Allee effects and the evolution of polymorphism in cyclic parthenogens

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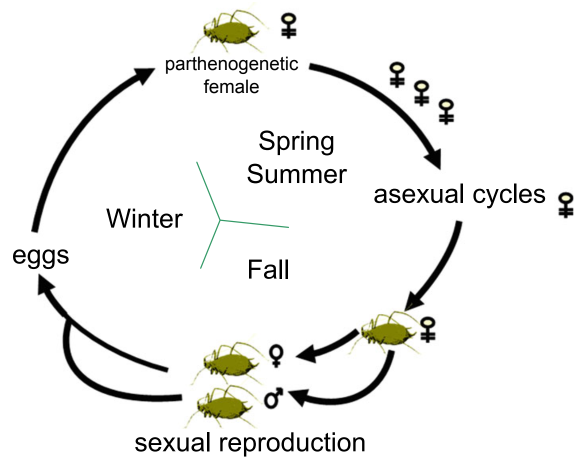
Many plant parasites mix sexual and asexual reproduction

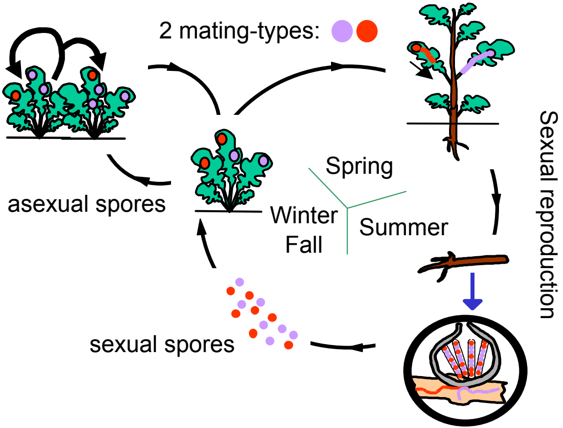
- e.g. the pea aphid *Acyrthosiphon pisum*



- coupling between **sex** and **dormancy**

Many plant parasites mix sexual and asexual reproduction

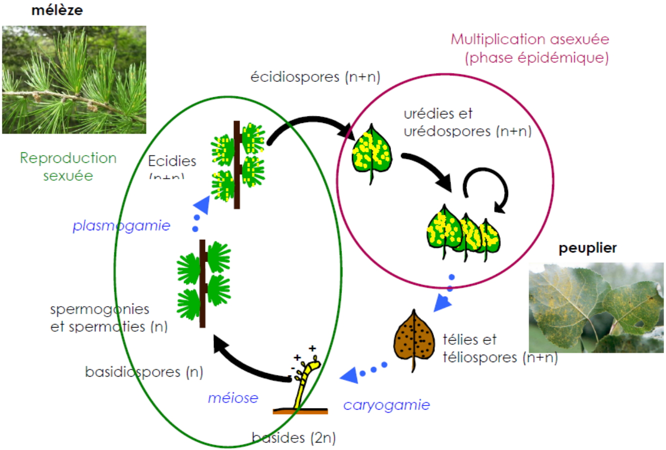
- e.g. the canola backleg fungus *Leptosphaeria maculans*



- mating prior to surviving

Many plant parasites mix sexual and asexual reproduction

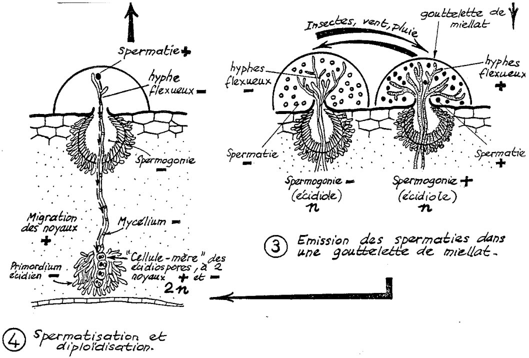
- e.g. the poplar rust fungus *Melampsora larici-populina*



- mating after survival

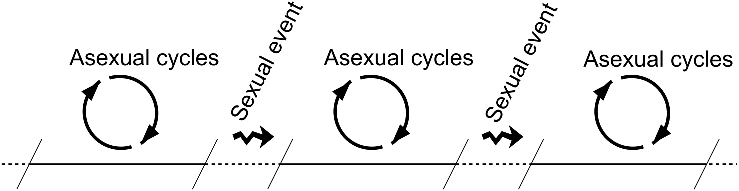
Mating occurs in diverse ways in fungi

- e.g. the poplar rust fungus *Melampsora larici-populina*



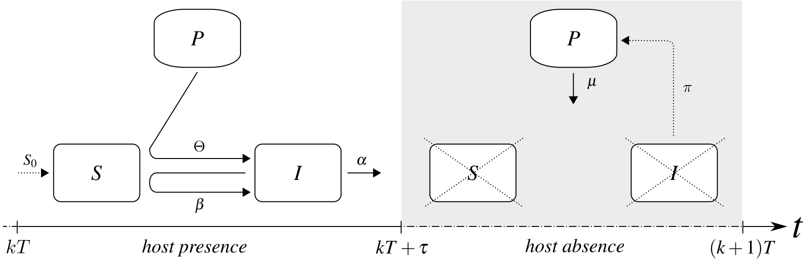
- our **mating function** will be bilinear in mating types densities
- or with a balanced “sex-ratio,” **quadratic** in parasite density
- mating limitation translates into positive density dependence

Interplay between sexual and asexual reproduction

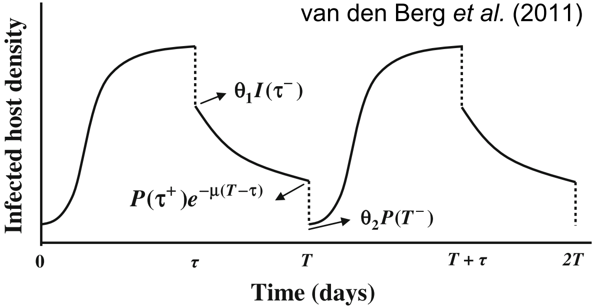


- **Can sexual reproduction promote diversification?**
- From an ecological point of view, sexual reproduction refers to mate limitation or **positive density dependence**

Semi-discrete modelling



Asexual model



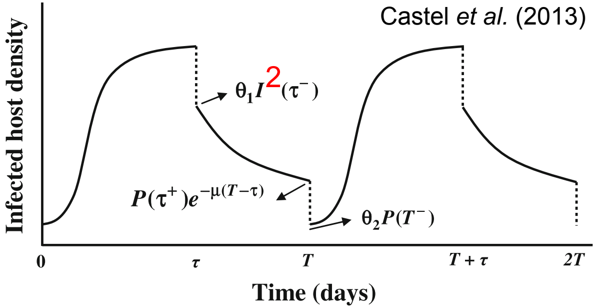
- **Growing season**: for all $t \in (0, \tau)$ modulo T

$$\frac{\mathrm{d}I}{\mathrm{d}t} = \beta(N - I)I\,, \quad P(\tau^+) = \theta_1 I(\tau^-)\,,$$

- **Inter-season**: for all $t \in (\tau, T)$

$$\frac{dP}{dt} = -\mu P\,, \quad I(T^+) = \theta_2 P(T^-)\,.$$

Sexual model



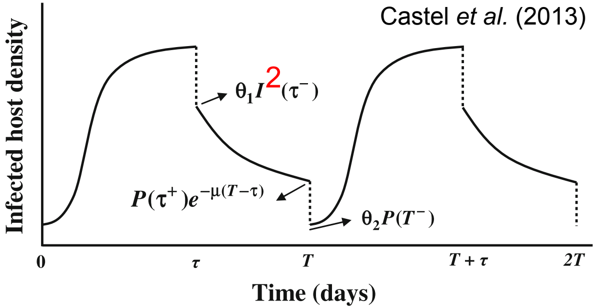
- **Growing season**: for all $t \in (0, \tau)$ modulo T

$$\frac{\mathrm{d}I}{\mathrm{d}t} = \beta(N - I)I\,, \quad P(\tau^+) = \theta_1 I^2(\tau^-)\,,$$

- **Inter-season**: for all $t \in (\tau, T)$

$$\frac{dP}{dt} = -\mu P\,, \quad I(T^+) = \theta_2 P(T^-)\,.$$

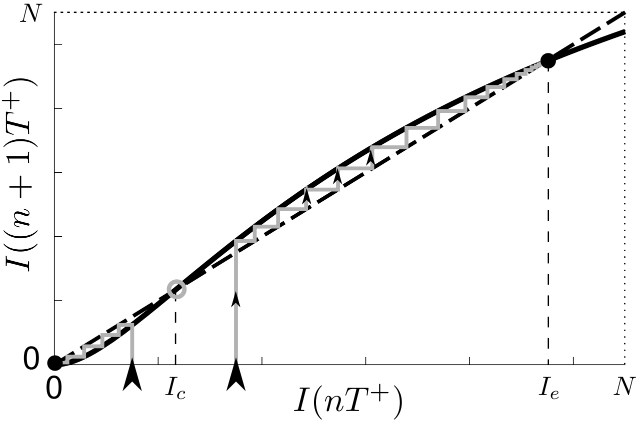
Sexual model



- The ecological model reduces to a single equation:

$$I((n+1)T^+) = \theta_1\theta_2 e^{-\mu(T-\tau)}\left(\frac{I(nT^+)N}{I(nT^+)+(N-I(nT^+))e^{-\beta N\tau}}\right)^2.$$

A strong Allee effect may drive the population to extinction



- $I < I_c$: "the probability to find a mate is critically low"

Trade-off (asexual) infection *vs.* (sexual) survival

- Gosme *et al.* (2009)[1] report a trade-off in the take-all disease of wheat fungus *Gaeumannomyces graminis var. tritici*

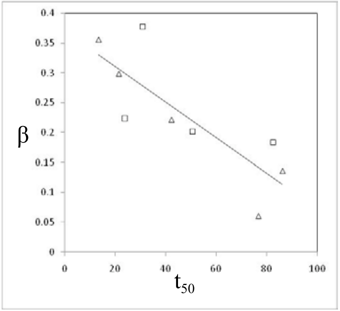


Fig 3. Infection efficiency (beta) as a function of the time at which 50% of the propagules have decayed in soil (t_{50})

- Mathematically, we let $\mu = f(\beta)$

[1] See also Carson (1998), Abang *et al.* (2006), Sommerhalder *et al.* (2011)

Evolutionary invasion analysis

- resident population **1** at ecological attractor $I_1^\circ(t, \beta_\mathbf{1})$
- challenged by a small mutant subpopulation **2** with trait $\beta_\mathbf{2}$
- haploid species (*e.g.* ascomycete fungi)
- ecological trait β coded by a single multi-allelic locus

$\Rightarrow$ **probability 1/2** of inheriting either parental allele

$$P_2(\tau) \propto \frac{1}{2} I_1(\tau) I_2(\tau)\,.$$

- mutant multiplication factor

$$\frac{I_2(T^+)}{I_2(0)} \propto \underbrace{\mathrm{e}^{\beta_\mathbf{2}\tau(N-\bar{I}_1^\circ(\beta_\mathbf{1}))}}_{\text{multiplication}} \times \underbrace{I_1^\circ(\tau, \beta_\mathbf{1})}_{\text{mating}} \times \underbrace{\mathrm{e}^{-f(\beta_\mathbf{2})(T-\tau)}}_{\text{survival}}$$

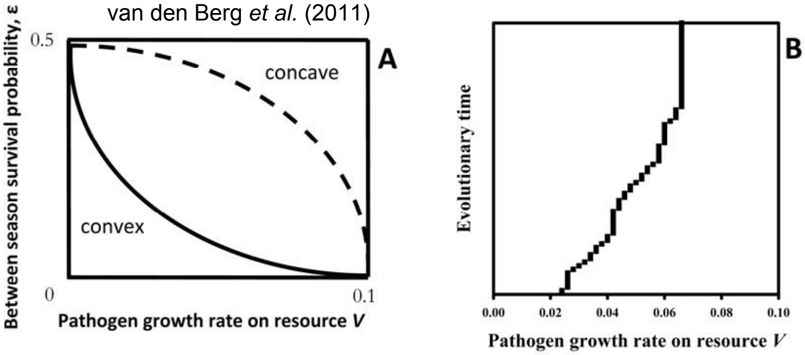
- invasion fitness

$$s(\beta_\mathbf{1}, \beta_\mathbf{2}) = (f(\beta_\mathbf{1}) - f(\beta_\mathbf{2}))(T - \tau) - (\beta_\mathbf{1} - \beta_\mathbf{2})(N - \bar{I}_1^\circ(\beta_\mathbf{1}))$$

Asexual model

- Regardless whether the trade-off is concave or convex, **evolutionary branching is impossible**

van den Berg *et al.* (2011)

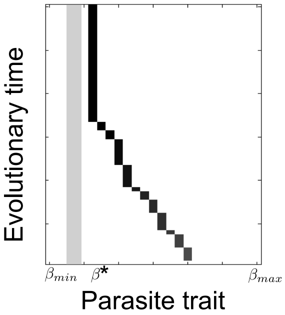


- Evolution leads to a **monomorphic** endpoint

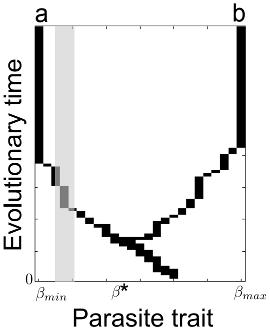
Sexual model

$$\frac{\partial^2}{\partial {\beta_2}^2} s(\beta_1, \beta_2)\Big|_{\beta_1=\beta_2=\beta} = -f''(\beta)(T-\tau).$$

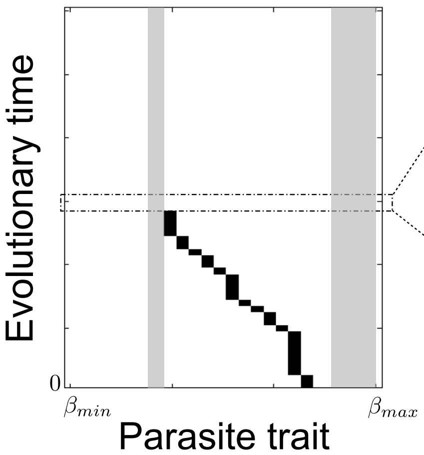
Convex trade-off: f'' $>$ 0



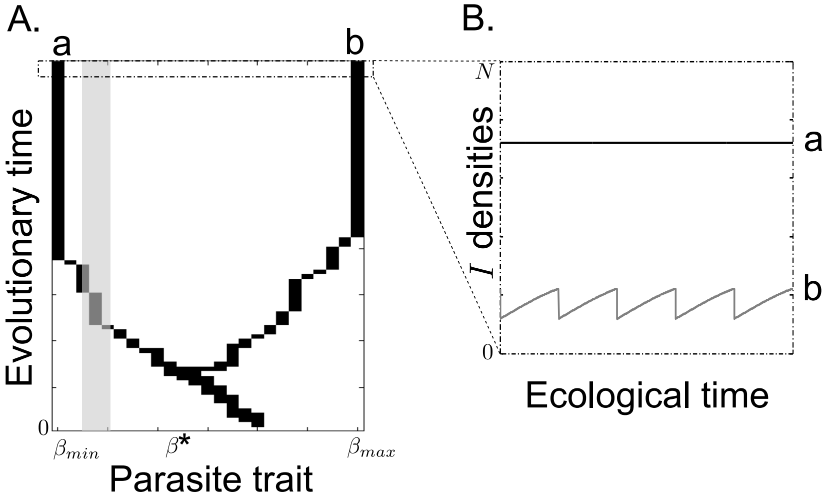
Concave trade-off: f'' $<$ 0



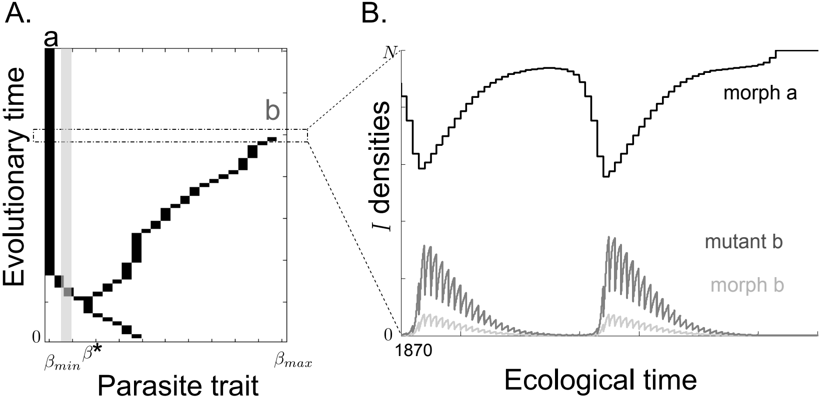
Sexual model - evolutionary extinction (Allee effect)



Sexual model - reproductive polymorphism



Sexual model - evolutionary exclusion - asexuality lost



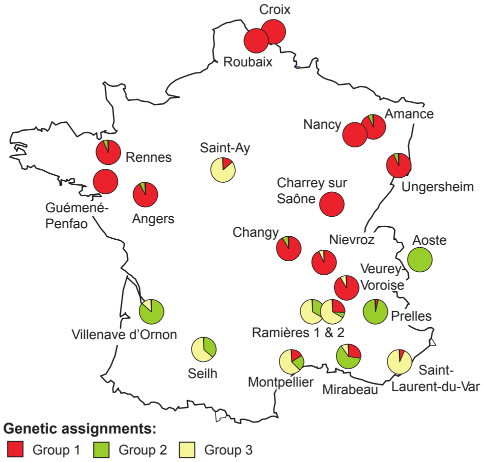
Ecological and evolutionary implications of obligate sex

- Strong Allee effect
- Evolutionary extinction
- Reproductive polymorphism (new mechanism)
- Lost of asexual reproduction

These results echo with recent population genetics studies:

- Xhaard C *et al.* (2011) The genetic structure of the plant pathogenic fungus *M. larici-populina* on its wild host is extensively impacted by host domestication. *Mol. Ecol.*
- Dilmaghani *et al.* (2012) Migration patterns and changes in population biology associated with the worldwide spread of the oilseed rape pathogen *L. maculans*. *Molecular Ecology*.

Reproductive polymorphism in the poplar rust fungus

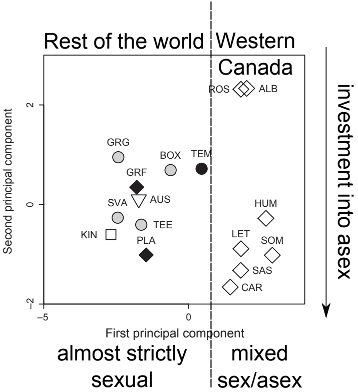


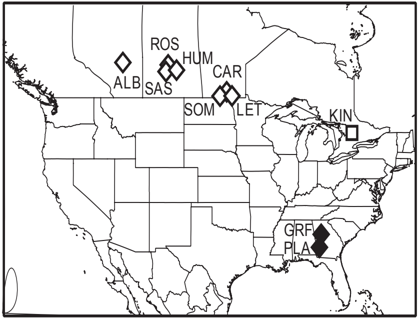
group 1 'virulent-sexual' - group 2 'avirulent-sexual' - group 3 'avirulent-asexual'

Xhaard *et al.* (2011)

Reproductive polymorphism in the canola blackleg fungus

- Polymorphism in Western Canada





Dilmaghani *et al.* (2012)

Thank you

Castel MK, Mailleret L, Andrivon D, Ravigné V, Hamelin FM (2014) Allee effects and the evolution of polymorphism in cyclic parthenogens. *The American Naturalist*, in press.