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Seasonality and the evolutionary divergence of plant parasites

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8th European Conference on Mathematical and Theoretical
Biology
Kraków, 28 June - 2 July 2011

Biotrophic plant parasites

- ▶ **feed, grow and reproduce on their living host plant**
- ▶ **cause massive damage to staple food crops**



- ▶ **ubiquitous coexistence of related plant parasite species¹**

¹Brasier, 1987

Temporal heterogeneity in host availability

- ▶ Spatial host heterogeneity promotes evolutionary divergence²



- ▶ Can seasonality promote evolutionary divergence as well?

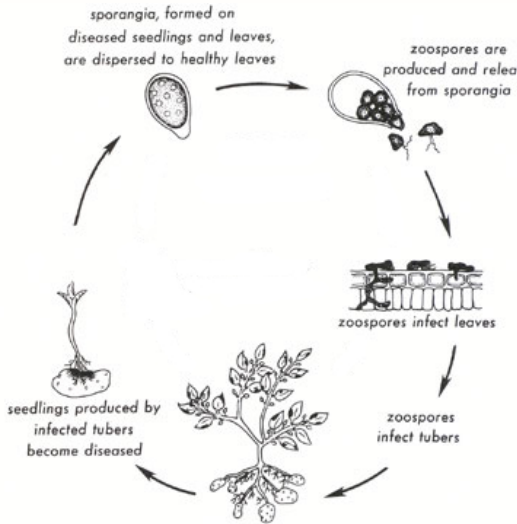


²Gudelj *et al.*, 2004

Biotrophic parasites' life cycle: Potato Late Blight

During early spring

- ▶ **Primary infection phase:** seedlings' infection by **inoculum from previous seasons**

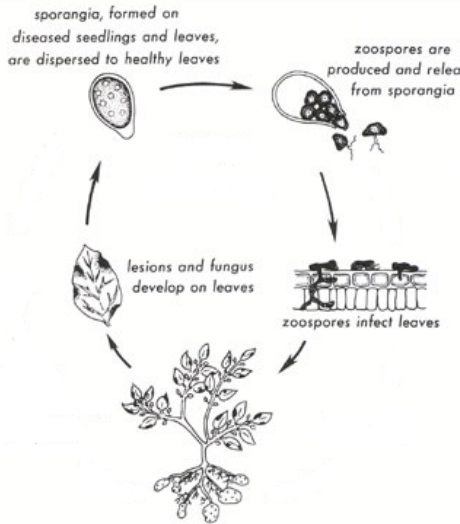


Biotrophic parasites' life cycle: Potato Late Blight

During the **season**

- ▶ **Secondary infection** phase: the parasite spreads from host to host through **inoculum from the current season**

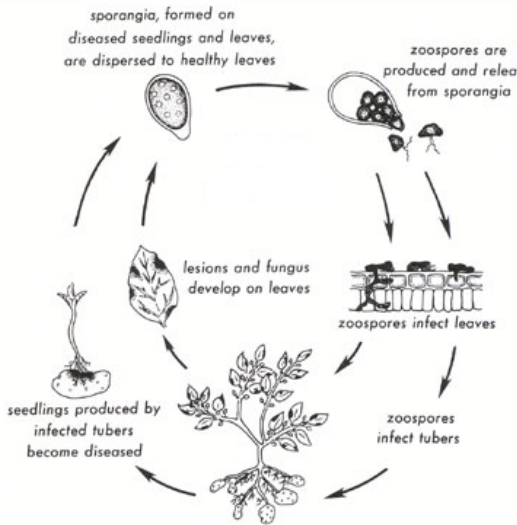
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Biotrophic parasites' life cycle: Potato Late Blight

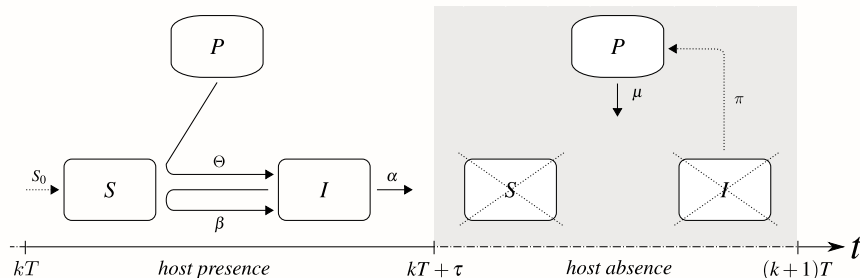
Two **complementary** transmission routes:

- ▶ **between** season transmission
- ▶ **within** season contagion



Model Basic Assumptions

(1) **Different** important **time windows** in such epidemic systems:



(2) Fast primary infection.

This requires a mixed **continuous/discrete** modelling framework

The ecological model in compact form³

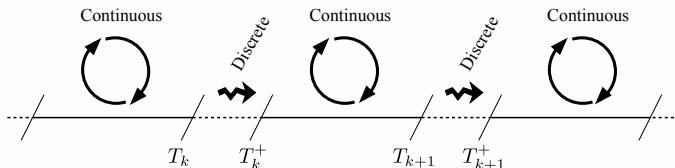
With the **continuous part**

$$\begin{cases} \dot{S} = -\sum_i \beta_i S I_i, & \text{Susceptible/healthy hosts} \\ \dot{I}_i = \beta_i S I_i - \alpha I_i. & \text{Infected/infectious hosts, } r \text{ or } m \end{cases}$$

And the **discrete part**

$$\begin{cases} S((n+1)T^+) = S_0 \exp(-\sum_i F_i((n+1)T)), \\ I_i((n+1)T^+) = S_0 [1 - \exp(-\sum_i F_i((n+1)T))] \times \left(\frac{F_i((n+1)T)}{\sum_i F_i((n+1)T)} \right), \end{cases}$$

$$\text{with } F_i((n+1)T) = \pi e^{-\mu_i(T-\tau)} \frac{\theta}{\delta} I_i(nT + \tau).$$



³Mailleret et al., 2011

The ecological model in compact form³

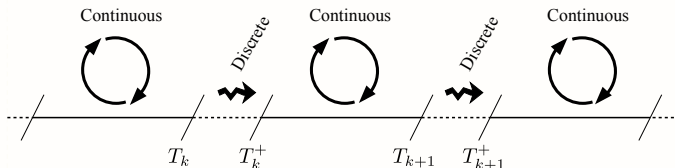
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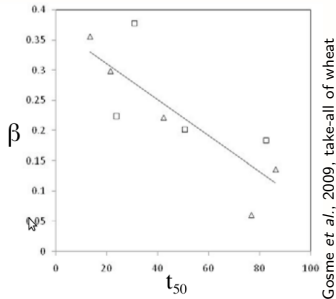


³Mailleret et al., 2011

Evolutionary trade-off

Experimental evidence⁴ of a negative relationship between

- ▶ **within season transmission ability**
- ▶ **season-to-season survival ability**



higher infection rate \Leftrightarrow lower season-to-season survival

To **capture** this, let $\mu = f(\beta)$, **with $f' > 0$.**

⁴Abang et al. 2006, Carson 1998.

Evolutionary invasion analysis

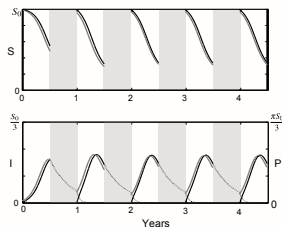
Adaptive Dynamics, a framework to address phenotypical evolution

- ▶ consider a **resident** population at ecological “equilibrium”,
- ▶ **challenge** it with a small **mutant** sub-population

Assuming the resident is at a T -periodic equilibrium $(S_r^\circ(\cdot), I_r^\circ(\cdot))$,

let

$$\bar{S}_r = \frac{1}{T} \int_0^T S_r^\circ(t) dt.$$



Evolutionary invasion analysis

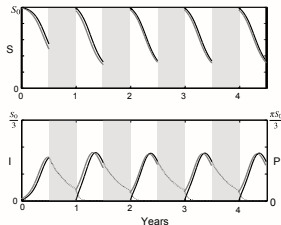
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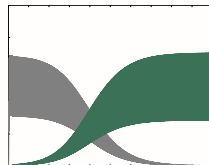
Invasion fitness

The mutant invasion criterion is define by the **invasion fitness**:

$$s(\beta_r, \beta_m) = (\beta_m - \beta_r) \bar{S}^\circ(\beta_r) \tau - (f(\beta_m) - f(\beta_r))(T - \tau)$$

- ▶ The small mutant can invade provided

$$s(\beta_r, \beta_m) > 0.$$



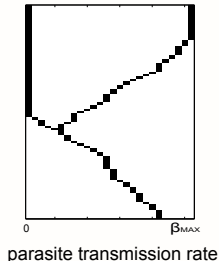
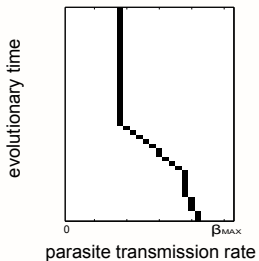
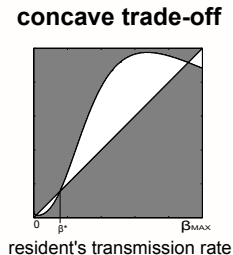
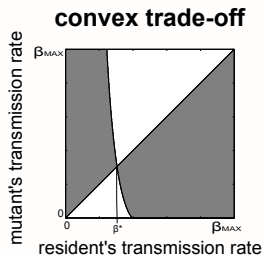
We are interested in **singular traits** β^* s.t.

$$D_2 s(\beta^*, \beta^*) = 0.$$

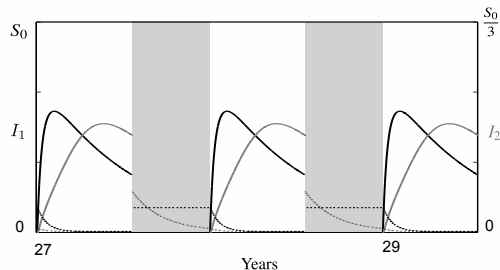
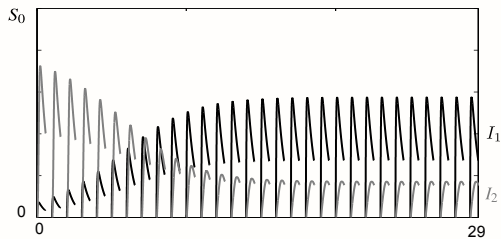
The necessary condition for a branching point reads

$$D_{22} s(\beta^*, \beta^*) = -f''(\beta^*)(T - \tau) > 0.$$

Evolutionary dynamics

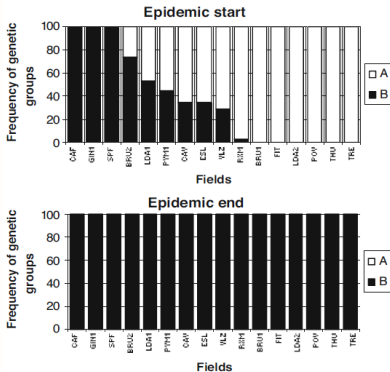


Ecological dynamics at the dimorphic evolutionary endpoint



Conclusion

- ▶ (evolution can promote) ecological niche differentiation through time partitioning⁵



⁵from Montarry et al., 2007

Thank you for your attention!



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Supporting agricultural research
for sustainable development



Annexes

Full model with two strains

{	$\dot{P}_i = -\Delta P_i,$	Primary inoculum, type r or m
	$\dot{S} = -\sum_i \Theta P_i S - \sum_i \beta_i S I_i,$	Susceptible/healthy hosts
	$\dot{I}_i = \Theta P_i S + \beta_i S I_i - \alpha I_i.$	Infected/infectious hosts, r or m
<hr/>		
{	$P_i(\tau^+) = P_i(\tau) + \pi I_i(\tau),$	Transition from growing season to winter season. $t = \tau.$
	$S(\tau^+) = 0,$	
	$I_i(\tau^+) = 0.$	
<hr/>		
{	$\dot{P}_i = -\mu_i P_i.$	Overwintering. $t \in (\tau, T).$
	<hr/>	
{	$P_i(T^+) = P_i(T),$	Beginning of a new cycle. $t = T.$
	$S(T^+) = S_0,$	
	$I_i(T^+) = 0.$	

Annexes

Making primary infections fast

- ▶ Let $\delta = \varepsilon\Delta$, $\theta = \varepsilon\Theta$, with $0 < \varepsilon \ll 1^6$.
- ▶ The **within-season** model writes, in a **slow-fast form**,

$$\begin{cases} \varepsilon \dot{P}_i = -\delta P_i, & \text{Primary inoculum} \\ \varepsilon \dot{S} = -\sum_i \theta P_i S - \sum_i \varepsilon \beta_i S I_i, & \text{Susceptible/healthy plants} \\ \varepsilon \dot{I}_i = \theta P_i S + \varepsilon \beta_i S I_i - \varepsilon \alpha I_i. & \text{Infected/Infectious Plants} \end{cases}$$

- ▶ And neglecting terms in $O(\varepsilon)$

$$\begin{cases} P \rightarrow 0, \\ S \rightarrow S_0 \exp\left(-\sum_i \frac{\theta}{\delta} P_{i,0}\right), \\ I \rightarrow S_0 \left[1 - \exp\left(-\sum_i \frac{\theta}{\delta} P_{i,0}\right)\right] \left(\frac{\frac{\theta}{\delta} P_{i,0}}{\sum_i \frac{\theta}{\delta} P_{i,0}}\right). \end{cases}$$

where $P_{i,0} = P_i((n+1)T^+) = \pi e^{-\mu_i(T-\tau)} I_i(nT + \tau)$.

⁶Madden and van den Bosch (2002)

Annexes

Making primary infections fast

- ▶ Defining fast time $t' = t/\varepsilon$,
- ▶ The **within-season** model writes, in a **slow-fast form**,

$$\begin{cases} \dot{P}'_i = -\delta P_i, & \text{Primary inoculum} \\ \dot{S}' = -\sum_i \theta P_i S - \sum_i \varepsilon \beta_i S I_i, & \text{Susceptible/healthy plants} \\ \dot{I}'_i = \theta P_i S + \varepsilon \beta_i S I_i - \varepsilon \alpha I_i. & \text{Infected/Infectious Plants} \end{cases}$$

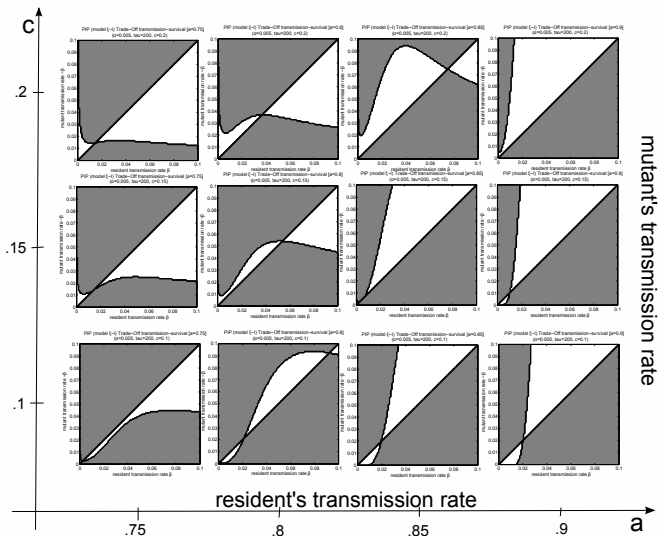
- ▶ And **neglecting terms** in $O(\varepsilon)$

$$\begin{cases} P \rightarrow 0, \\ S \rightarrow S_0 \exp\left(-\sum_i \frac{\theta}{\delta} P_{i,0}\right), \\ I \rightarrow S_0 \left[1 - \exp\left(-\sum_i \frac{\theta}{\delta} P_{i,0}\right)\right] \left(\frac{\frac{\theta}{\delta} P_{i,0}}{\sum_i \frac{\theta}{\delta} P_{i,0}}\right). \end{cases}$$

where $P_{i,0} = P_i((n+1)T^+) = \pi e^{-\mu_i(T-\tau)} I_i(nT + \tau)$.

Annexes

PIP robust around the branching point with a respect to the trade-off



Annexes

PIP robustness around the branching point with a respect to the season length

