Adaptive dynamics

via an example of host-pathogen coevolution

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Adaptive dynamics

A mathematical framework for modelling adaptive evolution in (possibly complex) ecological systems

Stefan Geritz

Hans Metz

Worked example of this talk: Best et al. 2010, Am. Nat.

Theory and many more examples:
http://mathstat.helsinki.fi/~kisdi/addyn.htm

Host-pathogen model

- Susceptible: $\frac{dS}{dt} = b(N)S - \mu S - \beta SI$ sterilizing disease

  Infected: $\frac{dI}{dt} = \beta SI - (\mu + \alpha)I$ no recovery

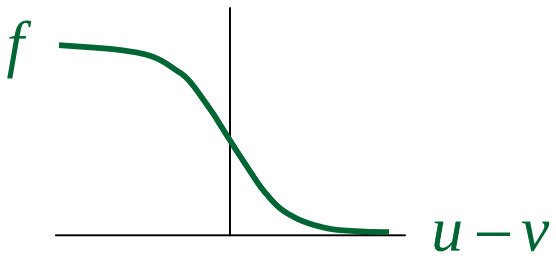
- Density-dependent birth rate: $b(N) = b_0 - qN,\ N = S + I$

- If the host and the pathogen are viable ($b_0 > \mu, \beta > \frac{q(\mu+\alpha)}{b_0-\mu}$) then there is a unique stable interior equilibrium $(\hat{S}, \hat{I})$

Traits and trade-offs

- Host strains differ in resistance, u
  Pathogen strains differ in infectivity, v

  Transmission rate $\beta(u,v) = \beta_0 f(u-v)$



arms race

- Cost of resistance in the birth rate: $b_0(u)$ decreasing
  Cost of infectivity: $\beta_0(v)$ decreasing

Traits and trade-offs

$$f(u-v) = 1 - \frac{1}{1+\exp(-c(u-v))}$$

$$b_0(u) = b_{0\max} - (b_{0\max} - b_{0\min})\frac{u-u_{\min}}{(1+p_b)(u_{\max}-u_{\min}) - p_b(u-u_{\min})}$$

$$\beta_0(v) = \beta_{0\max} - (\beta_{0\max} - \beta_{0\min})\frac{v-v_{\min}}{(1+p_\beta)(v_{\max}-v_{\min}) - p_\beta(v-v_{\min})}$$

$$u_{\min} = 0, u_{\max} = 10, b_{0\min} = 0.5, b_{0\max} = 3, p_b = 4,$$
$$v_{\min} = 0, v_{\max} = 10, \beta_{0\min} = 0.5, \beta_{0\max} = 10, p_\beta = -0.4,$$
$$c = 2, \alpha = 2, \mu = 0.2, q = 0.5, \phi_u = 1, \phi_v = 1$$

Resident equilibrium

- Single host and single pathogen strain

$$\left.\begin{aligned} \frac{dS}{dt} &= (b_0(u) - qN)S - \mu S - \beta(u,v)SI \\ \frac{dI}{dt} &= \beta(u,v)SI - (\mu+\alpha)I \end{aligned}\right\} \longrightarrow \hat{S}(u,v), \hat{I}(u,v)$$

with $\beta(u,v) = \beta_0(v)\, f(u-v)$

Pathogen mutant

- Mutant pathogen strain v_{mut}

$$\frac{dS}{dt} = (b_0(u) - qN)S - \mu S - \beta(u,v)SI - \beta(u,v_{mut})SI_{mut}$$

$$\frac{dI}{dt} = \beta(u,v)SI - (\mu + \alpha)I$$

$$\frac{dI_{mut}}{dt} = \beta(u,v_{mut})SI_{mut} - (\mu + \alpha)I_{mut}$$

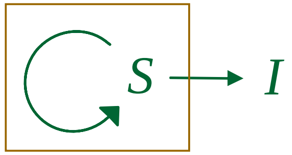
Pathogen mutant

- The mutant is initially rare, linearize at $I_{mut} \to 0$

$$\left.\begin{aligned}\frac{dS}{dt} &= (b_0(u)-qN)S-\mu S-\beta(u,v)SI \\ \frac{dI}{dt} &= \beta(u,v)SI-(\mu+\alpha)I\end{aligned}\right\} \longrightarrow \hat{S}(u,v), \hat{I}(u,v)$$

$$\frac{dI_{mut}}{dt} = [\underbrace{\beta(u,v_{mut})\hat{S}(u,v)-(\mu+\alpha)}_{r(v_{mut},u,v)\ \text{invasion fitness of the pathogen}}]I_{mut}$$

Host mutant



- Once infected, the host never reproduces again

$$\left.\begin{aligned}\frac{dS}{dt} &= (b_0(u) - qN)S - \mu S - \beta(u,v)SI\\ \frac{dI}{dt} &= \beta(u,v)SI - (\mu+\alpha)I\end{aligned}\right\} \longrightarrow \hat{S}(u,v), \hat{I}(u,v)$$

$$\frac{dS_{mut}}{dt} = \underbrace{[b_0(u_{mut}) - q\hat{N}(u,v) - \mu - \beta(u_{mut},v)\hat{I}(u,v)]}_{s(u_{mut},u,v)\ \text{invasion fitness of the host}} S_{mut}$$

Small mutation steps

- Assume small mutation steps: $|u_{mut} - u|, |v_{mut} - v|$ are $O(\varepsilon)$

$$s(u_{mut}, u, v) = \xcancel{s(u,u,v)} + s_1(u,u,v)(u_{mut} - u) + O(\varepsilon^2)$$

$$r(v_{mut}, u, v) = \xcancel{r(v,u,v)} + r_1(v,u,v)(v_{mut} - v) + O(\varepsilon^2)$$

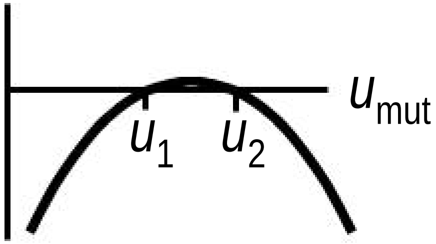
Invasion of a mutant

- The mutant *may* invade if its invasion fitness is positive

$$\Pr(invasion) = \begin{cases} cs_1(u_{mut}, u, v)(u_{mut} - u) & \text{if positive} \\ 0 & \text{otherwise} \end{cases}$$

(stochastic branching process, see e.g. Jagers 1975)

- Invasion implies fixation (Geritz 2005 “bending theorem”)



$s \in C^2 \Rightarrow$ coexistence of similar strains is possible only near $u : s_1(u, u, v) = 0$

Trait substitution sequence

- Trait substitution

$$\Delta u = \underbrace{(m\hat{S}\cdot\Delta T)}_{\Pr(\mathit{mutation})} \cdot \underset{\uparrow}{\frac{1}{2}} \cdot \underbrace{cs_1(u,u,v)(u_{mut}-u)}_{\Pr(\mathit{invasion}\,|\,\mathit{beneficial})} \cdot \underbrace{(u_{mut}-u)}_{\mathit{change}}$$

$\Pr(\mathit{beneficial})$
assuming symmetric mutations

Trait substitution sequence

- Trait substitution

$$\Delta u = (m\hat{S} \cdot \Delta T) \cdot \frac{1}{2} \cdot c s_1(u,u,v)(u_{mut} - u) \cdot (u_{mut} - u)$$

- Infrequent mutations: trait substitution sequence
- $|u_{mut} - u|, |v_{mut} - v| \to 0$: canonical equation

$$\frac{du}{dT} = \phi_u \hat{S}(u,v) s_1(u,u,v)$$

$$\frac{dv}{dT} = \phi_v \hat{I}(u,v) r_1(v,u,v)$$

Trait substitution sequence

- Canonical equation

$$\frac{du}{dT} = \phi_u \hat{S}(u,v) s_1(u,u,v)$$

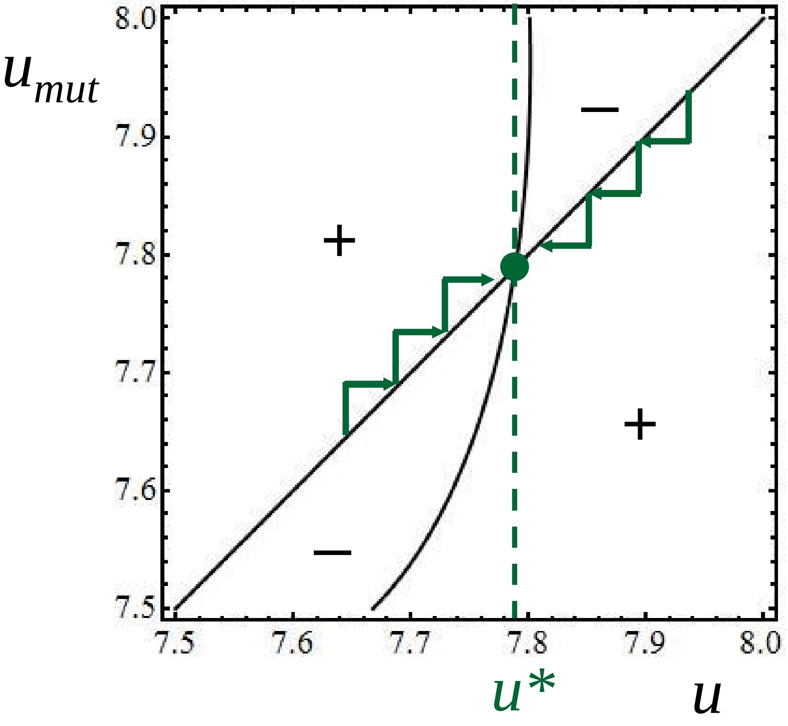
$$\frac{dv}{dT} = \phi_v \hat{I}(u,v) r_1(v,u,v)$$

- Fixed point (u^*, v^*) : $s_1(u^*, u^*, v^*) = r_1(v^*, u^*, v^*) = 0$
  called singularity; asympt. stability = convergence stability

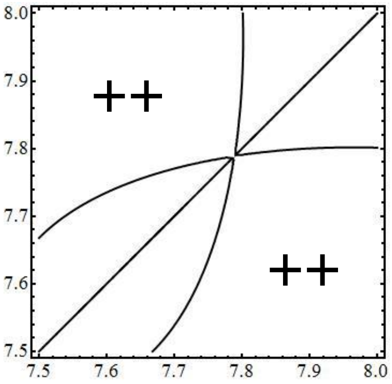
- Evolutionary cycles (chaos), evolution to extinction, evolutionary suicide

Only host evolves

- Pairwise invasibility plot: sign plot of $s(u_{mut}, u, \bar{v})$ ($\bar{v}$ fixed)



u^* convergence stable
NOT evolutionarily stable
coexistence in the nbh



Evolutionary singularities (1D)

- Convergence stability: the fixed point of $\frac{du}{dT} = \phi_u \hat{S}(u,v) s_1(u,u,\bar{v})$ is stable if

$$s_{11}(u^*,u^*,\bar{v}) + s_{12}(u^*,u^*,\bar{v}) < 0$$

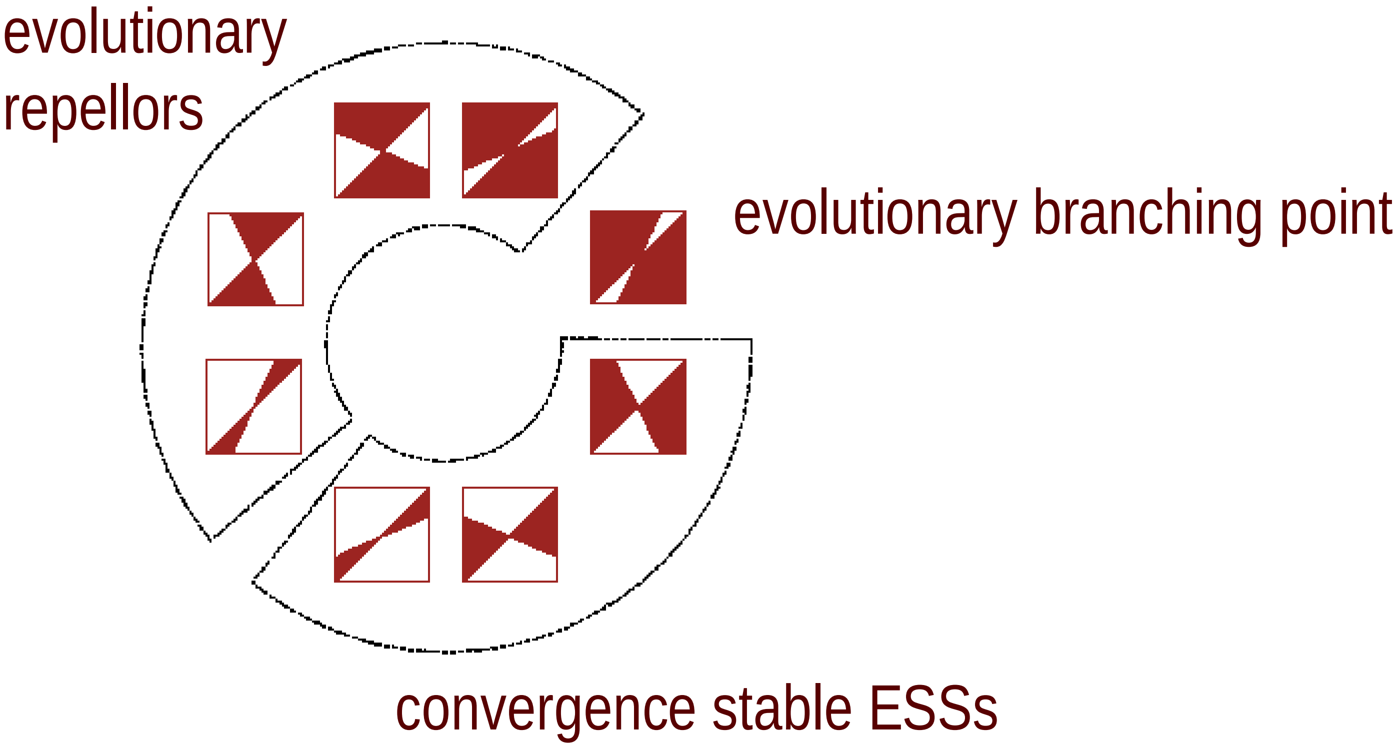
- No evolutionary stability: from second-order expansion

$$s_{11}(u^*,u^*,\bar{v}) > 0$$

- Coexistence by mutual invasibility

$$s_{12}(u^*,u^*,\bar{v}) < 0$$

Evolutionary singularities (1D)



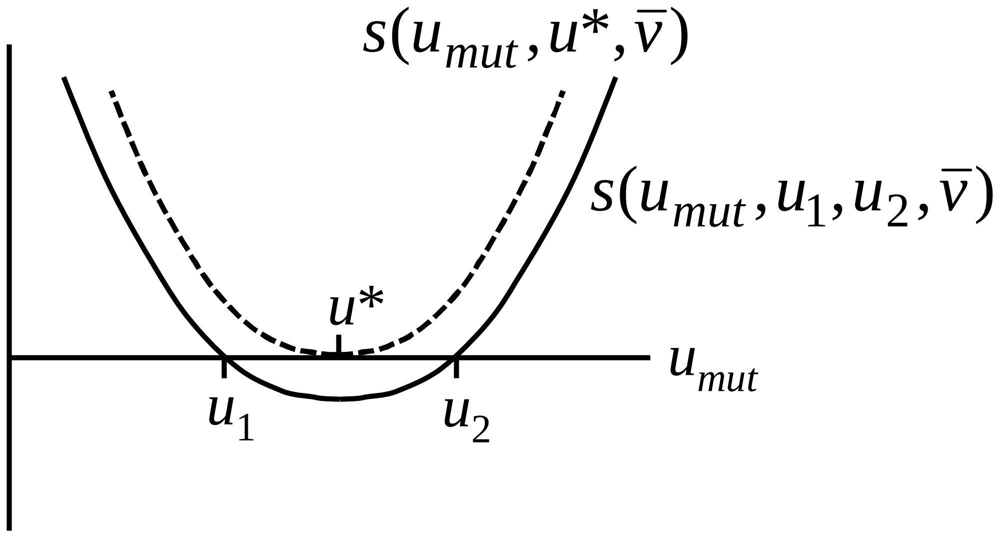
evolutionary repellors

evolutionary branching point

convergence stable ESSs

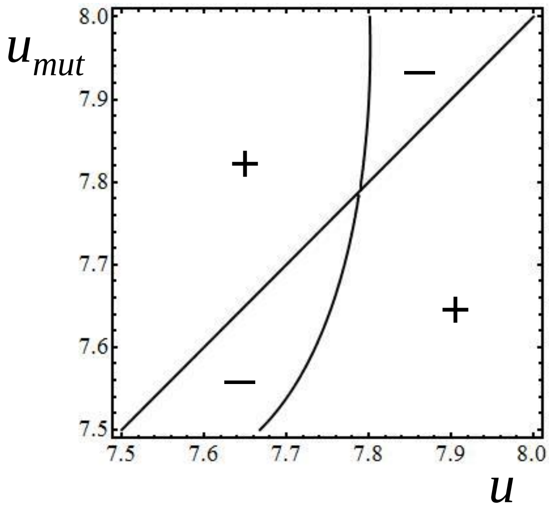
Evolutionary singularities (1D)

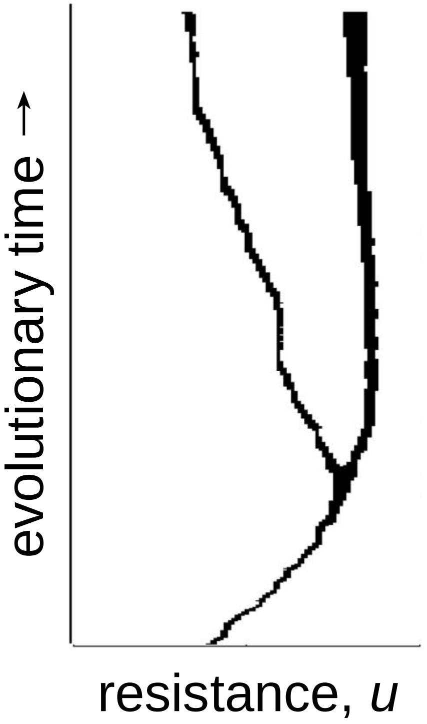
- Evolutionary branching (Geritz et al. 1998)



Only host evolves

- The host undergoes evolutionary branching





Only pathogen evolves

- Optimal pathogen strain ($\bar{u}$ fixed)

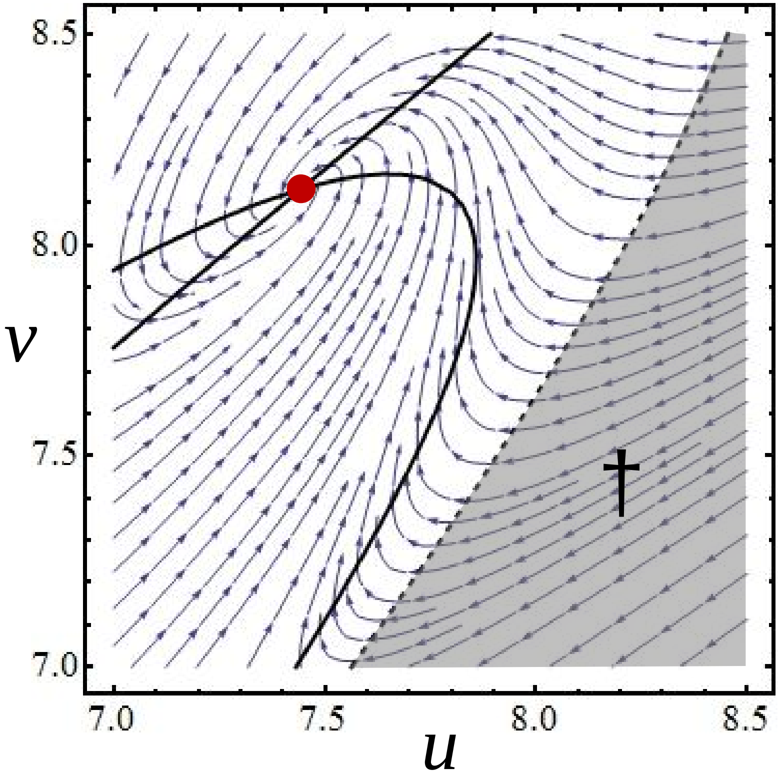
1D feedback: no coexistence, optimal pathogen minimizes *S*

$$\frac{dI_{mut}}{dt} = [\underbrace{\beta(\bar{u}, v_{mut})\boxed{\hat{S}(\bar{u}, v)} - (\mu + \alpha)}_{r(v_{mut}, \bar{u}, v) > 0 \;\Leftrightarrow\; \beta(\bar{u}, v_{mut}) > \frac{\mu + \alpha}{\hat{S}(\bar{u}, v)} = \beta(\bar{u}, v)}]I_{mut}$$

v evolves to maximize $\beta(\bar{u}, v) = \beta_0(v) f(u - v)$

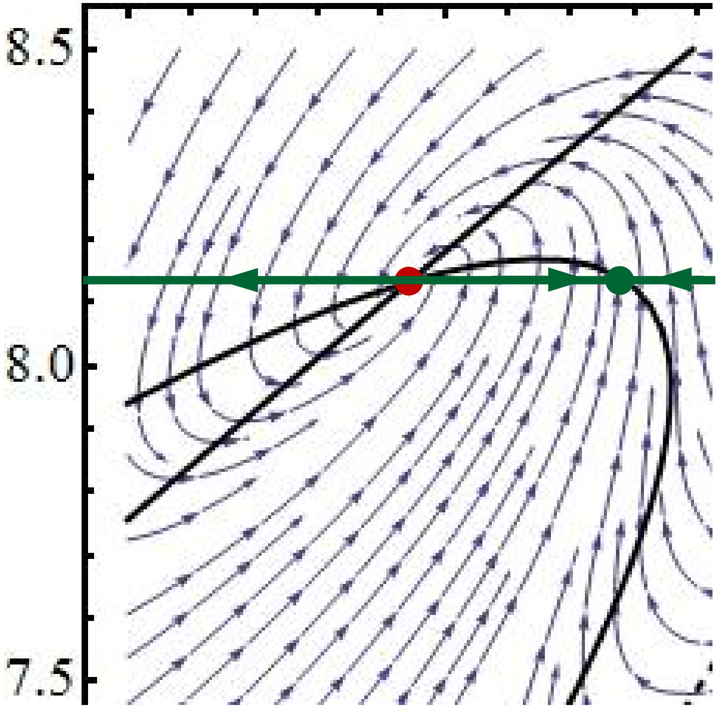
Both host and pathogen evolve

- Canonical equation: (u^*, v^*) attracting



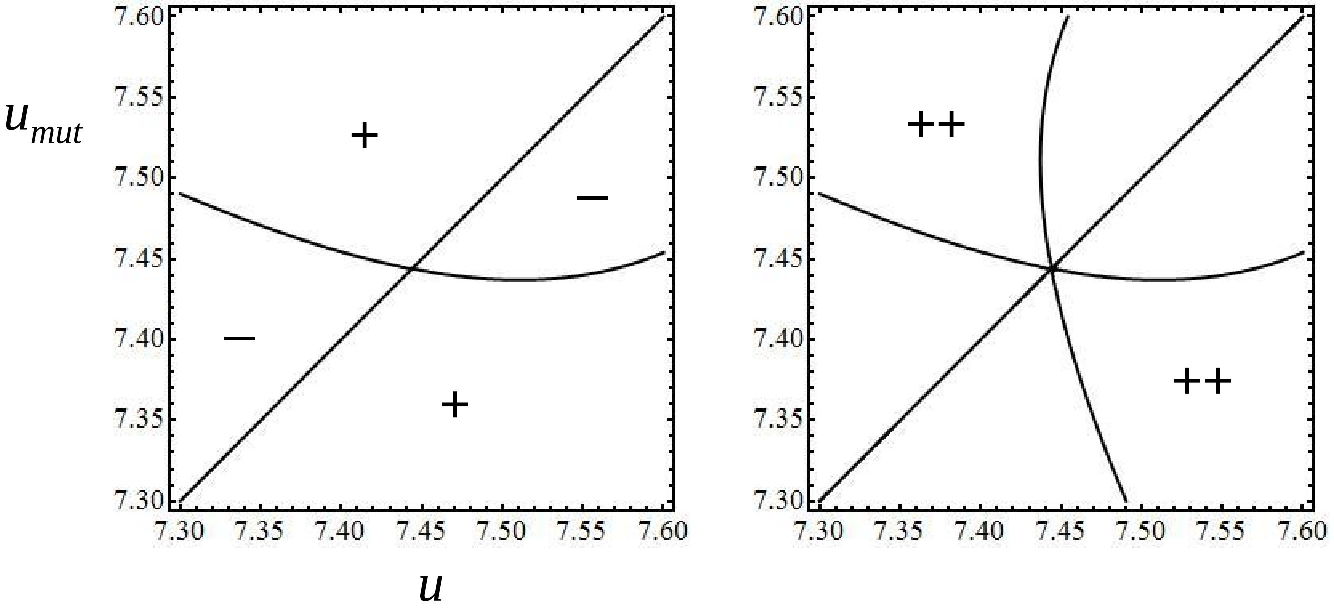
Both host and pathogen evolve

- Canonical equation: (u^*, v^*) attracting

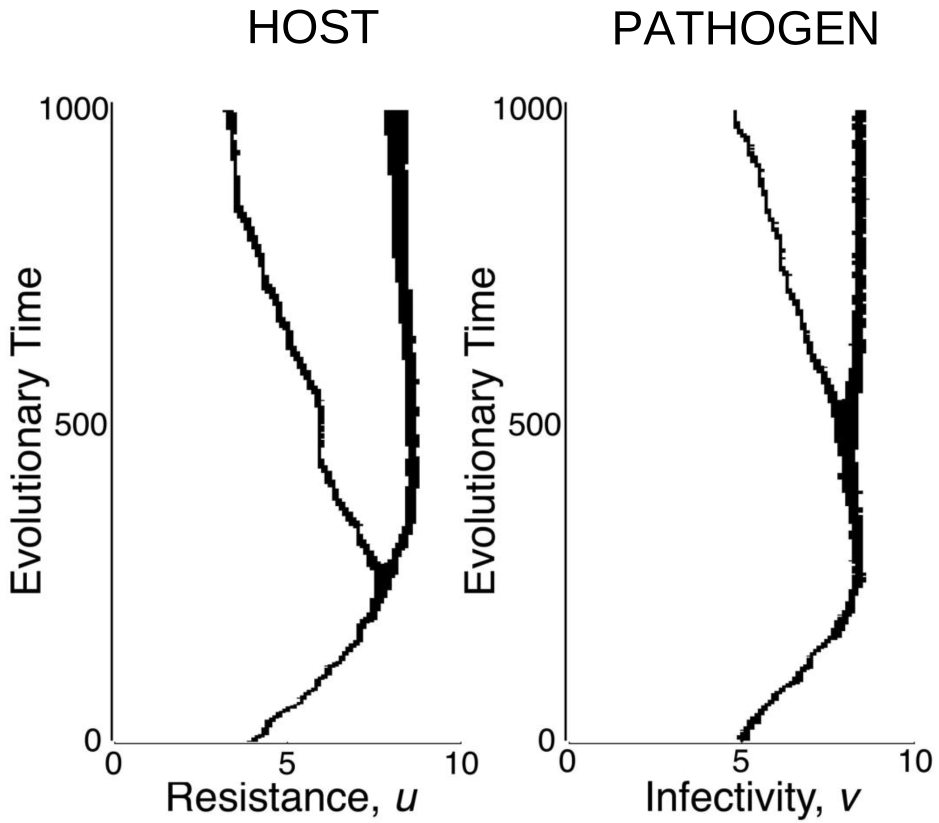


Both host and pathogen evolve

- At the convergence stable singularity (u^*, v^*)
  - the pathogen maximizes $\beta(u^*, v)$ as a function of v
  - the host is not evolutionarily stable and coexistence is possible



Both host and pathogen evolve



HOST

PATHOGEN

Both host and pathogen evolve

- Pathogen mutant with only 1 host strain:

$$\frac{dI_{mut}}{dt} = [\beta(u,v_{mut})\boxed{\hat{S}(u,v)} - (\mu+\alpha)]I_{mut}$$

- Host mutant with only 1 pathogen strain:

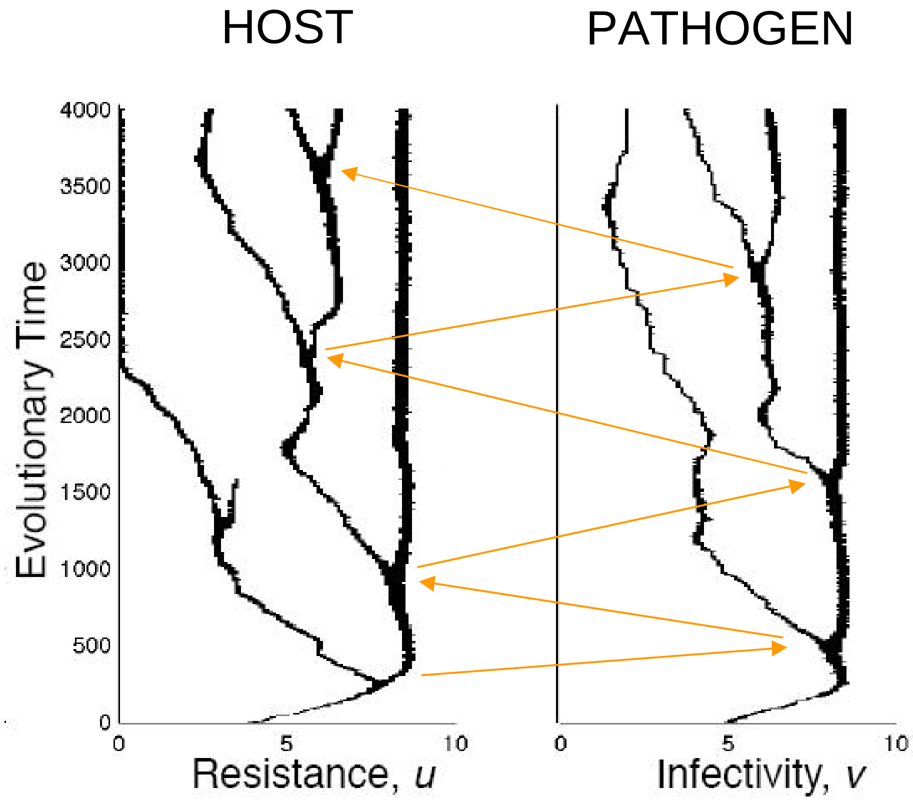
$$\frac{dS_{mut}}{dt} = [b_0(u_{mut}) - q\boxed{\hat{N}(u,v)} - \mu - \beta(u_{mut},v)\boxed{\hat{I}(u,v)}]S_{mut}$$

- Pathogen mutant with 2 host strains:

$$\frac{dI_{mut}}{dt} = [\beta(u_1,v_{mut})\boxed{\hat{S}_1(u,v)} + \beta(u_2,v_{mut})\boxed{\hat{S}_2(u,v)} - (\mu+\alpha)]I_{mut}$$

- …

Both host and pathogen evolve



cheater + resistant specialist + generalist

Adaptive dynamics

- Main assumptions
  - clonal inheritance (alleles are inherited clonally!)
  - small mutational steps (local analysis)
  - mutations occur only infrequently (time scale separation)
  - the mutant is initially rare (invasion fitness)

Adaptive dynamics

- Dynamics of long-term evolution
  - evolutionary branching
  - coevolution of strains after branching; repeated branching
  - coevolution of different species
  - evolution to extinction, evolutionary suicide
  - evolutionary cycles (Red Queen)
  - multiple traits; function-valued traits
  - critical function analysis (shape of trade-off functions)

- Models of (almost) arbitrary ecological complexity
  - invasion fitness + analysis numerically

Homework assignment

Numerical (use functions and parameters as given on slide 5):

- Find the singularity (u^*,v^*) of the host-pathogen coevolution model
  (this should agree with the figure on slide 21)

- Construct the pairwise invasibility plot of the host for the range
  $(u_1, u_2) = (7,8)$ when the pathogen is fixed at $\bar{v} = v^*$
  (parts of this range are shown on slides 15 and 23)

- Construct the pairwise invasibility plot of the pathogen for any fixed host.
  Explain why the plot is skew symmetric (when mirrored on the main diagonal,
  "+" parts map onto "-" parts and *vice versa*).

Analytical

- The joint evolution of host and pathogen may exhibit a limit cycle. Show that if ϕ_u increases, the fixed point of the canonical equation may undergo a Hopf bifurcation. (You may want to use some information shown on slide 22.)