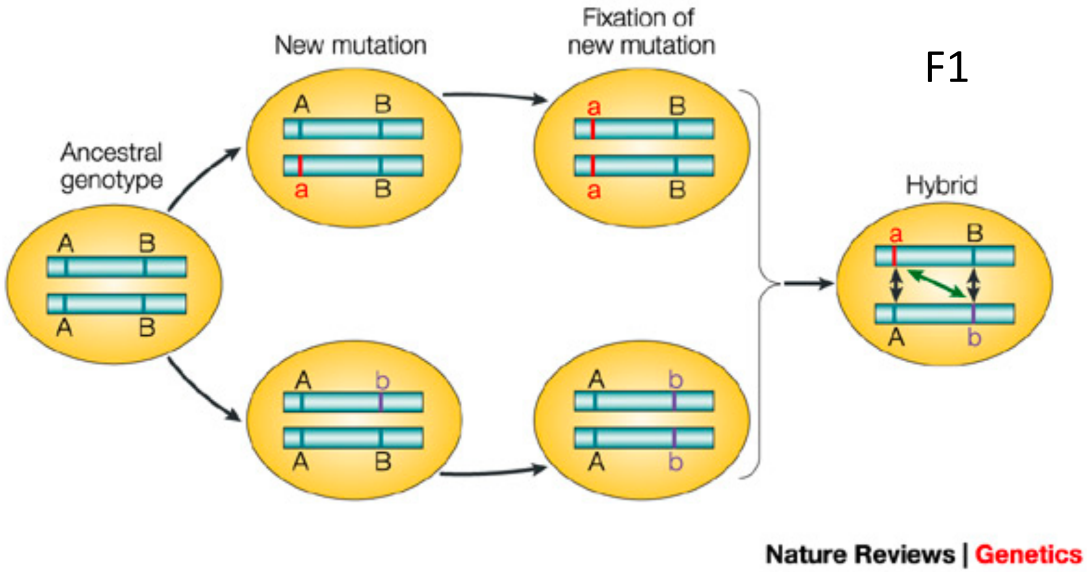


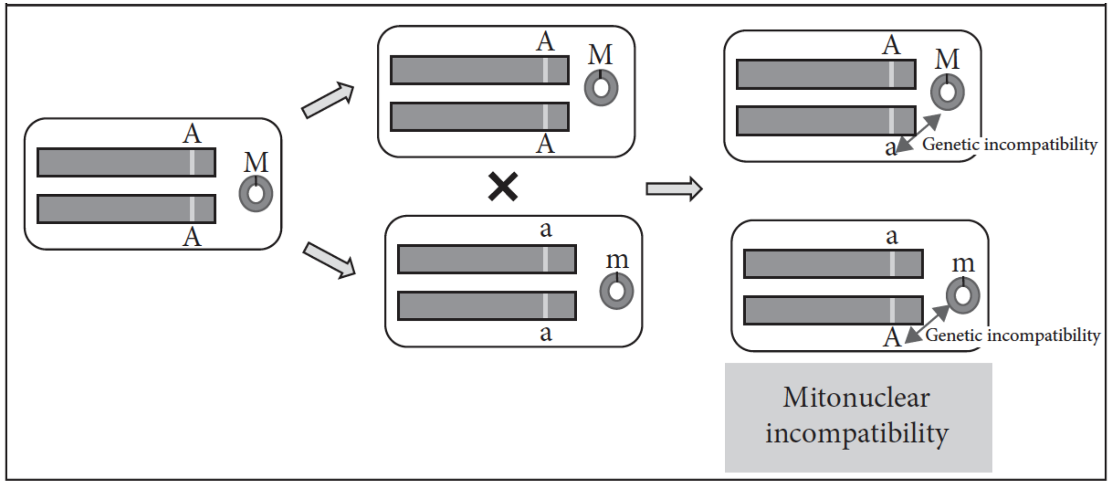
New mutation
Fixation of
new mutation
Ancestral
genotype
Hybrid
A
B
a
b
Nature Reviews | Genetics

Mitonuclear DMIs



F1s vs. F2s and dominance effects





F1

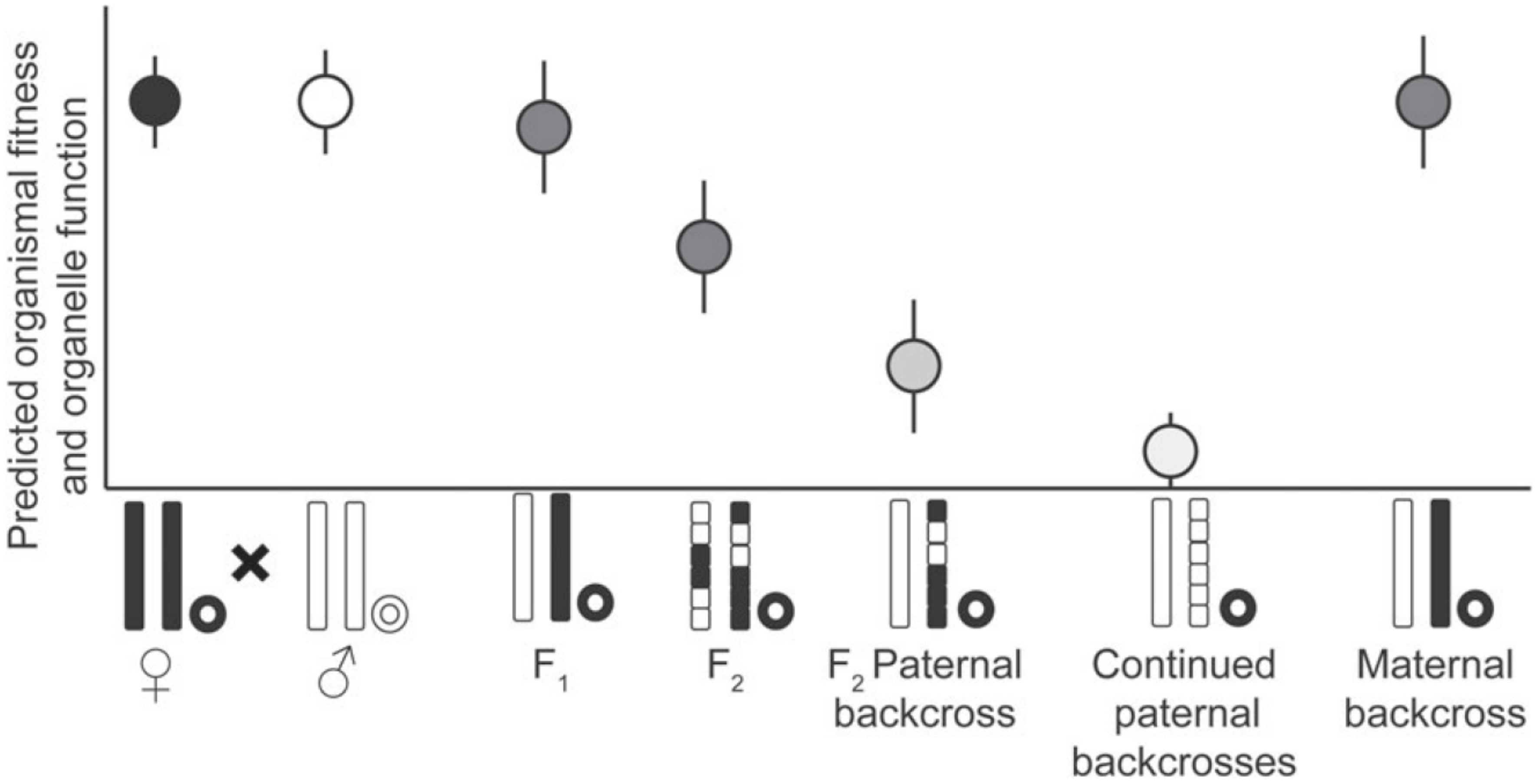
Later hybrids

aabb

vs.

AAm or aaM

Mitonuclear hybrid breakdown



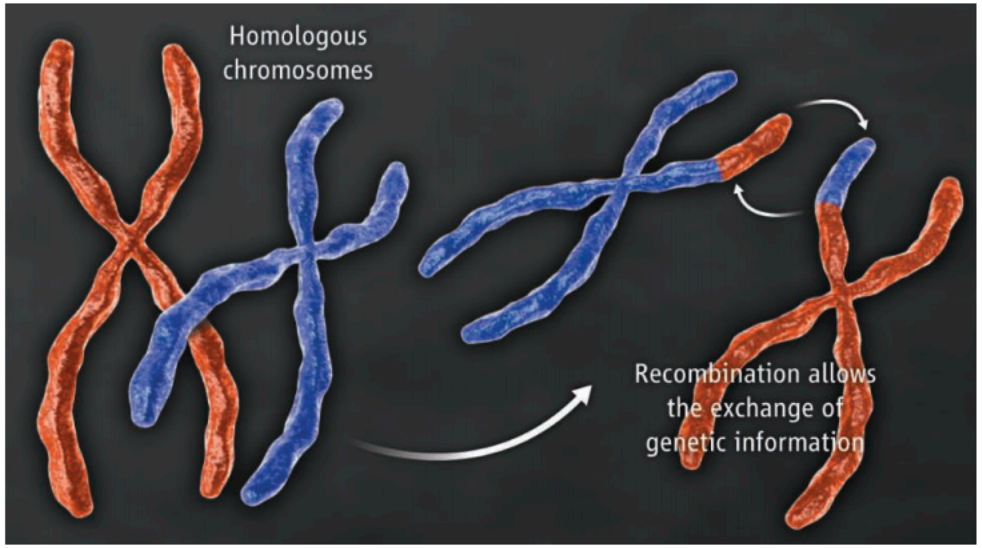
Hill et al. 2019

Nuclear speciation genes

- Gene that follows DMI model and creates reproductive isolation
- Wu and Ting identified 5 in 2004
- Many more have been identified, but the list remains fairly short
- Is there a universal speciation gene or set of genes?

PRDM9

- Only speciation gene identified in mammals (most are in flies)
- Controls recombination hotspots
- One of the fastest evolving genes



An outsized role for mitonuclear DMIs

- Only 13 loci (or 1 linked locus)
- Evolves quickly
- Critical energetic functions
- Can't tolerate slight incompatibilities?
- Lots of interactions
- May be a hotspot for speciation genes

MOLECULAR ECOLOGY

Molecular Ecology (2012) doi: 10.1111/mec.12006

INVITED REVIEW AND META-ANALYSES

A disproportionate role for mtDNA in Dobzhansky–Muller incompatibilities?

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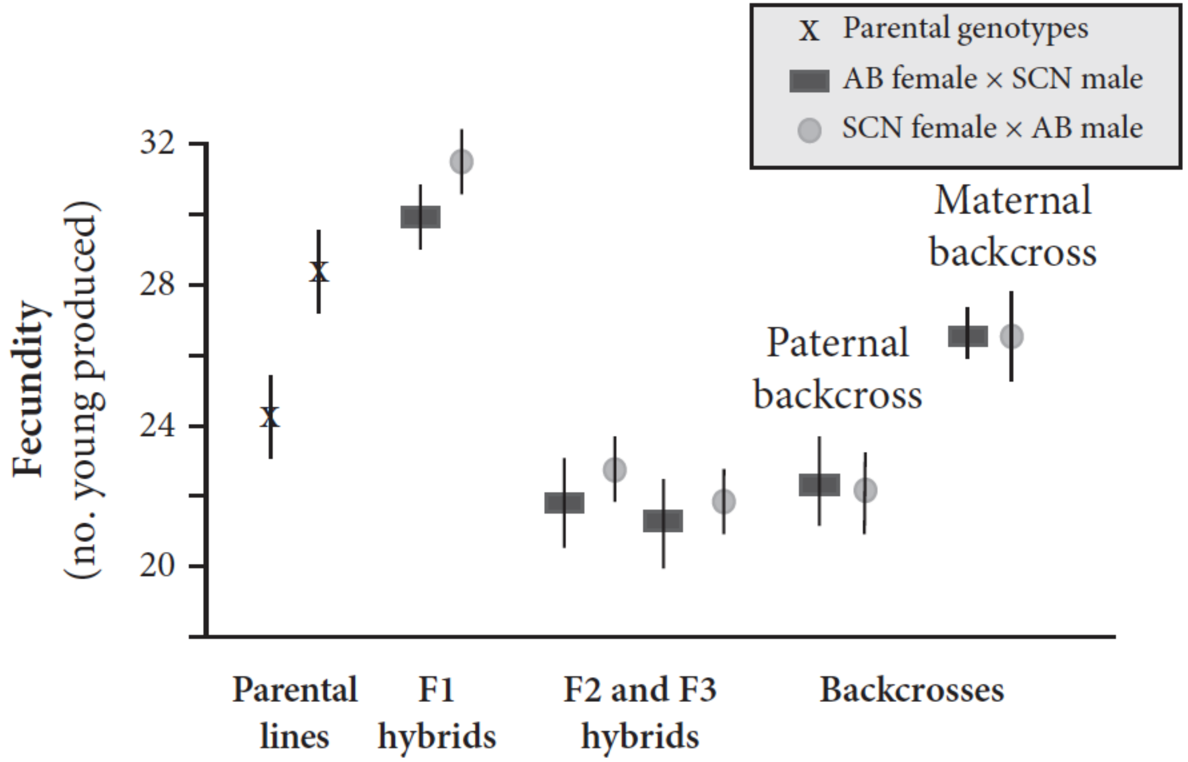
Evidence for mitonuclear speciation

Table 1 Examples of systems with evidence of a cytonuclear basis of reproductive isolation or cytonuclear effects on fitness. In some cases, the evidence remains indirect and/or speculative

Taxon	References
Animals	
Arthropods (*Acanthoscelides*, *Callosobruchus*, *Encarsia*, *Drosophila*, *Nasonia*, *Tigriopus*)	Sackton *et al.* (2003), Dowling *et al.* (2007b), Ellison *et al.* (2008), Niehuis *et al.* (2008), Meiklejohn *et al.* (2013), Đorđević *et al.* (2015), Gebiola *et al.* (2016), Immonen *et al.* (2016)
Nematodes (*Caenorhabditis*)	Zhu *et al.* (2015), Chang *et al.* (2016)
Vertebrates (*Anguilla*, *Ambystoma*, Centrarchidae, *Chamaeleo*, *Eopsaltria*, *Mus*, *Passer*)	Nagao *et al.* (1998), Bolnick *et al.* (2008), Gagnaire *et al.* (2012), Lee-Yaw *et al.* (2014), Trier *et al.* (2014), Bar-Yaacov *et al.* (2015), Morales (2016)
Fungi	
Yeast (*Saccharomyces*)	Zeyl *et al.* (2005), Lee *et al.* (2008), Chou *et al.* (2010), Paliwal *et al.* (2014), Spirek *et al.* (2015)
Plants	
Angiosperms (numerous)	Reviewed in Levin (2003), Greiner *et al.* (2011)

Sloan et al. 2017

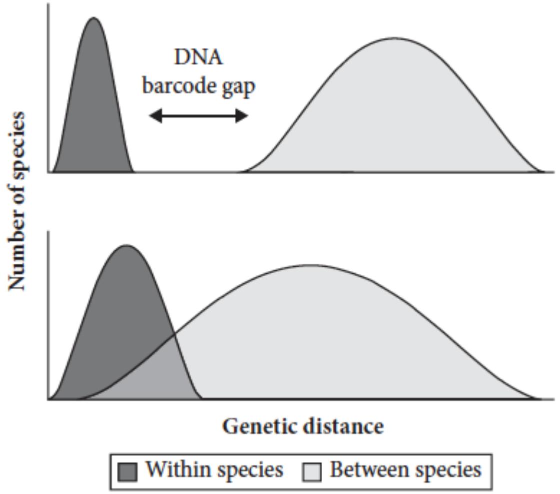
Best case study

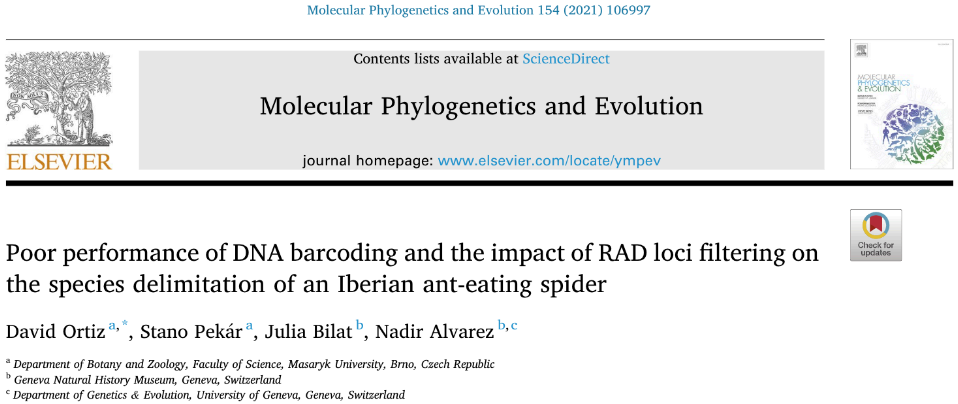


- Fast mt evolution
- Good evidence for nuclear coevolution
- Hybrids show mito dysfunction as predicted
- Incompatibilities map to N-mt genes

DNA barcode gap

- First proposed as a taxonomic tool
- Hill considers it diagnostic of the speciation process
- Works well in birds
- Doesn't work well in lineages with slow mt mutation rates (e.g., corals)

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ELSEVIER

Poor performance of DNA barcoding and the impact of RAD loci filtering on the species delimitation of an Iberian ant-eating spider

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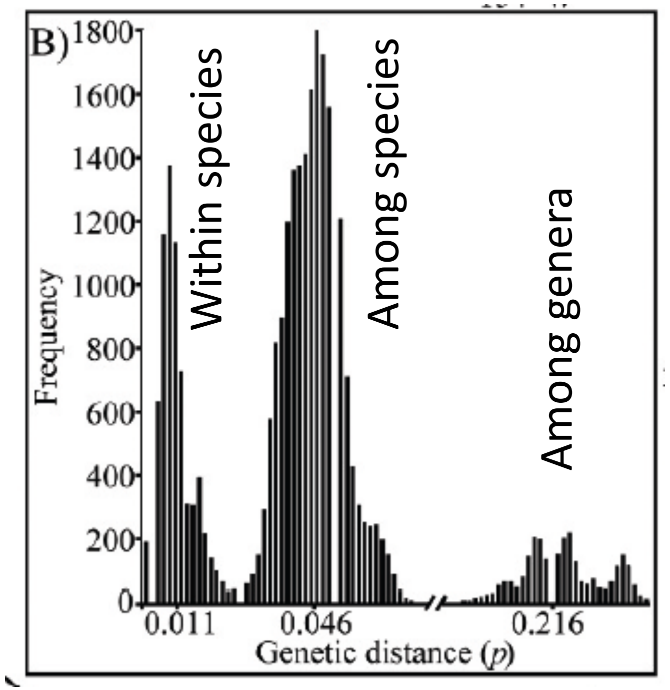
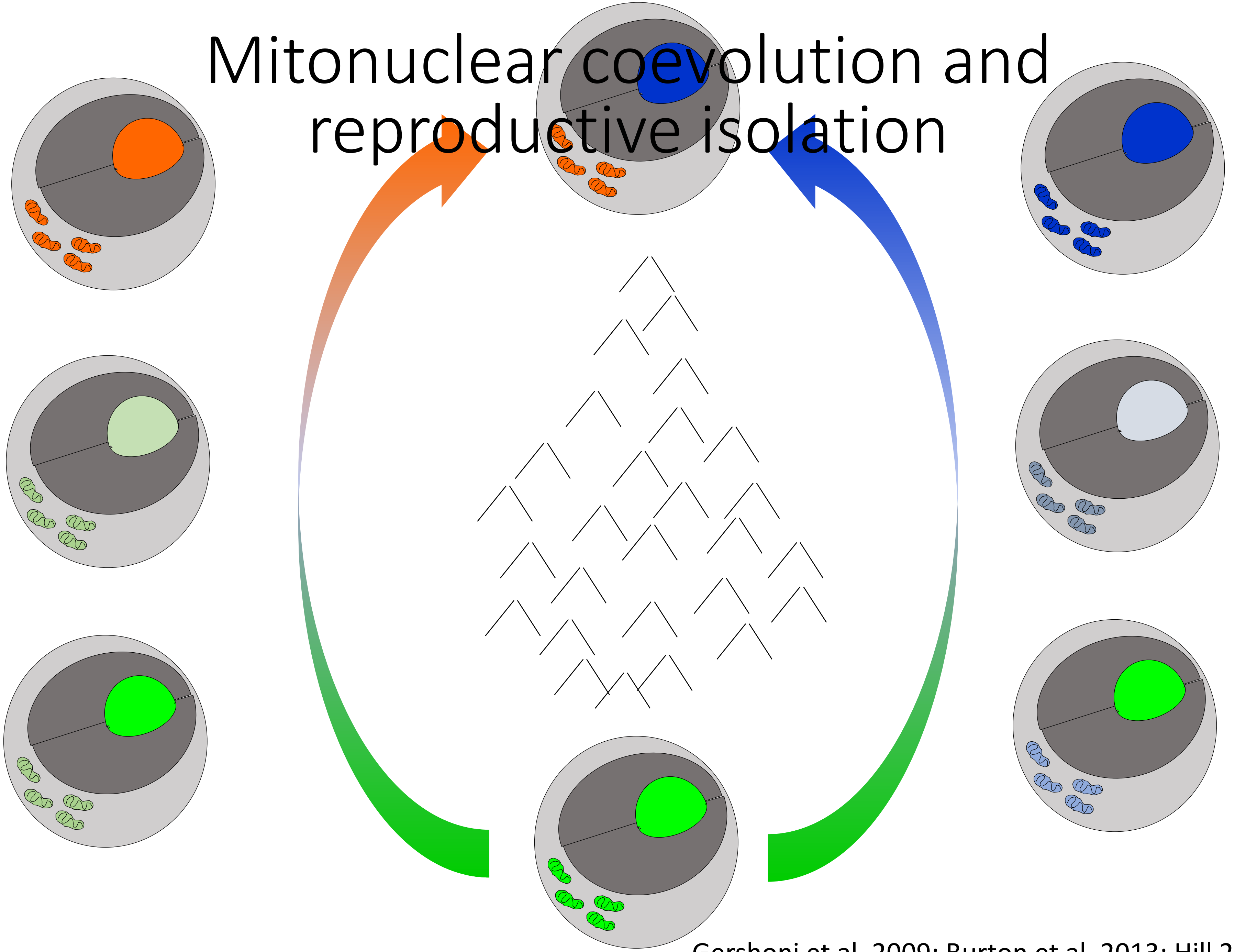


Craft et al. 2008

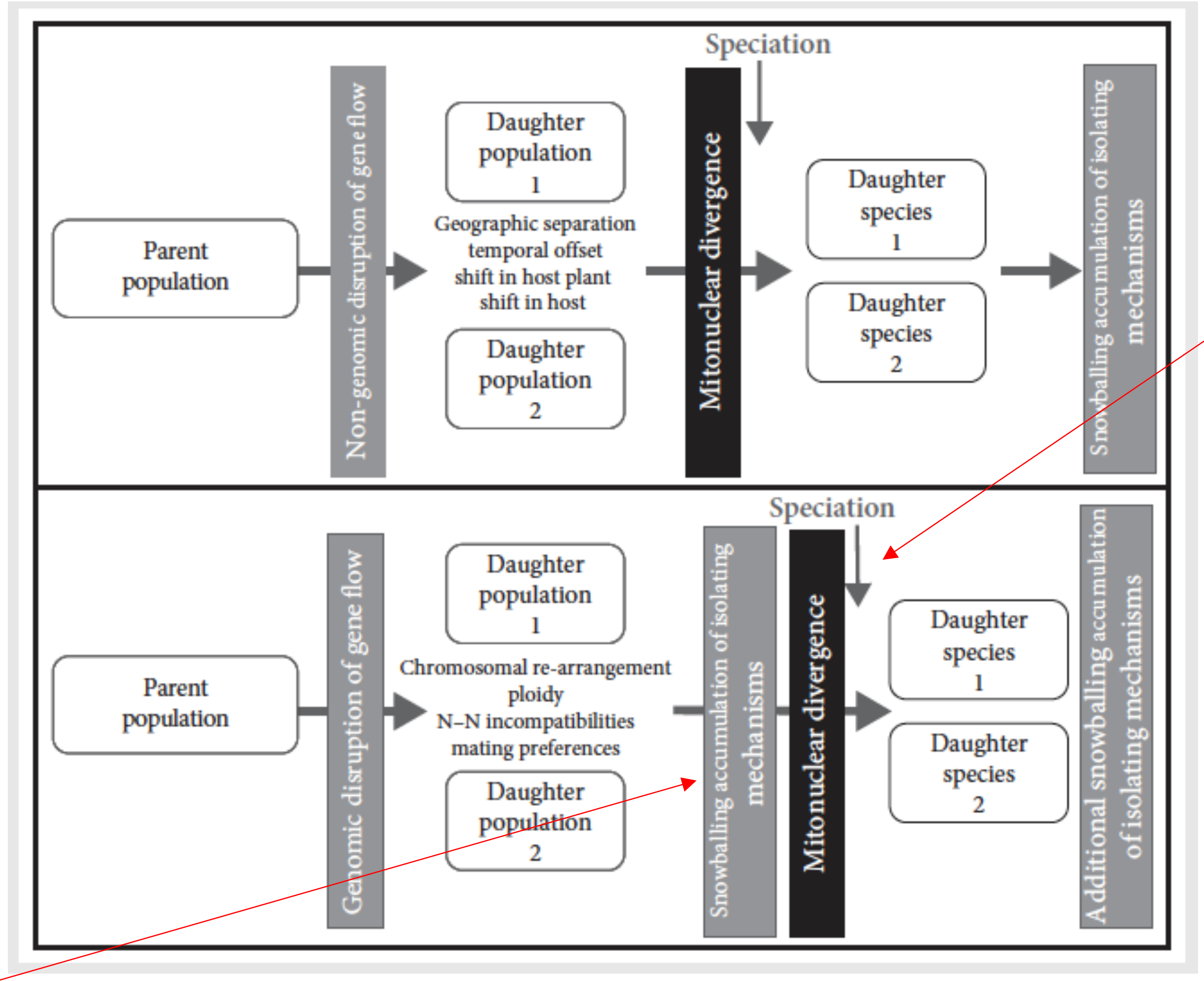
Adaptive vs. neutral mitonuclear speciation

Mitonuclear coevolution and reproductive isolation



Gershoni et al. 2009; Burton et al. 2013; Hill 2016

Some fallacies

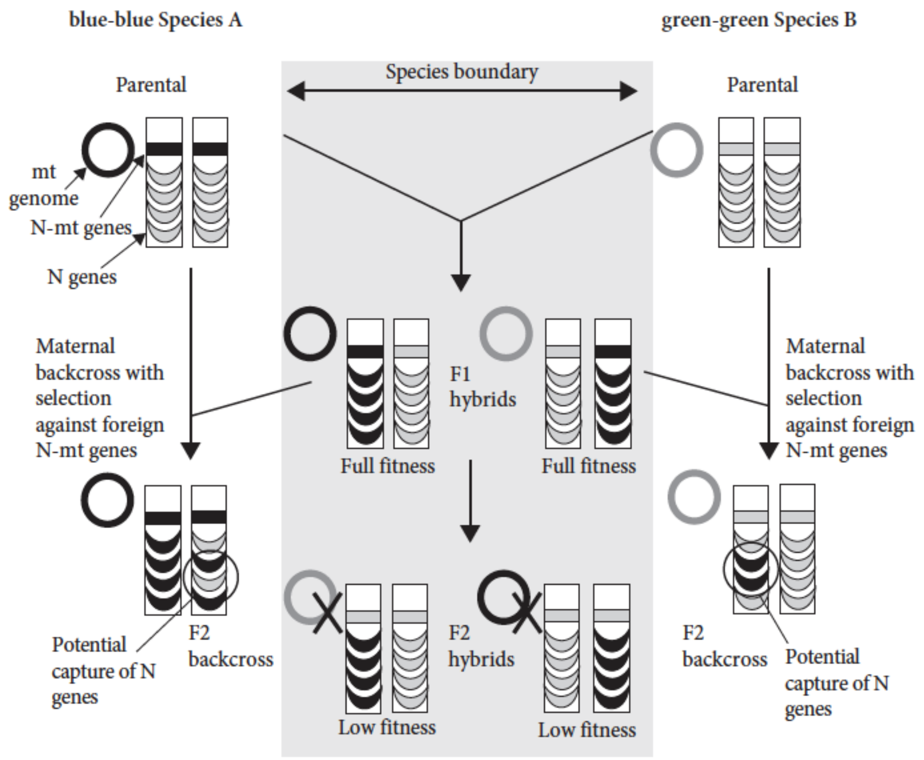


How long might this take?

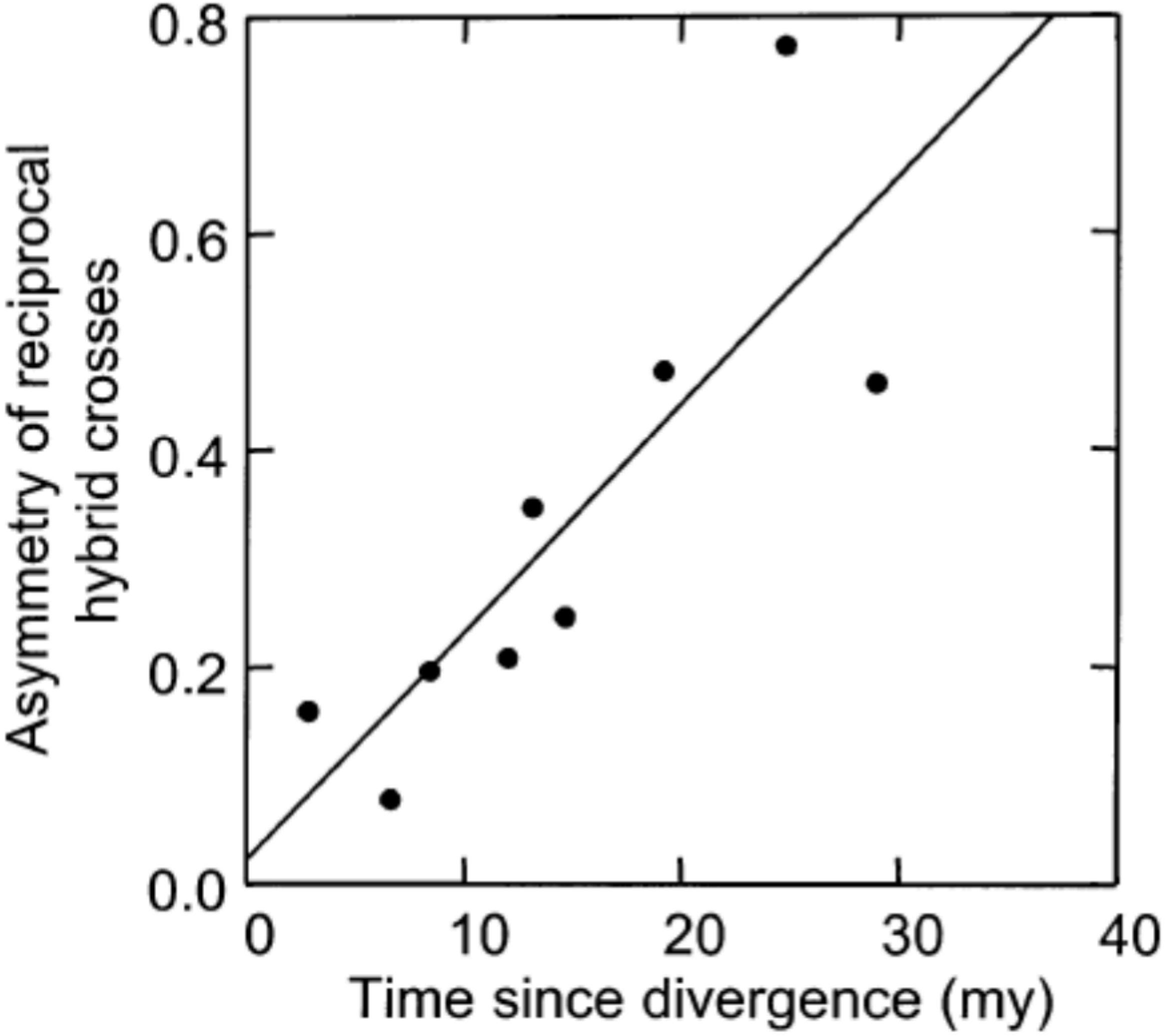
Populations are reproductively isolated without gene flow, but aren't species yet

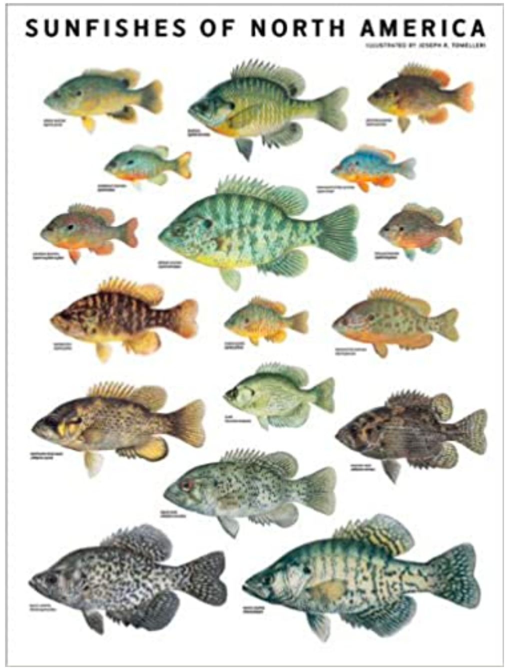
Mitonuclear speciation provides a mechanism for the biological species concept

- a species is a population that is genetically isolated from other populations by incompatibilities in uniquely coadapted mt and N-mt genes **(Hill, 2016, 2017, 2018).**



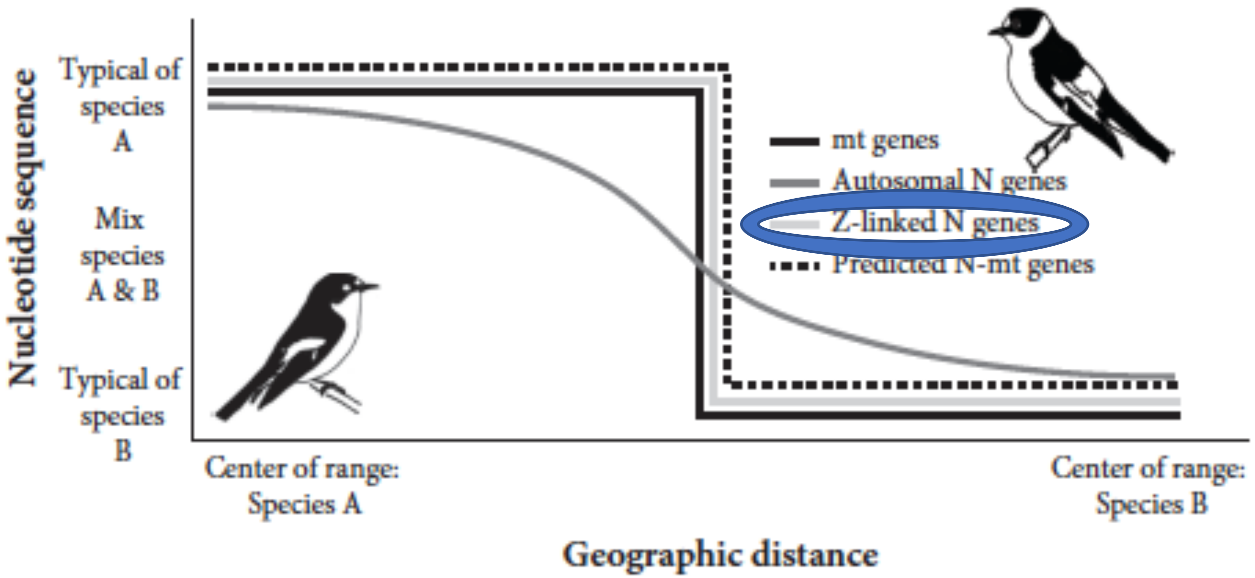
Some other evidence for mitonuclear speciation

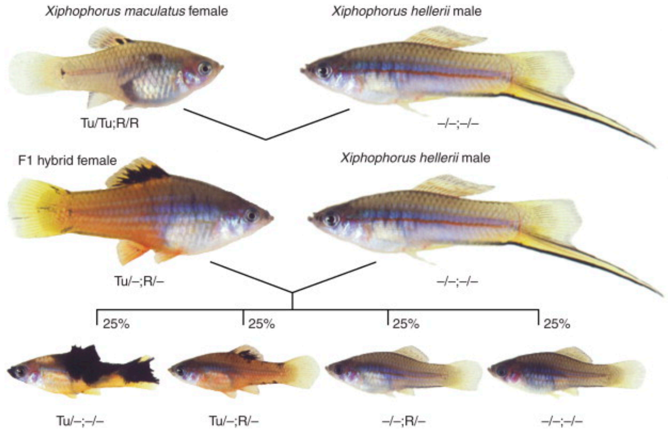


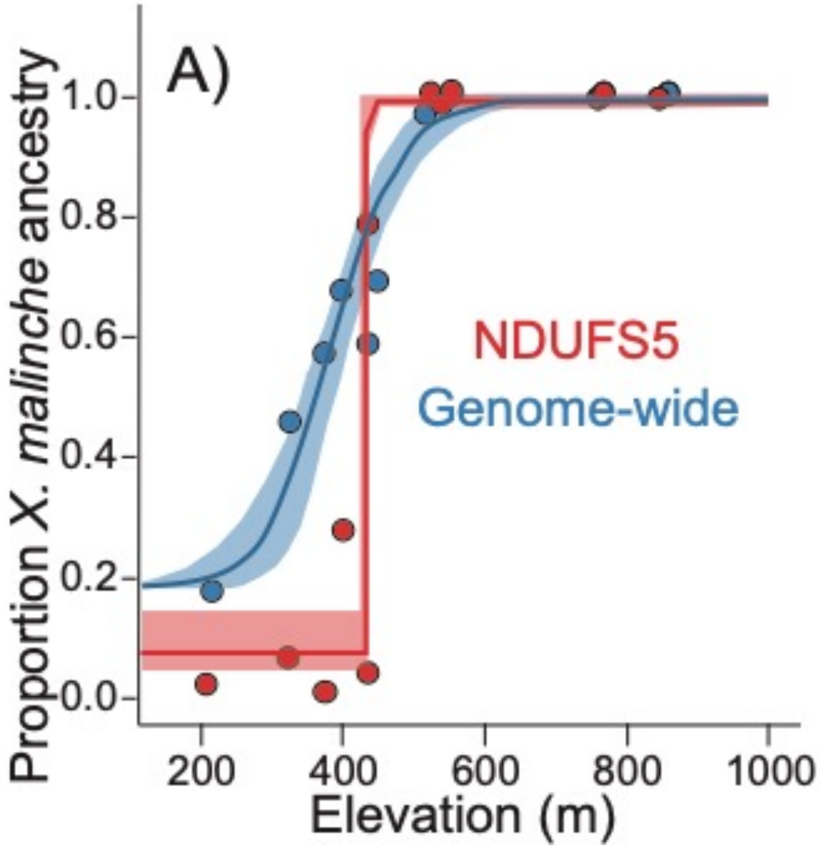


Bolnick and Near 2005

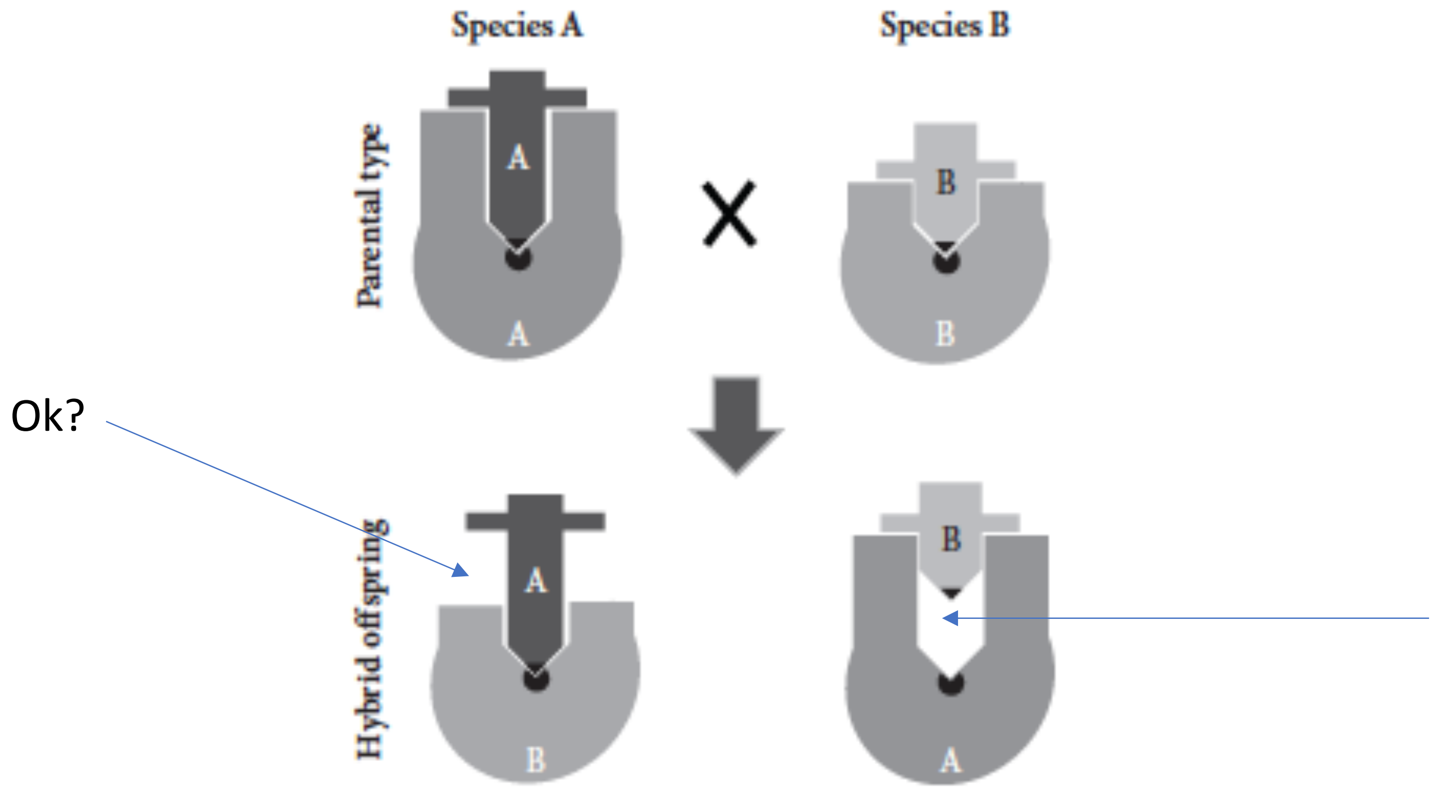
Clinal data


Nucleotide sequence
Typical of species A
Mix species A & B
Typical of species B
mt genes
Autosomal N genes
Z-linked N genes
Predicted N-mt genes
Center of range: Species A
Center of range: Species B
Geographic distance


Xiphophorus maculatus female
Xiphophorus hellerii male
Tu/Tu;R/R
–/–;–/–
F1 hybrid female
Xiphophorus hellerii male
Tu/–;R/–
–/–;–/–
25%
25%
25%
25%
Tu/–;–/–
Tu/–;R/–
–/–;R/–
–/–;–/–


A)
Proportion X. malinche ancestry
1.0
0.8
0.6
0.4
0.2
0.0
NDUFS5
Genome-wide
200
400
600
800
1000
Elevation (m)

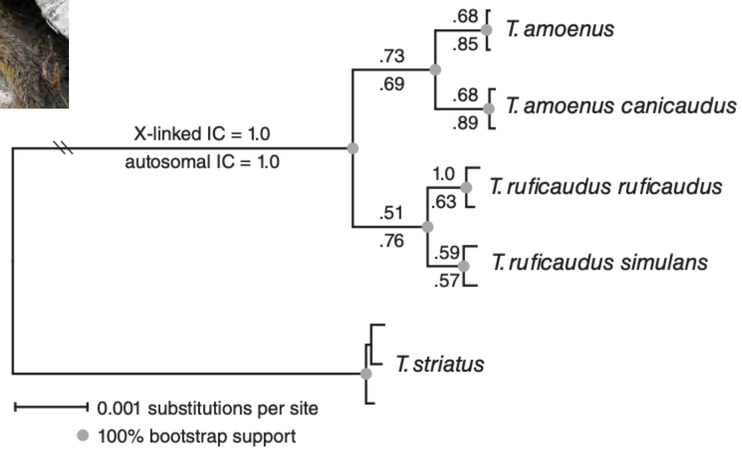
Darwin’s corollary to Haldane’s rule



Compatible mitonuclear interactions: No hybrid dysfunction

Incompatible mitonuclear interactions: Hybrid dysfunction

Introgression



- Nuclear introgression across species boundaries via hybridization is common
- Mt introgression is also common
- ~20% of phylogenetic studies show mitonuclear discordance
- Often mt genomes are captured w/o nuclear gene flow

Table 2. Divergence and support for the alternative phylogenies.

Linkage group	Contigs	Average length	Divergence (ingroup[1])	Divergence (total[2])	Informative loci[3]	Species tree[4]	Potential introgression[5]	Other trees[6]
Autosomes	8558	321	0.33%	1.82%	1848 (21.6%)	1596 (86.4[illegible])	20 (1.1%)	232 (12.5%)
X chromosome	201	256	0.25%	1.32%	24 (11.9%)	20 (83.3[illegible])	1 (4.2%)	3 (12.5%)

Good et al. 2015

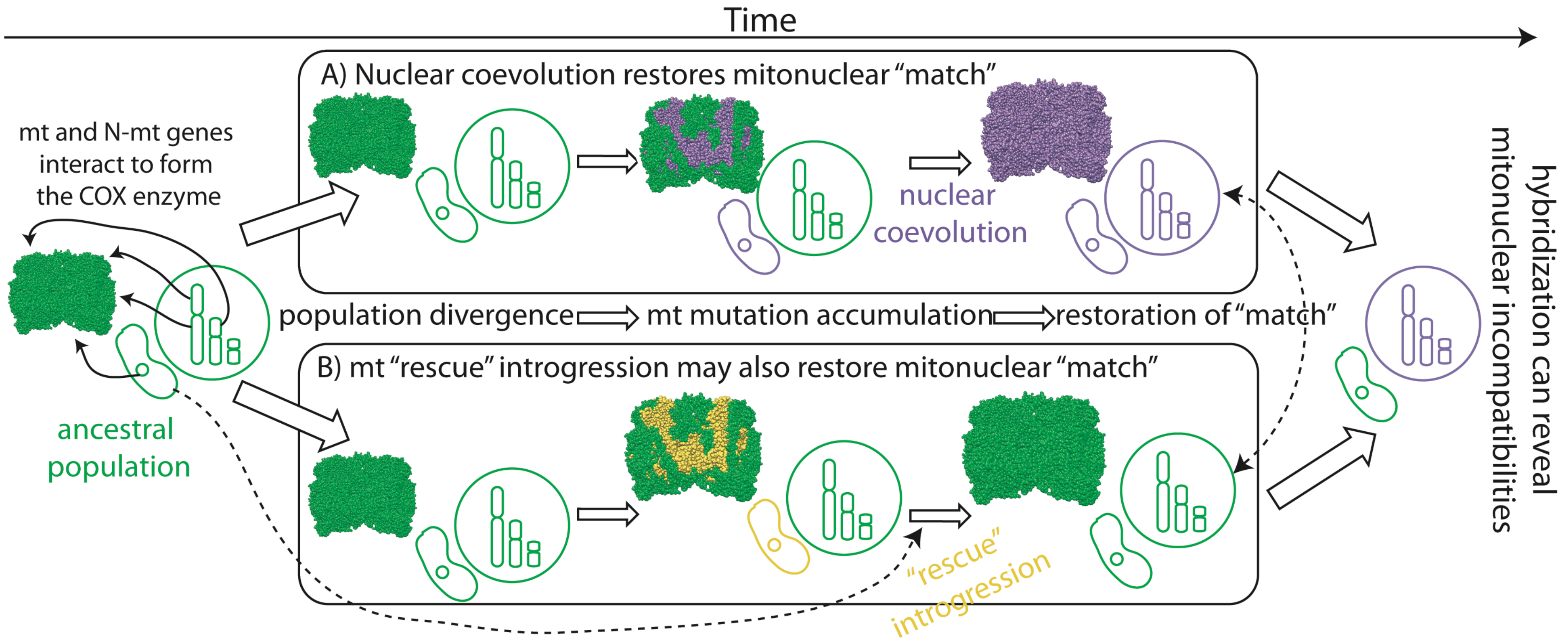
Causes for mt introgression

- Many authors invoke adaptive reasons, but do not follow up
- Good evidence for adaptive introgression of pt in sunflowers (reciprocal transplants)
- Lots of neutral reasons too:
  - Sex-biased dispersal
  - Haldane’s rule
  - Sexual selection
  - Haplodiploidy
  - Selfish genes/drive

Paradox of mt introgression

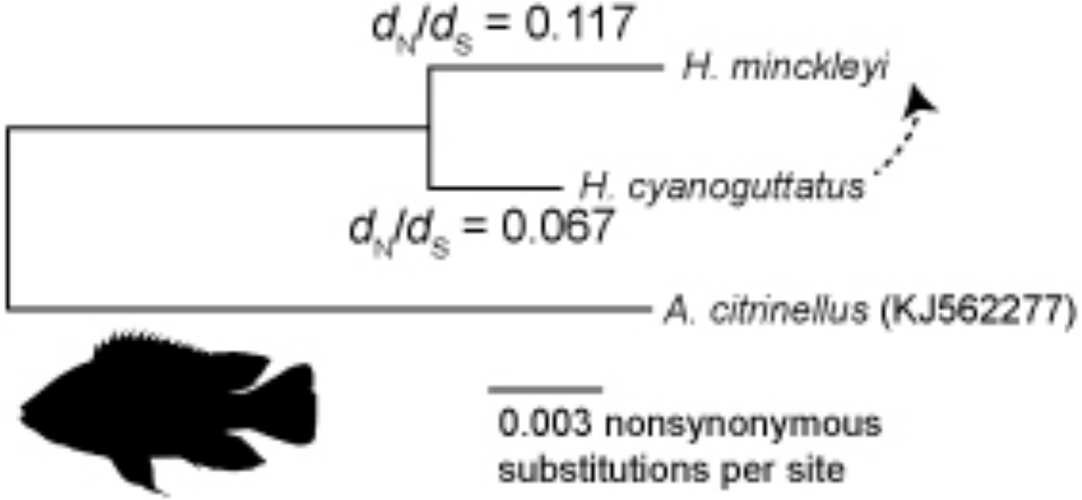
- How can mt genomes create species boundaries and then blatantly disregard them?

Resolutions



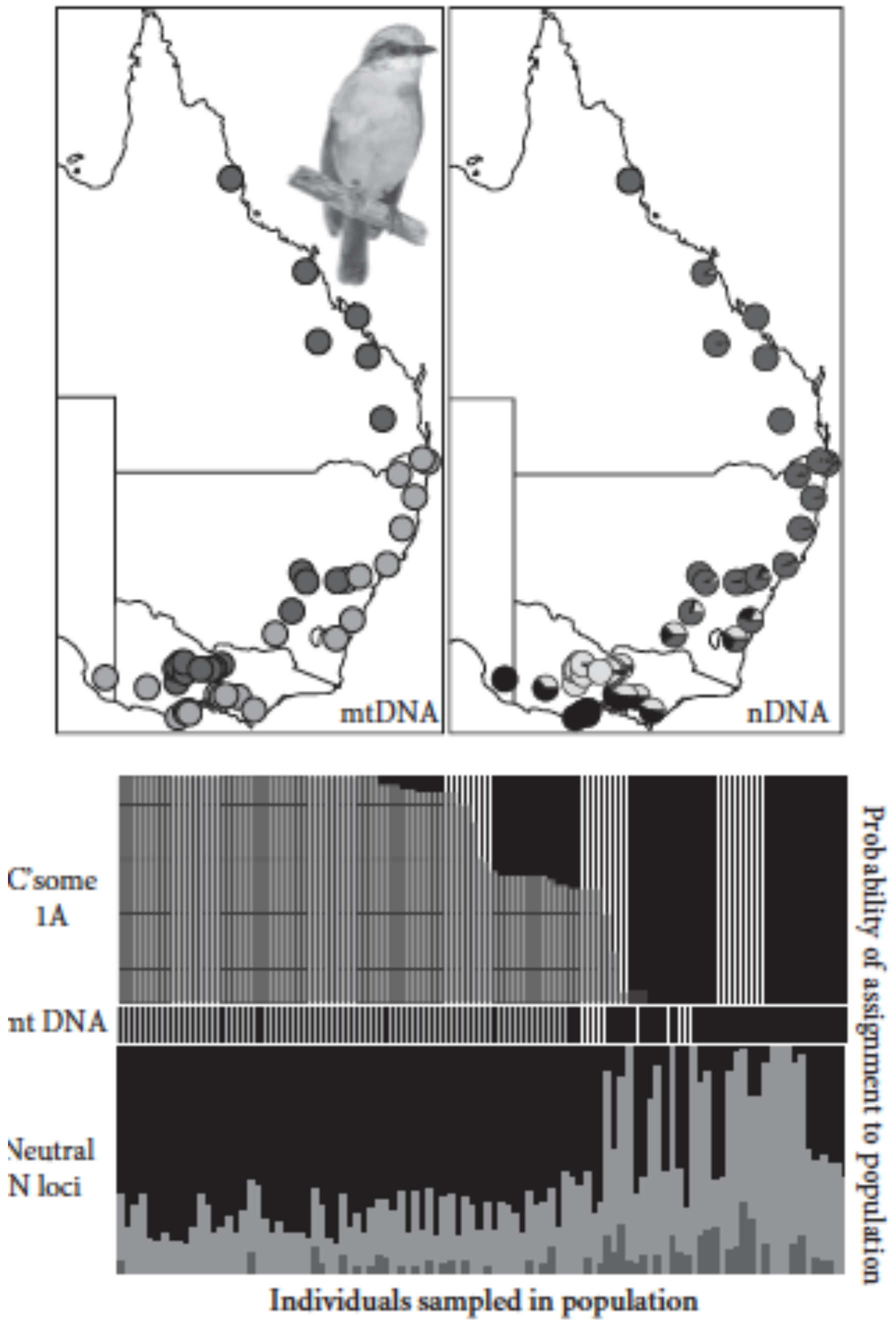
Rescue introgression

- Little evidence – 2 case studies

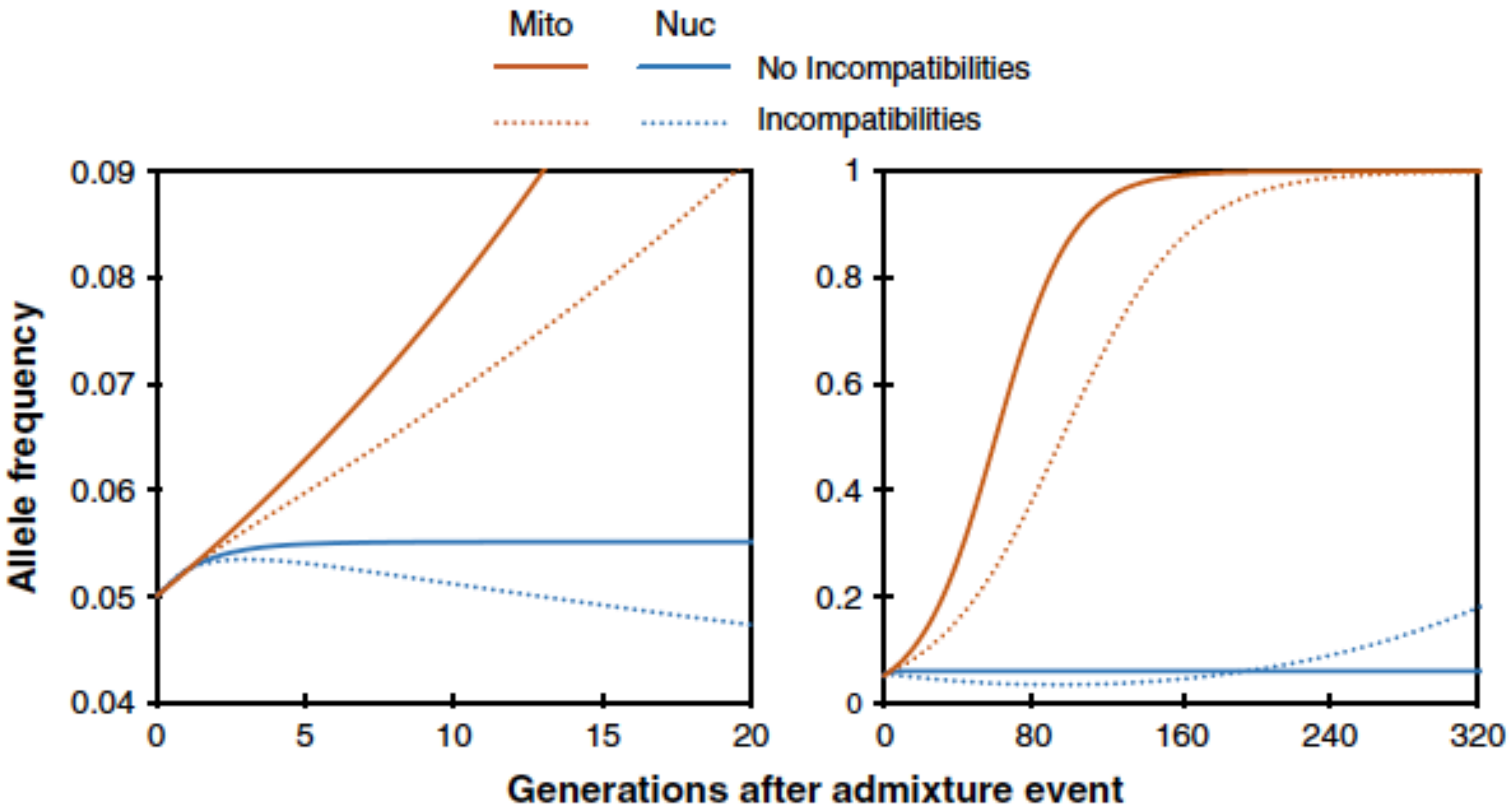


Co-introgression

- Allows mt introgression without breaking up coadapted mt and N-mt complexes
- A few cases
- Including NDUFS5



Difficulties in co-introgression



Sloan et al. 2017

Table 3 Predicted conditions that would favour alternative evolutionary responses to mitochondrial mutation accumulation

	Conditions promoting...	
	Compensatory co-evolution and mitonuclear incompatibilities	Adaptive mitochondrial introgression/replacement
Mitochondrial mutation rates	Higher rates	Lower rates
Effective Population Size	Large or symmetric population sizes	Small or asymmetric population sizes
Population Subdivision	More subdivision	Less subdivision
Divergence Time	More ancient divergence	More recent divergence
Cotransmission of nuclear and mitochondrial loci (e.g. inbreeding)	More cotransmission	Less cotransmission
Constraints on mitochondrial function	Intense constraints	Relaxed constraints

Sloan et al. 2017

Final thoughts

- Mitonuclear speciation definitely occurs, but how important is it in eukaryotic reproductive isolation?
- Active area of research…