Solving Games for Life

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Darwin’s Postulates

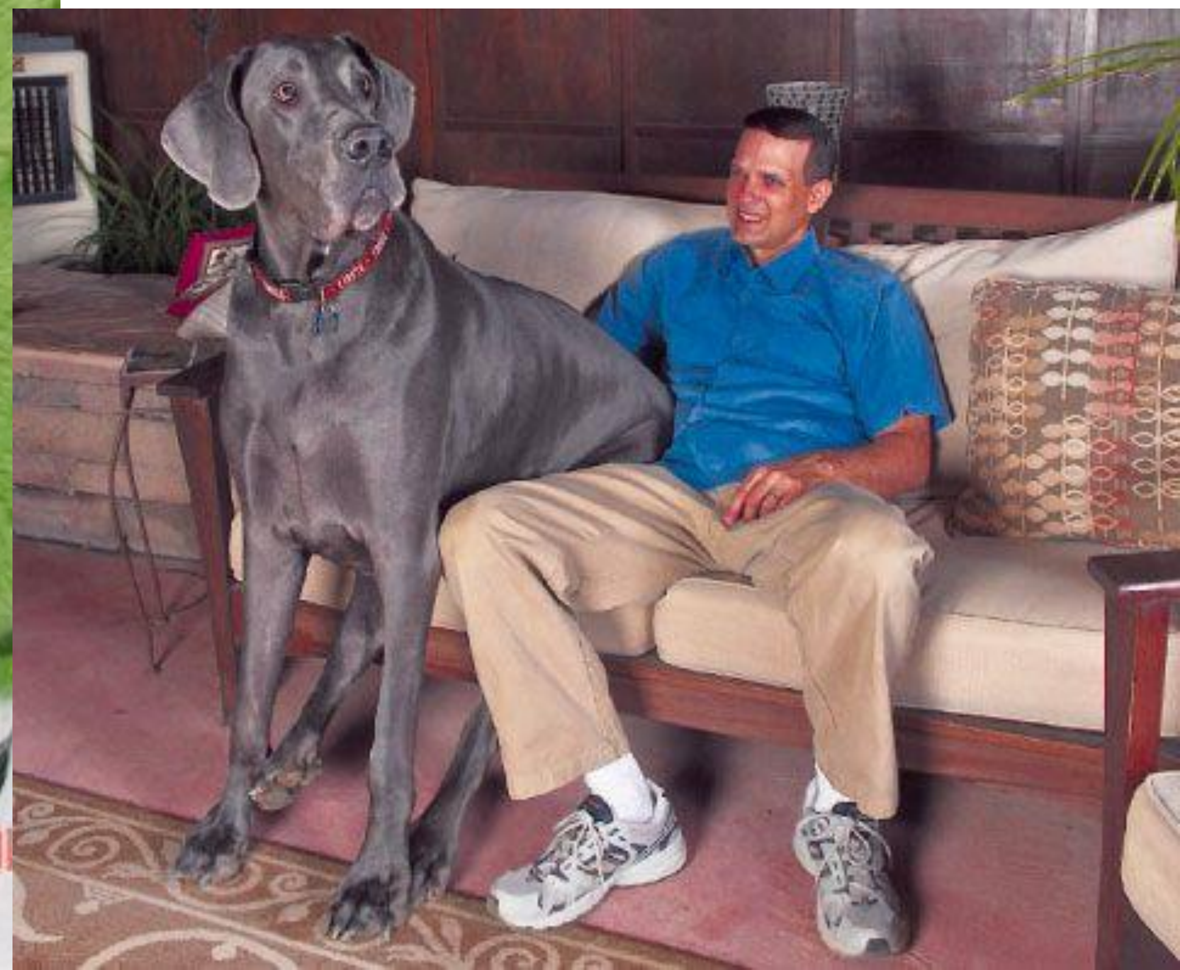
- Heritable Variation
- Struggle for Existence
- Variation influences the Struggle

“In the survival of favoured individuals and races, during the constantly-recurring struggle for existence, we see a powerful and ever-acting form of selection”

Darwin's Postulates as a Game

- **Heritable Variation**: Organisms possess strategies u ε **U**
- **Struggle for Existence:** Fitness (per capita growth rate) $G = (1/x)(\partial x/\partial t)$ and at some point $\partial G/\partial x < 0$

How big is my strategy set



Variation Influences the Struggle

- Fitness Generating Function: $G(v,\mathbf{u},\mathbf{x})$
- v = strategy of focal individual
- $\mathbf{u}$ = vector of extant strategies among others
- $\mathbf{x}$ = vector of population sizes associated with each extant strategy, where x_i is the population size of strategy u_i in the population


I have a strategy …
I just don’t know how to find it

Darwinian Dynamics

- Ecological Dynamics: $$\frac{dx_i}{dt} = x_i \, G|_{v=u_i}$$
- Strategy Dynamics: $$\frac{du_i}{dt} = k \frac{\partial G}{\partial v}\bigg|_{v=u_i}.$$
  evaluated at $v = u_i$
- Invasion Structured: Rather than letting the u_i*'s* evolve, introduce new u_i*'s* into the population

Recipe for an Evolutionary Game

- Select a model of population dynamics
- Select an evolutionary strategy
- Place bounds on the set of evolutionarily feasible strategies
- Introduce strategy of individual, and strategies of others into the population model

Competition Model of Coevolution

- Ecological Model: $\partial x / \partial t = rx(K-x)/K$

- Let carrying capacity be a function of the individual's strategy, v
- Let the competitive effect of others be a function of the individual's strategy, v, and the strategies of others, $\mathbf{u}$.

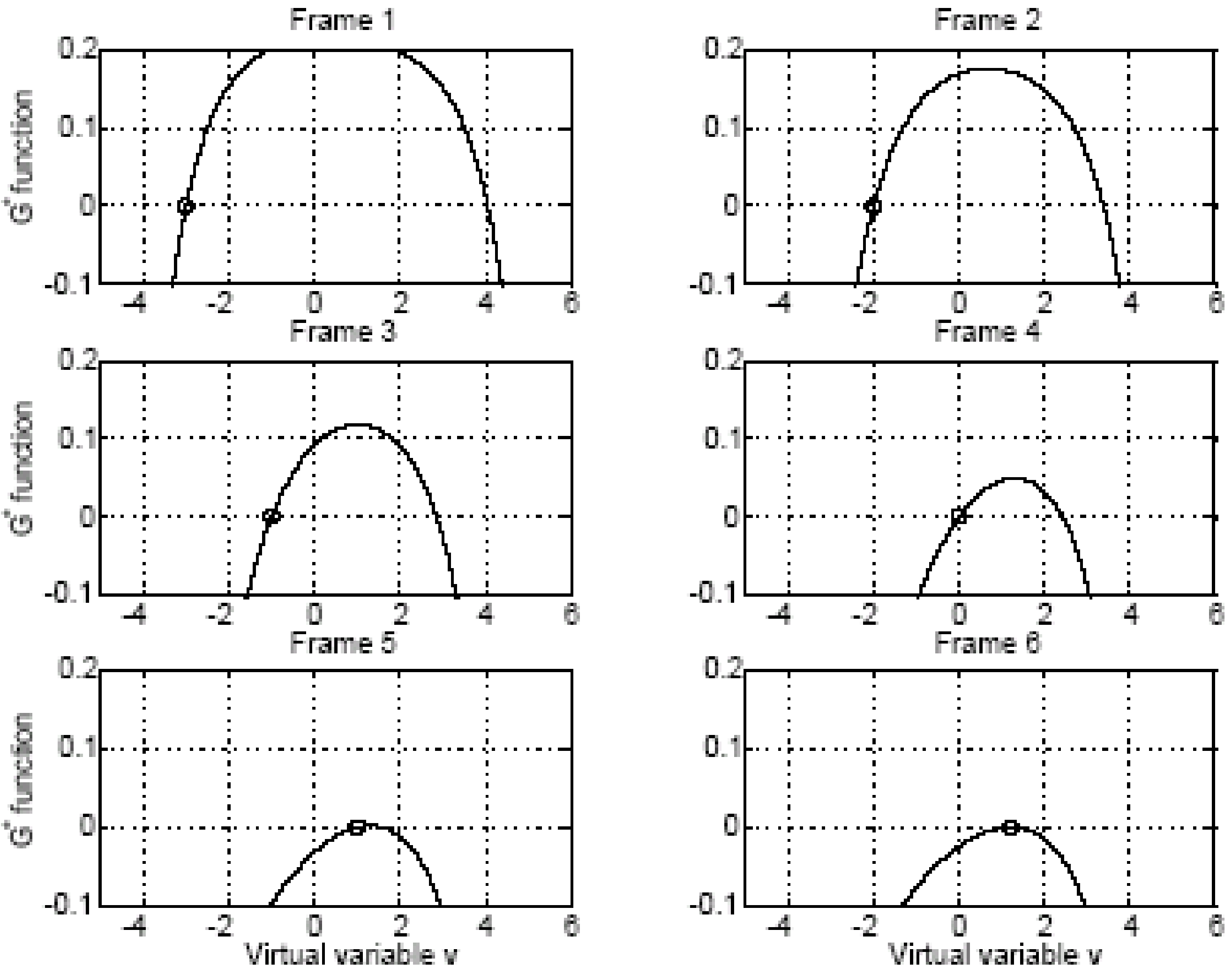
Fitness Generating Function

$$G(v,\mathbf{u},\mathbf{x}) = (r/K(v))[K(v)-\Sigma x_i \alpha(v,u_i)]$$

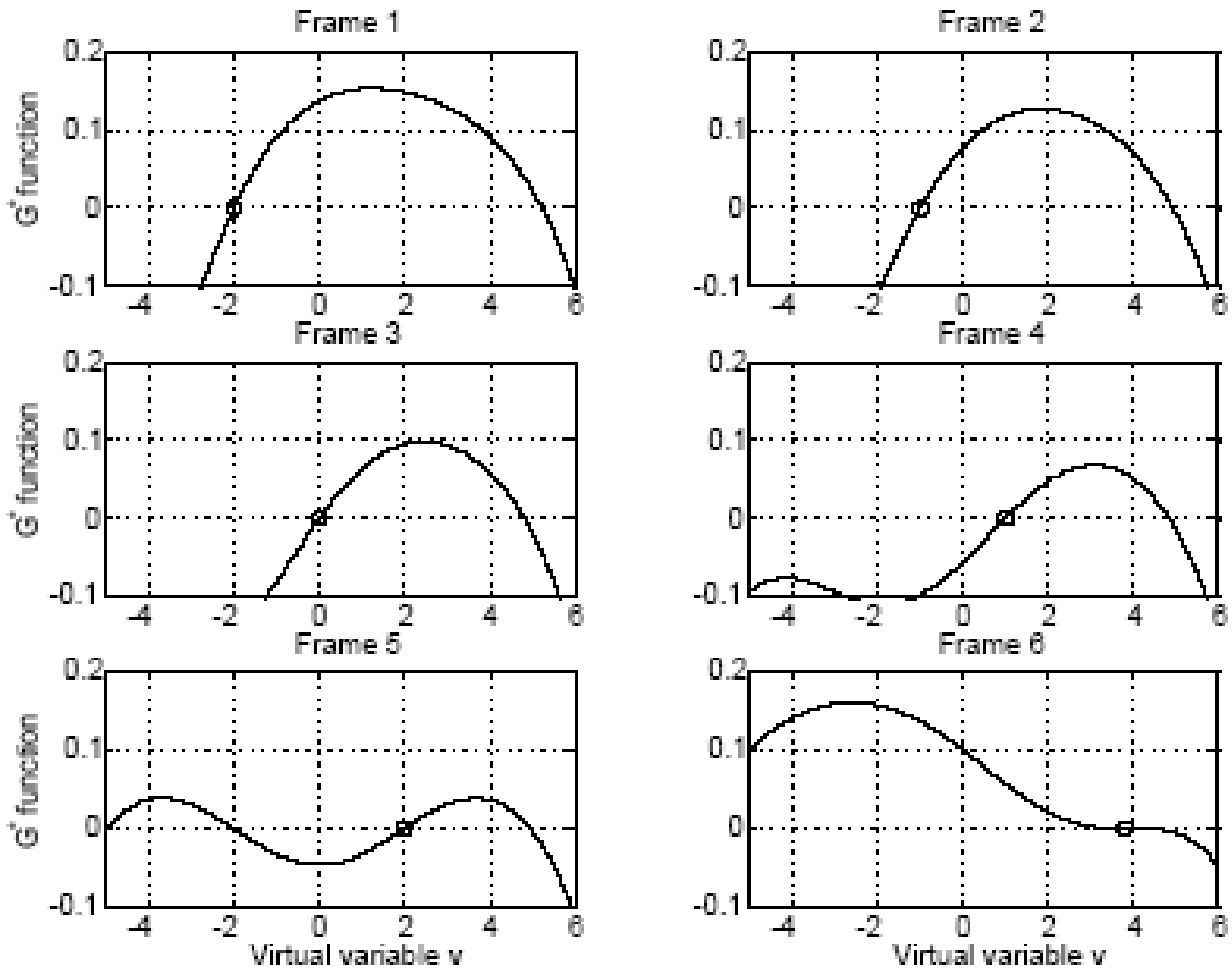
where

$$\alpha(v,u_i) = 1 + exp\left[-\frac{(v-u_j+\beta)^2}{2\sigma_a^2}\right] - exp\left[-\frac{\beta^2}{2\sigma_a^2}\right]$$

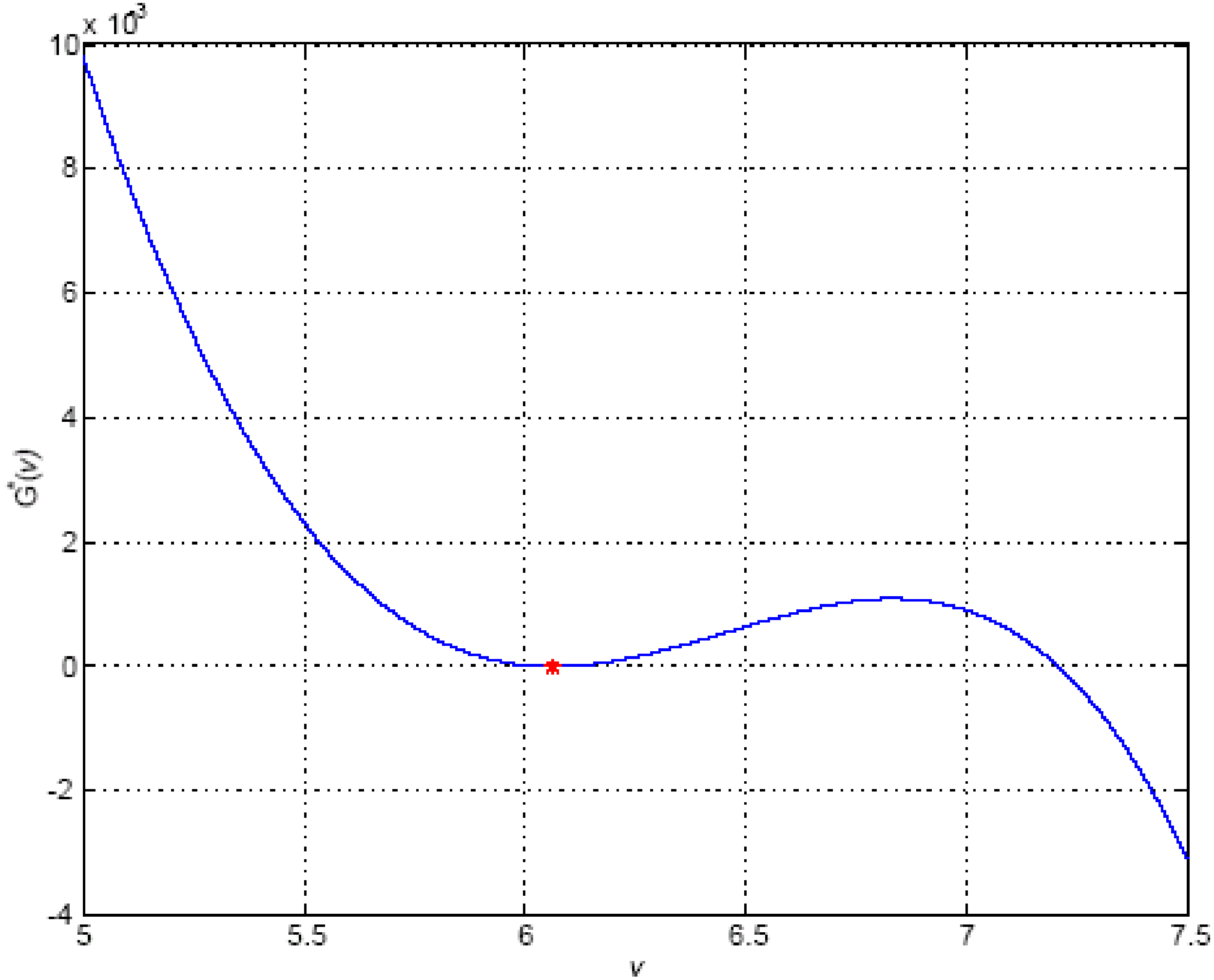
$$K(v) = (K_m)\exp[-v^2/2\sigma^2_K]$$



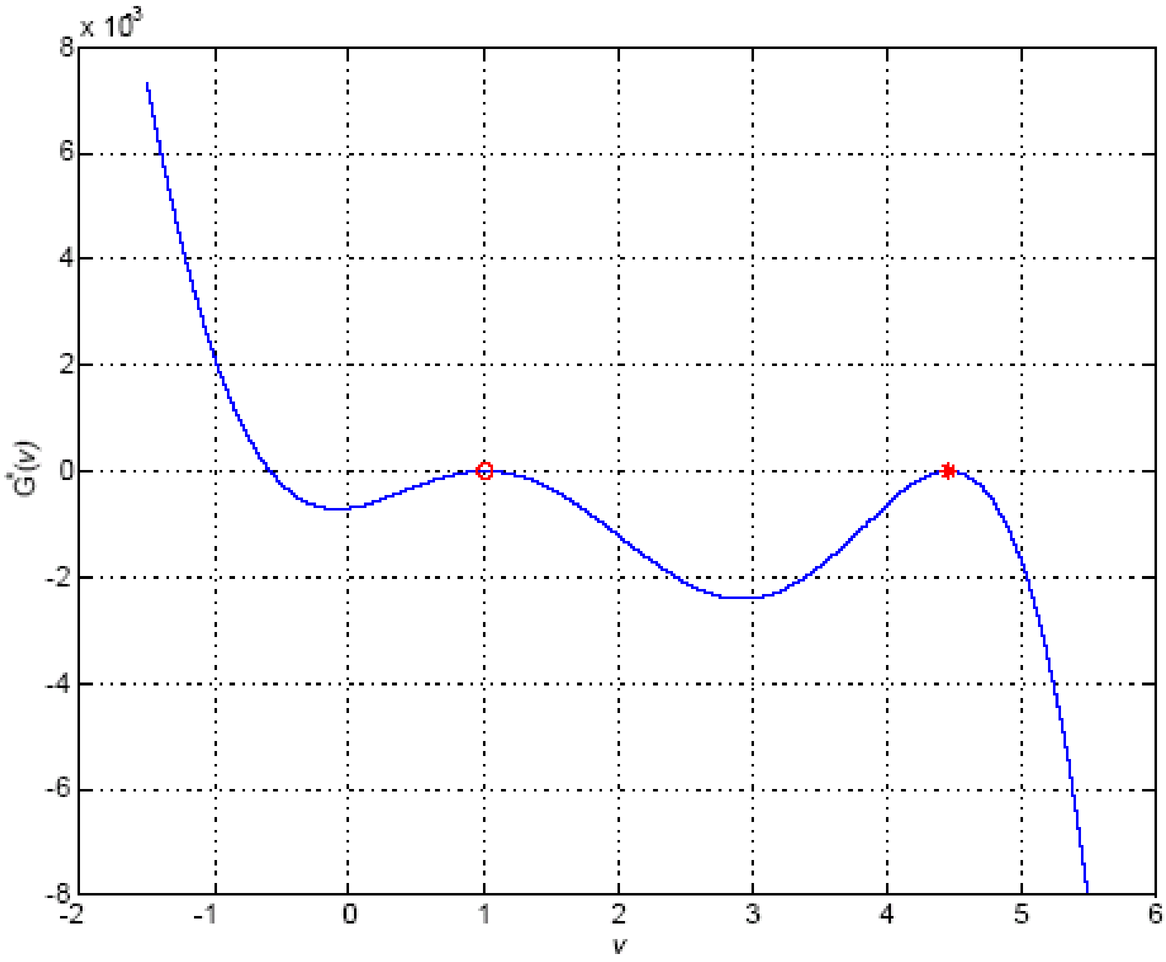
Strategy Dynamics showing the "escalator effect"



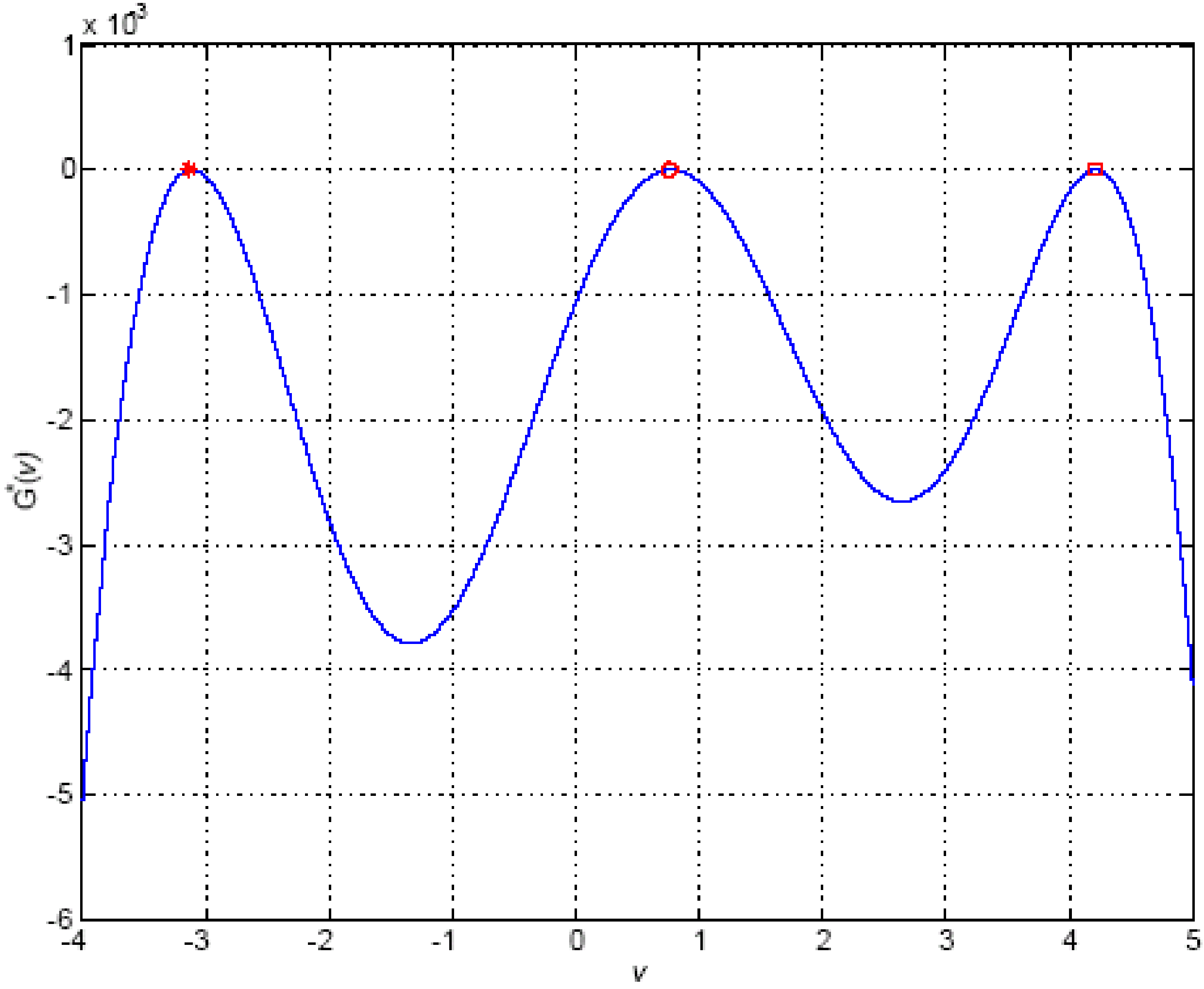
Strategy dynamics leading to a minimum on the adaptive landscape



Evolutionarily Stable Minimum



Convergent stable and local evolutionary maxima



Convergent stable and Global Evolutionary Maxima

Evolutionarily Stable Strategy

"A strategy which cannot be invaded by alternative strategies when it is common in the population"

An ESS can contain one or more "species". To be the outcome of natural selection it must be convergent stable and be global maxima on the adaptive landscape at the ESS

Definition 1 (ESS-scalar). *A coalition strategy $u_c \in \mathcal{U}$ is said to be an evolutionarily stable strategy (ESS) for the equilibrium point $\mathbf{x}^* = [x_c^*, x_m^*] = [x_c^*, 0]$ if, for all feasible strategies u_m, $\mathbf{x}^*$ remains as the stable equilibrium with respect to population dynamics. It is said to be a local (global) ESS if $\mathbf{x}^*$ is a local (global) ecologically stable equilibrium.*

$$G(v, [u_c, u_m], [x_c^*, 0])\big|_{v=u_c} = 0$$

$$\left.\frac{\partial G(v, [u_c, u_m], [x_c^*, 0])}{\partial v}\right|_{v=u_c} = 0$$

$$\left.\frac{\partial G(v, [u_c, u_m], [x_c, 0])}{\partial x_c}\right|_{v=u_c,\ x_c=x_c^*} < 0$$

- Apaloo et al., 2009 Evol. Ecol. Res.

ESS Maximum Principle

- Each strategy of the ESS must maximize $G(v,\mathbf{u}^*,\mathbf{x}^*)$ evaluated at $v = u_i^*$ and $\mathbf{u}^*,\mathbf{x}^*$.
- Because of the escalator effect $G(v,\mathbf{u}^*,\mathbf{x}^*) = 0$ at $v = u_i^*$
- This requires that $\partial G/ \partial v = 0$ and $(\partial^2 G/ \partial v^2) < 0$ at $v = u_i^*$ and $\mathbf{u}^*,\mathbf{x}^*$.

This is just a long-winded way of saying the strategy is a peak on the adaptive landscape

Adaptations are no regret strategies: Nash!!!

Convergence Stability

- When perturbed from the ESS in terms of **u*** and/or **x*** (or any other convergent stable point) the Darwinian Dynamics returns the community to **u*, x***

Definition 5 (covergence stable-scalar). *A strategy $u_c \in \mathcal{U}$ is said to be convergence stable for the equilibrium point $[x_c^*, x_m^*] = [x_c^*, 0]$ if there is a value $\varepsilon > 0$ such that for any strategy u_m with an associated equilibrium point $[0, x_m^*]$ in an ε neighbourhood of u_c, there is a value $\delta > 0$ such that for any strategy v at a δ vicinity of u_m with $u_m \neq u_c$,*

$$G(v, [u_c, u_m], [0, x_m^*]) > 0 \text{ whenever } |v - u_c| < |u_m - u_c| . \quad (6)$$

This just says that evolution by natural selection can get you there!

Neighborhood Invader Strategy

- When perturbed from the ESS in terms of **u*** and/or **x*** (or minimum point) the strategy **u*, x*** can invade

Definition 3 (NIS-scalar). *A strategy* $u_c \in \mathcal{U}$ *is said to be a neighbourhood invader strategy (NIS) for the equilibrium point* $\mathbf{x}^* = [x_c^*, x_m^*] = [x_c^*, 0]$ *if, when the population using* u_c *is rare* $(x_c = \varepsilon \simeq 0)$, *for any scalar strategy* u_m *in a close neighbourhood of* u_c, $N(u_c)$ *with* $u_m \neq u_c$,

$$G(v, [u_c, u_m], [0, x_m^*])|_{v=u_c} > 0. \qquad (5)$$

This just says that I can invade when rare

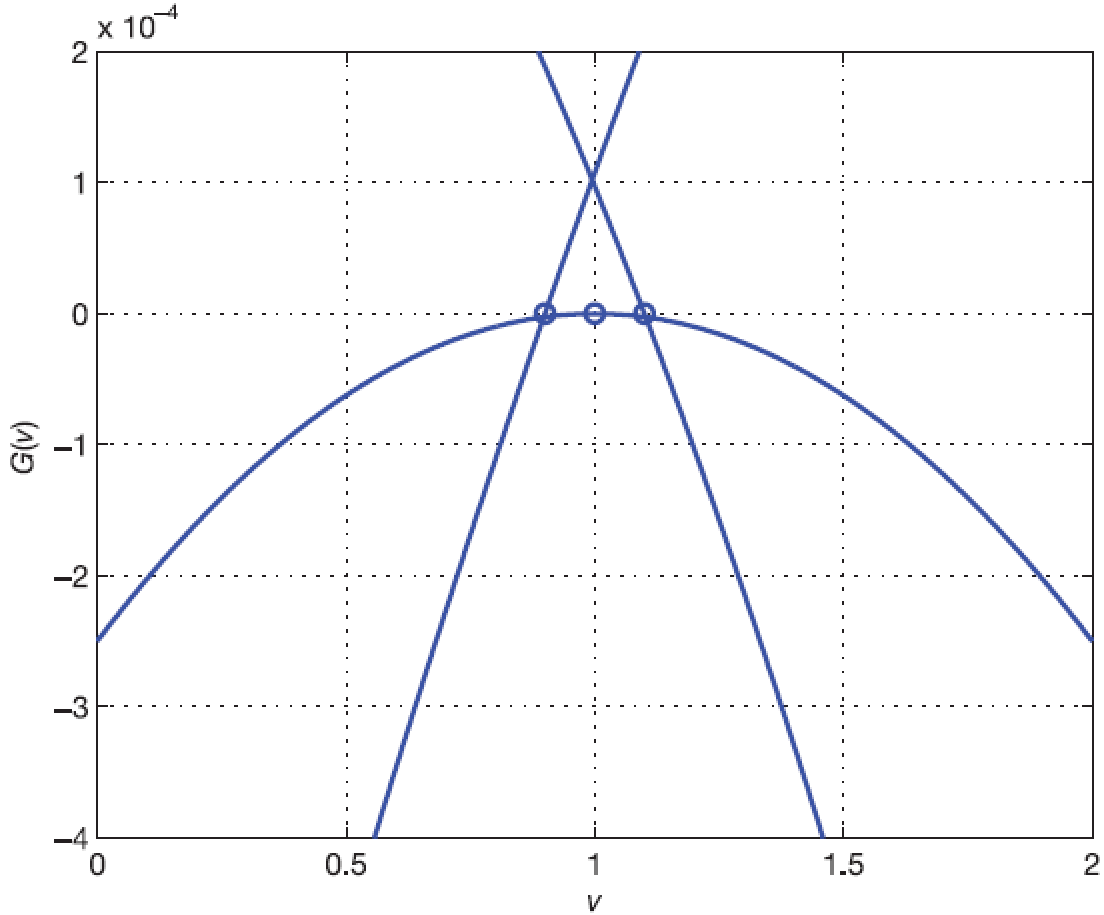
Conditions for NIS and Convergence Stability

$$S_2 = \left(\frac{\partial^2 G(v, [u_c, u_m], [0, x_m^*])}{\partial {u_m}^2} + 2 \frac{\partial^2 G(v, [u_c, u_m], [0, x_m^*])}{\partial u_m \partial x_m^*} \frac{\partial x_m^*}{\partial u_m} + \frac{\partial^2 G(v, [u_c, u_m], [0, x_m^*])}{\partial {x_m^*}^2} \left(\frac{\partial x_m^*}{\partial u_m} \right)^2 + \frac{\partial G(v, [u_c, u_m], [0, x_m^*])}{\partial x_m^*} \frac{\partial^2 x_m^*}{\partial {u_m}^2} \right) \Bigg|_{v = u_m = u_c^*}$$

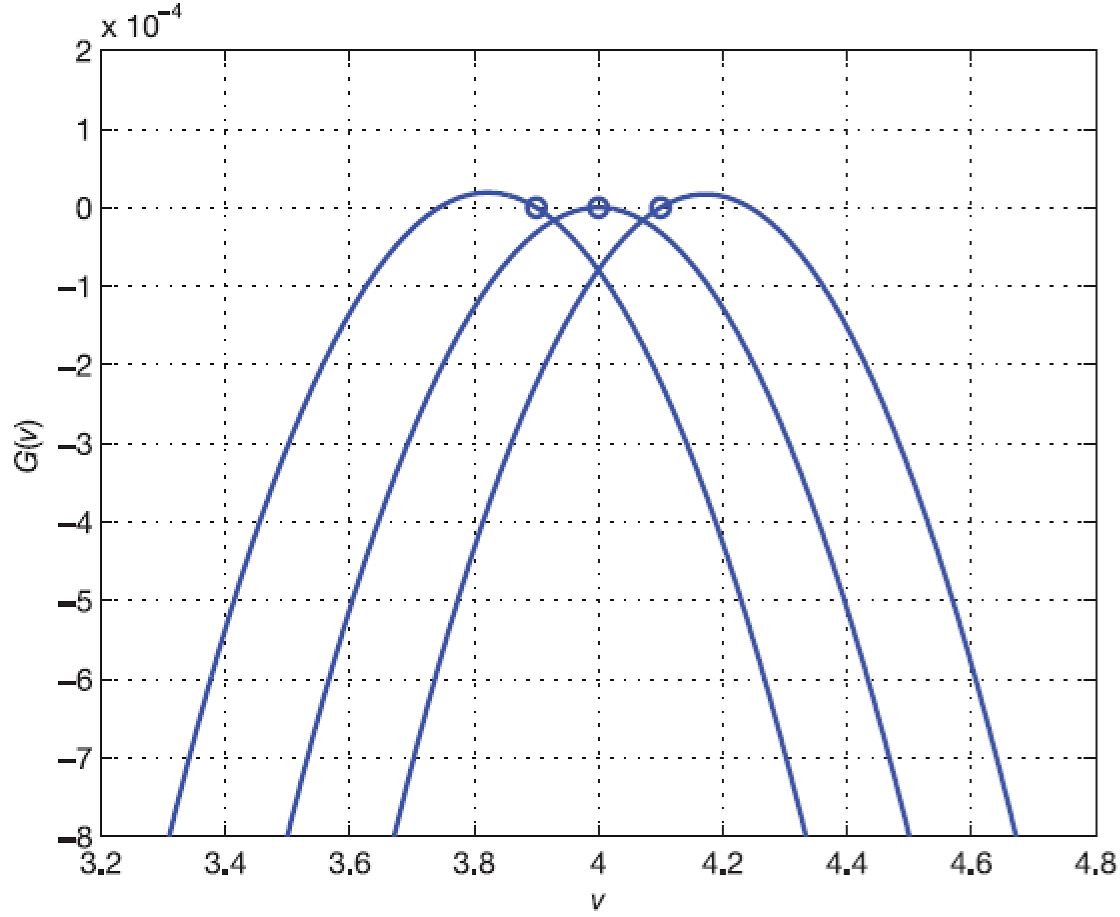
$$S_3 = \left(\frac{\partial^2 G(v, [u_c, u_m], [0, x_m^*])}{\partial v^2} + \frac{\partial^2 G(v, [u_c, u_m], [0, x_m^*])}{\partial u_m \partial v} + \frac{\partial^2 G(v, [u_c, u_m], [0, x_m^*])}{\partial v \partial x_m^*} \frac{\partial x_m^*}{\partial u_m} \right) \Bigg|_{v = u_m = u_c}$$

Ugly and Beautiful at the same time!!

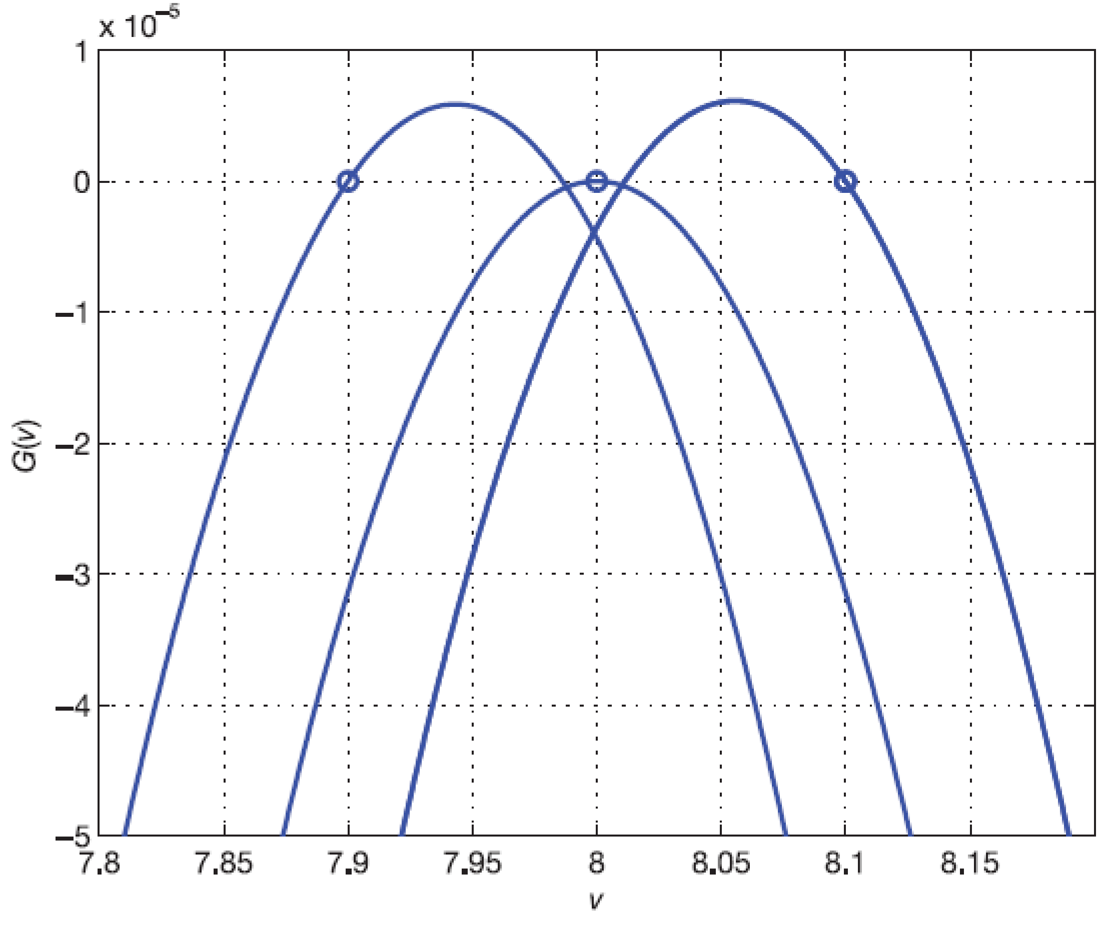
Convergent Stable ESS that is NIS



ESS, Not Convergent Stable, not NIS



ESS, Convergent Stable but not NIS

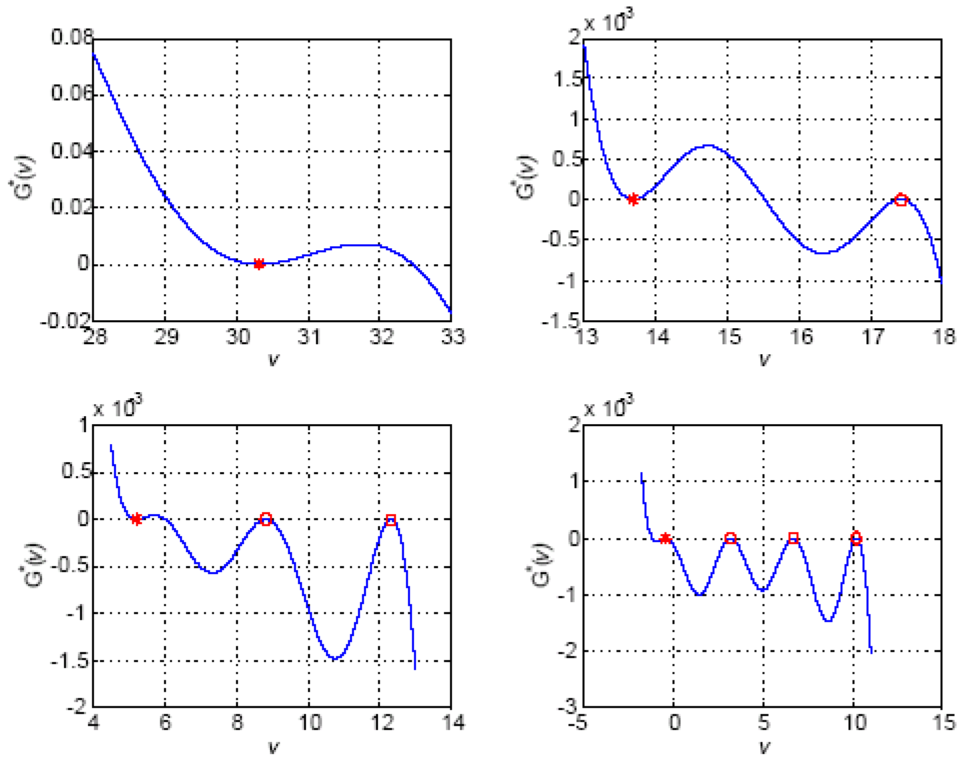


Evolutionary Stability

- Comes down to ESS, NIS and convergence stable
- Produces 8 combinations of which 6 are permissible
- An ESS that is NIS must be convergent stable
- A convergent stable minimum must be NIS
- **These are geeky but useful results!**

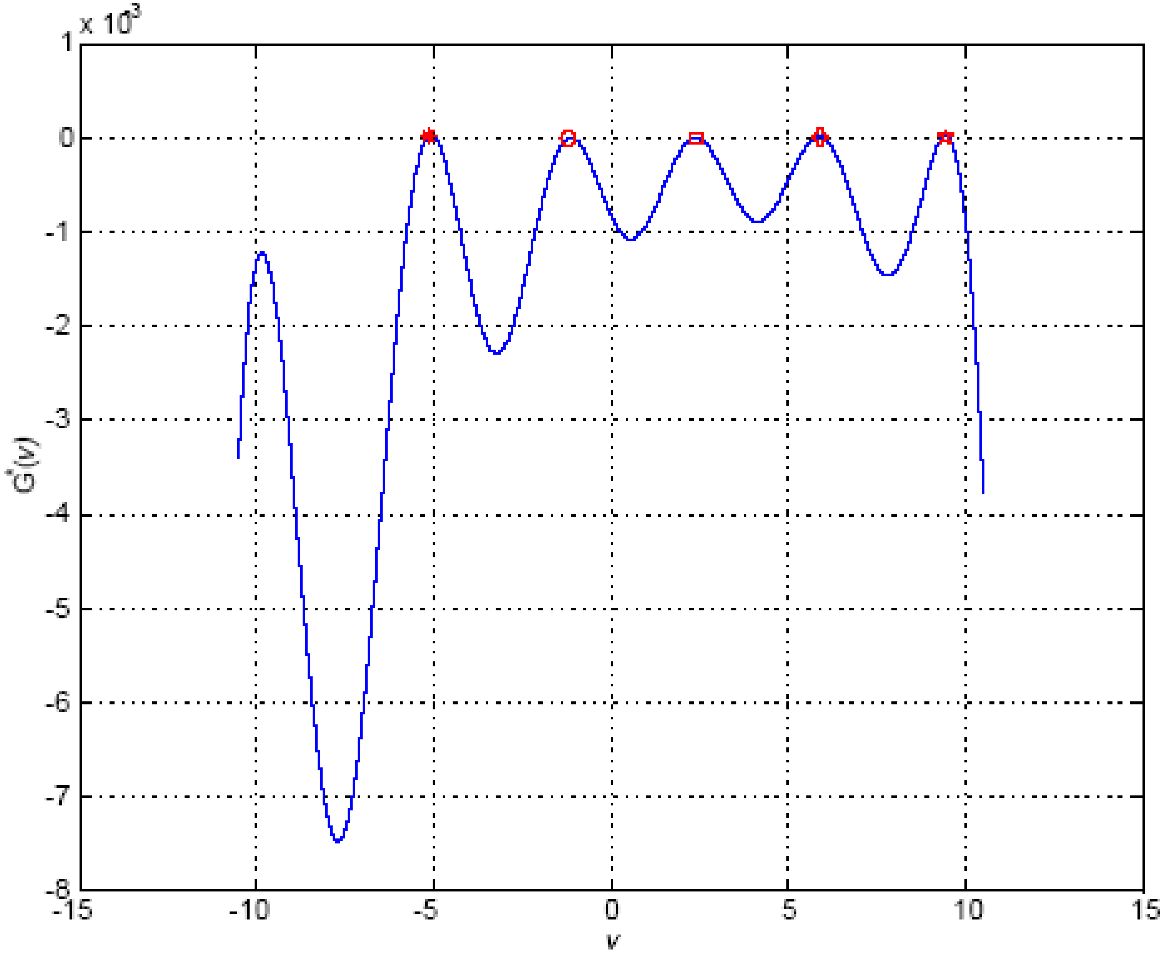
In search of my ESS

Adaptive Radiation by Adaptive Speciation



Convergent stable points for a 5 strategy ESS

The Darwinian Niches



The adaptive landscape for 5 species ESS

Most species most of the time are at or near their ESSs?

Nature is a dull subset of what is evolutionarily feasible and ecologically acceptable



We are the same G-function


My G-function is
different

Now for the predator’s G-function

Predator-Prey Model

$$\partial x_1/\partial t \quad = x_1 G_1 = x_1 r_1 (1 - x_1/K) - b x_2$$

$$\partial x_2/\partial t = x_2 G_2 = x_2 r_2 (1 - x_2/(c b x_1))$$

Prey's Fitness Generating Function

$$G_1(v,\mathbf{u},\mathbf{x}) = (r/K(v))[K(v)-\Sigma x_i \alpha(v,u_i)] - \Sigma x_j b(v,u_j)]$$

Where

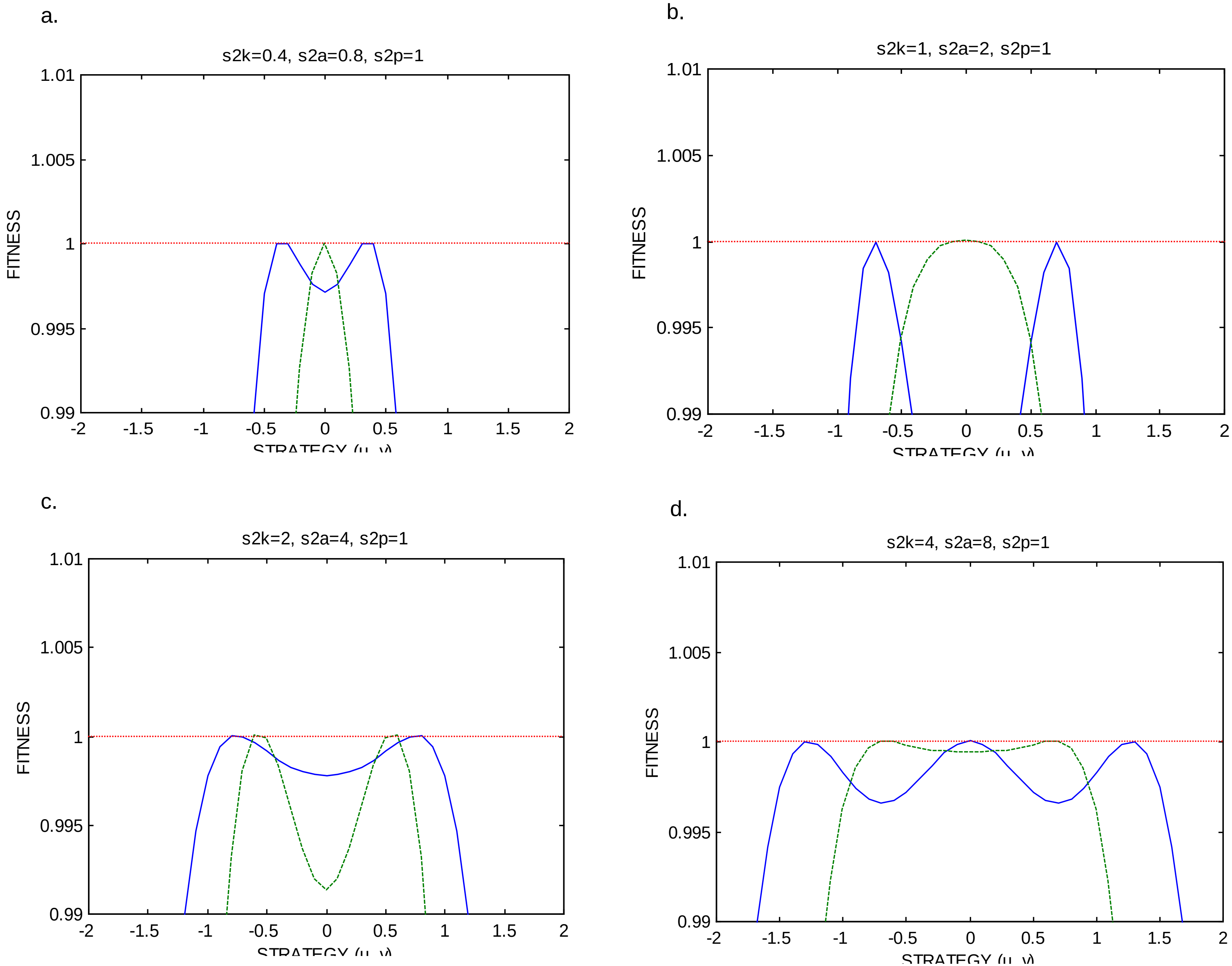
$$b(v,u_j) = b_{max}\exp[-(v-u_j)^2 / \sigma^2_b]$$

Predator's G-function

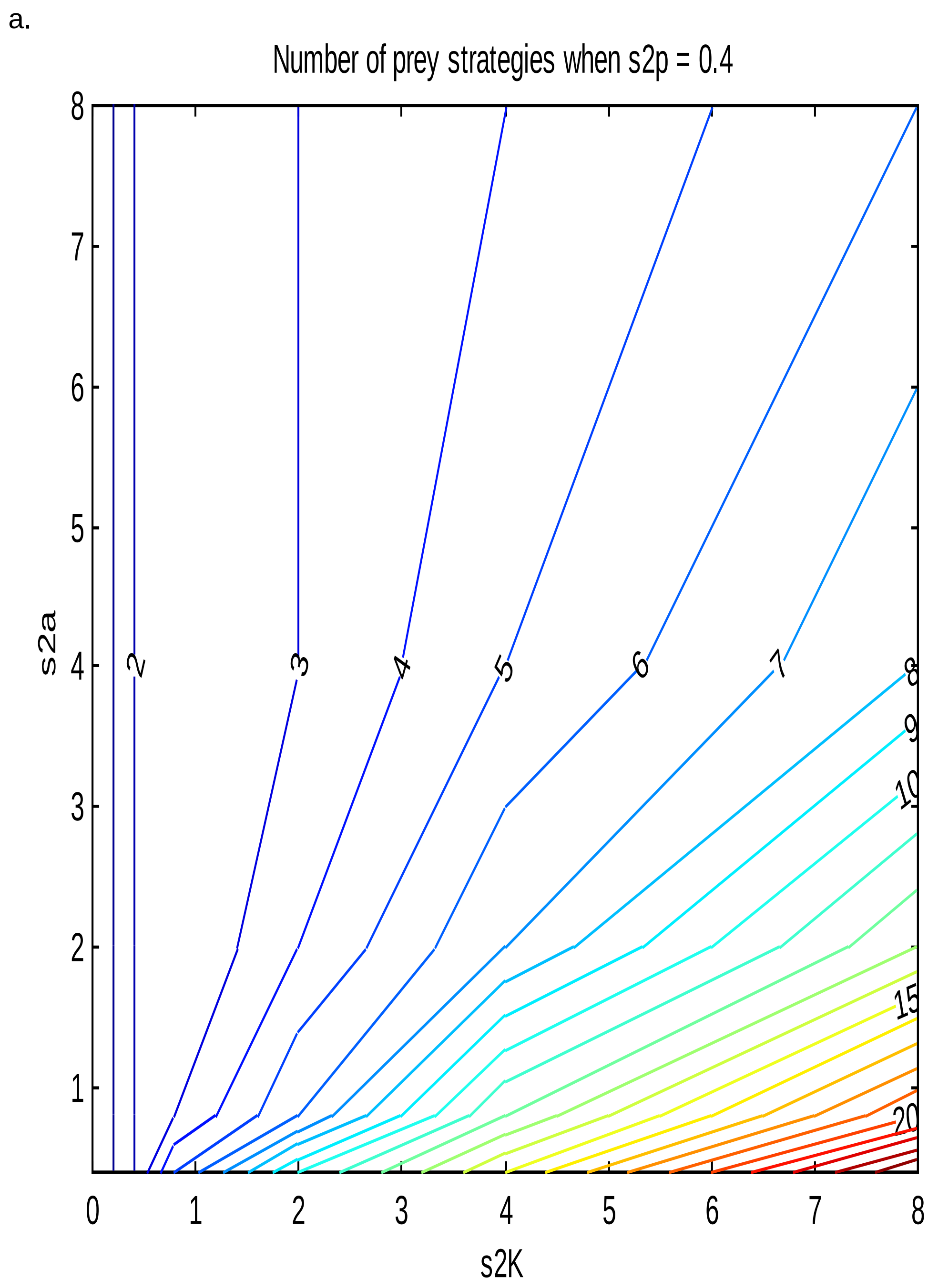
$$G_2(v,\mathbf{u},\mathbf{x}) = r_j[1 - \Sigma x_j/(c\ \Sigma x_i b(v,u_j))]$$

Where

$$b(v,u_i) = b_{\mathrm{max}}\mathrm{exp}[-(v - u_i)^2 / \sigma^2_{\mathrm{b}}]$$

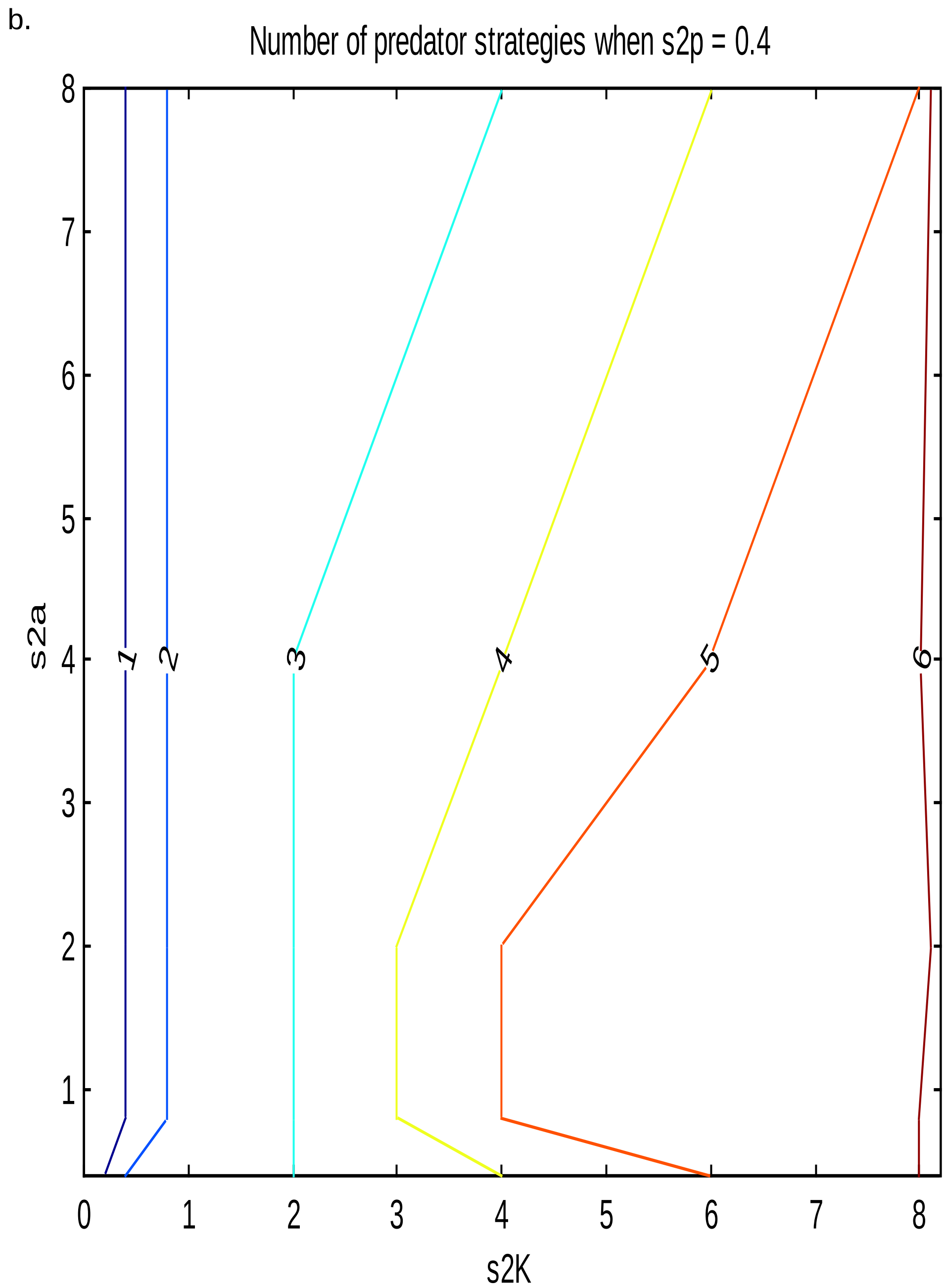


More Darwinian Niches



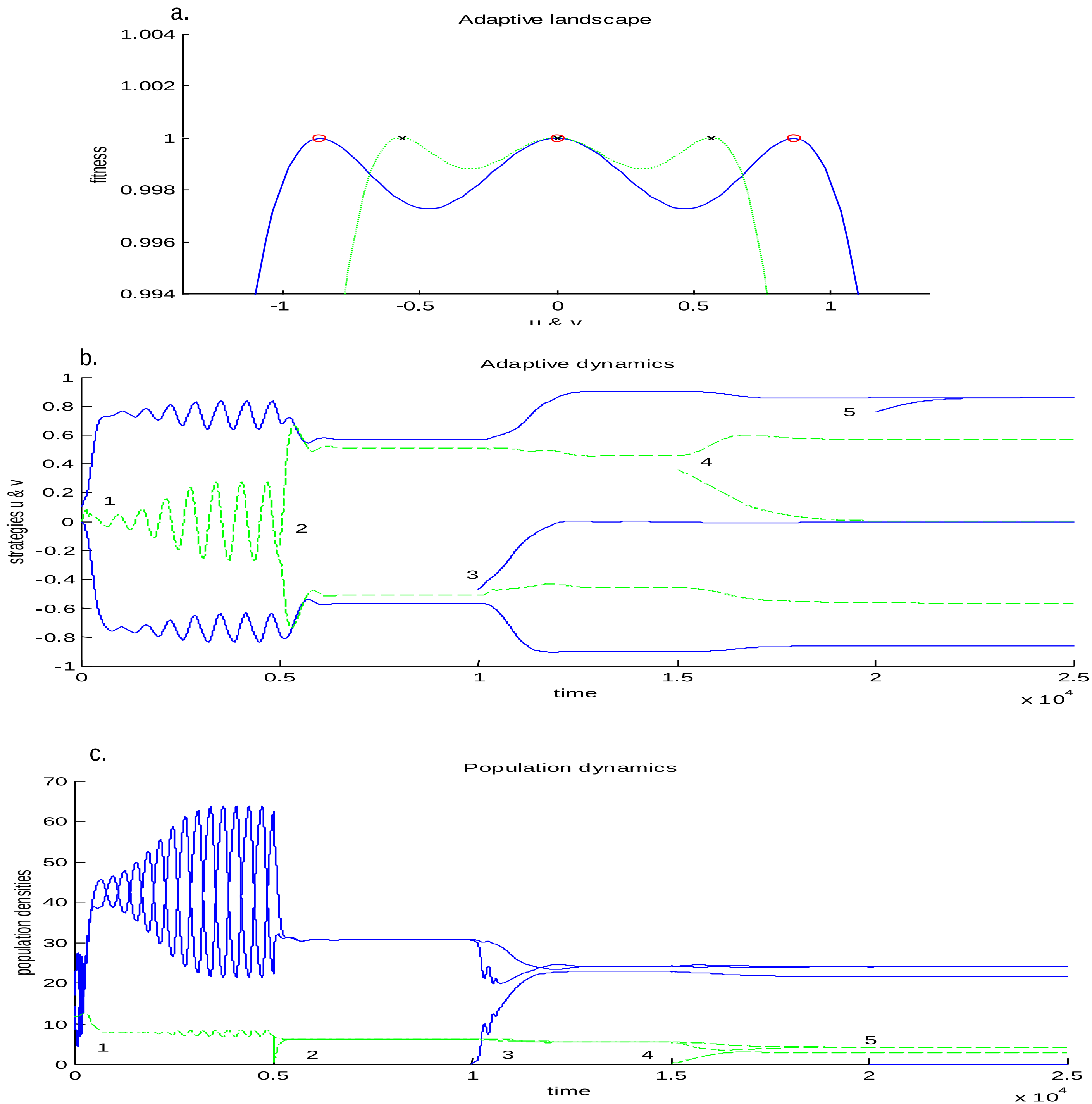
Lines of equal Biodiversity for the prey

y-axis is σ^2_K
x-axis is σ^2_a



Lines of equal Biodiversity for the predator

y-axis is σ^2_K
x-axis is σ^2_a


a.
Adaptive landscape
fitness
1.004
1.002
1
0.998
0.996
0.994
-1
-0.5
0
0.5
1
b.
Adaptive dynamics
strategies u & v
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1
0
0.5
1
1.5
2
2.5
time
x 10^4
1
2
3
4
5
c.
Population dynamics
population densities
70
60
50
40
30
20
10
0
0
0.5
1
1.5
2
2.5
time
x 10^4
1
2
3
4
5

Nature is the Product of Natural Selection
Natural Selection is a Game