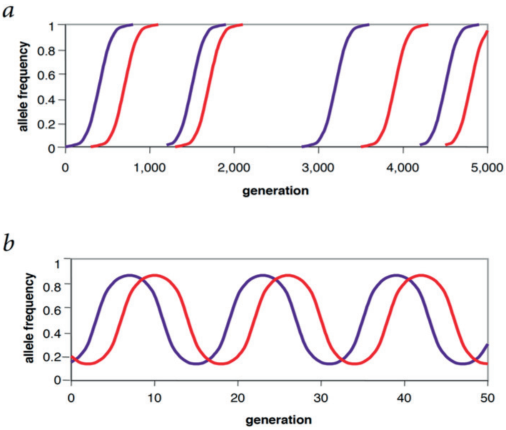
# Evolutionary vs. ecological time scales in host-parasite coevolution

Daniel Živković

# Typical host parasite concepts

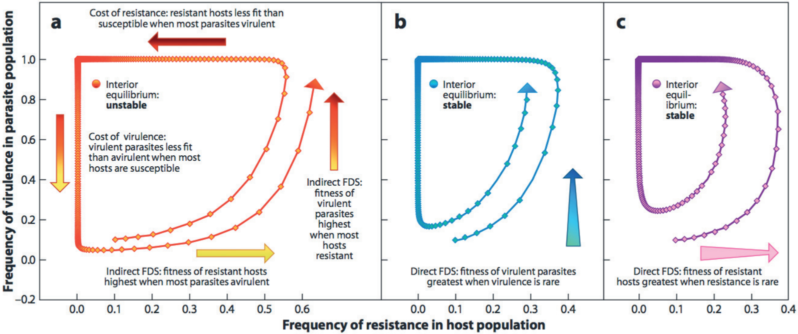



Arms race
Recurrent sweeps

Trench warfare

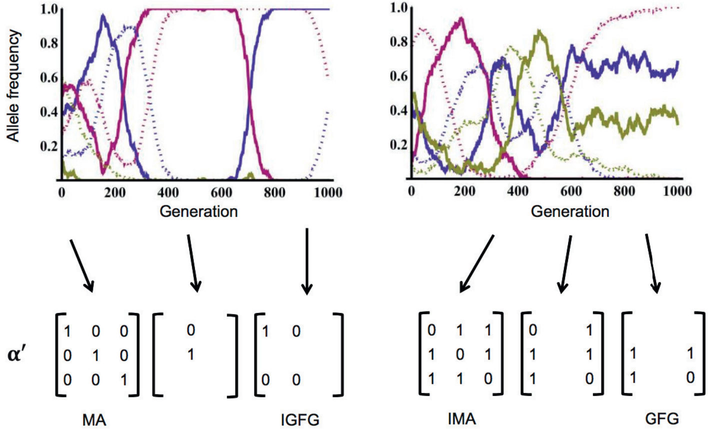
Woolhouse MEJ, JP Webster, E Domingo, B Charlesworth, and BR Levin (2002). Biological and biomedical implications of the co-evolution of pathogens and their hosts. Nature Genet 32: 569-577.

# Cycling of alleles




Brown JKM, and A Tellier (2011). Plant-Parasite Coevolution: Bridging the gap between genetics and ecology. Annu Rev Phytopathol 49: 345-367.

# Merging models




Dybdahl MF, CE Jenkins, and SL Nuismer (2014). Identifying the molecular basis of host-parasite coevolution: merging models and mechanisms. Am Nat 184: 1-13.

# A system of coupled differential equations

$$\frac{dH_i}{dt} = H_i \left[ b_i(1 - c_{h_i}) - d_i - \sum_{j=1}^{A} \alpha_{ij}\beta_{ij}(1 - c_{p_j}) \sum_{k=1}^{A} I_{kj} \right] \tag{1}$$

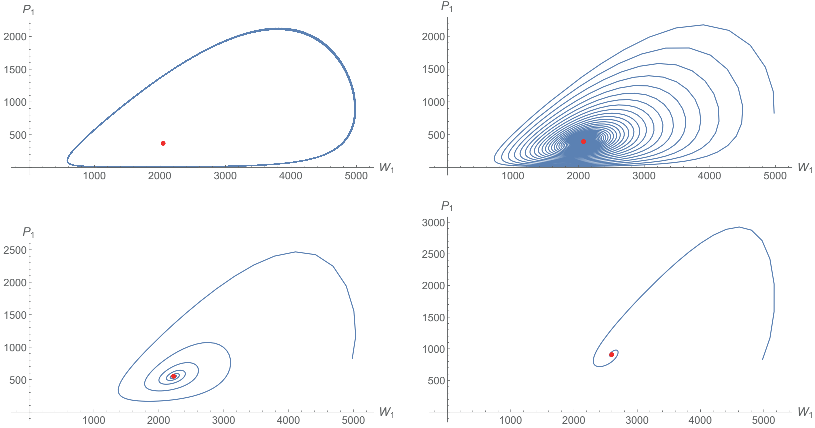
$$+ b_i(1 - c_{h_i}) \sum_{j=1}^{A} (1 - s_{h_i}) I_{ij},$$

$$\frac{dI_{ij}}{dt} = I_{ij}(-d_i - \delta_{ij}) + H_i \left[ \alpha_{ij}\beta_{ij}(1 - c_{p_j}) \sum_{k=1}^{A} I_{kj} \right]. \tag{2}$$

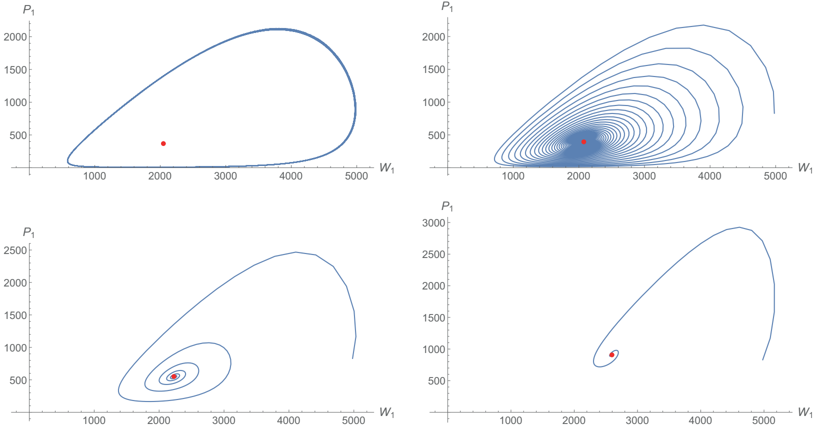
The change in the effective population size over time is obtained from (1) and (2) as

$$\frac{dN_{\text{eff}}}{dt} = \sum_{i=1}^{A} H_i \left[b_i(1-c_{h_i}) - d_i\right] + \sum_{i=1}^{A} b_i(1-c_{h_i}) \sum_{j=1}^{A}(1-s_{h_i})I_{ij} + \sum_{i=1}^{A}\sum_{j=1}^{A} I_{ij}(-d_i - \delta_{ij}). \quad (3)$$

# Stability analysis in a nutshell



# Stability analysis in a nutshell

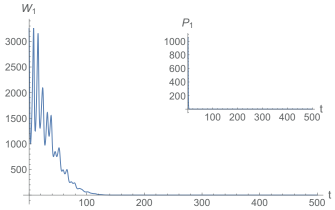


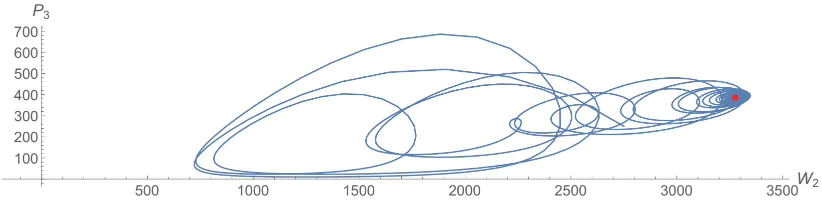

$$\hat{W}_1 = \frac{(\delta + d_1)(b_1(1 - c_{h_1})s_{h_1} + \delta)}{\beta(1 - c_{p_1})(-b_1(1 - c_{h_1})(1 - s_{h_1}) + \delta + d_1)},$$

$$\hat{P}_1 = \frac{(\delta + d_1)(b_1(1 - c_{h_1}) - d_1)}{\beta(1 - c_{p_1})(-b_1(1 - c_{h_1})(1 - s_{h_1}) + \delta + d_1)}.$$

# Transition from three to two alleles

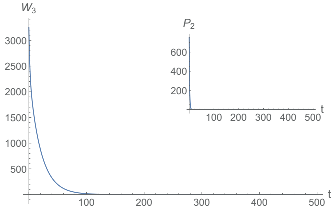
$$\begin{pmatrix} 0 & 1 & 1 \\ 1 & 0 & 1 \\ 1 & 1 & 0 \end{pmatrix} \longrightarrow \begin{pmatrix} & & \\ & 0 & {\color{red}1} \\ & 1 & 0 \end{pmatrix}$$

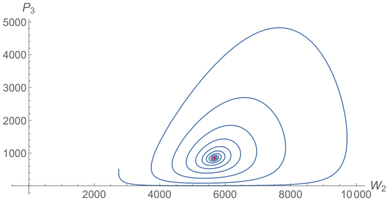


# Transition from three to two alleles

$$\begin{pmatrix} 0 & 1 & 1 \\ 1 & 0 & 1 \\ 1 & 1 & 0 \end{pmatrix} \longrightarrow \begin{pmatrix} 0 & 1 \\ 1 & \color{red}{1} \end{pmatrix}$$



# The forward equation

- Let $f(y,t)dy$ be the expected number of loci, in which the derived allele has a frequency in $(y, x+dy)$, $0 < y < 1$, at time $t$.

  Evans *et al.* (2007):

  $$\frac{\partial}{\partial t} f(y,t) = \frac{1}{2}\frac{\partial^2}{\partial y^2}\{b(y,t)f(y,t)\} - \frac{\partial}{\partial y}\{a(y)f(y,t)\},$$

  with appropriate initial conditions at time zero; the boundary conditions are

  $$\lim_{y\downarrow 0} yf(y;t) = \theta \lim_{y\downarrow 0} \frac{\rho(t)}{(1-y)}$$

  and

  $$\lim_{y\uparrow 1} f(y;t) \text{finite}.$$

- Now, let $b(y,t) = y(1-y)/\rho(t)$ and $a(y) = 2\sigma y(1-y)[y + h(1-2y)]$.

  Via $g(y,t) = y(1-y)f(y,t)$ we obtain

$$
\begin{aligned}
\frac{\partial}{\partial t} g(y,t) = & \frac{1}{2\rho(t)} y(1-y) \frac{\partial^2}{\partial y^2} \{g(y,t)\} \\
& - 2\sigma y(1-y) \frac{\partial}{\partial y} \{[y + h(1-2y)] g(y,t)\},
\end{aligned}
$$

  with appropriate initial conditions at time zero; the boundary conditions are

$$
\lim_{y \downarrow 0} g(y;t) = \theta \lim_{y \downarrow 0} \frac{y\rho(t)}{y(1-y)} = \theta \rho(t)
$$

  and

$$
\lim_{y \uparrow 1} g(y;t) = 0.
$$

# The system of ODEs for the moments

- Let $\mu_n(t) = \int\limits_0^1 y^n g(y,t)dx$ for $n = 0, 1, 2, \ldots$.

  Via integration by parts we obtain

$$\mu_0'(t) = \frac{\theta}{2} - \frac{1}{\rho(t)}\mu_0(t) + 2\sigma\left\{h[\mu_0(t) - 2\mu_1(t)] + (1-2h)[\mu_1(t) - 2\mu_2(t)]\right\},$$

$$\begin{aligned}\mu_j'(t) = \frac{1}{2\rho(t)}&\left[(j+1)j\mu_{j-1}(t) - (j+2)(j+1)\mu_j(t)\right]\\ &+ 2\sigma h\left[(j+1)\mu_j(t) - (j+2)\mu_{j+1}(t)\right]\\ &+ 2\sigma(1-2h)\left[(j+1)\mu_{j+1}(t) - (j+2)\mu_{j+2}(t)\right], \quad j \geq 1.\end{aligned}$$

# The system of ODEs in matrix form

$$\mathbf{M}'(t) = \left\{ \frac{1}{\rho(t)} \mathbf{B} + 2\sigma \left[ h\mathbf{A}_1 + (1-2h)\mathbf{A}_2 \right] \right\} \mathbf{M}(t) + \boldsymbol{\Theta}.$$

Even a finite version of this system can not be solved!

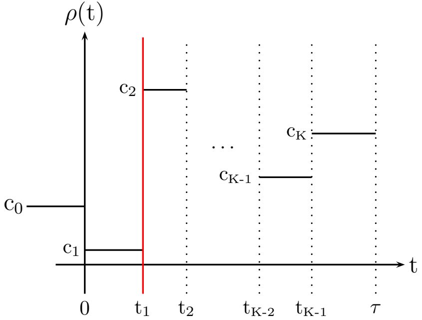
Therefore, we set $\rho(t) = c_1$ to obtain

$$\mathbf{M}'(t) = \mathbf{C}_1 \mathbf{M}(t) + \boldsymbol{\Theta},$$

where $\mathbf{C}_1 = \mathbf{B}/c_1 + 2\sigma \left[ h\mathbf{A}_1 + (1-2h)\mathbf{A}_2 \right]$. This differential equation can be solved in terms of a matrix exponential as

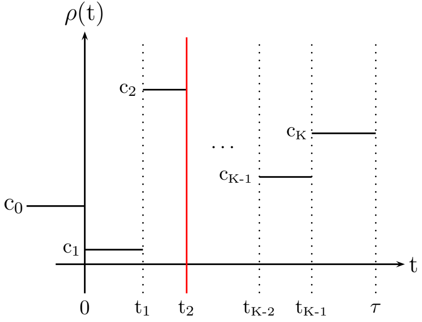
$$\mathbf{M}(t) = \exp\left(\mathbf{C}_1 t\right) \mathbf{M}(0) + \left[\exp(\mathbf{C}_1 t) - \mathbf{I}\right] \mathbf{C}_1^{-1} \boldsymbol{\Theta}.$$

# Building up an algorithm



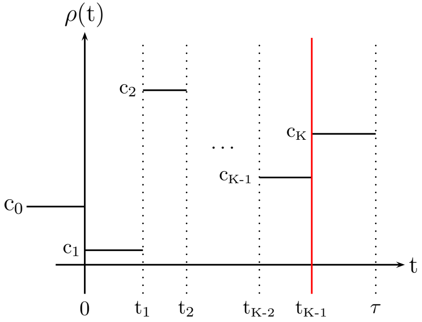

$$\mathbf{M}(t) = \exp\left(\mathbf{C}_1 t\right)\mathbf{M}(0) + \left[\exp(\mathbf{C}_1 t) - \mathbf{I}\right]\mathbf{C}_1^{-1}\,\boldsymbol{\Theta}, \quad 0 \leq t < t_1.$$

# Building up an algorithm



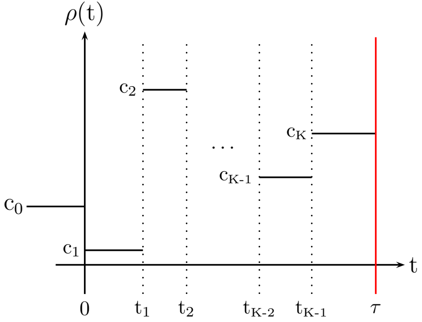

$$\mathbf{M}(t) = \exp\left(\mathbf{C}_2(t - t_1)\right)\mathbf{M}(t_1) + \left[\exp(\mathbf{C}_2(t - t_1)) - \mathbf{I}\right]\mathbf{C}_2^{-1}\,\boldsymbol{\Theta}, \quad t_1 \leq t < t_2.$$

# Building up an algorithm



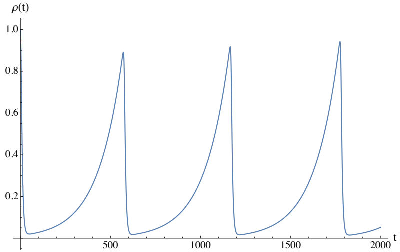

$$\mathbf{M}(t) = \exp\left(\mathbf{C}_{k-1}(t - t_{k-2})\right)\mathbf{M}(t_{k-2}) + \left[\exp(\mathbf{C}_{k-1}(t - t_{k-2})) - \mathbf{I}\right]\mathbf{C}_{k-1}^{-1}\,\boldsymbol{\Theta},$$
$$t_{k-2} \le t < t_{k-1}.$$

# Building up an algorithm

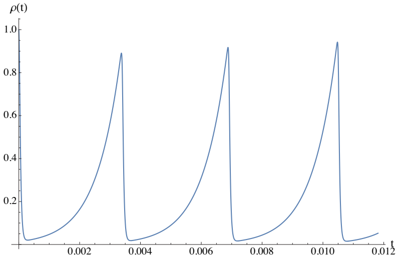



$$\mathbf{M}(t) = \exp\left(\mathbf{C}_K(t - t_{K-1})\right)\mathbf{M}(t_{K-1}) + \left[\exp(\mathbf{C}_K(t - t_{K-1})) - \mathbf{I}\right]\mathbf{C}_K^{-1}\,\boldsymbol{\Theta}, \qquad t_{k-1} \leq \tau.$$

# Measurable time scales



# Measurable time scales



# Measurable time scales