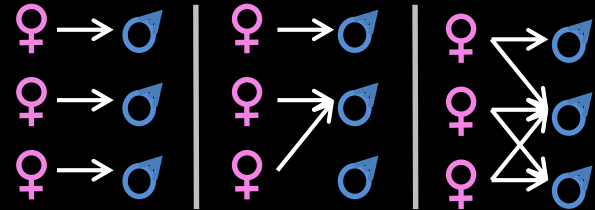


# Influence of mating system and sex chromosome system on sex-biased dispersal evolution

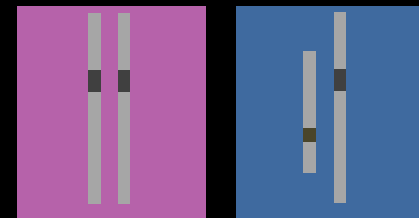
Thomas Brom, Manuel Massot, David Laloï

# Outlines

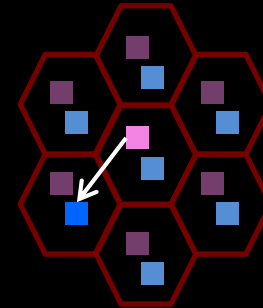
- Number of mates



- Genetic architecture



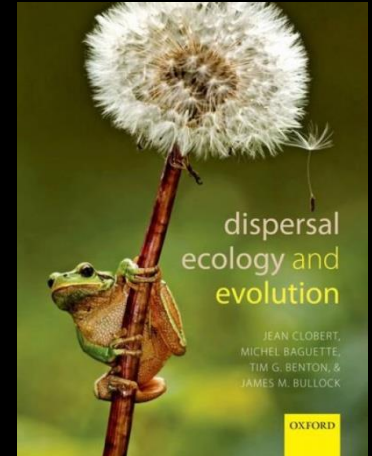
- Extra-pair copulations



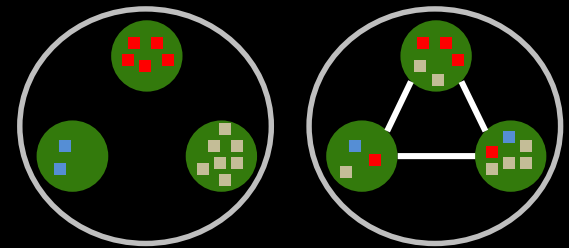
# Dispersal

- Dispersal: movement with potential consequences for gene flow

(Ronce 2007 Annu. Rev. Ecol. Evol. Syst.)



- Consequences at various scales
  - Gene flow
  - Individual life history
  - Population demography
  - Metapopulation dynamic



# Sex-biased dispersal

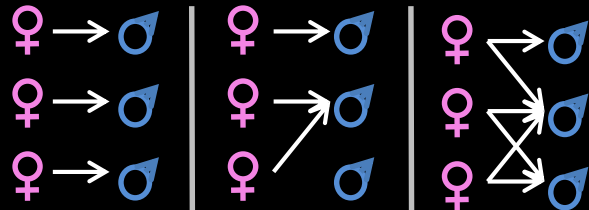
---

- One of the most studied phenomenon of dispersal  
(Dobson 2013 Anim. Behav.)
- Sex-biased dispersal : one sex emigrating more frequently or moving a greater distance
- A seminal paper: Greenwood (1980) Anim. Behav. Mating systems, philopatry and dispersal in birds and mammals.

# Sex-biased dispersal

- Why (sex-biased) dispersal ? (Henry et al. 2016 Am. Nat.)
  - Resource competition
  - Inbreeding avoidance
  - Dispersal cost
  - Mating system
  - Kin selection
- Any difference between the sex can promote sex-biased dispersal (cost or benefits)

# Influence of the number of mates on sex-biased dispersal evolution



Brom et al (2016) Anim. Behav.

# Greenwood (1980): Mammals / Birds

	Mammals	Birds
Dispersal	Male biased	Female biased
Mating system	Polygyny	Monogamy

- Polygyny: males strongly compete
  - Strong benefits to dispersal males



- Monogamy: males defend resources
  - Males benefit of philopatry



# Following Greenwood

- Mating system definition
  - Resource defense ?
  - Mate acquisition ?
  - Mate choice ?
  - Mate number ?
- Greenwood (1980) forget kin competition (Dobson 2013)
  - Asses kin competition intensity



# Question & methods

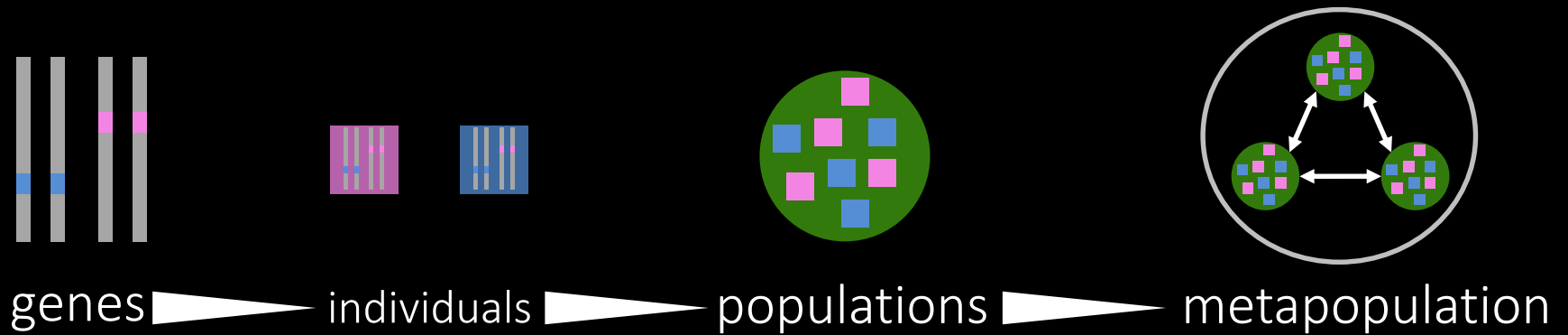
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- How the number of mates influence sex-biased dispersal evolution through kin competition.
- Individual based model
  - Model each individual, its properties, its behaviors. Results emerge from the simulation.
  - Taking into account stochastic phenomena (Gros et al. 2008)

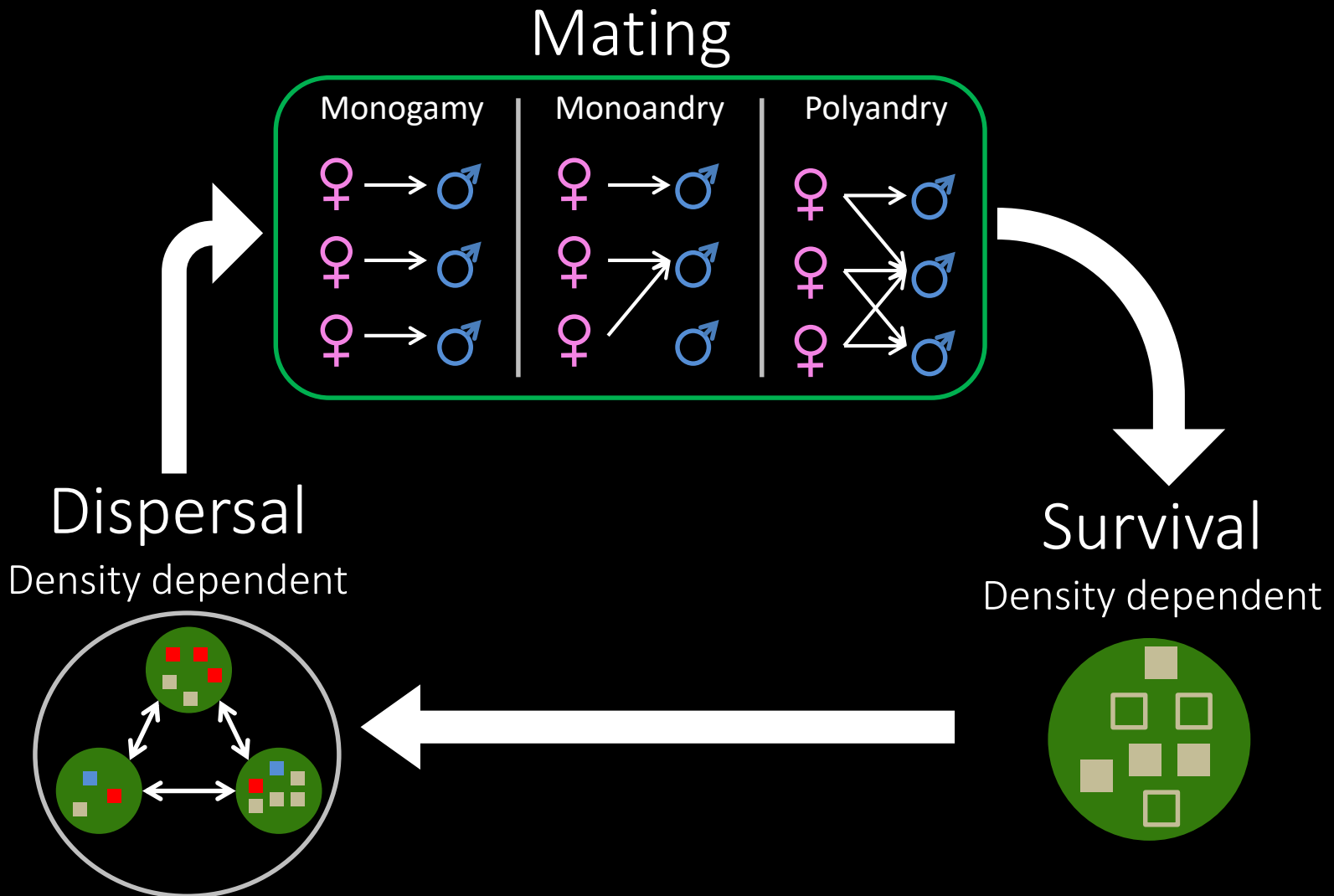
# The model

---

# Sexually reproducing diploid organisms

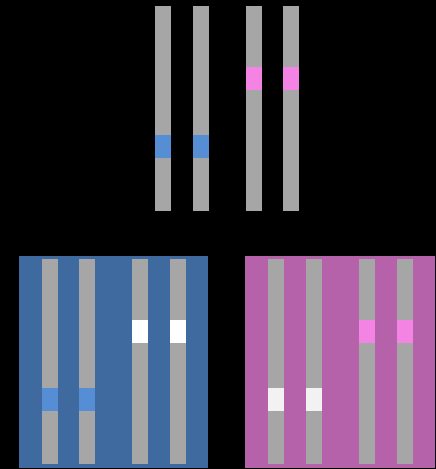


# Life cycle

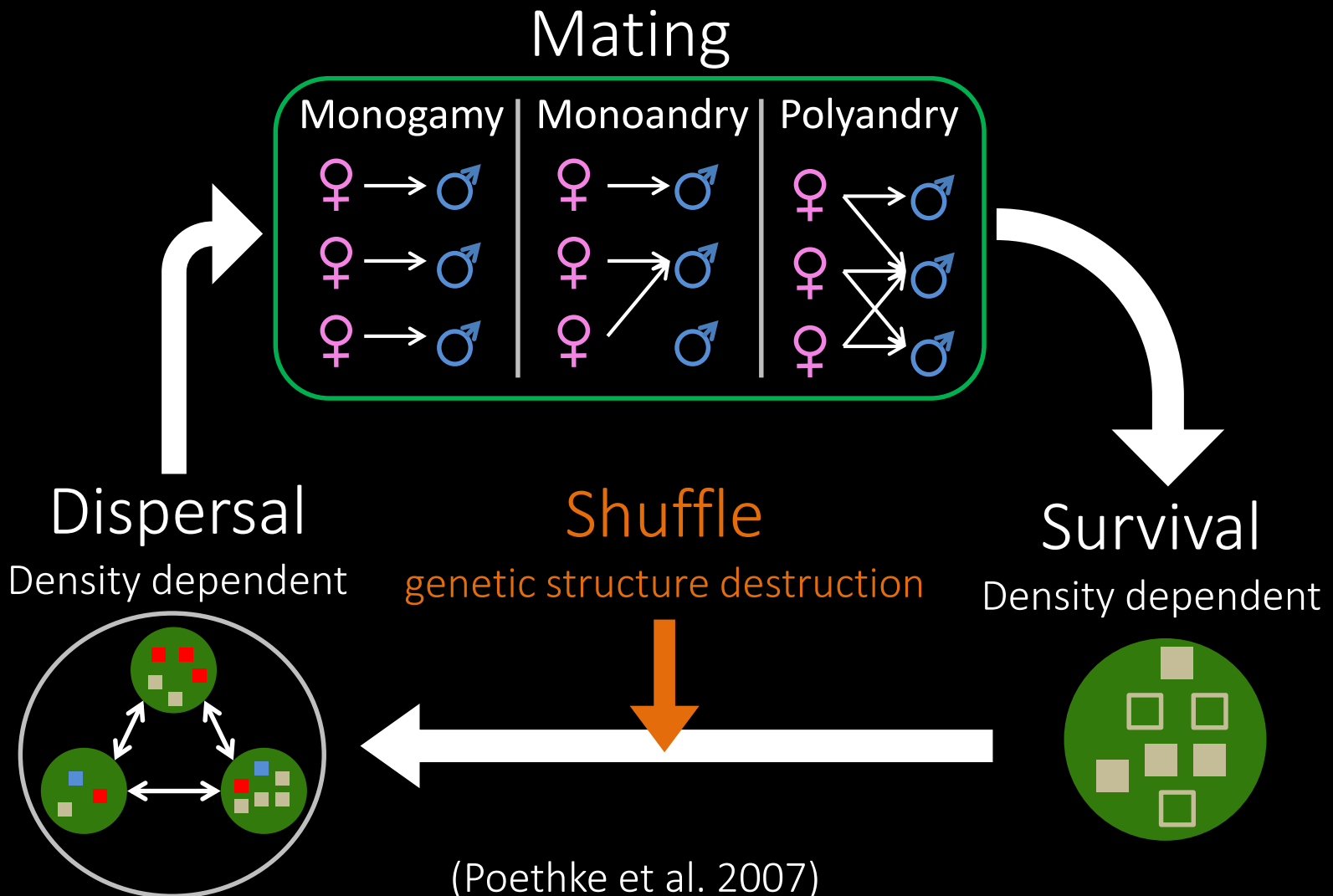


# Dispersal evolution

- Dispersal genes
  - Autosomes - Independent loci
  - Sex-dependent locus expression
  - Mutations
- Benefits / cost of dispersal
  - Natural selection → Equilibrium

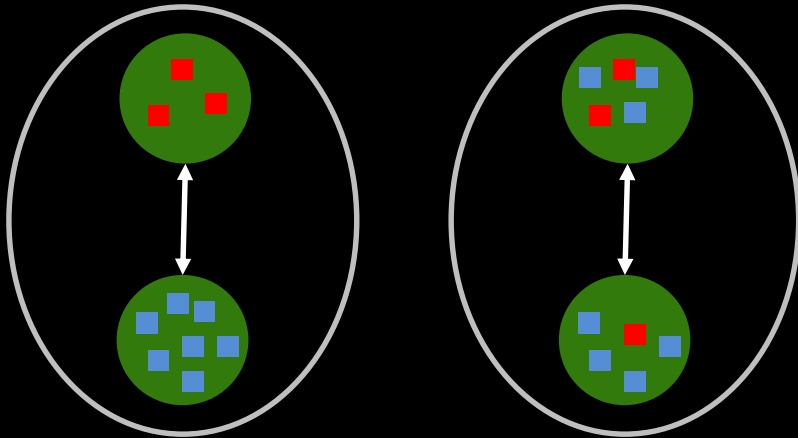


# Test kin competition effect



# Genetic structure and shuffle

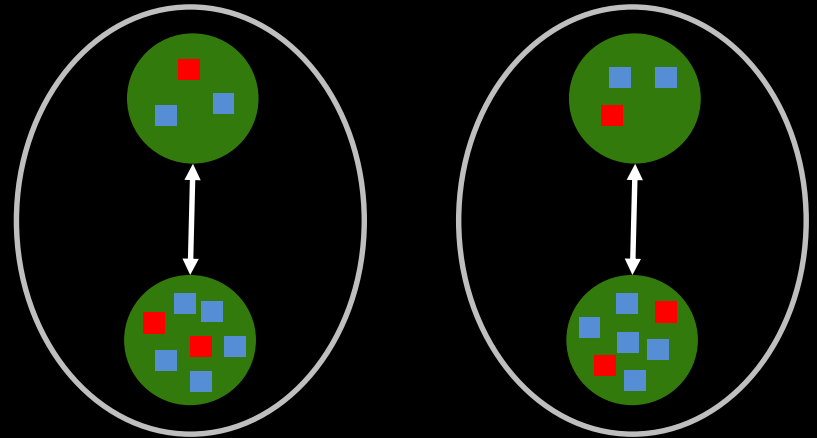
WITH  
genetic structure



BEFORE  
dispersal

AFTER  
dispersal

WITHOUT  
genetic structure

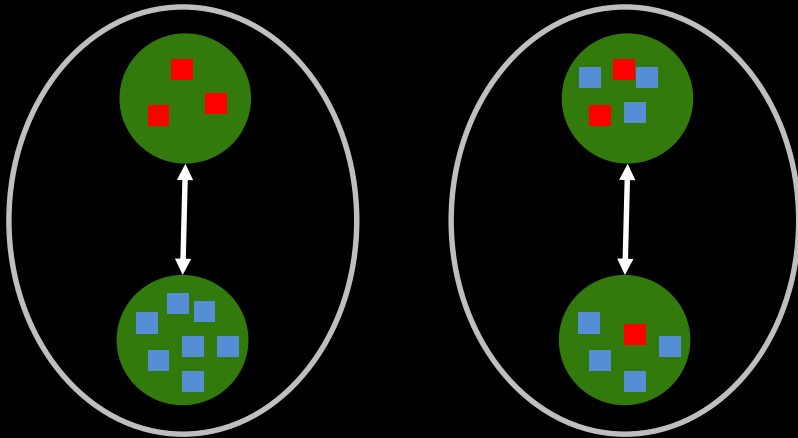


BEFORE  
dispersal

AFTER  
dispersal

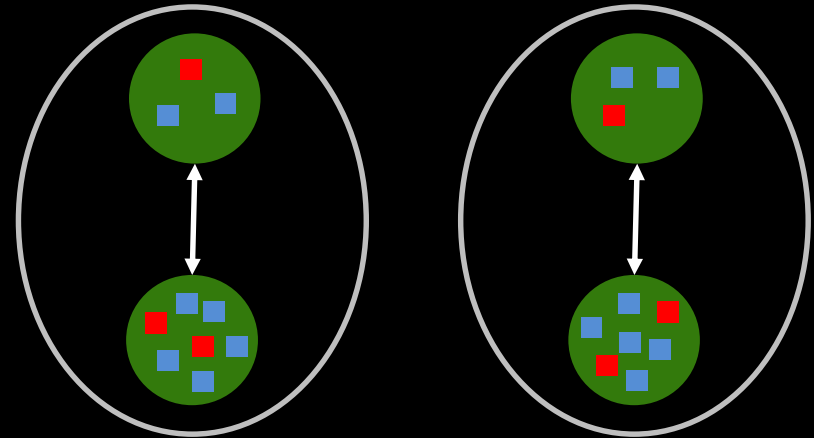
# Genetic structure and shuffle

WITH  
genetic structure



Less kin competition with  
dispersal

WITHOUT  
genetic structure



Dispersal do not change kin  
competition



# Results

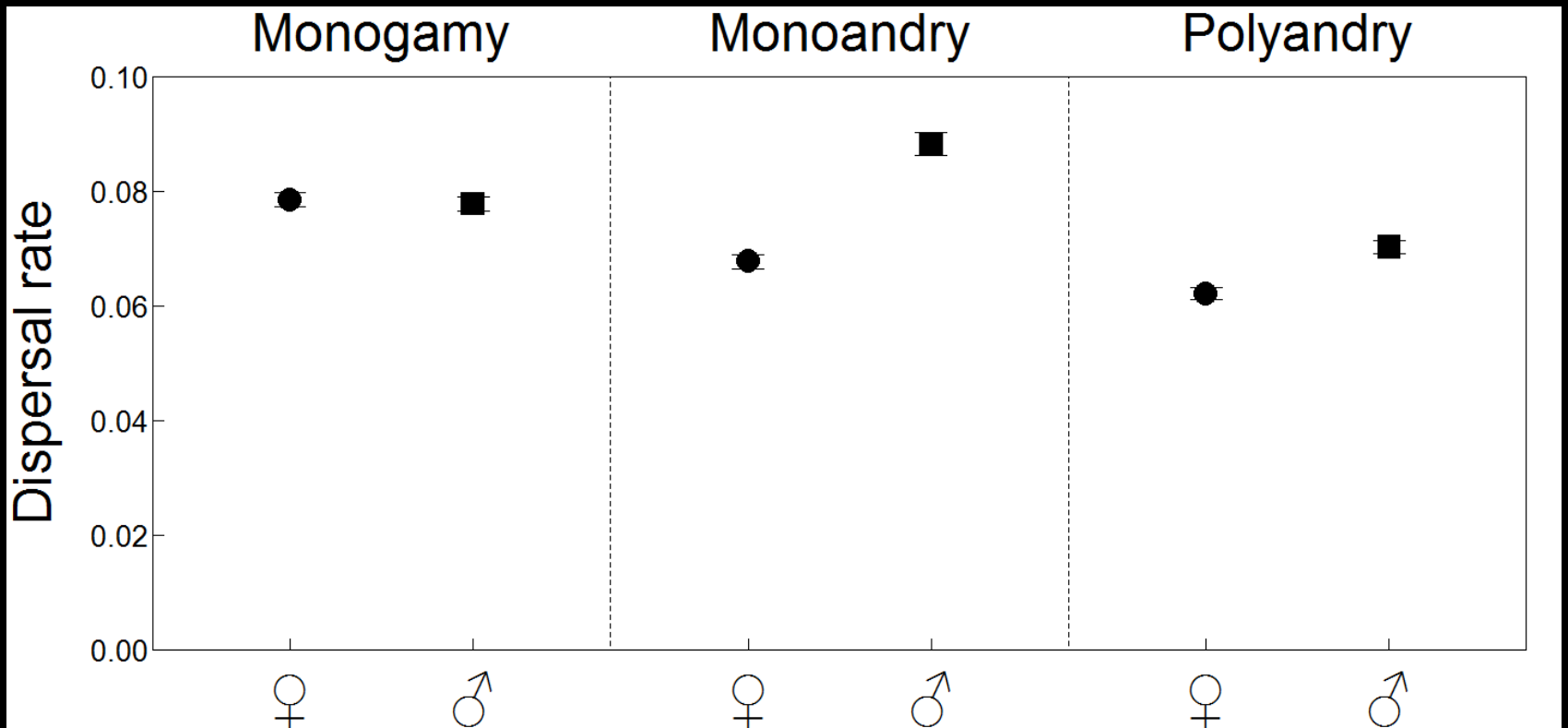
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# Sex-biased dispersal

WITH genetic structure

■ males

● females



# Sex-biased dispersal

WITH genetic structure

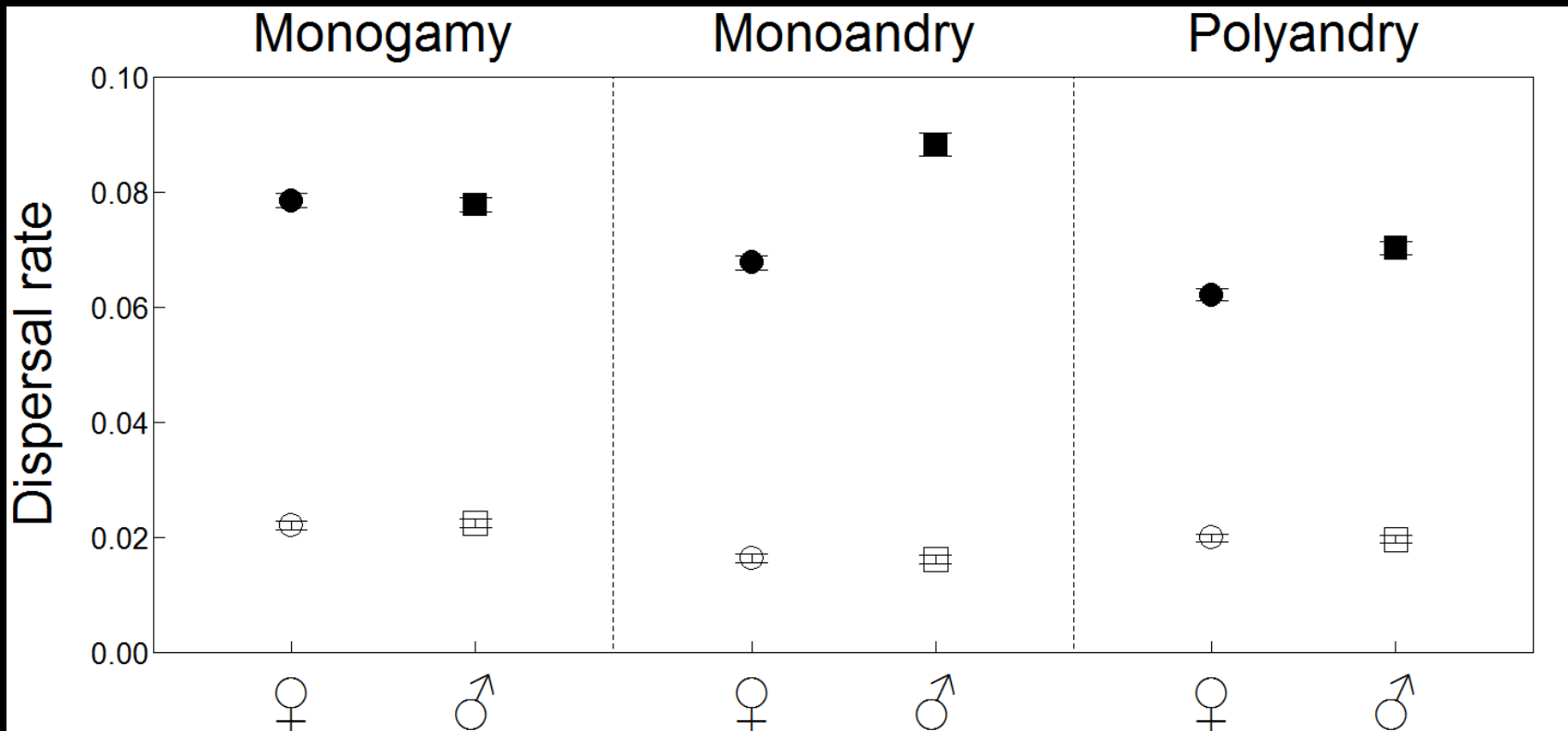
■ males

● females

WITHOUT genetic structure

□ males

○ females



# Environmental stochasticity effect

WITH genetic structure

WITHOUT genetic structure

■ males

□ males

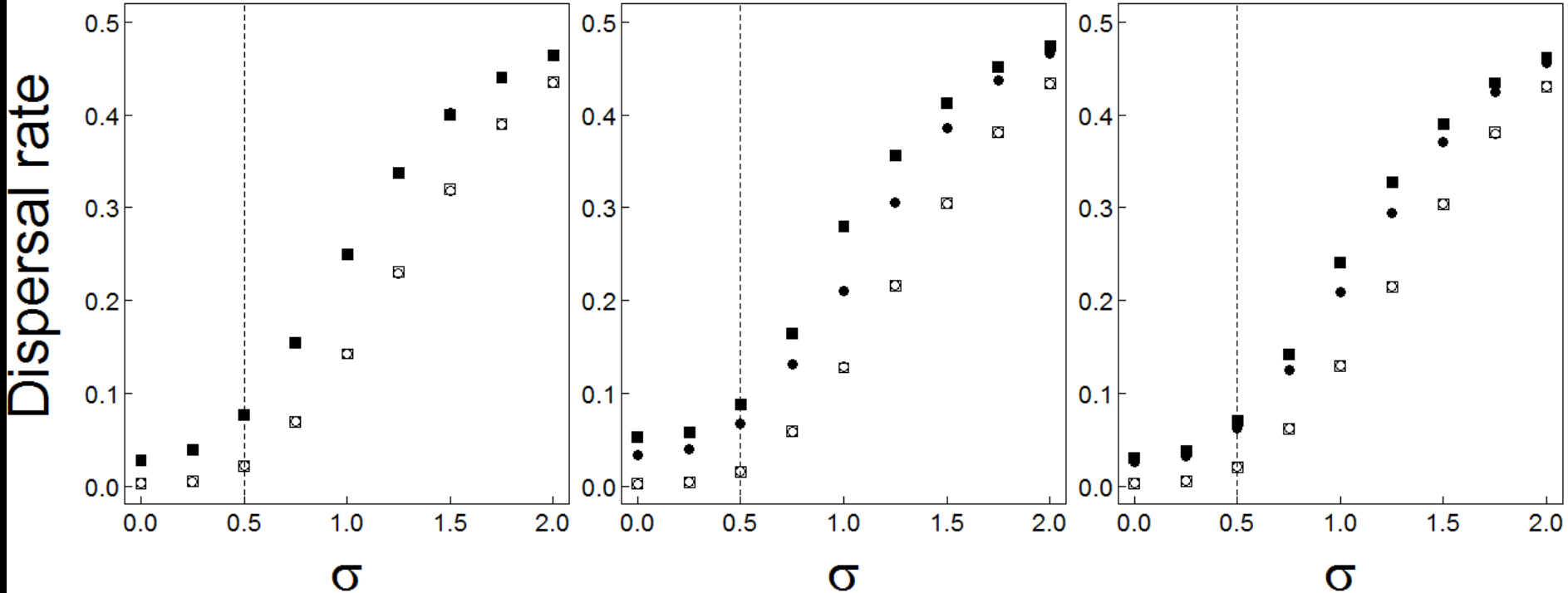
● females

○ females

Monogamy

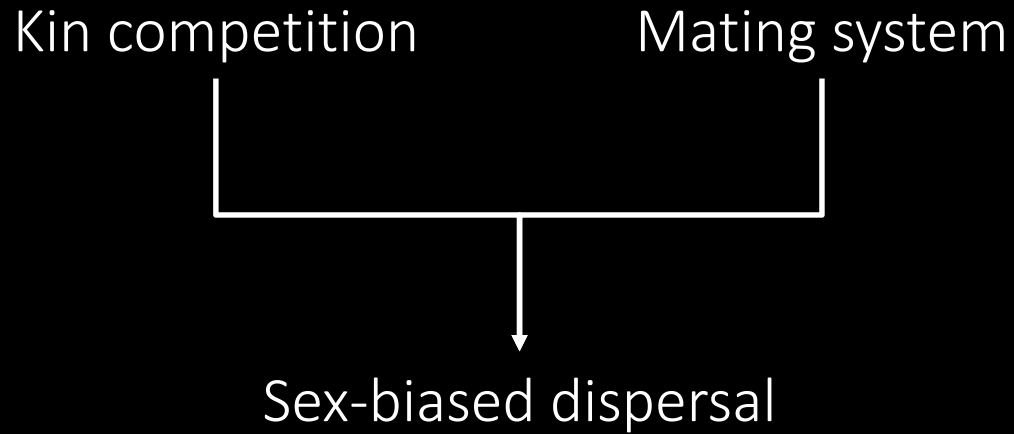
Monoandry

Polyandry



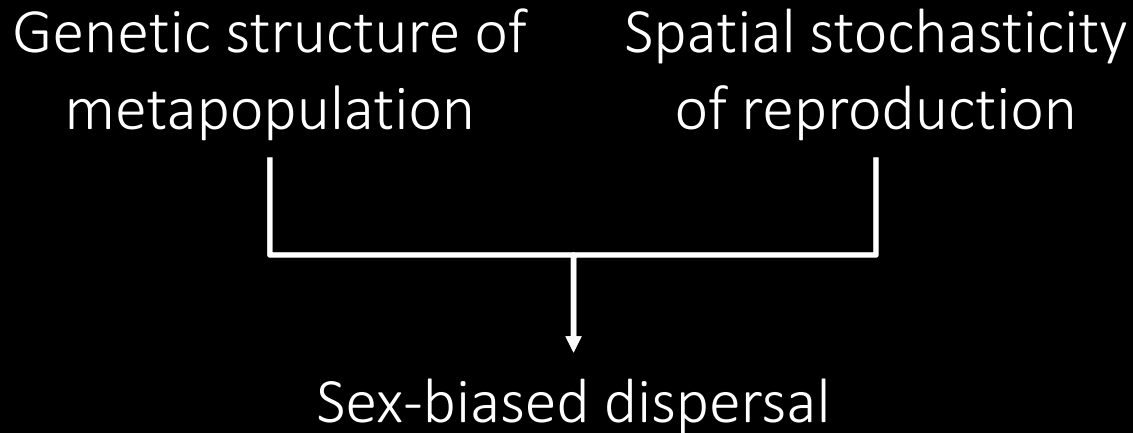
# Discussion

---



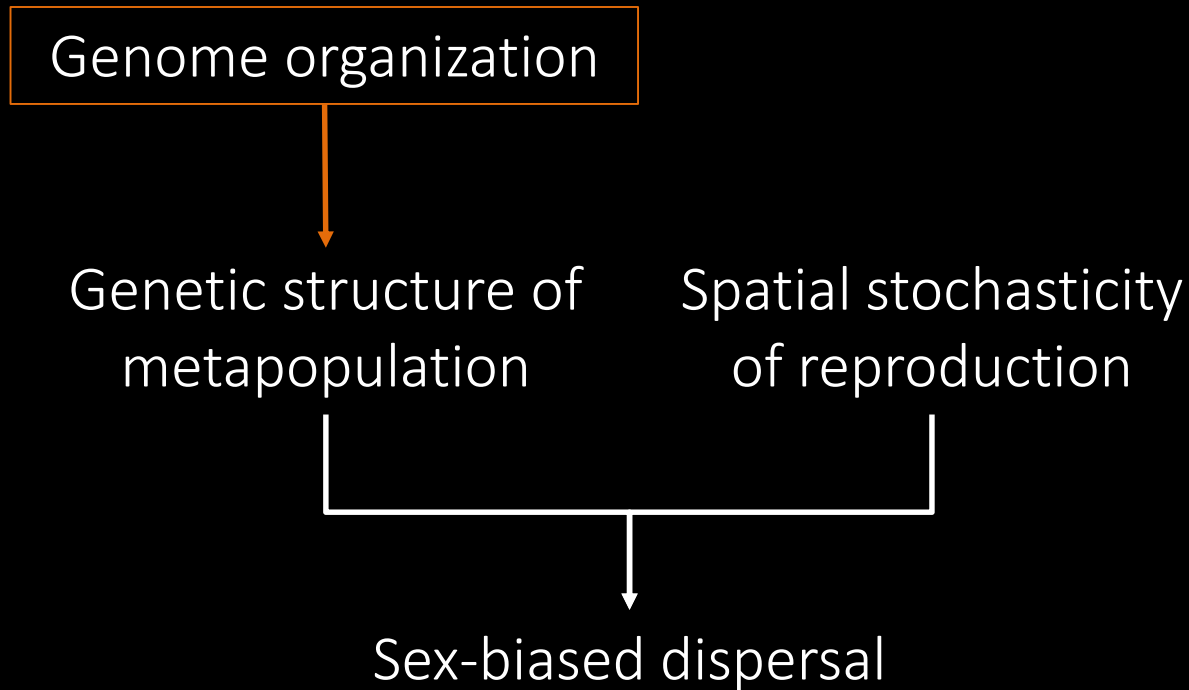
# Discussion

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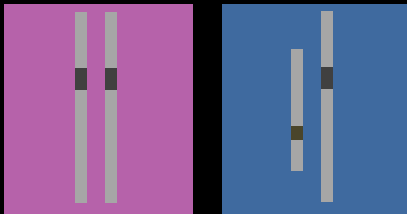


# Discussion

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# Influence of sex-chromosome system on sex-biased dispersal evolution



Brom et al (submitted) Evolution



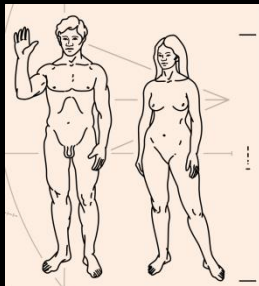
# Heterogamety

- Greenwood 1980 → Is opposite patterns of dispersal observed in mammals and birds linked to sex determination chromosomes ?

♂

X

Y



♀

X

X

♂

Z

Z



♀

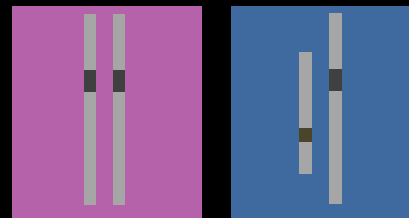
Z

W

# Heterogamety model

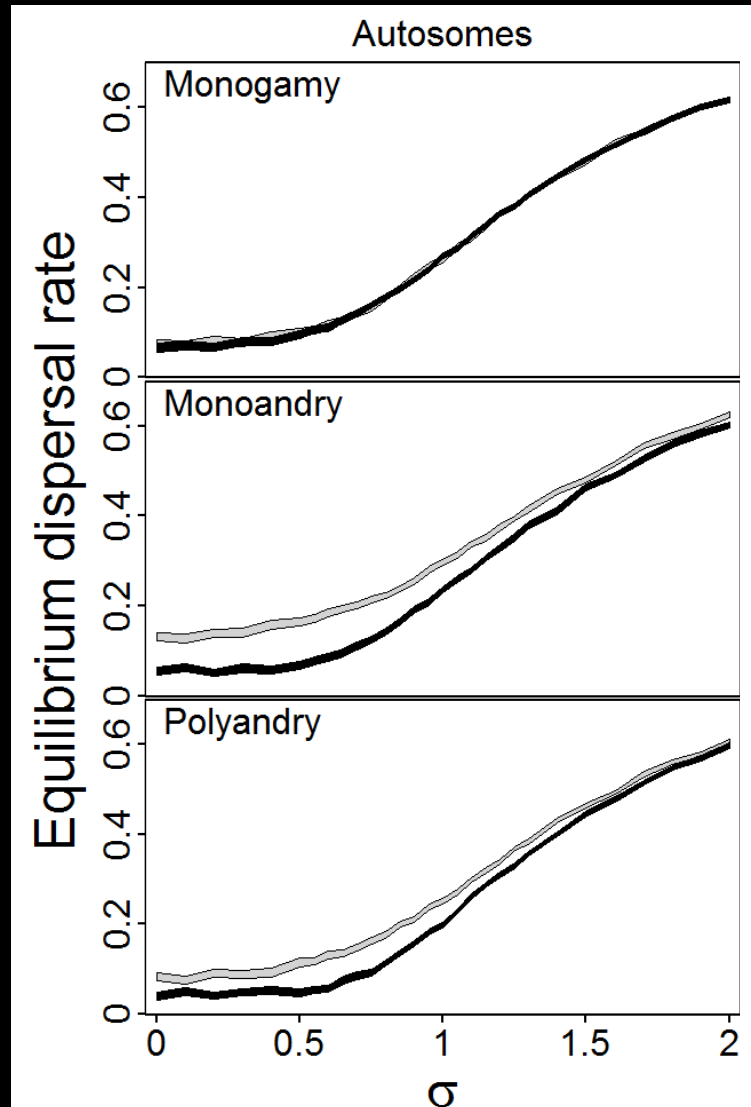
- Same IBM than before

- Dispersal loci
  - Sexual chromosomes

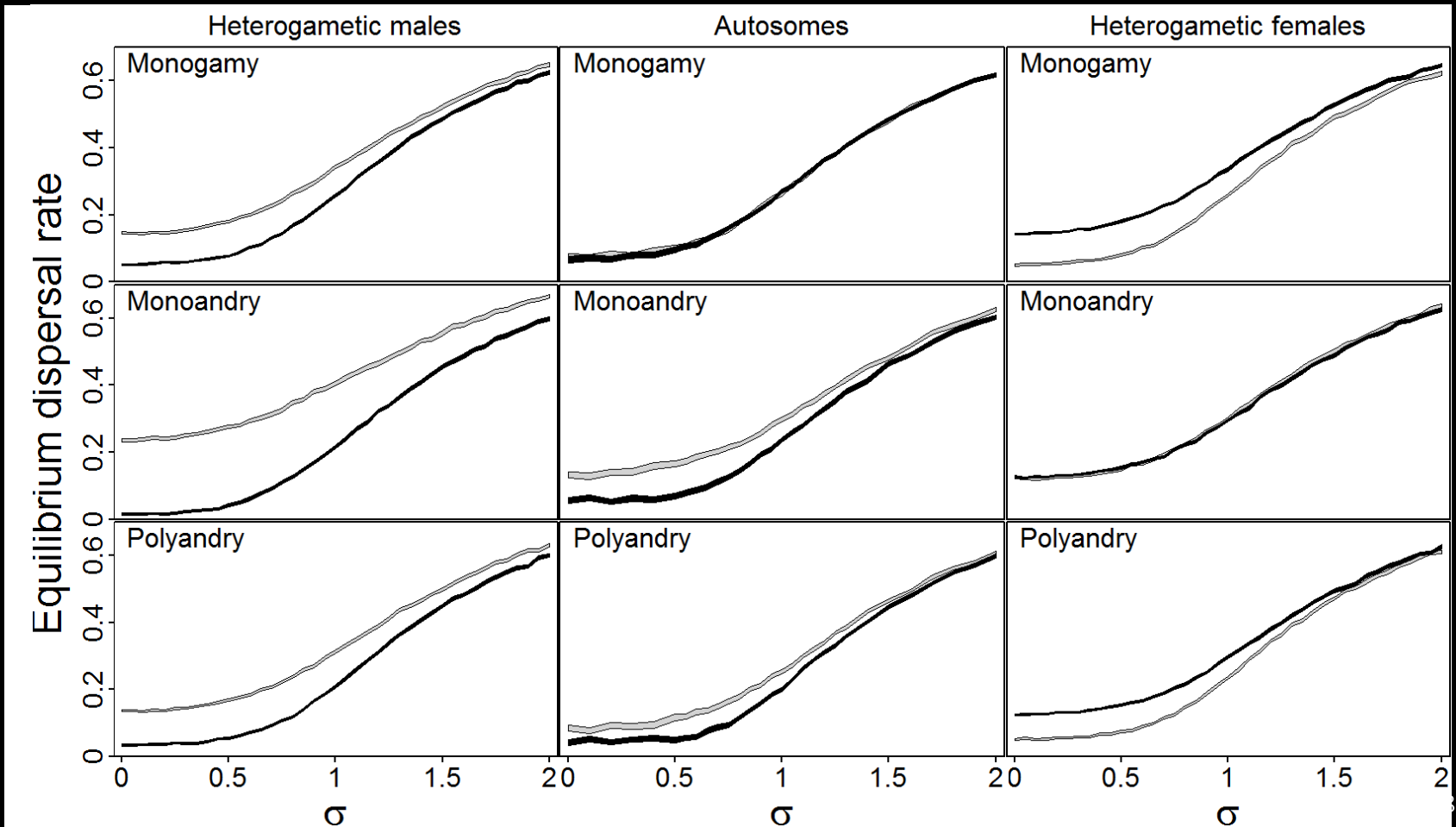
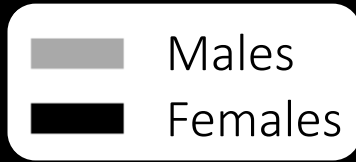
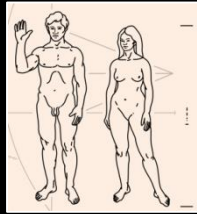


- Density independent dispersal

# Results: density independent dispersal



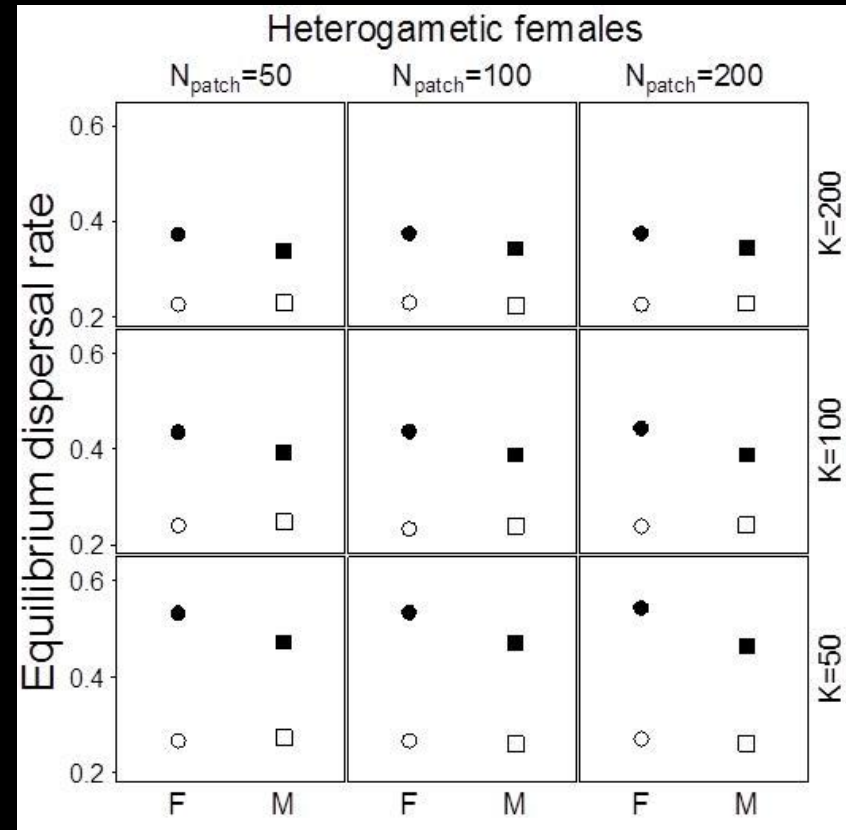
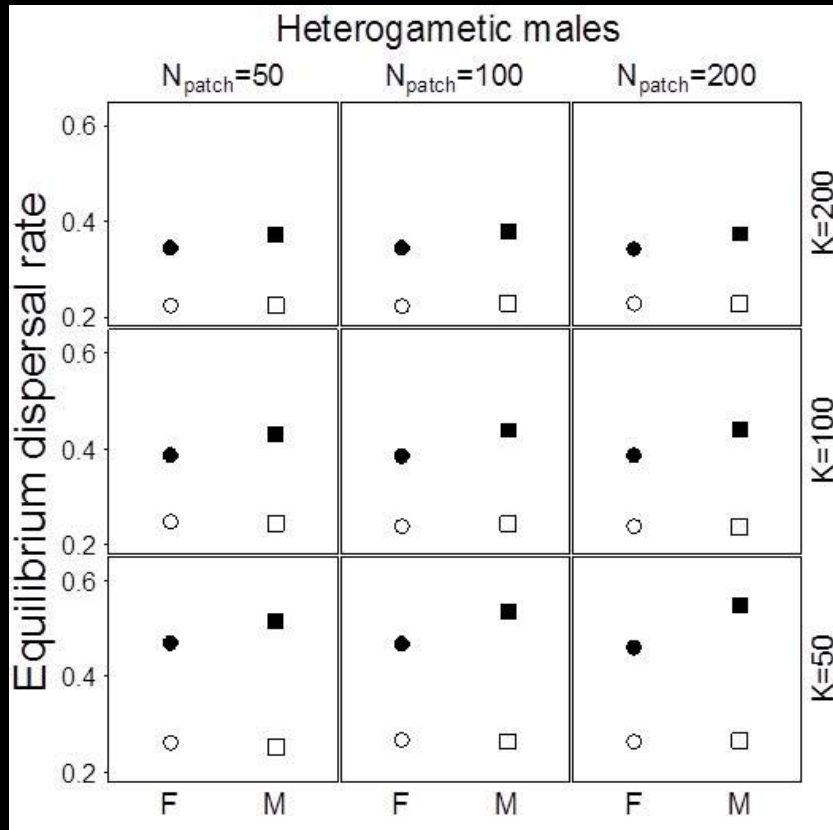
# Results



# Shuffle, $K$ and $N_{\text{patch}}$ in monogamy



Monogamy



# Conclusions

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- Genetic architecture can be important
- Mating system still have an effect
- Dispersal is multifactorial
- Different equilibriums between sex-chromosomes and autosomes
  - Genomic conflicts

# Perspectives

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- Evolution of mating system ? Coevolution ?
- Mating systems are complex
  - Resource defense ?
  - Mate choice ?
  - Extra pair copulation ?

# Perspectives

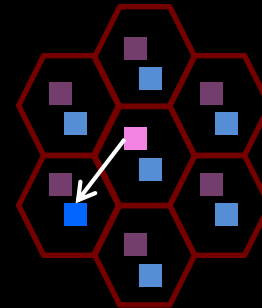
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- Evolution of mating system ? Coevolution ?
- Mating systems are complex
  - Resource defense ?
  - Mate choice ?
  - Extra pair copulation ?



# Influence of extra-pair copulation on sex-biased dispersal evolution

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# Introduction : birds case

- Female biased dispersal

Mabry et al. (2013) PLoS One



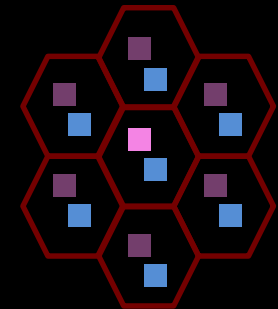
- Monogamy ?

– Extra Pair Copulation (EPC) in many species

Griffith et al. (2002) Molecular Ecology

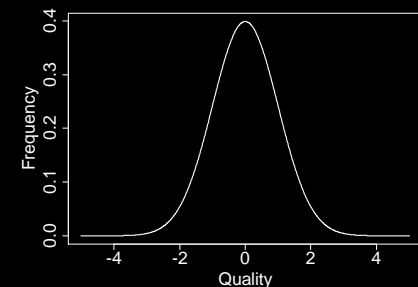
# Methods : mating

- Monogamy: only 1 female and 1 male reproduce on each patch



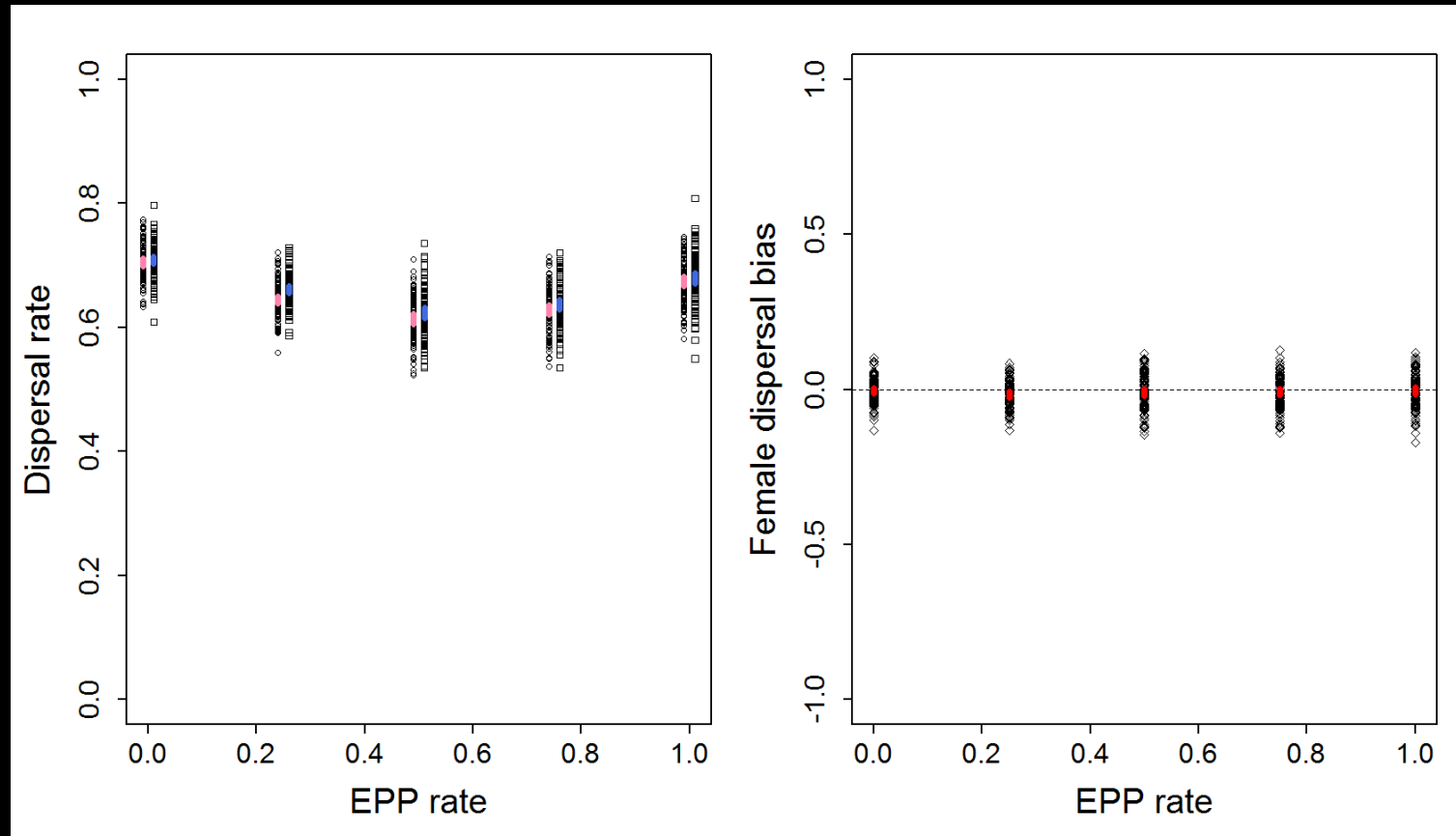
- Extra-pair copulation:
  - With 1 other mated male of the adjacent patch
  - EPP rate: % of newborns from EP male

- Random mating or “best-of” choice
  - Non heritable normally distributed quality



# Results : taking into account EPC

## Random mating

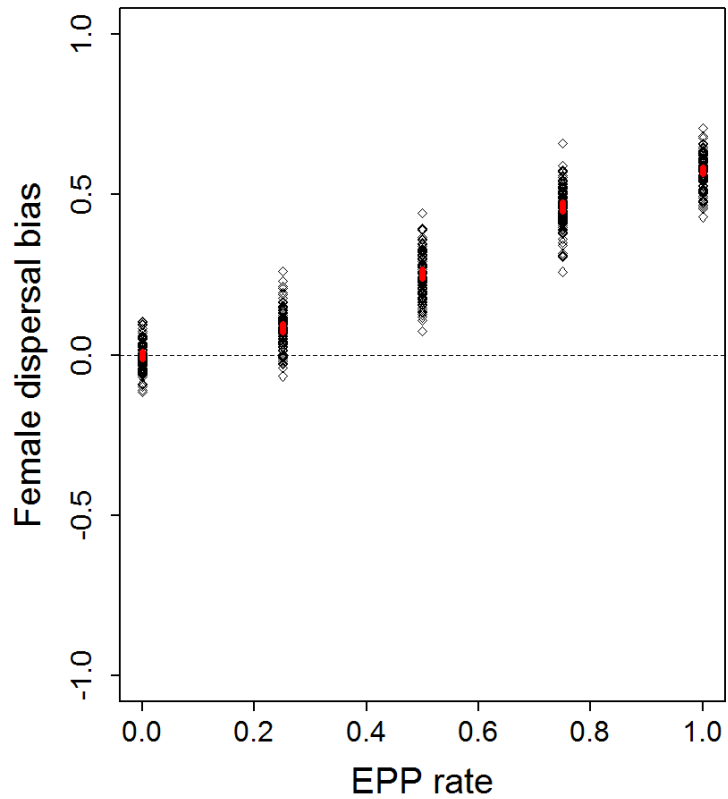
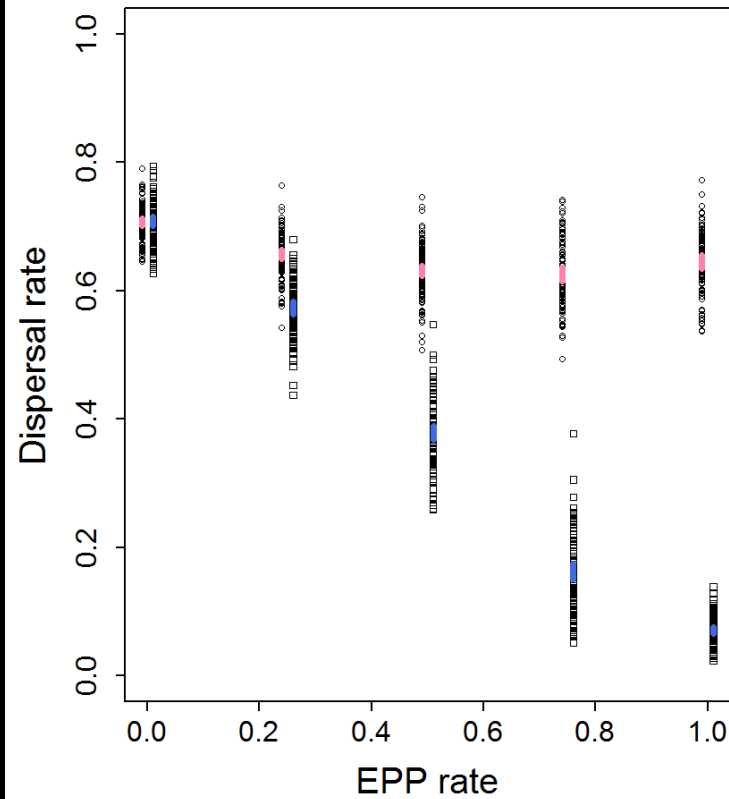


# Results : taking into account EPC

---

- Without choice:
  - No bias.
  - Lower dispersal rate with middle values of EPC rate.
- Intermediate level of EPP:
  - Reduced kin competition because of the multiple paternity in each patch

# Results : female mate choice



# Results : female mate choice

- With choice:
  - Male dispersal rate decrease as extra-pair copulation rate increase.
- Mate choice
  - Mating depend more on quality and less on the number of male in the population/patch.
  - Low benefit to disperse
- Increasing level of EPP
  - Increasing benefit of reproduction for high quality male

# New question

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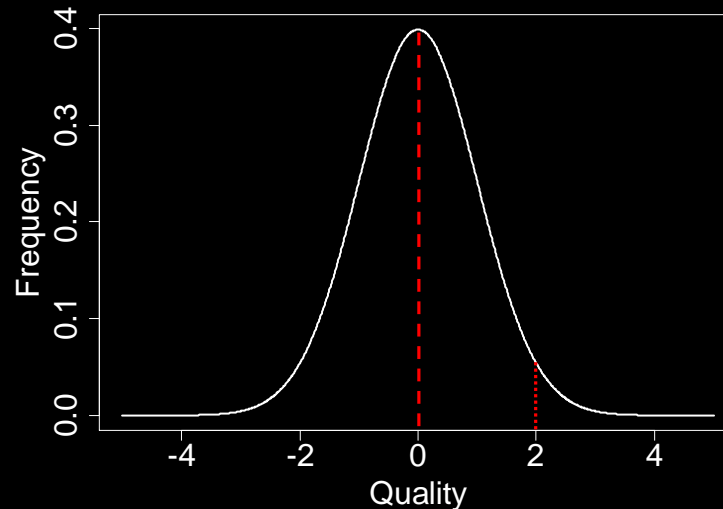
## ➤ Effect of quality

- What happen if dispersal strategy can change with individual quality ?

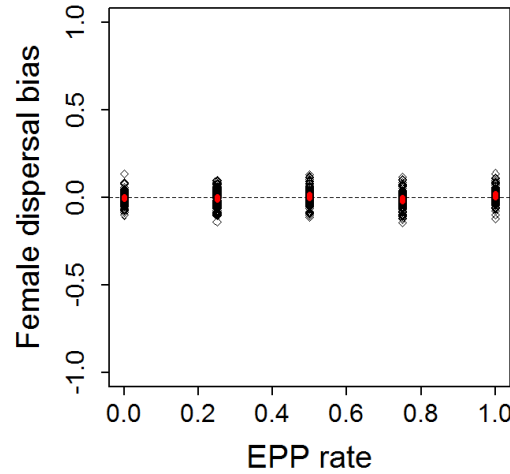
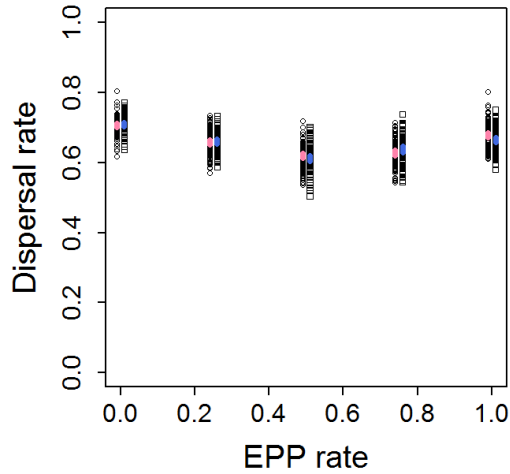


# Quality dependend dispersal

- Two loci:
  - High quality dispersal strategy
  - Low quality dispersal strategy
- High or low quality depending on a fixed threshold

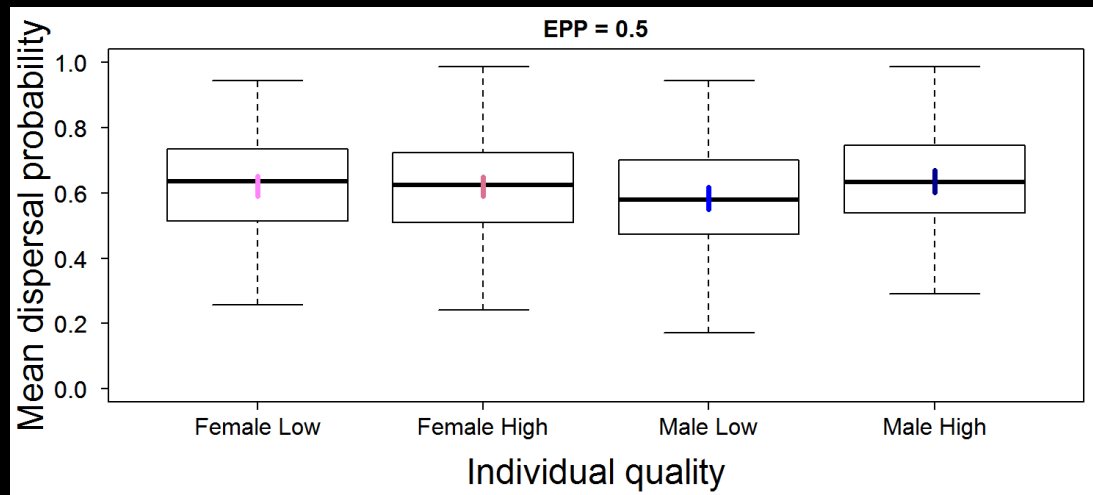


# No choice control

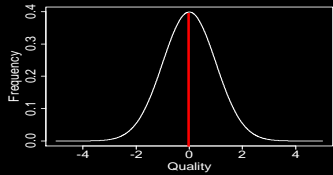


Same pattern than in quality independent dispersal

High and low quality strategies are the same



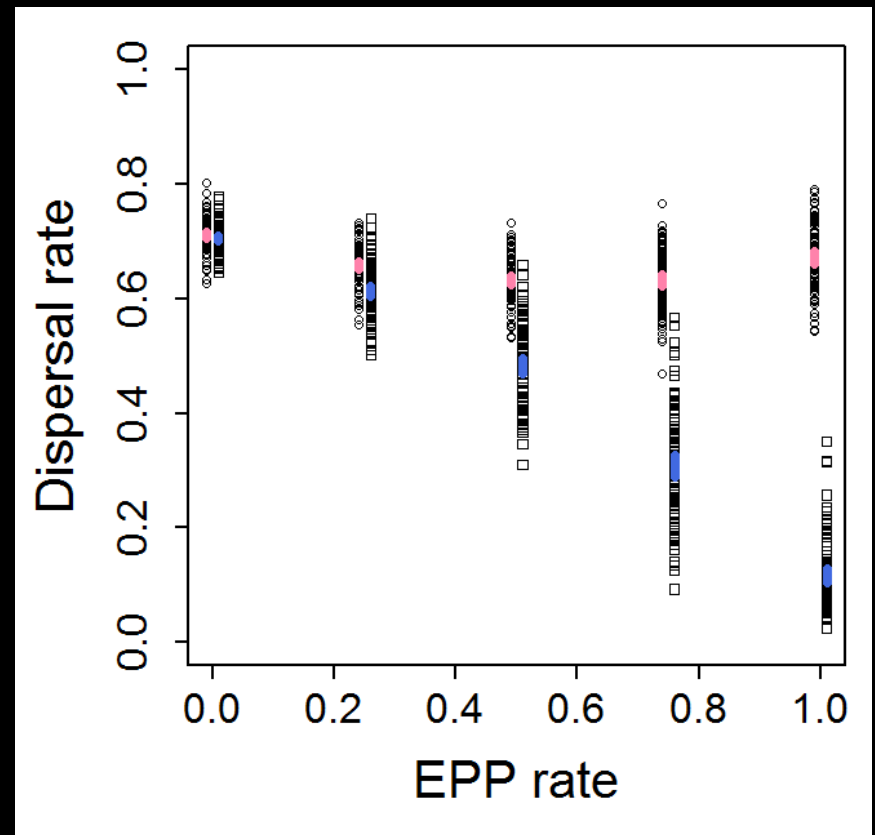
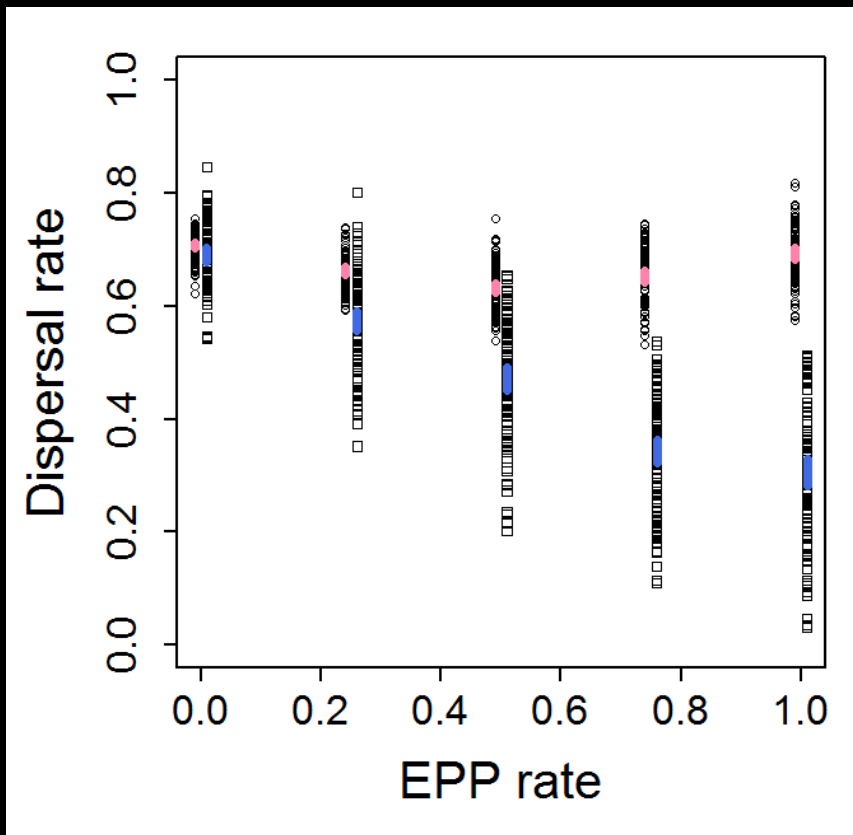
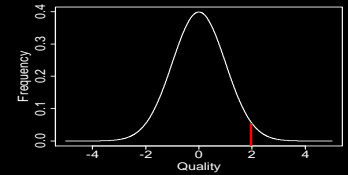
# Results: Quality dependend dispersal



➤ 0

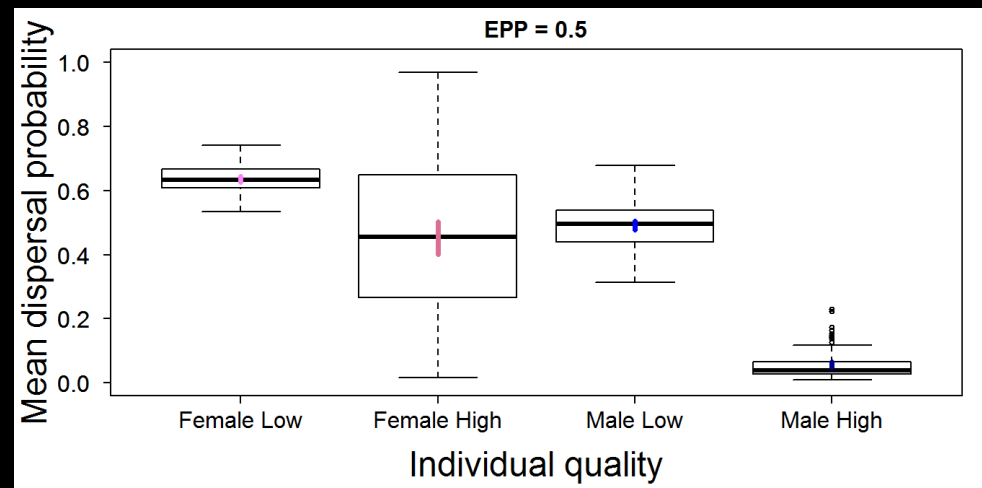
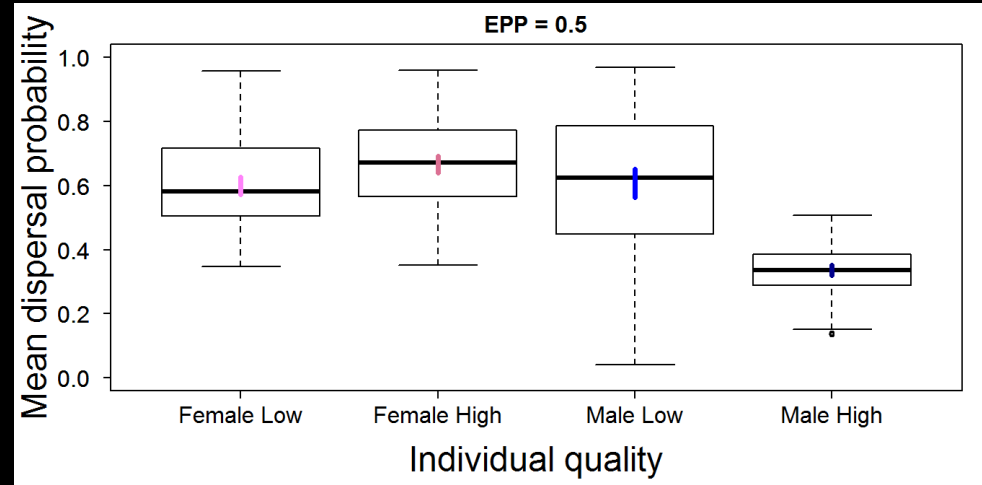
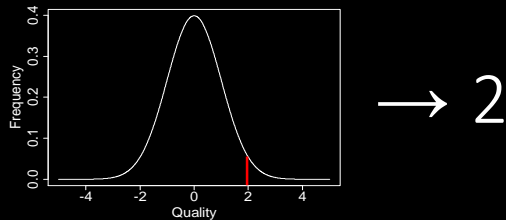
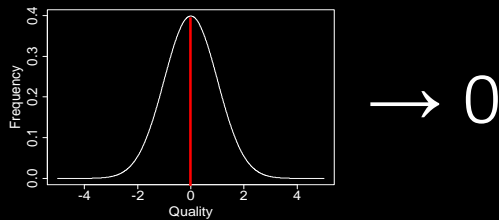
## Quality threshold

➤ 2



# Results: Quality dependend dispersal

## Quality threshold



# Results: Quality dependend dispersal

---

- Dispersal do not evolves in the same way for low and high quality males.
- High quality male do no disperse
  - High probability of beeing choose
  - Low benefit to disperse
  - Cost of dispersal (death) avoidance

# Discussion

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- Conditional dispersal strategy need more attention
- EPP rate: obligation of extra-pair copulation
  - amplified effect
- Importance of genetic mating system

# Perspectives

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- Overlapping or non overlapping generation change results.
- Sex-biased dispersal
  - Rate
  - Distance

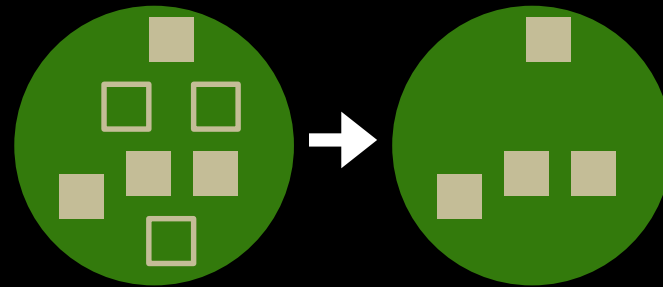
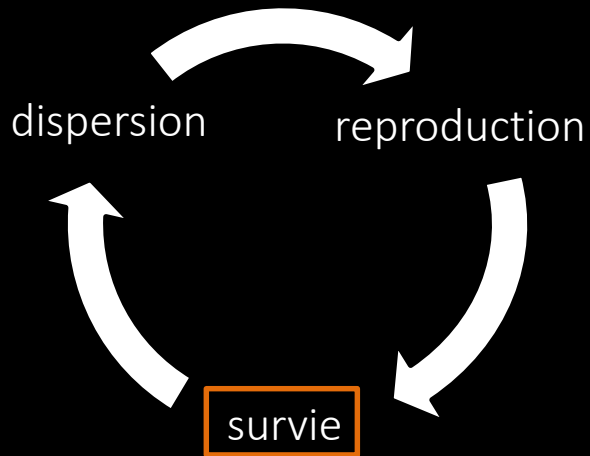
# Acknowledgement

- Manuel Massot (IEES-Paris)
- David Laloï (IEES-Paris)
- Stéphane Legendre (ENS)
- You (for your attention)





Dispersion sexe biaisée

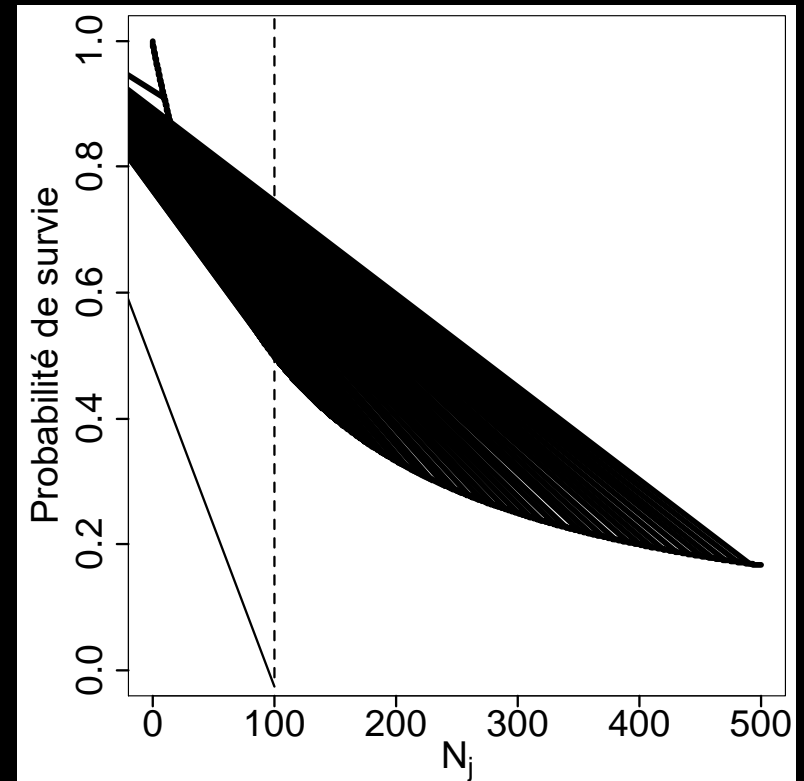


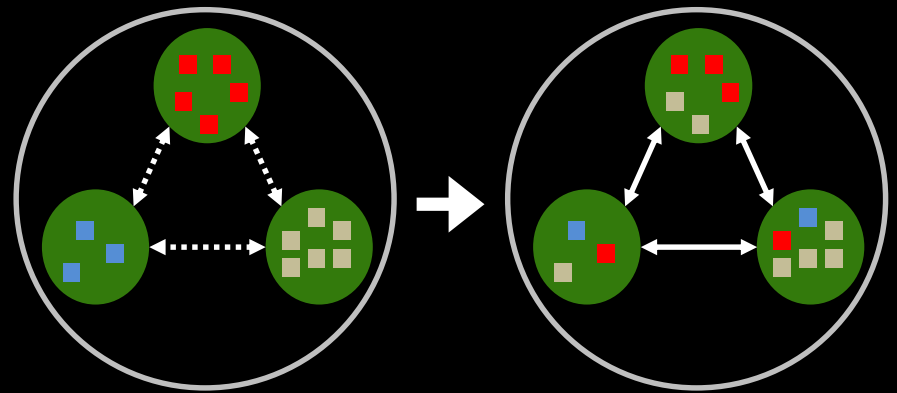
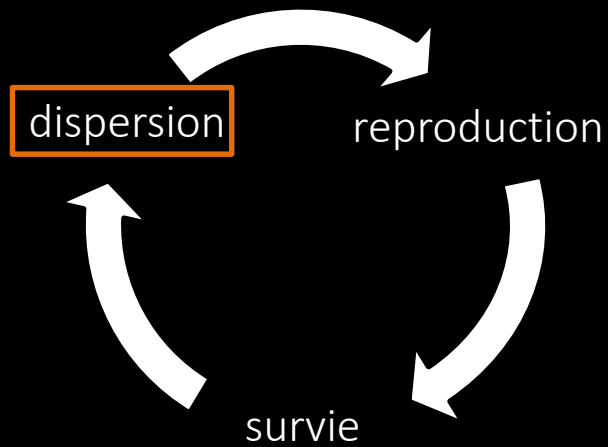
$$S = \frac{1}{(1 + \alpha N_j)^\beta}$$


---


$$\alpha = (\lambda^{1/\beta} - 1) / K$$

$N_j$  = nombre d'individus sur la parcelle  $j$   
 $K$  = capacité de la parcelle  
 $\beta$  = facteur de densité dépendance  
 $\lambda$  = taux de croissance de la population

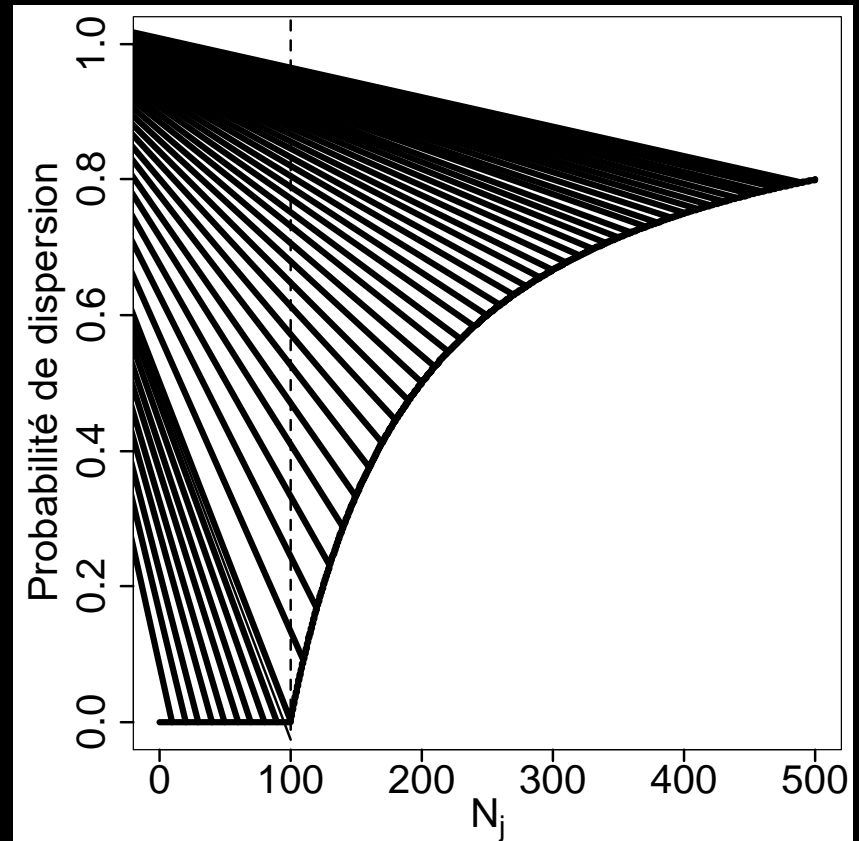




## Densité dépendante

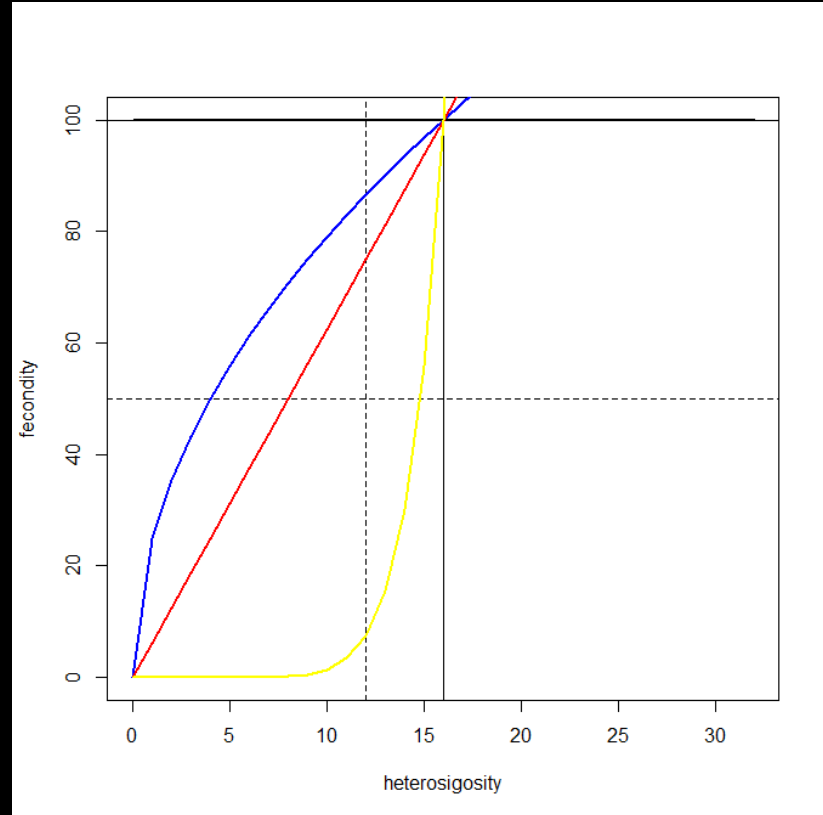
$$dp_i = \begin{cases} 0 & \text{if } N_j/K \leq ds_i \\ 1 - \frac{ds_i}{N_j/K} & \text{if } N_j/K > ds_i \end{cases}$$

$dp_i$  = probabilité de dispersion de l'individu  $i$   
 $ds_i$  = stratégie de dispersion de l'individu  $i$   
 $N_j$  = nombre d'individus sur la parcelle  $j$   
 $K$  = capacité de la parcelle



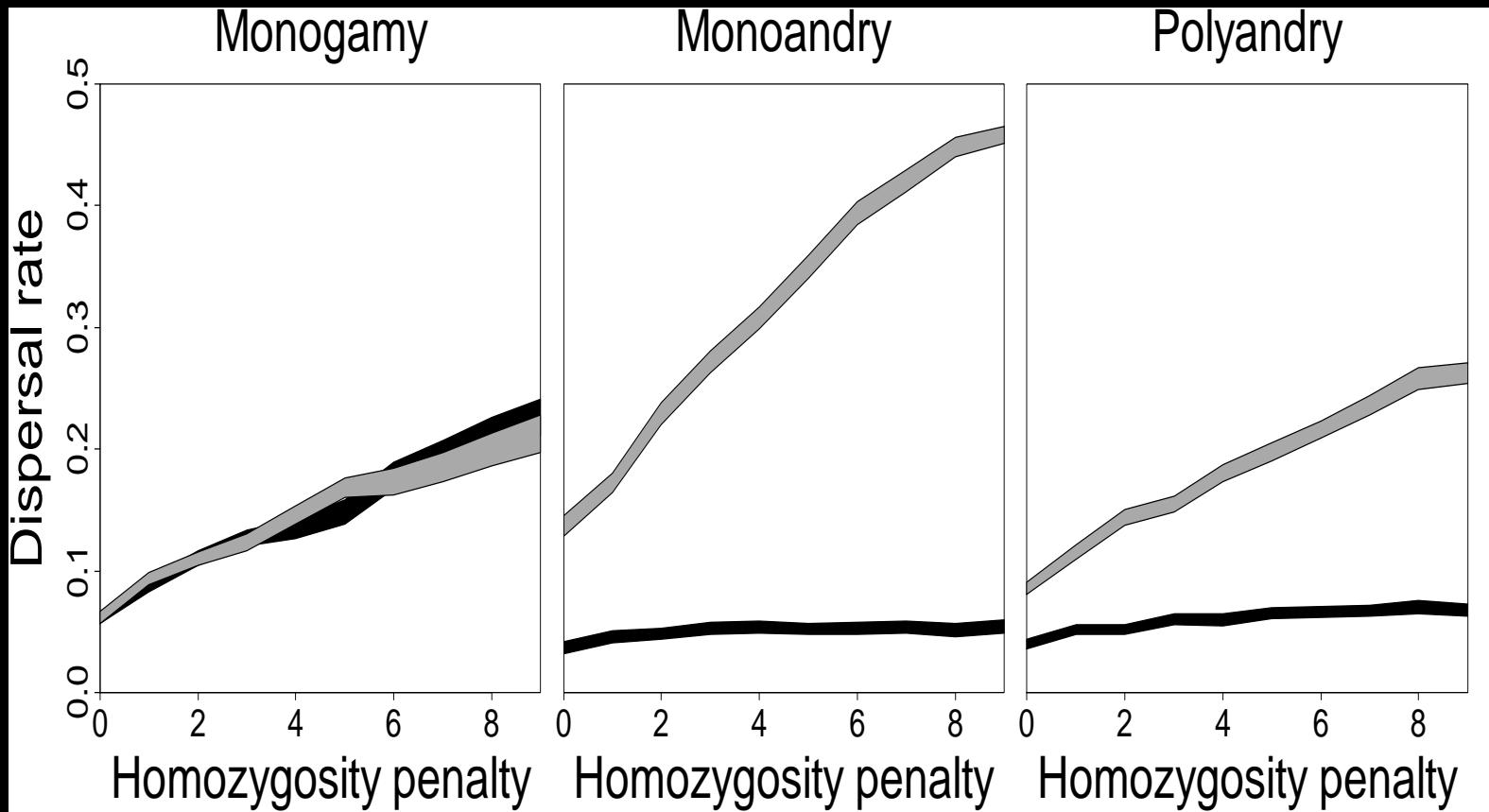
# Consanguinité

$$F_i = \begin{cases} F_i & \text{if } H_i \geq 0.5 \\ F_i * (2H_i)^p & \text{if } H_i < 0.5 \end{cases}$$



0 ; 0.5 ; 1 ; 9

# Effet de la consanguinité



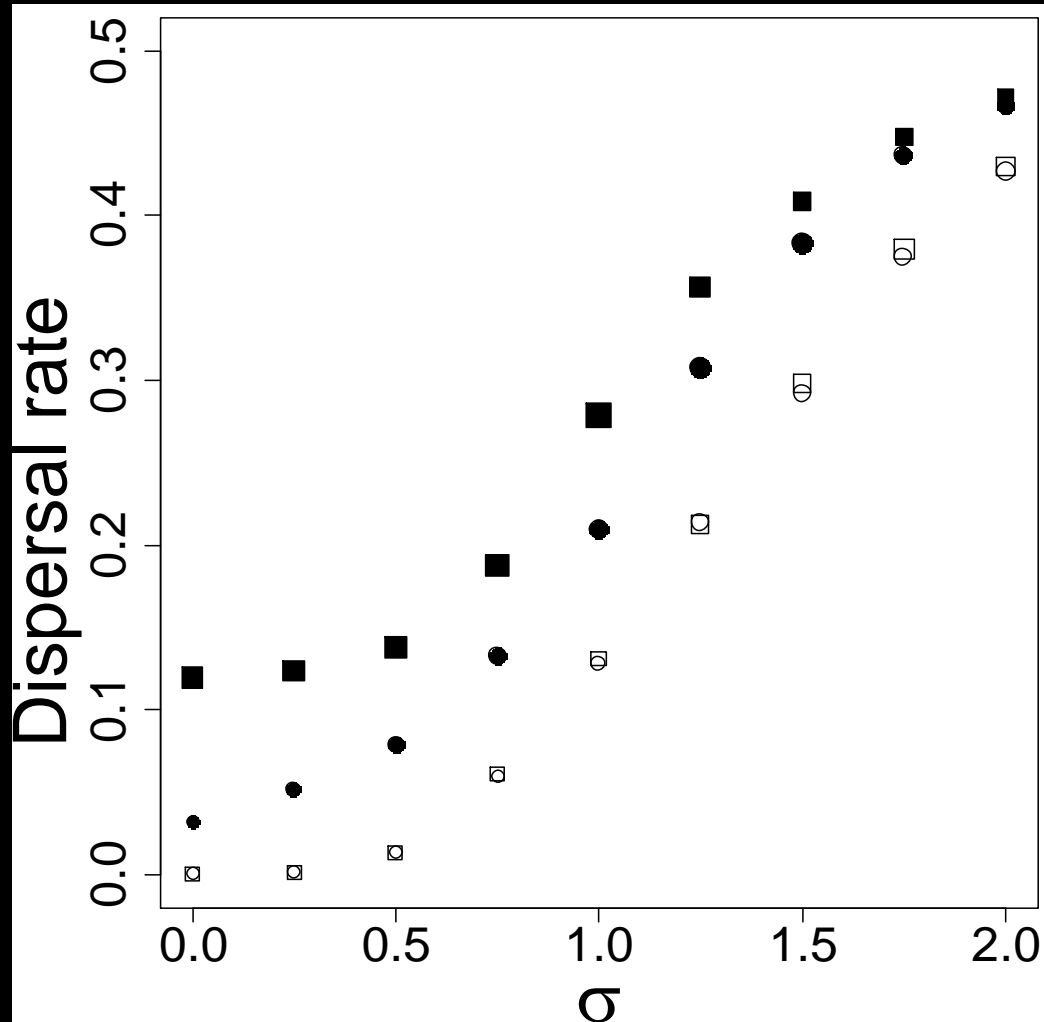
**Fig. 3.** Dispersal rate at equilibrium for males (grey) and females (black) plotted against homozygosity cost on fecundity for the three mating systems studied. Other parameters fixed to their base value as in Table 1. Line width indicates 95% confidence interval built by bootstrapping the results of 100 replicate simulation runs.

# Paramètres de la simulation

**Table 1:** Simulation parameters

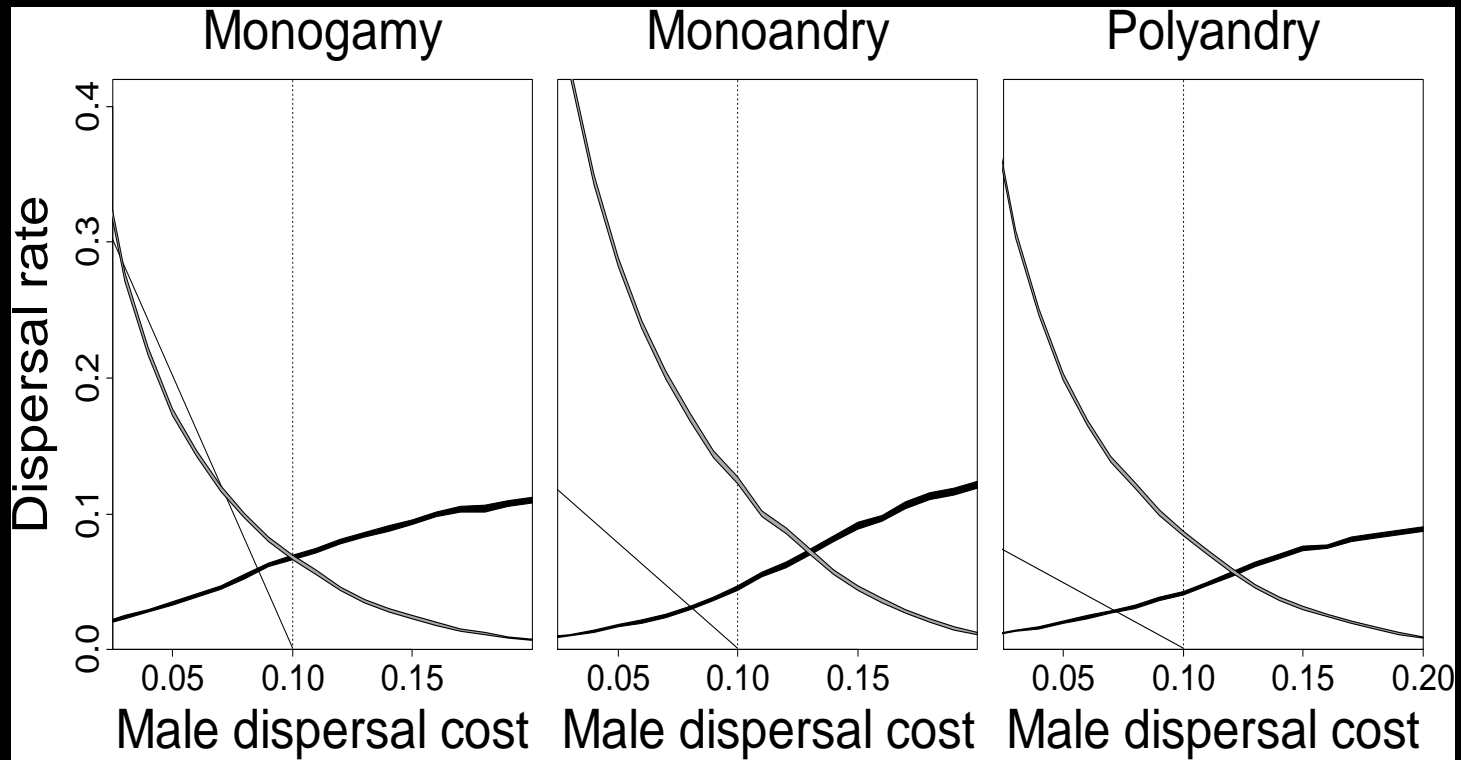
Name	Sy	Base
	mbol	value
Patch capacity	$K$	100
Number of patches	$n_{\text{pat}}$	100
	ch	
Dispersal mortality	$\mu$	0.1
Mean patch quality	$\lambda$	2
Heterogeneity in patch quality	$\sigma$	0.25
Intensity of density dependence	$\beta$	1
Primary sex ratio	$sr_b$	0.5
Homozygosis penalty coefficient	$\rho$	0
Mutation frequency on dispersal alleles	$f_s$	0.001
Mutation standard deviation on dispersal alleles	$sd_s$	0.05
Mutation frequency on neutral alleles	$f_n$	0.001

# Effet de la stochasticité



**Fig. 2.** Dispersal rate at equilibrium in the monoandrous mating system for females (circles) and males (squares) as a function of heterogeneity in patch quality ( $\sigma$ ). Filled symbols: standard model, open symbols: shuffled model. Other parameters fixed to their base value as in Table 1. Height of symbols represents 95% confidence interval built by bootstrapping the results of 100 replicate simulation runs (to ensure visibility, minimal height of symbols is 0.033 dispersal rate unit).

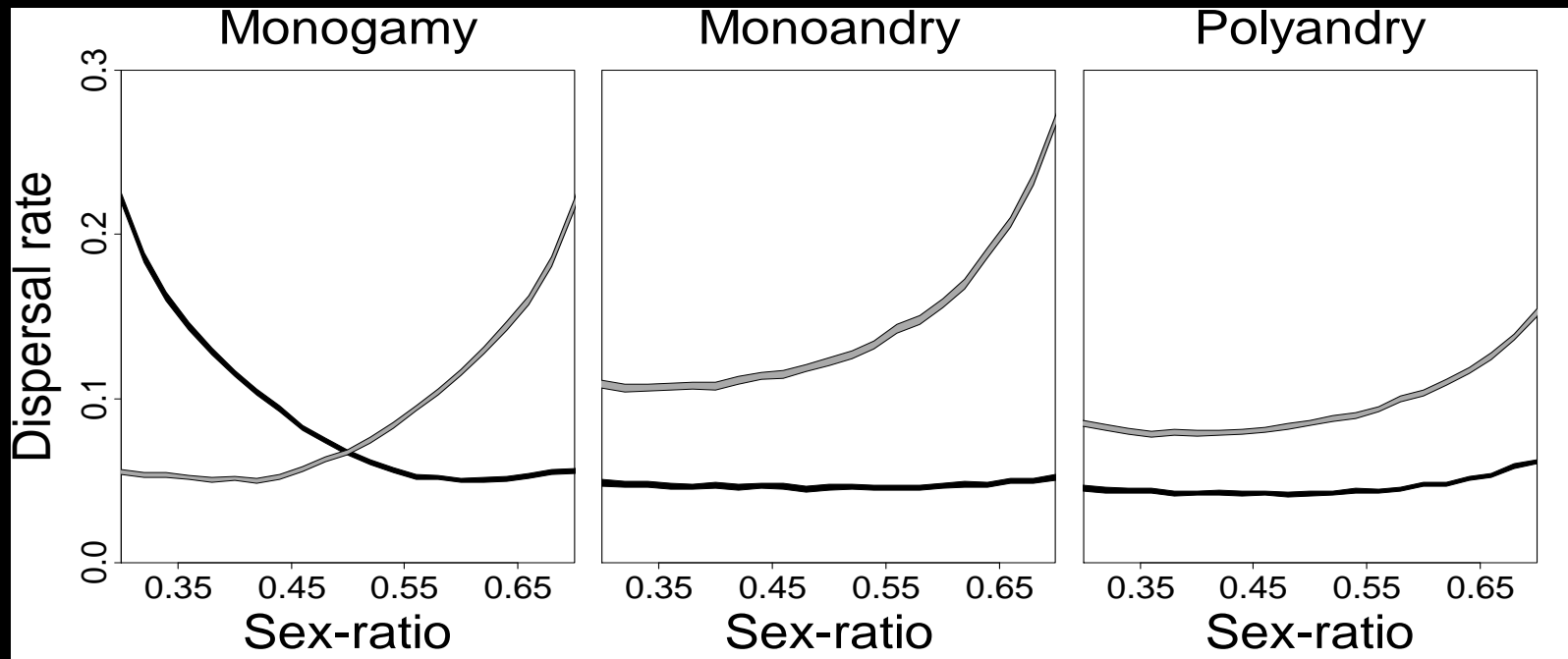
# Coût différent entre mâles et femelles



**Fig. 4.** Dispersal rate at equilibrium for males (grey) and females (black) for a range of male dispersal costs and for the three mating systems studied. Female dispersal cost  $\mu = 0.1$ . Other parameters fixed to their base value as in Table 1. The vertical line shows equality of dispersal costs between males and females. Line width indicate 95% confidence interval built by bootstrapping the results of 1000 replicate simulation runs.

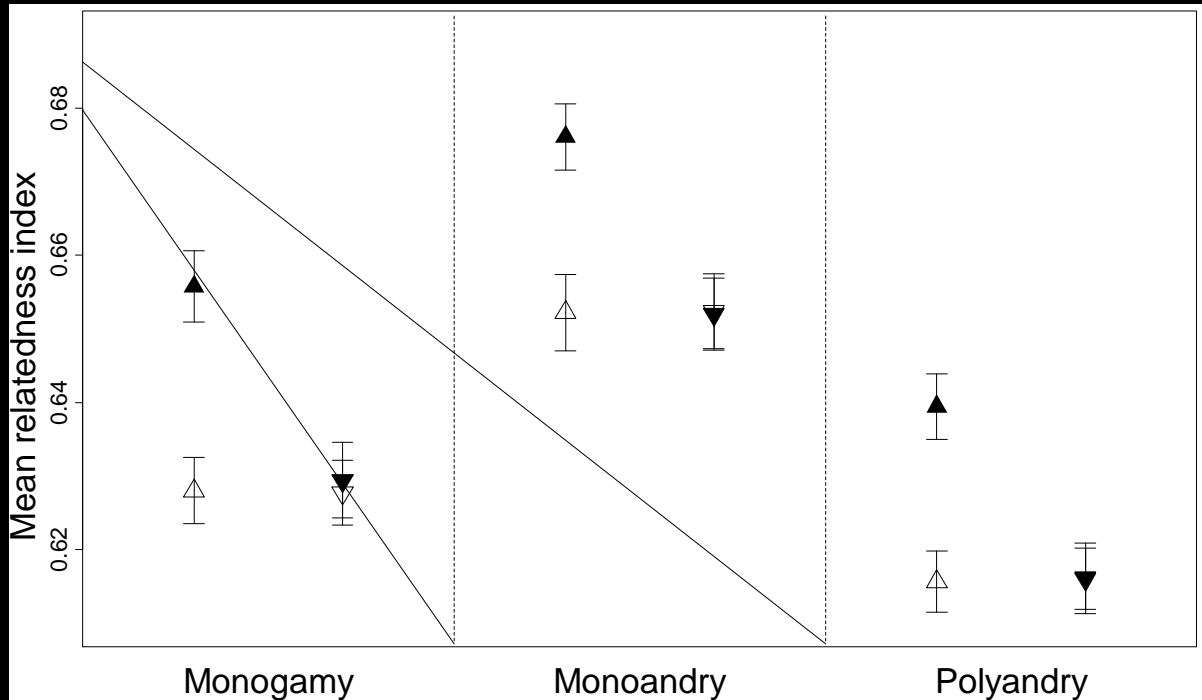


# Effet du sexe ratio



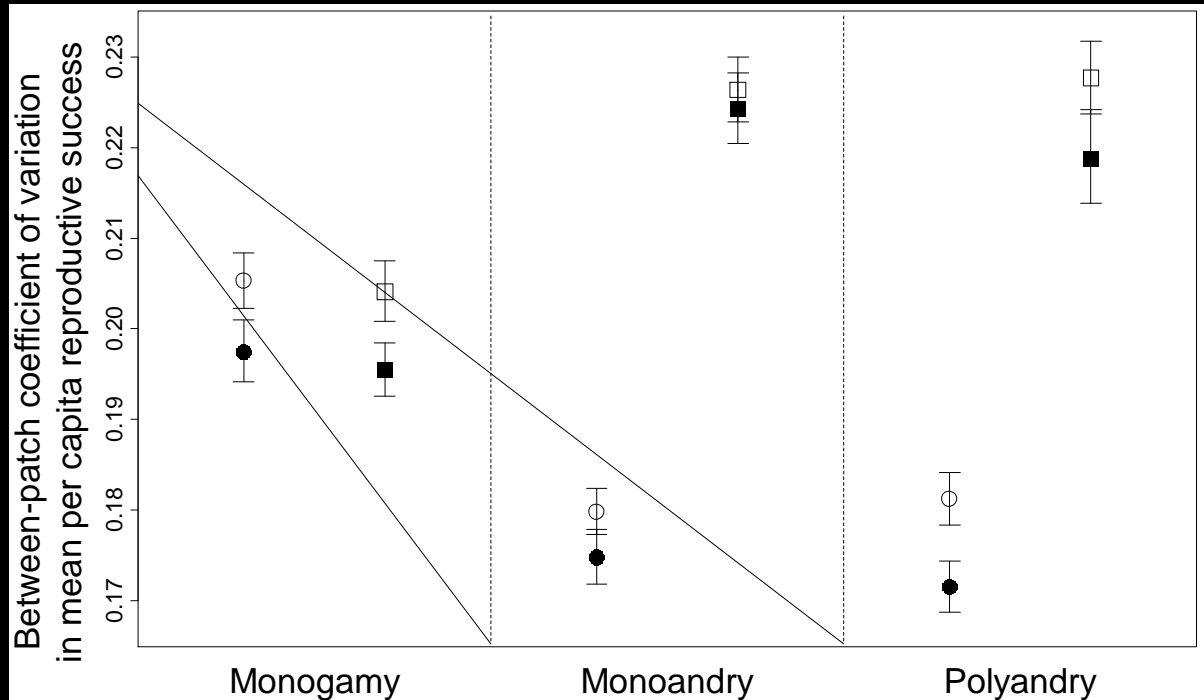
**Fig. 5.** Dispersal rate at equilibrium for males (grey) and females (black) when the sex-ratio (proportion of males) varies for the three mating systems studied. Other parameters fixed to their base value as in Table 1. Line width indicates 95% confidence interval built by the bootstrapping results of 100 replicate simulation runs.

# Apparentement



**Fig. S1.** Mean relatedness index before dispersal between individuals of same patches (upward triangle) and from different patches (downward triangle) in standard (filled symbols) and shuffled (open symbols) model for the three mating systems studied. Parameters fixed to their base value as in Table 1. Error bars indicate 95% confidence interval built by bootstrapping the results of 100 replicate simulation runs.

# Stochasticité spatiale de la reproduction



**Fig. S2.** Between-patch coefficient of variation in mean per capita reproductive success for females (circles) and males (squares) in the standard (filled symbols) and shuffled (open symbols) models for the three mating systems studied. Parameters fixed to their base value as in Table 1. Error bars indicate 95% confidence interval built by bootstrapping results of the 100 replicate simulation runs.

# Coût de dispersion

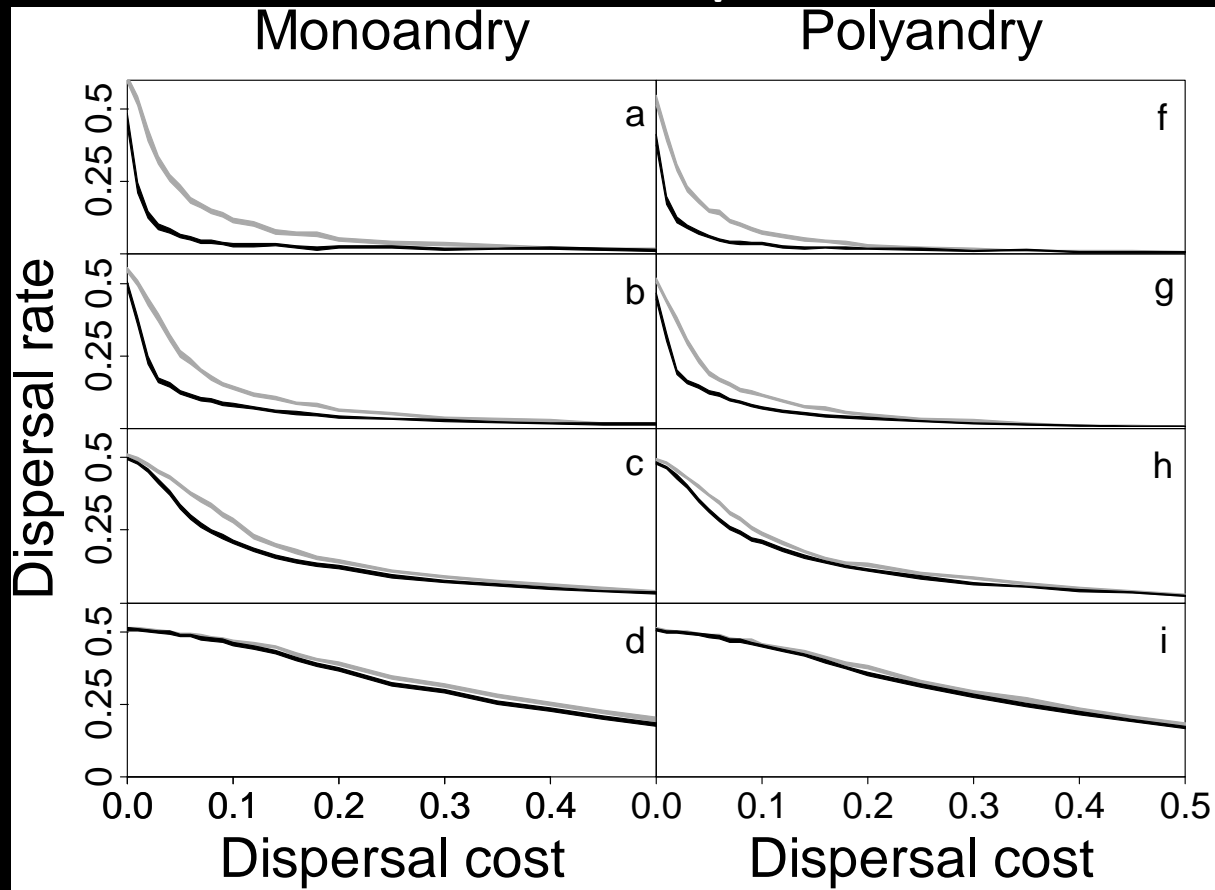


Fig. S3. Dispersal rate at equilibrium for males (grey) and females (black) in monoandry and polyandry with increasing heterogeneity in patch quality from top to base panels: a,f:  $s=0$ ; b,g:  $s=0.5$ ; c,h:  $s=1$ ; d,i:  $s=2$ . Other parameters fixed to their base value as in Table 1. Line width indicates 95% confidence interval built by bootstrapping the results of 100 replicate simulation runs.

# Densité indépendante

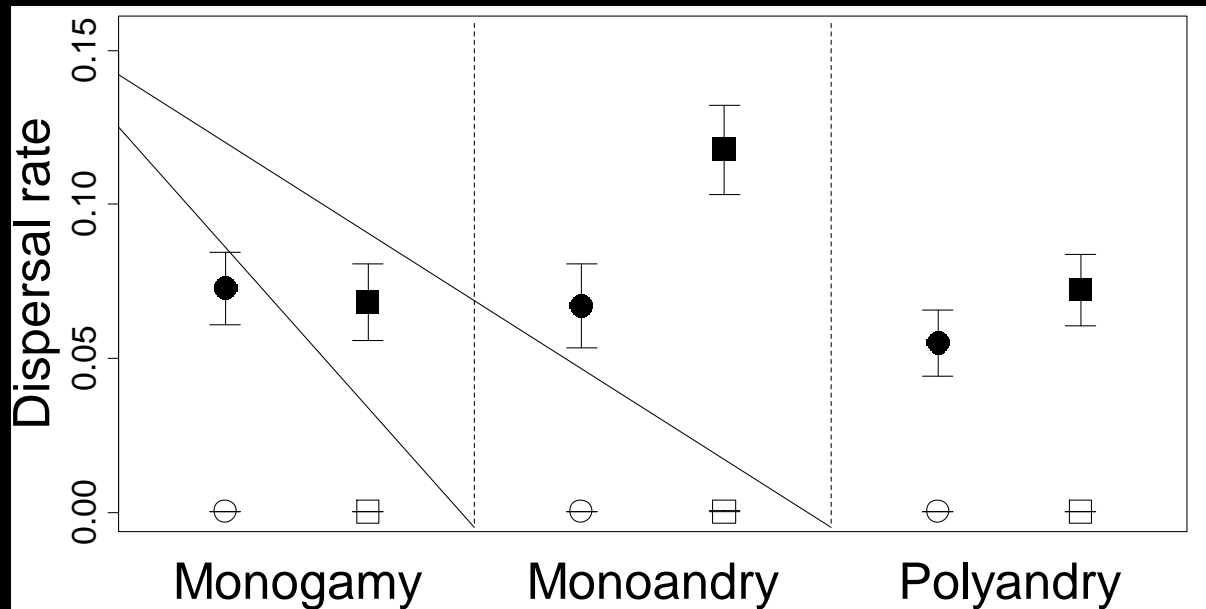


Fig. S4. Density independent dispersal rate at equilibrium for females (circles) and males (squares) in the standard (black) and the shuffled (blank) models for the three mating systems studied. Parameters fixed to their base value as in Table 1. Line width indicates 95% confidence interval built by bootstrapping the results of 100 replicate simulation runs. We test density independent dispersal simply by setting  $d_{pi} = d_{si}$ : the probability of dispersal of an individual is equal to the value of its adaptive trait, the dispersal strategy.

Hétérogamétie

# Hétérogamétie coût de la dispersion

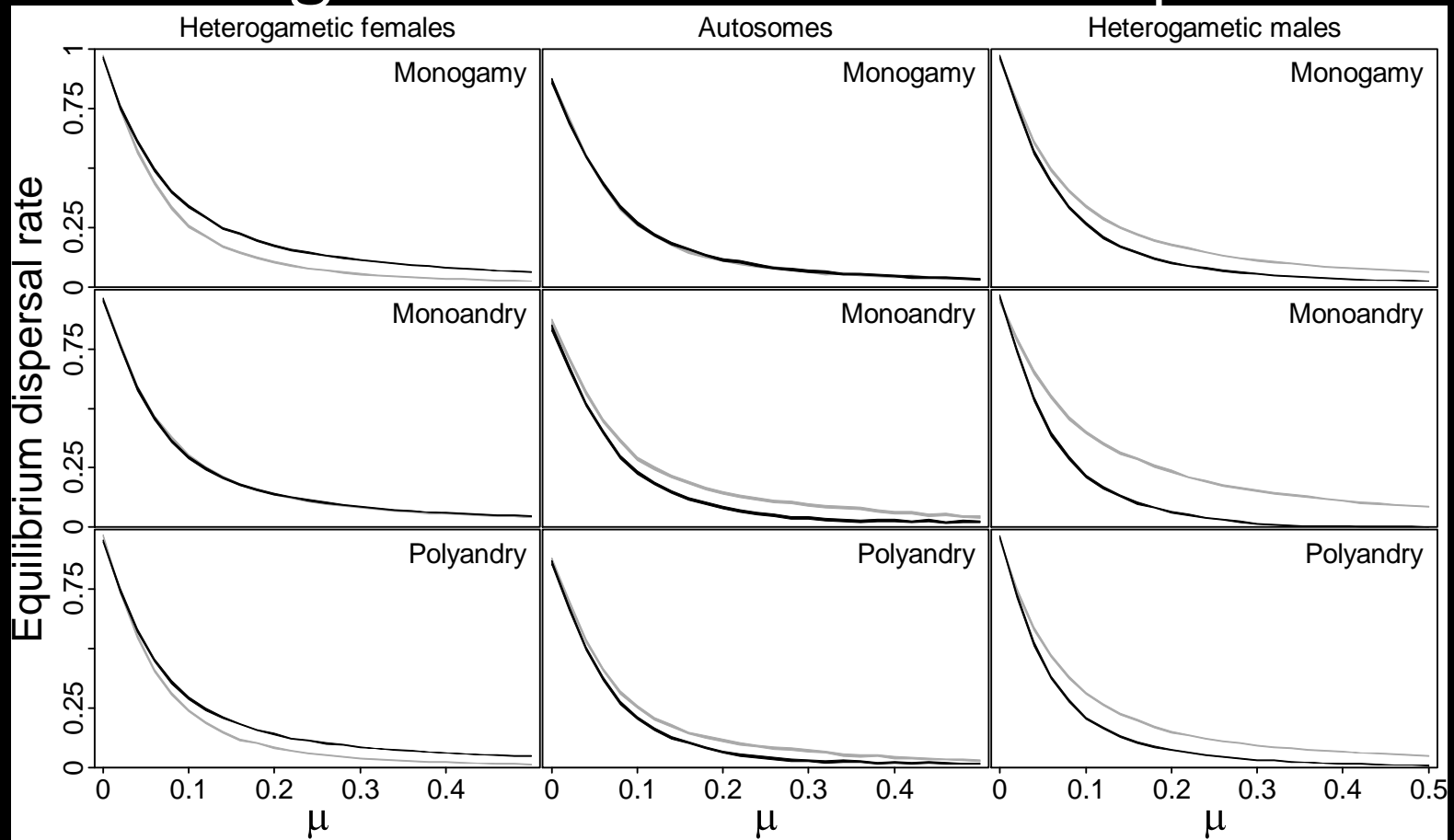
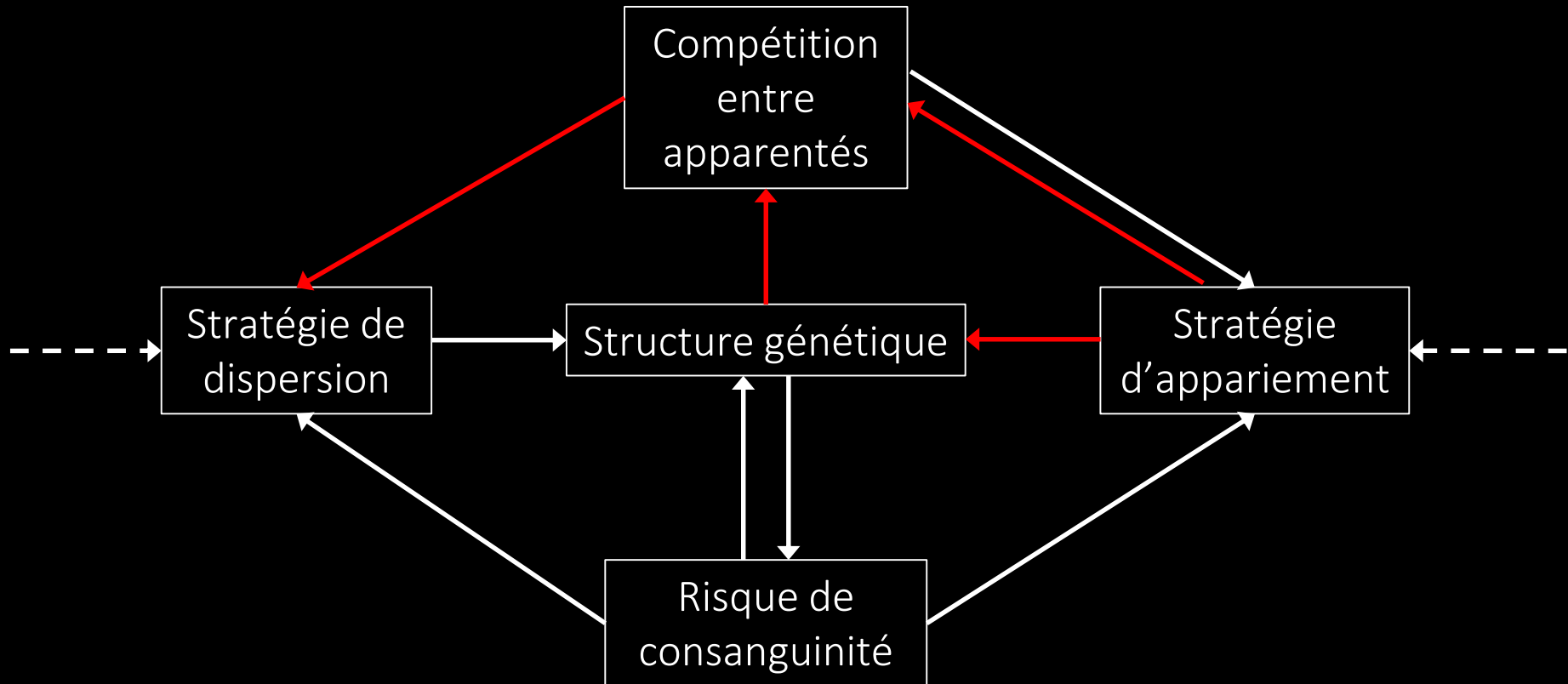


Figure 2. Dispersal rate at equilibrium for females (black) and males (grey) as a function of heterogametic systems (and the associated genetic systems coding for dispersal), dispersal cost  $\mu$ , and the three mating systems considered. Model parameters are  $\beta = 2$ ,  $\beta = 1$ ,  $\mu = 0.1$ ,  $n_{\text{patch}} = 100$ , and  $K = 100$ . Line width indicates 95% confidence intervals built by bootstrapping the results of 100 replicate simulation runs.

# Perspectives *in silico*

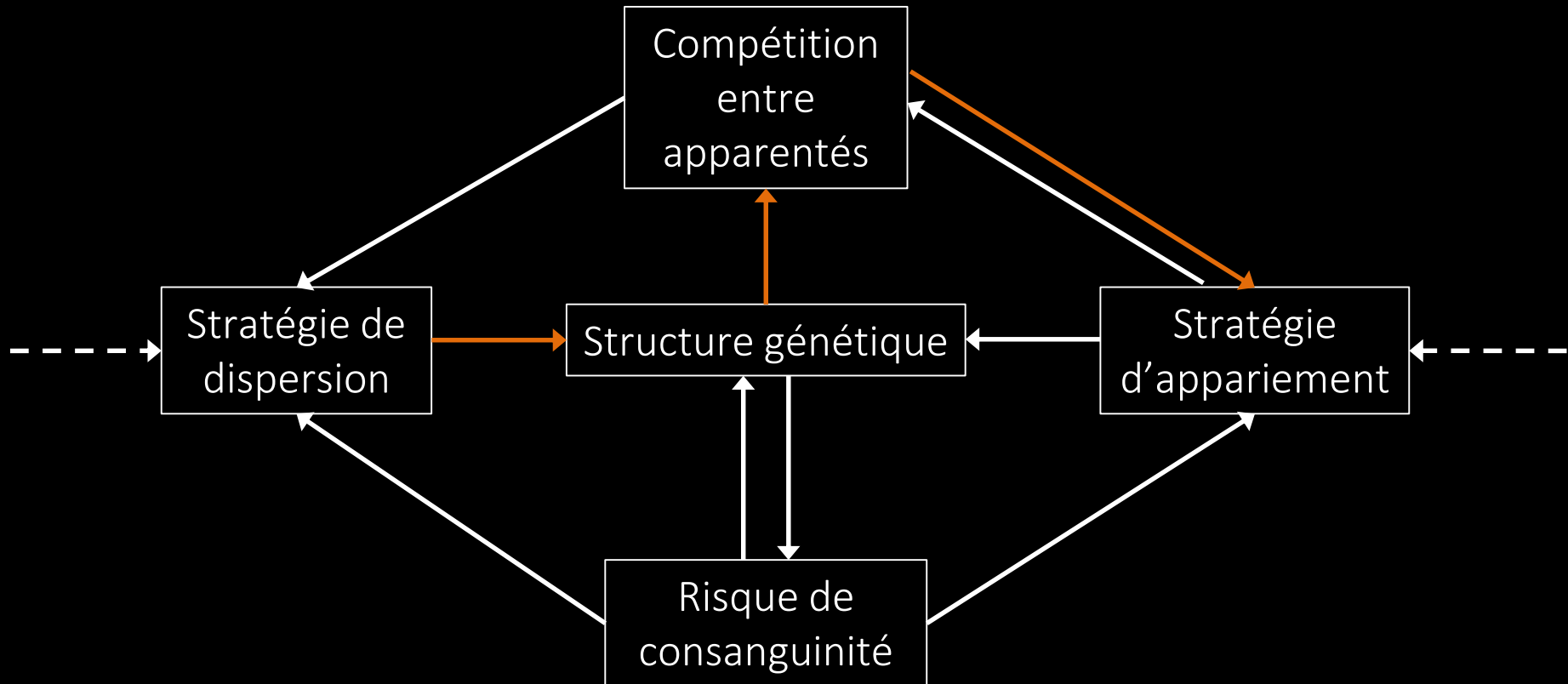
Appariement → Dispersion





# Perspectives *in silico*

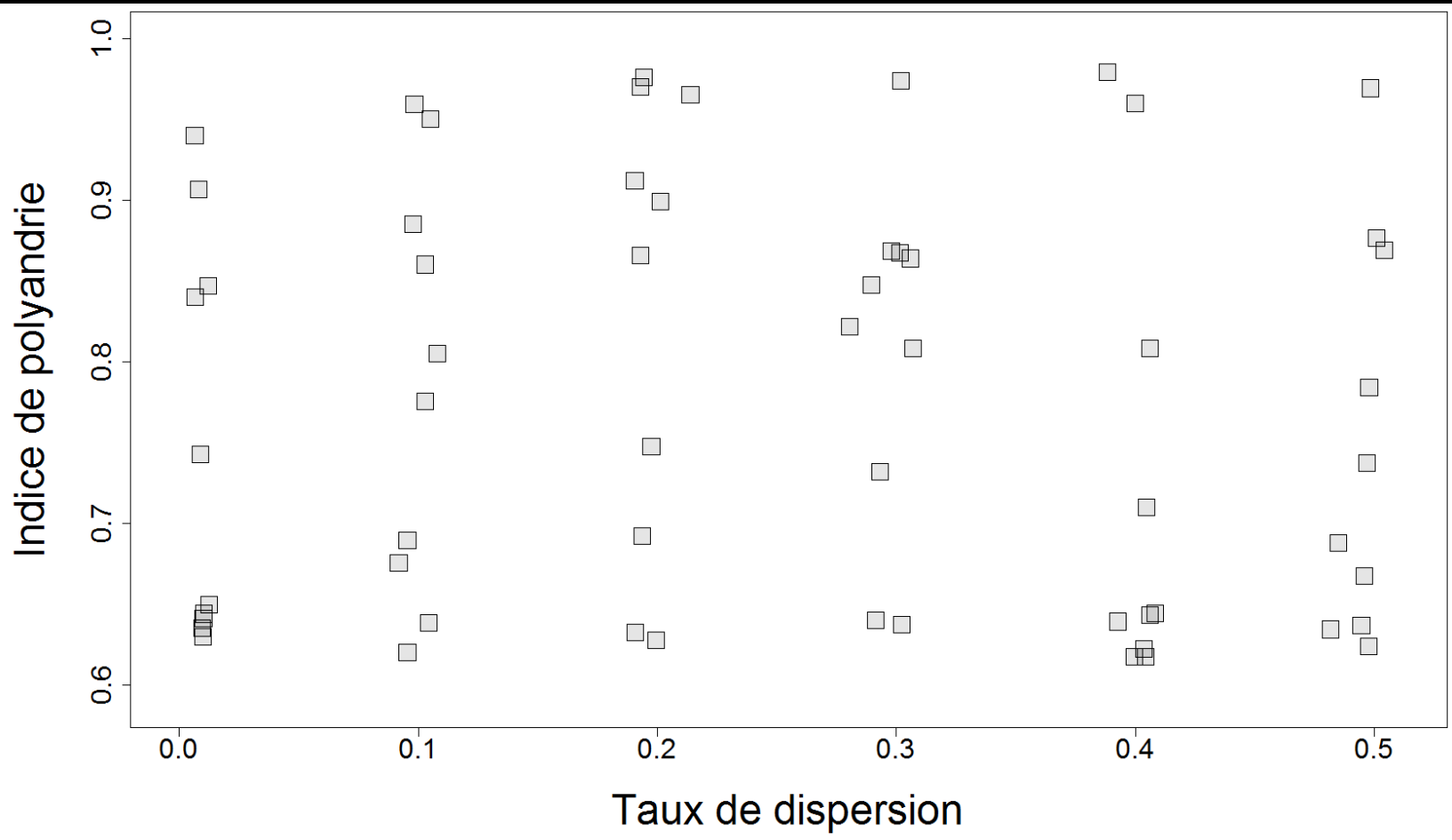
Dispersion → Appariement



# Dispersion $\rightarrow$ Appariement

Coût de la polyandrie

■ aucun

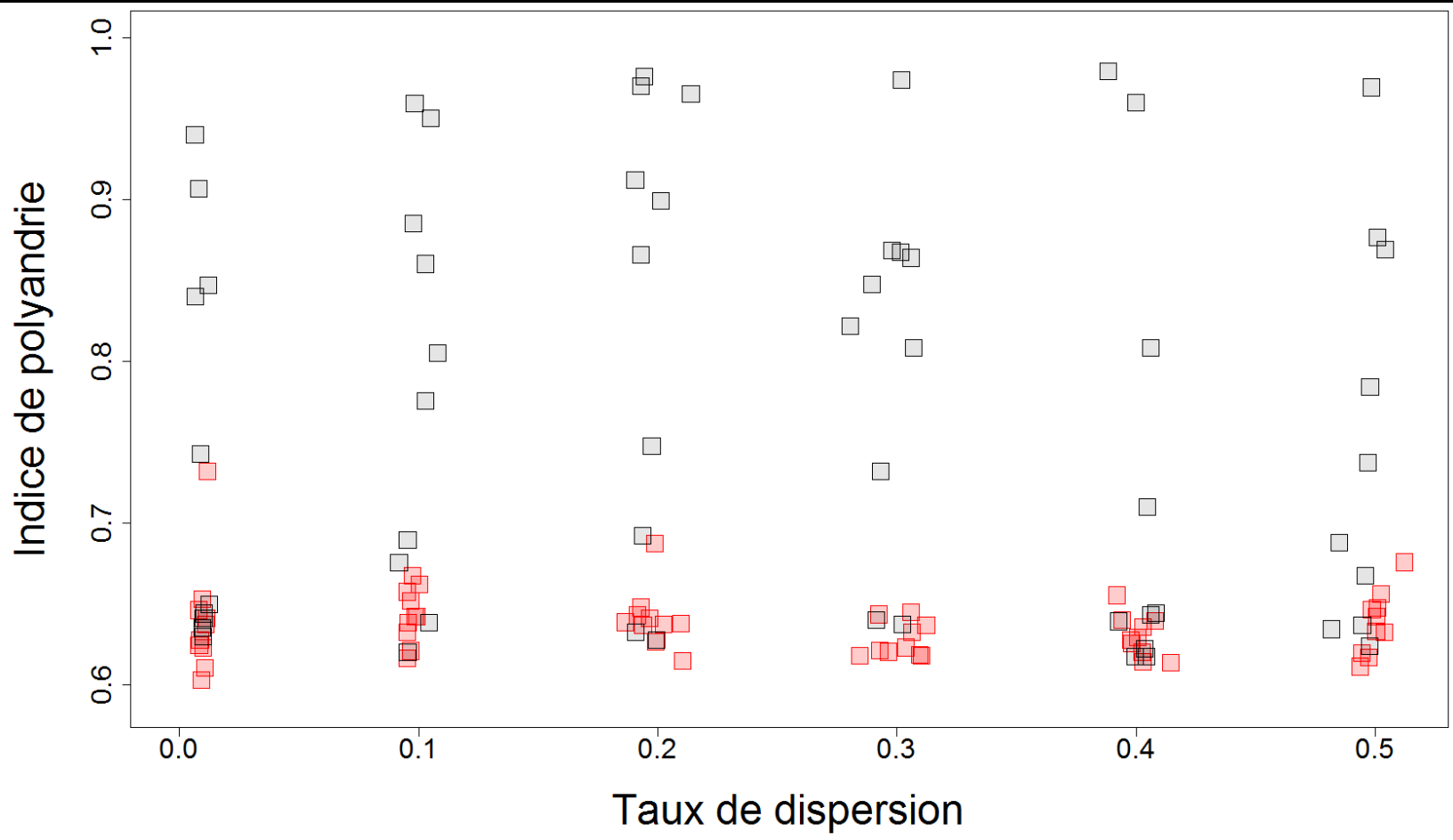


# Dispersion $\rightarrow$ Appariement

Coût de la polyandrie

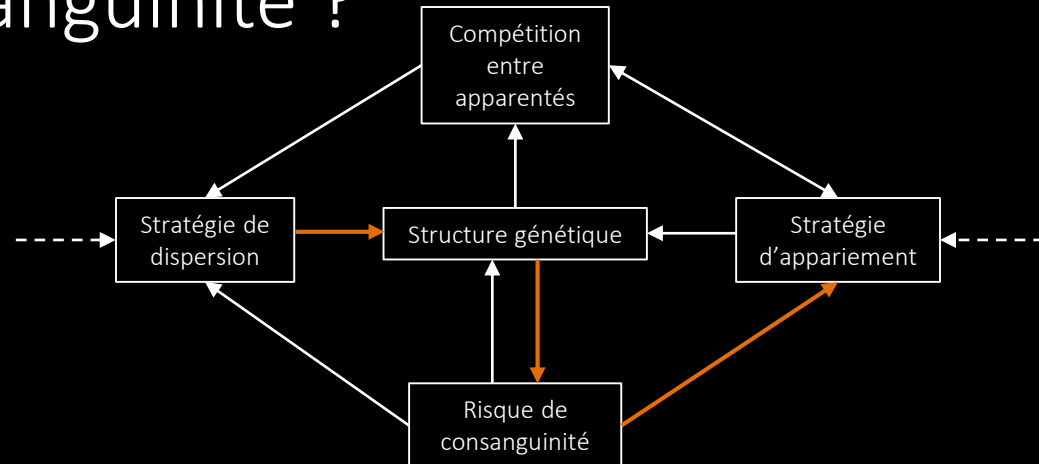
□ aucun

□ faible



# Dispersion → Appariement

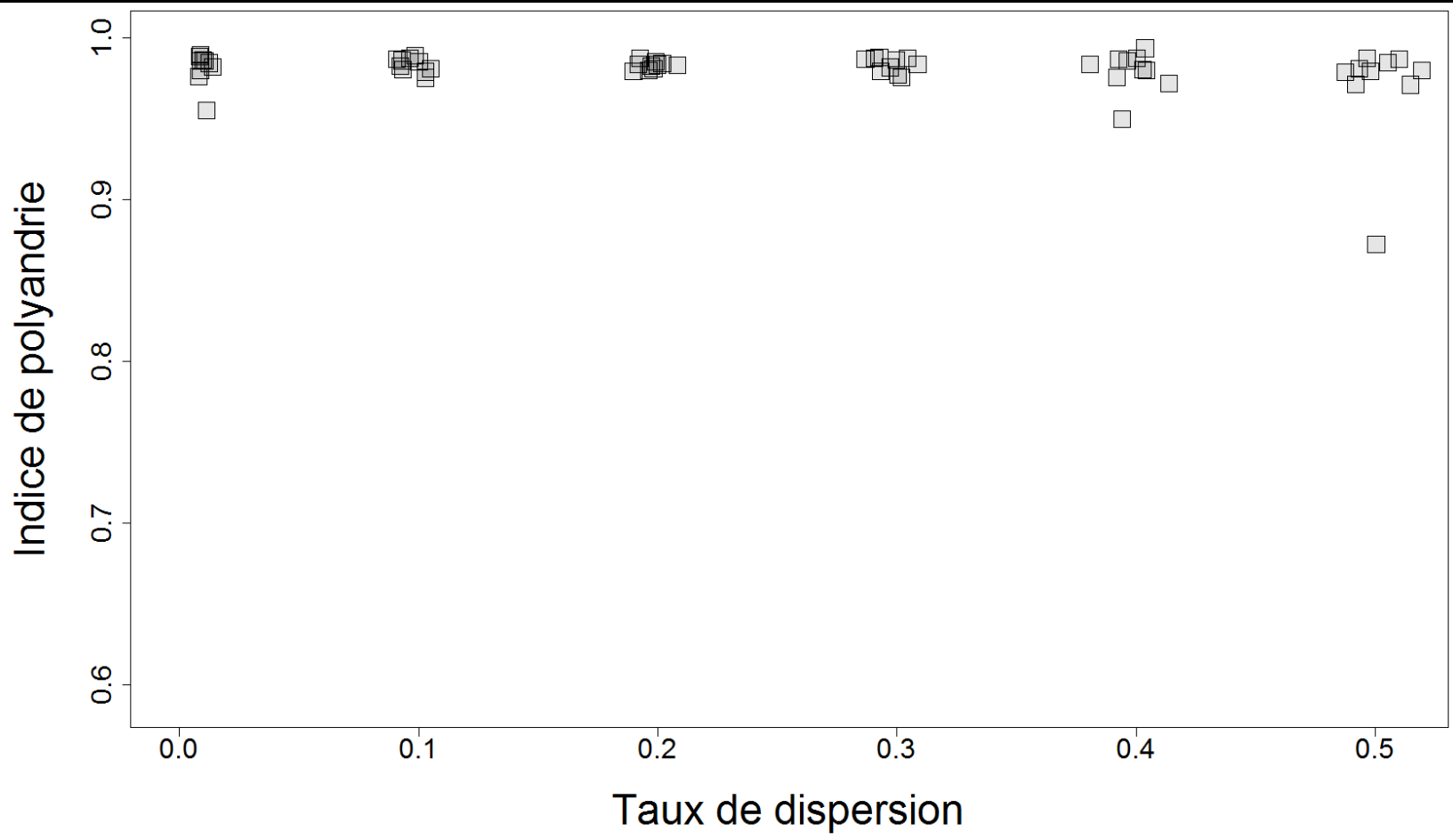
- La stratégie de dispersion ne modifie pas l'évolution de la stratégie d'appariement via la compétition entre apparentés
- Dépression de consanguinité ?



# Dispersion → Appariement

Coût de la polyandrie

■ aucun

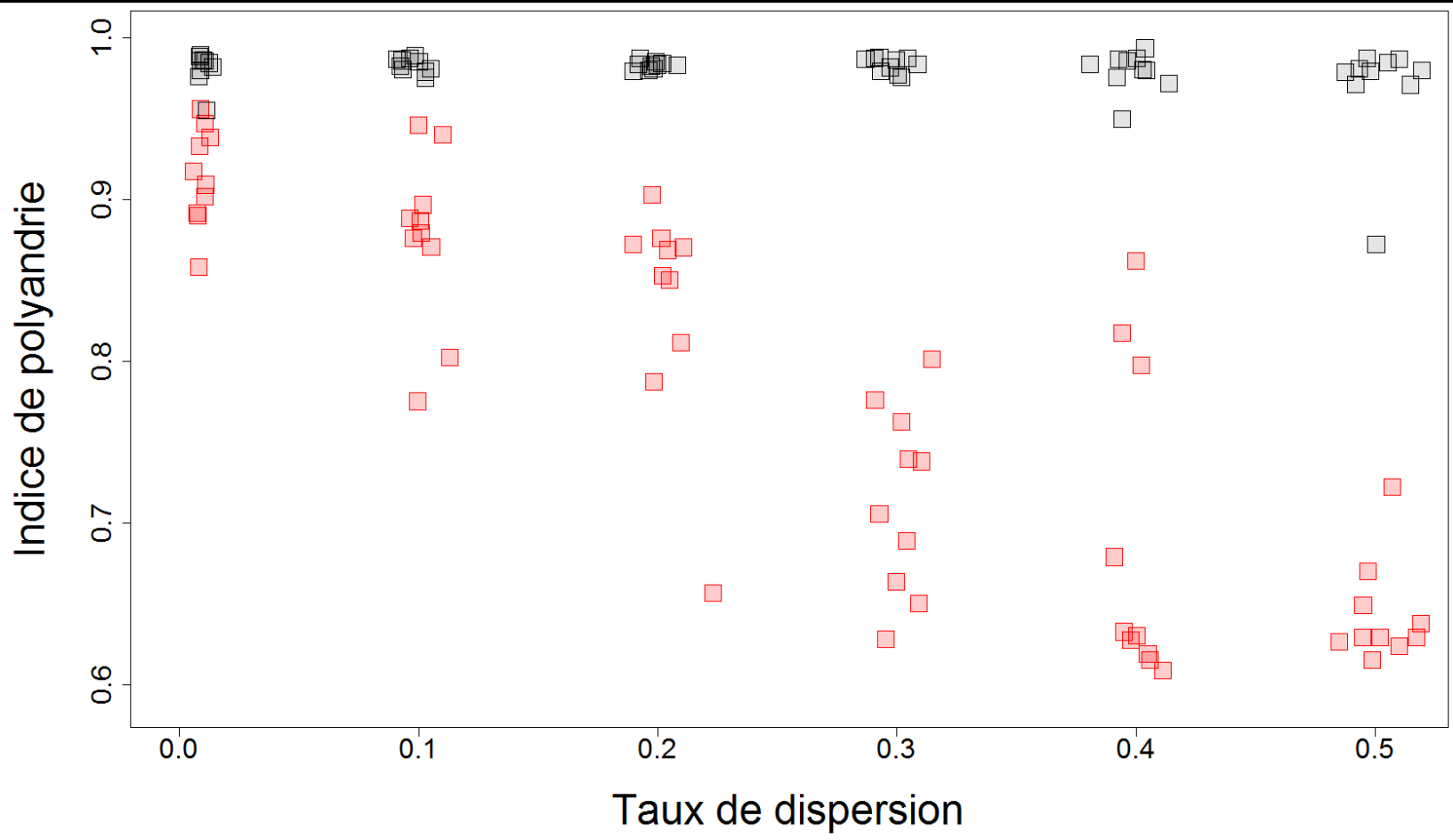


# Dispersion $\rightarrow$ Appariement

Coût de la polyandrie

□ aucun

□ faible



# Dispersion → Appariement

---

- Dépression de consanguinité ?
  - Influence de la stratégie de dispersion sur la stratégie d'appariement

Prochaine étape:

Appariement ↔ Dispersion

# Conflits génomiques



# Schéma autosomes VS hétérochromosomes

Modèle de conflit entre autosomes et hétérochromosomes

Individu homogamétique      Individu hétérogamétique

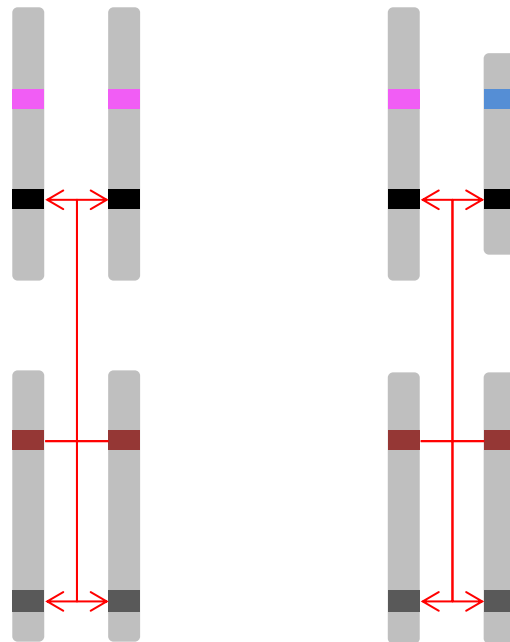
Gènes:

du sexe

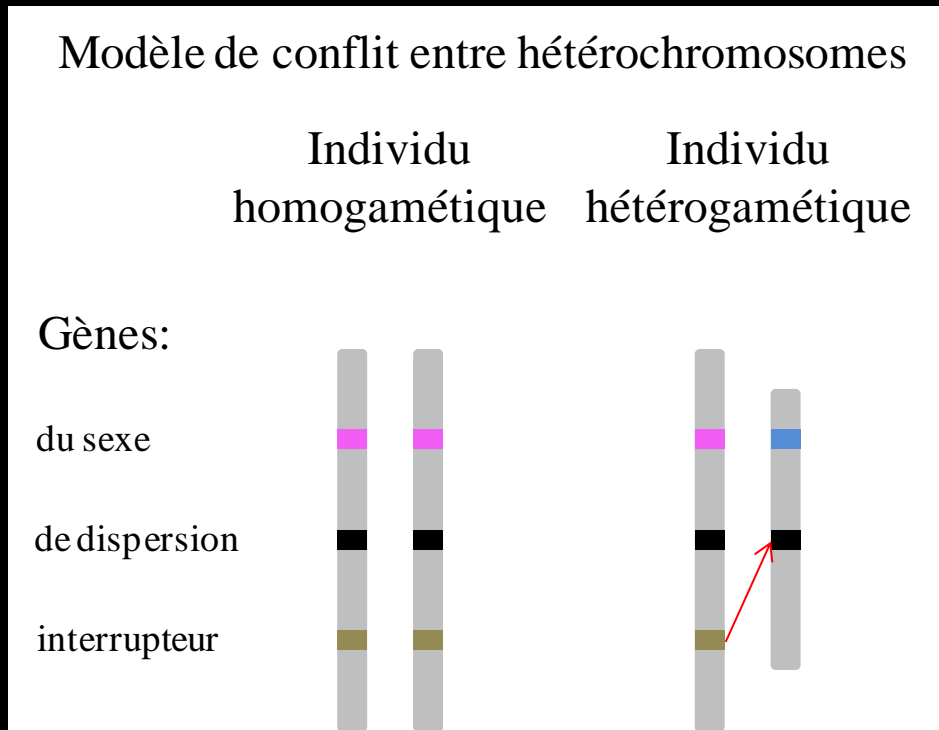
de dispersion

régulateur

de dispersion



# Schéma hétérochromosome VS hétérochromosome



# Y inerte

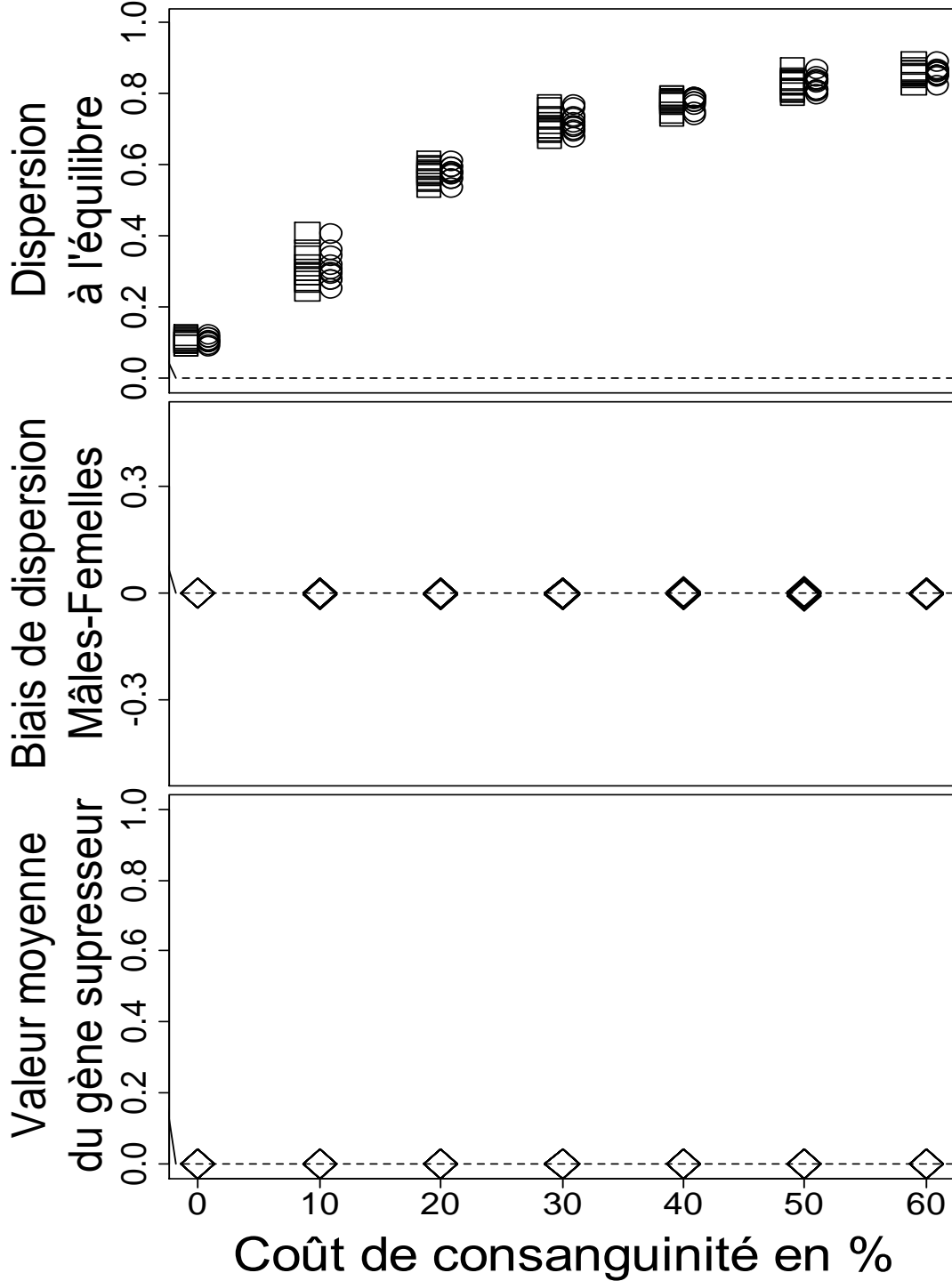
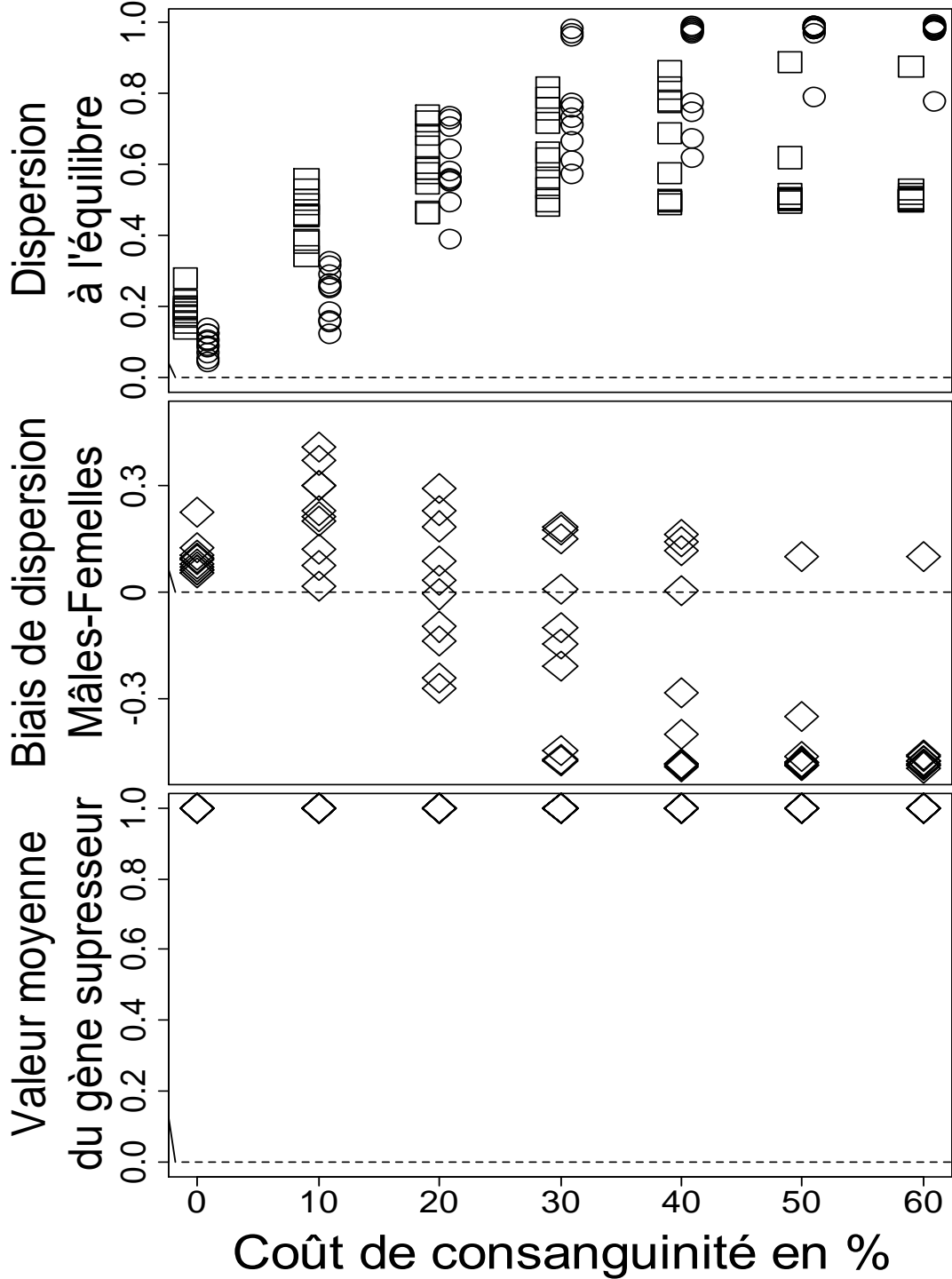
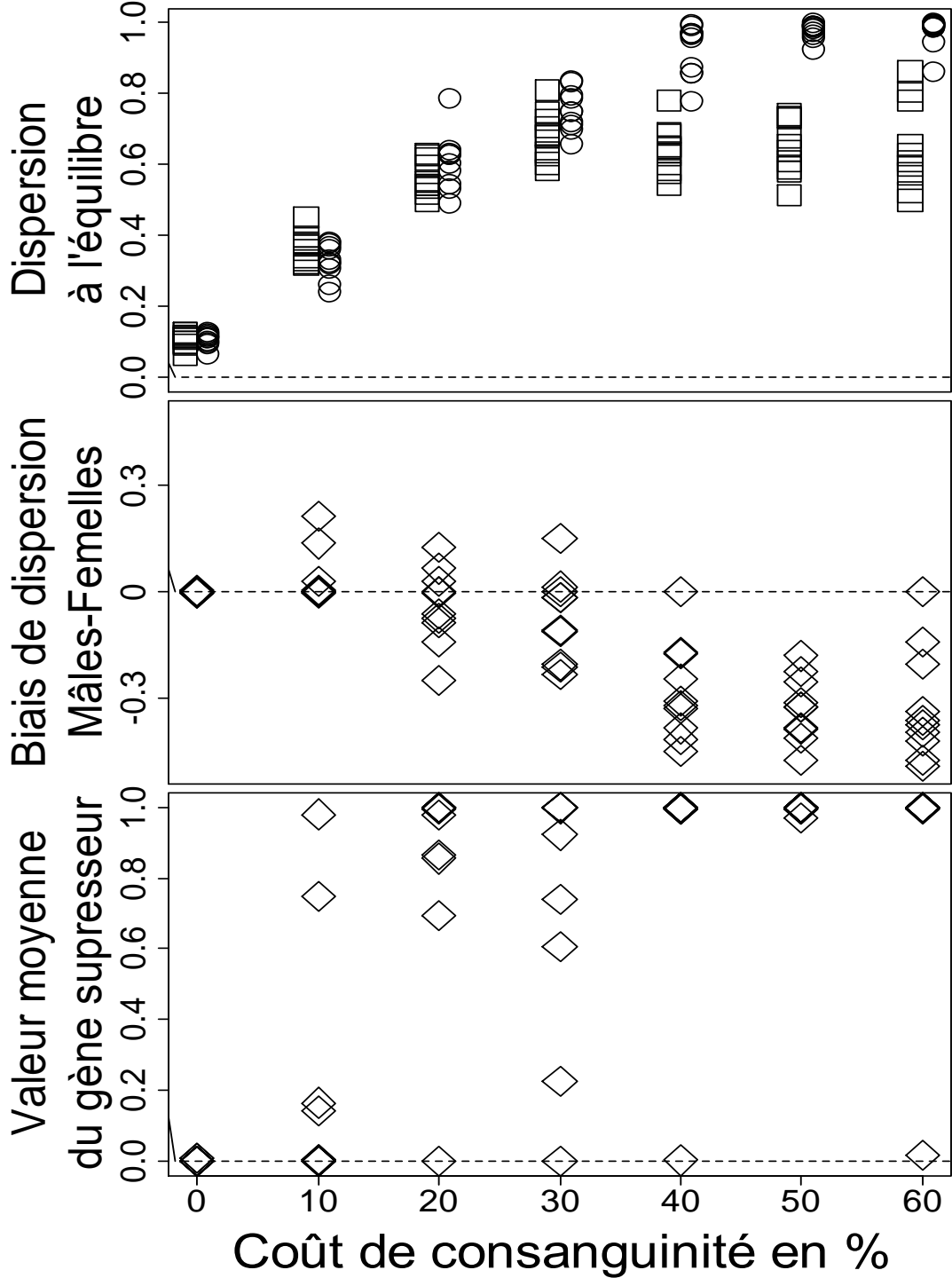


Figure 3 : Evolution de la dispersion en fonction du coût de consanguinité lorsque le chromosome Y est inerte. Mâles hétérogamétiques. Pour le premier panel, les mâles sont représentés par des carrés, les femelles par des ronds, les figurés ont été légèrement décalés pour permettre une meilleur lecture.



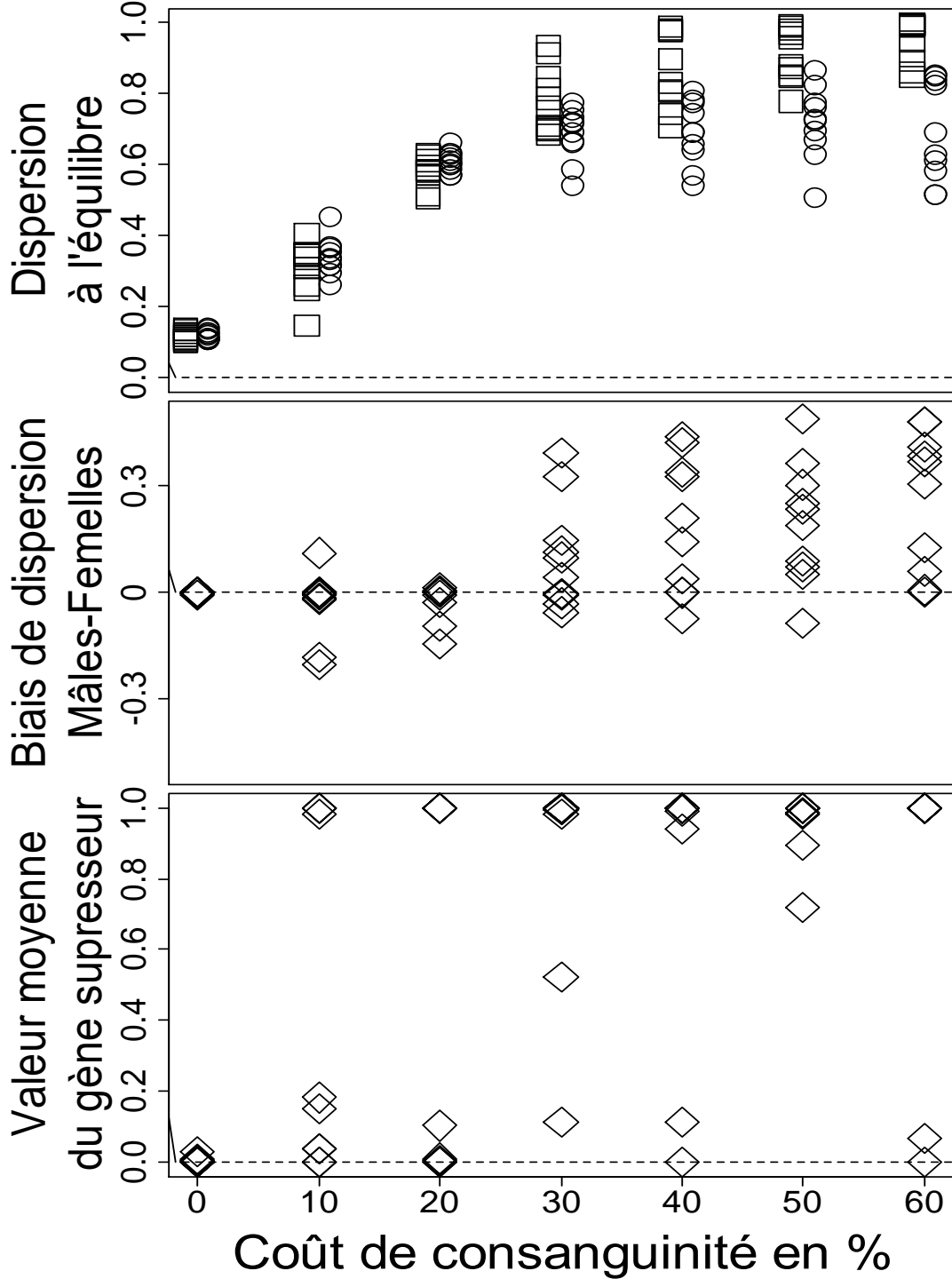
# Suppresseur à 1

Figure 4 : Evolution de la dispersion en fonction du coût de consanguinité lorsque le gène supresseur est fixé à une valeur de 1. Mâles hétérogamétiques. Pour le premier panel, les mâles sont représentés par des carrés, les femelles par des ronds, les figurés ont été légèrement décalés pour permettre une meilleur lecture.



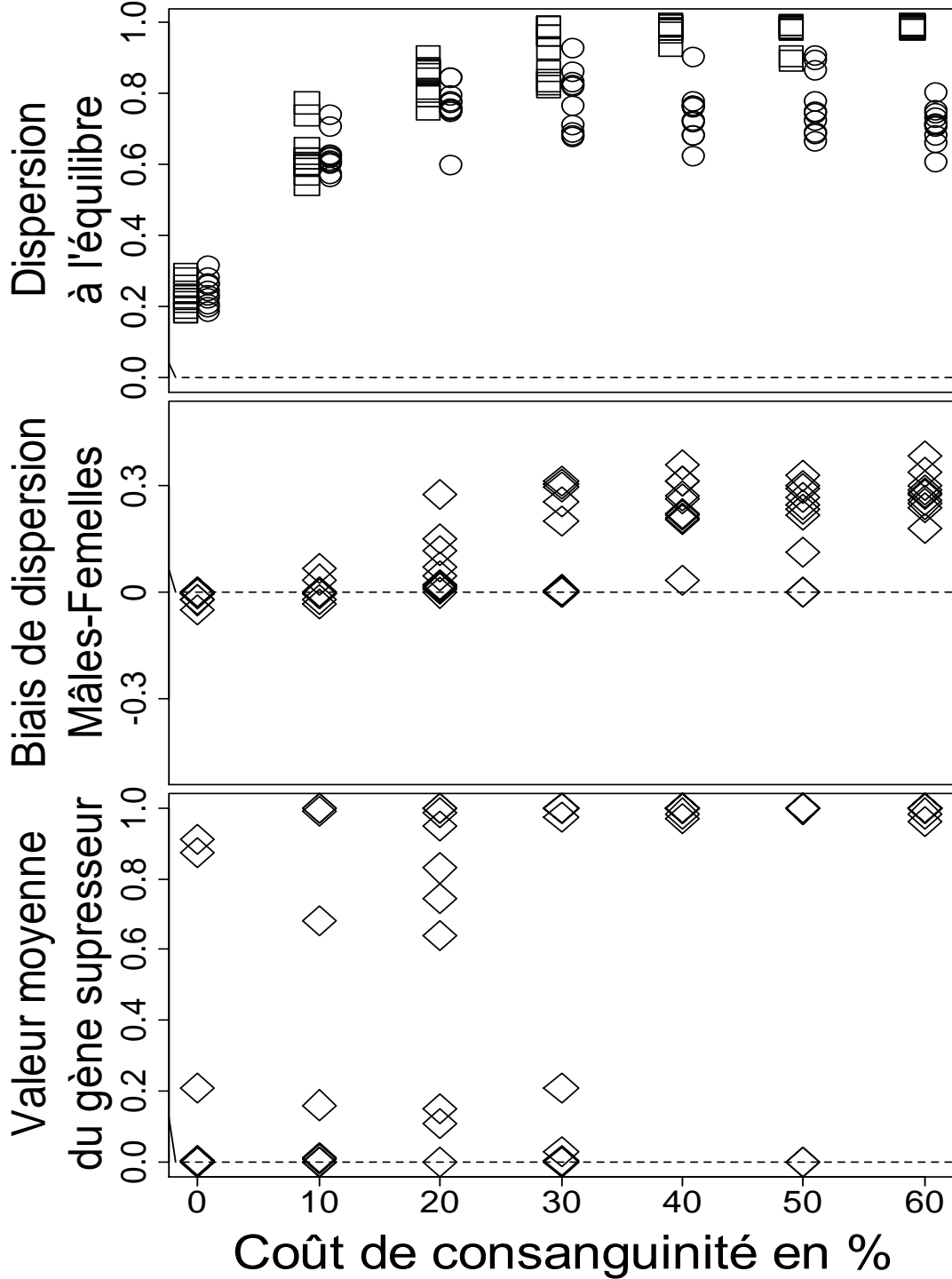
# Suppresseur évoluant librement mâles hétérog

Figure 5 : Evolution de la dispersion en fonction du coût de consanguinité (le gène suppresseur évolue librement). Mâles hétérogamétiques. Pour le premier panel, les mâles sont représentés par des carrés, les femelles par des ronds, les figurés ont été légèrement décalés pour permettre une meilleur lecture.



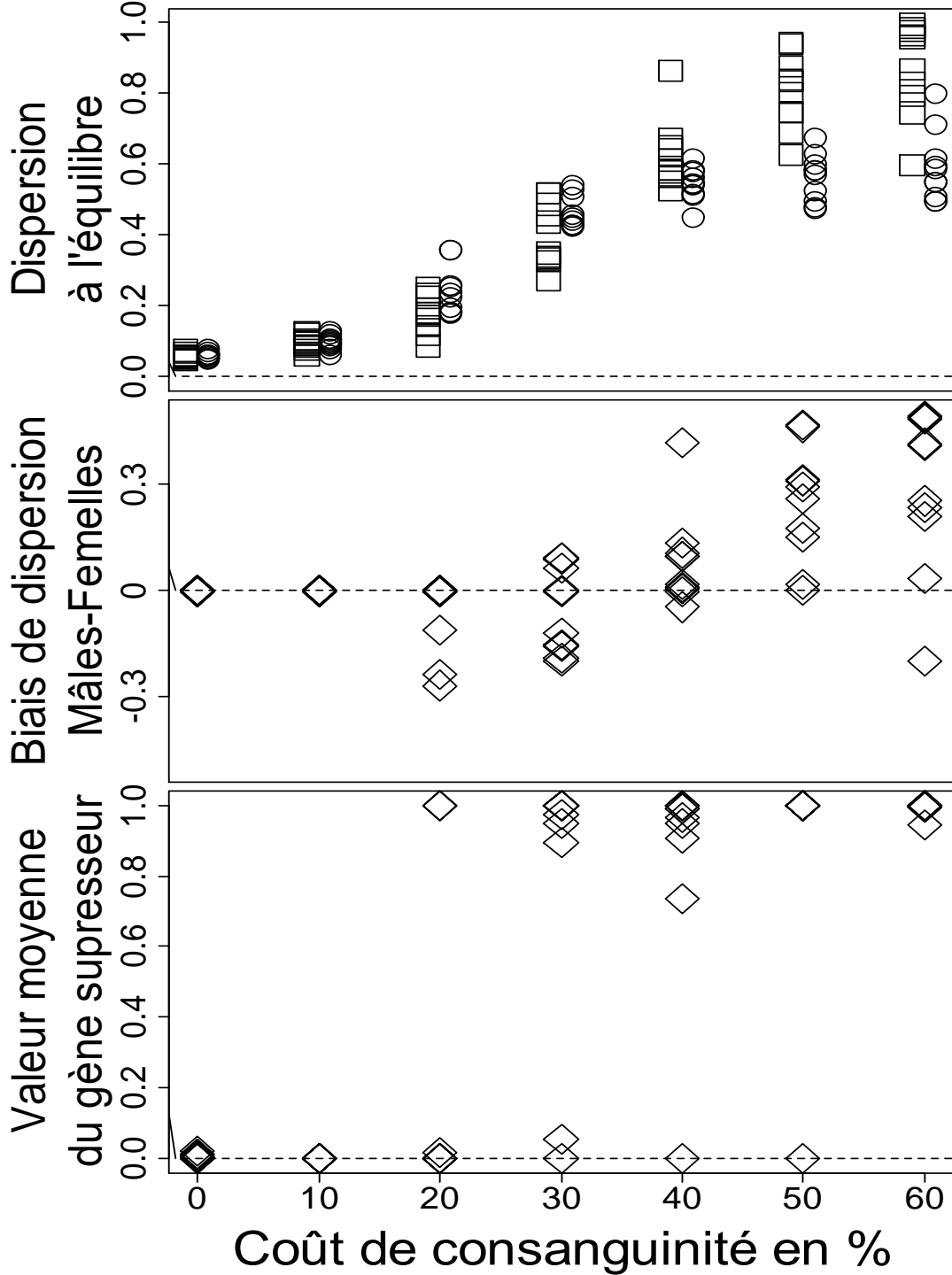
# Suppresseur évoluant librement femelles hétérog

Figure 6 : Evolution de la dispersion en fonction du coût de consanguinité (le gène supresseur évolue librement). Femelles hétérogamétiques. Pour le premier panel, les mâles sont représentés par des carrés, les femelles par des ronds, les figurés ont été légèrement décalés pour permettre une meilleur lecture.  
 $n_p=50, K=50, \rho=10, s=5, \mu=0,1.$



# Suppresseur évoluant librement femelles hétérog c disp faible

Figure 7 : Evolution de la dispersion en fonction du coût de consanguinité avec un faible coût de la dispersion (le gène supresseur évolue librement). Femelles hétérogamétiques. Pour le premier panel, les mâles sont représentés par des carrés, les femelles par des ronds, les figurés ont été légèrement décalés pour permettre une meilleur lecture.  $n_p=50, K=50, \tau=10, s=5, \mu=0,05$ .



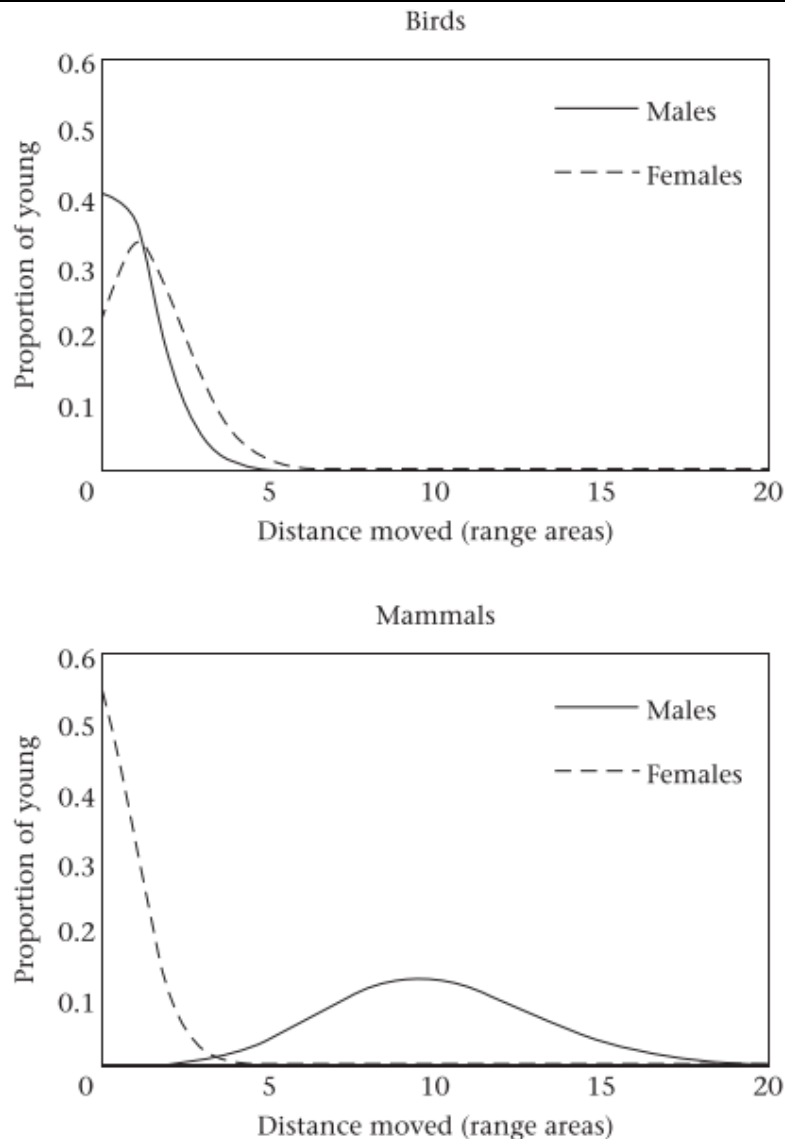
# Suppresseur évoluant librement femelles hétérog c disp important

Figure 8 : Evolution de la dispersion en fonction du coût de consanguinité avec un coût important de la dispersion (le gène supresseur évolue librement). Femelles hétérogamétiques. Pour le premier panel, les mâles sont représentés par des carrés, les femelles par des ronds, les figurés ont été légèrement décalés pour permettre une meilleur lecture.  
 $n_p=50, K=50, \rho=10, s=5, \mu=0,2.$



Variés

# Différence de patterns entre oiseaux et mammifères

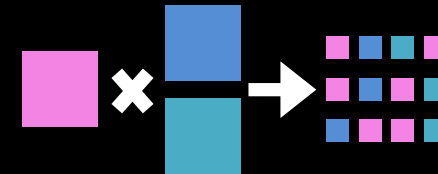
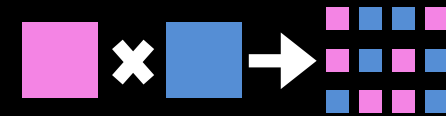
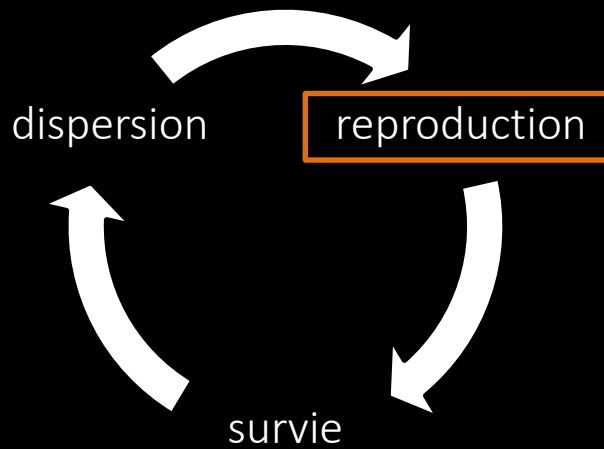


**Figure 2.** Idealized distributions of natal dispersal distances for (a) birds and (b) mammals in ranges from the natal area. All are Poisson distributions of dispersal distances, with the following mean movements: 0.9 for male birds, 1.5 for female birds; 10 for male mammals, 0.6 for female mammals. The area under each curve adds to 1.0, and mean dispersal distances were selected for the purposes of illustration.

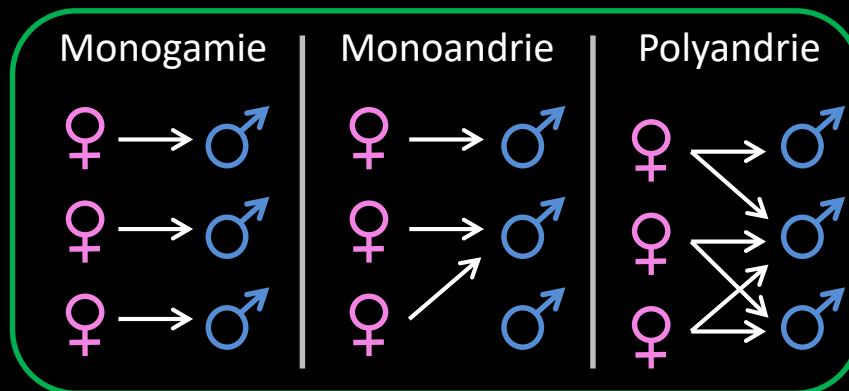
# Tableau d'apparentement

*Table 2:* Probability that a gene on a particular type of chromosome (row titles) will be identical by descent to a gene in a relative (column titles). Male sex assumed heterogametic; if female heterogametic, reverse sex titles

	Sex	Chromosome	Brother	Sister	Father or son	Mother or daughter
Normal Diploid	♀	X	$\frac{1}{4}$	$\frac{3}{4}$	$\frac{1}{2}$	$\frac{1}{2}$
	♂	X	$\frac{1}{2}$	$\frac{1}{2}$	0	1
		Y	1	0	1	0
	Either	Autosome	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$
Haplodiploid	♀	Any	$\frac{1}{4}$	$\frac{3}{4}$	$\frac{1}{2}$	$\frac{1}{2}$
	♂	Any	$\frac{1}{2}$	$\frac{1}{2}$	-	1



## Stratégies de reproduction fixées

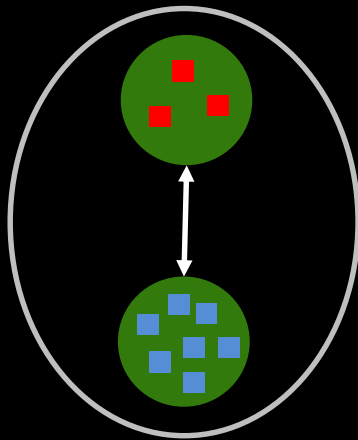


➤ compétition pour la reproduction

➤ structure génétique de la population

# Kin competition

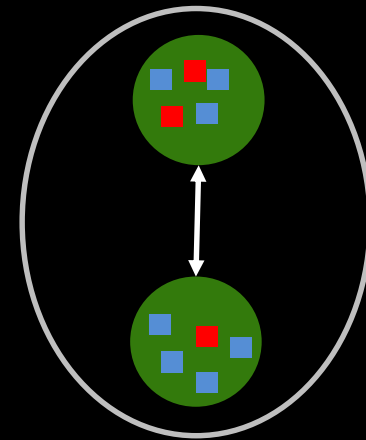
More genetic structure, more kin competition



BEFORE  
dispersal

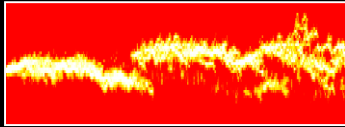
Local relatedness is  
higher than global  
relatedness

Dispersal  
→ reduce  
relatedness



AFTER  
dispersal

# Projects



*in silico*

- Mate choice evolution
- Mating strategy, genetic architecture, genomic conflicts → sex-biased dispersal evolution
- Extra-pair copulation → s-b dispersal evolution



*in vivo*

- Mother mating strategy → natal dispersal
- Mother stress (corticosterone) → natal dispersal
- Mating strategy → cloacal microbiome