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Seasonality and the evolutionary divergence of plant parasites

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Biotrophic plant parasites

Introduction

- 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

Introduction

Temporal heterogeneity in host availability

► Spatial host heterogeneity promotes evolutionary divergence²



Can seasonality promote evolutionary divergence as well?

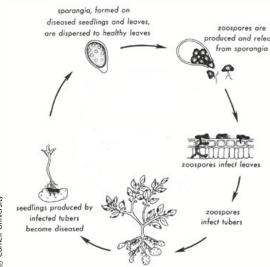


²Gudelj *et al.*, 2004

Biotrophic parasites' life cycle: Potato Late Blight

During early spring

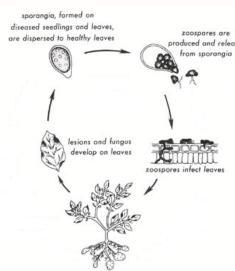
 Primary infection phase: seedlings' infection by inoculum from previous seasons



Biotrophic parasites' life cycle: Potato Late Blight

During the **season**

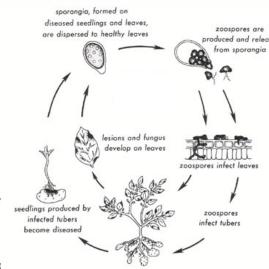
Secondary infection phase: the parasite spreads from host to host through inoculum from the current season



Biotrophic parasites' life cycle: Potato Late Blight

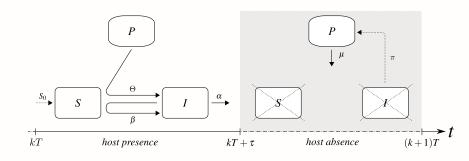
Two **complementary** transmission routes:

- 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 continous part

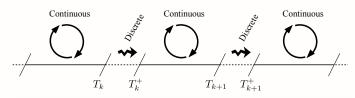
$$\begin{cases} \dot{S} = -\sum_{i} \beta_{i} S I_{i}, \\ \dot{I}_{i} = \beta_{i} S I_{i} - \alpha I_{i}. \end{cases}$$

Susceptible/healthy hosts

Infected/infectious hosts, r or m

And the discrete part

$$\begin{cases} S((n+1)T^{+}) &= S_{0} \exp\left(-\sum_{i} F_{i}((n+1)T)\right), \\ I_{i}((n+1)T^{+}) &= S_{0} \left[1 - \exp\left(-\sum_{i} F_{i}((n+1)T)\right)\right] \times \left(\frac{F_{i}((n+1)T)}{\sum_{i} F_{i}((n+1)T)}\right), \\ \text{with } F_{i}((n+1)T) &= \pi e^{-\mu_{i}(T-\tau)\frac{\theta}{\tau}} I_{i}(nT+\tau). \end{cases}$$



³Mailleret et al., 2011

The ecological model in compact form³

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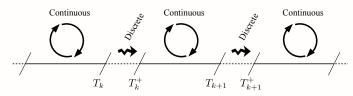
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Susceptible/healthy hosts

Infected/infectious hosts, r or m

And the discrete part

$$\left\{ \begin{array}{ll} S((n+1)T^+) & = & S_0 \exp \left(- \sum_i F_i((n+1)T) \right) \right), \\ I_i((n+1)T^+) & = & S_0 \left[1 - \exp \left(- \sum_i F_i((n+1)T) \right) \right] \times \left(\frac{F_i((n+1)T)}{\sum_i F_i((n+1)T)} \right), \\ \text{with } F_i((n+1)T) & = \pi \mathrm{e}^{-\mu_i(T-\tau)} \frac{\theta}{\delta} I_i(nT+\tau). \end{array} \right.$$

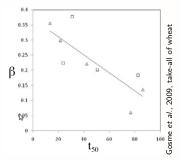


³Mailleret et al., 2011

Evolutionary trade-off

Experimental evidence⁴ of a negative relationship between

- within season transmission ability
- season-to-season survival ability



higher infection rate ⇔ lower season-to-season survival

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

⁴Abang et al. 2006, Carson 1998.

Biology

Evolutionary invasion analysis

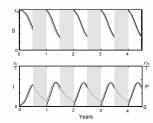
Adaptive Dynamics, a framework to address phenotypical evolution

- 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

$$\bar{S}_r = \frac{1}{\tau} \int_0^{\tau} S_r^{\circ}(t) \mathrm{d}t$$



Evolutionary invasion analysis

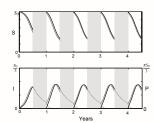
Adaptive Dynamics, a framework to address phenotypical evolution

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$$ar{S}_r = rac{1}{ au} \int_0^ au S_r^\circ(t) \mathrm{d}t \,.$$



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

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



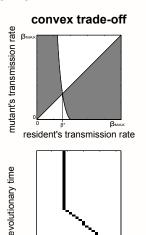
We are interested in **singular traits** β^* s.t.

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

The necessary condition for a branching point reads

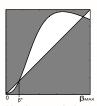
$$D_{22}s(\beta^*, \beta^*) = -f''(\beta^*)(T - \tau) > 0.$$

Evolutionary dynamics

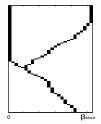


parasite transmission rate

concave trade-off

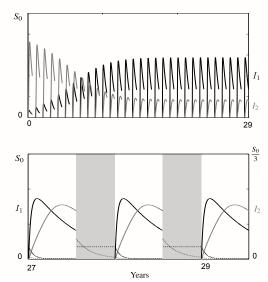


resident's transmission rate



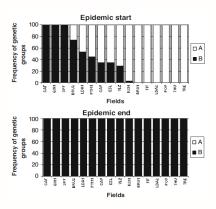
parasite transmission rate

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!







Full model with two strains

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

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,

$$\begin{cases} \varepsilon \dot{P}_{i} = -\delta \mathbf{P_{i}}, \\ \varepsilon \dot{S} = -\sum_{i} \theta \mathbf{P_{i}S} - \sum_{i} \varepsilon \beta_{i} S I_{i}, \\ \varepsilon \dot{I}_{i} = \theta \mathbf{P_{i}S} + \varepsilon \beta_{i} S I_{i} - \varepsilon \alpha I_{i}. \end{cases}$$

Primary inoculum Susceptible/healthy plants Infected/Infectious Plants

• And **neglecting terms** in $O(\varepsilon)$

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

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)

Making primary infections fast

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

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

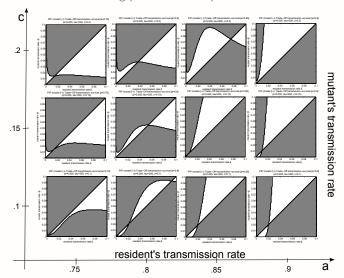
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.

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



PIP robustess around the branching point with a respect to the season legth

