Topics in evolutionary dynamics

Lecture 2: Phenotypic models

François Massol

3rd summer school on Mathematical Biology

São Paulo, February 2014

Lecture outline

1. Phenotypic vs. genotypic models
2. Game theory
3. Adaptive dynamics
4. Quantitative genetics

PHENOTYPIC VS. GENOTYPIC MODELS

Phenotypic vs. genotypic models

Genotype

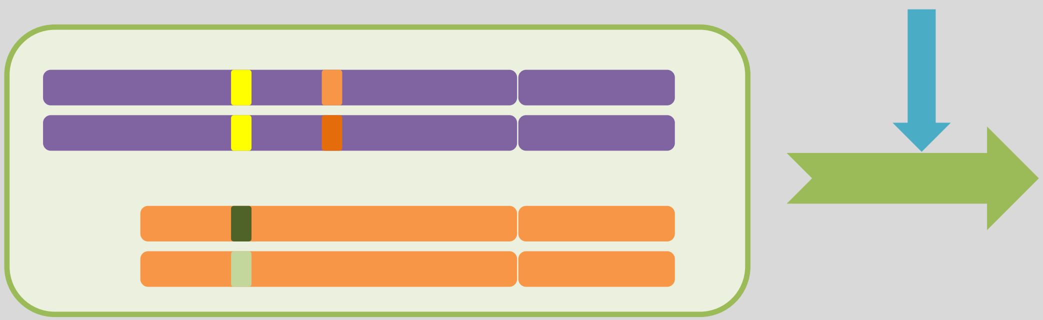
Environment

Phenotype
= value of one (or more) traits

Phenotypic vs. genotypic models

Genotype

Environment



Phenotype
= value of one (or more) traits

Different alleles (two per gene in diploids), → dominance ?

at different loci, → recombination ?

in interaction → epistasis ?

Phenotypic vs. genotypic models

"The **phenotypic gambit** is to examine the evolutionary basis of a character as if the very simplest genetic system controlled it: as if there were a haploid locus at which each distinct strategy was represented by a distinct allele, as if the payoff rule gave the number of offspring for each allele, and as if enough mutation occurred to allow each strategy the chance to invade."

A. Grafen, *in* Krebs & Davies 1984

Phenotypic vs. genotypic models

Phenotypic gambit in simpler words

1. Remove issues linked to genetic architecture
2. Remove issues linked to ploidy and dominance
3. No constraint on available mutations
4. Perfect inheritance

Phenotypic vs. genotypic models

Phenotypic gambit in simpler words

1. Remove issues linked to genetic architecture
2. Remove issues linked to ploidy and dominance
3. No constraint on available mutations
4. Perfect inheritance

If a model based on these (simplistic) assumptions explains some patterns, then we need not invoke genetic architecture, ploidy, mutation, etc. effects

Phenotypic vs. genotypic models

When to question phenotypic models? examples

1. The studied trait is linked to the mating system
2. The studied trait affects meiosis, recombination, etc.
3. The studied trait affects the dynamics of deleterious allele fixation

…

GAME THEORY

Game theory

Assumptions

- ✓ common rules for a given game
- ✓ players = rational

Definitions

- ✓ strategy = set of *a priori* decisions
- ✓ payoff = measure of player's success

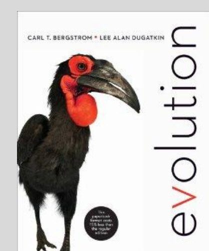
Goal of the game: maximize expected payoff

Game theory

Classic games: prisoner’s dilemma

		Suspect 2	
		Cooperate (refuse to testify)	**Defect (testify)**
Suspect 1	**Cooperate (refuse to testify)**	R = 1 year in jail / R = 1 year in jail	S = 5 years in jail / T = 0 years in jail
	Defect (testify)	T = 0 years in jail / S = 5 years in jail	P = 3 years in jail / P = 3 years in jail

Evolution, 1/e Figure 18.7



Classic games: prisoner's dilemma

Payoff matrix

$$\mathbf{W} = \begin{pmatrix} -1 & -5 \\ 0 & -3 \end{pmatrix}$$

Game theory

Classic games: prisoner's dilemma

Payoff matrix

$$\mathbf{W} = \begin{pmatrix} -1 & -5 \\ 0 & -3 \end{pmatrix}$$

$$w_{CC} = -1 \quad w_{CD} = -5$$

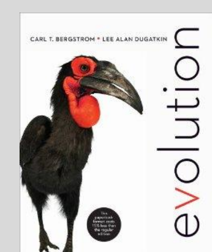
$$w_{DC} = 0 \quad w_{DD} = -3$$

Game theory

Classic games: hawks vs. doves

		Player 2: Hawk	Player 2: Dove
Player 1	Hawk	$\frac{v-c}{2}$, $\frac{v-c}{2}$	v, 0
	Dove	0, v	$\frac{v}{2}$, $\frac{v}{2}$

Evolution, 1/e Figure 18.13



Game theory

Classic games: hawks vs. doves

Payoff matrix

$$\mathbf{W} = \begin{pmatrix} (v-c)/2 & v \\ 0 & v/2 \end{pmatrix}$$

Classic games: hawks vs. doves

Payoff matrix

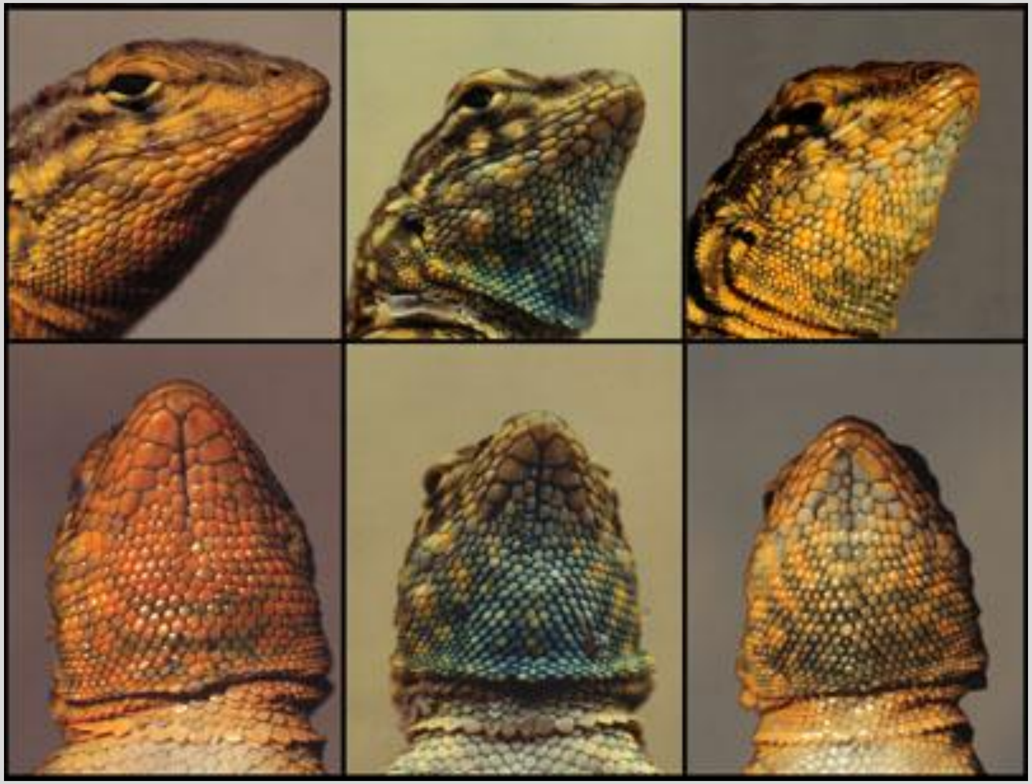
$$\mathbf{W} = \begin{pmatrix} (v-c)/2 & v \\ 0 & v/2 \end{pmatrix}$$

$$w_{HH} = \frac{v-c}{2} \qquad w_{HD} = v$$

$$w_{DH} = 0 \qquad w_{DD} = \frac{v}{2}$$

Game theory

Orange males: large territories, harems

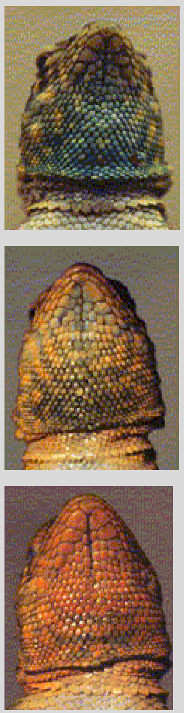


Yellow males: no territory, sneakers

Blue males: small-sized easily defended territories, one female

Sinervo & Lively 1996

Game theory



$$\begin{pmatrix} -\varepsilon & 1 & -1 \\ -1 & -\varepsilon & 1 \\ 1 & -1 & -\varepsilon \end{pmatrix}$$

Sinervo & Lively 1996

Game theory

Evolutionary stability

A strategy = evolutionarily stable strategy (ESS) iff not beatable by other strategies

$$\forall y \neq x, w_{yx} < w_{xx}$$

In practice: diagonal element higher than all other elements of the same column in the payoff matrix

Classic games: prisoner’s dilemma

Payoff matrix

$$\mathbf{W} = \begin{pmatrix} -1 & -5 \\ 0 & -3 \end{pmatrix}$$

Defecting is an ESS

Game theory

Classic games: hawks vs. doves

Payoff matrix

$$\mathbf{W} = \begin{pmatrix} (v-c)/2 & v \\ 0 & v/2 \end{pmatrix}$$

If $v > c$, hawks are ESS

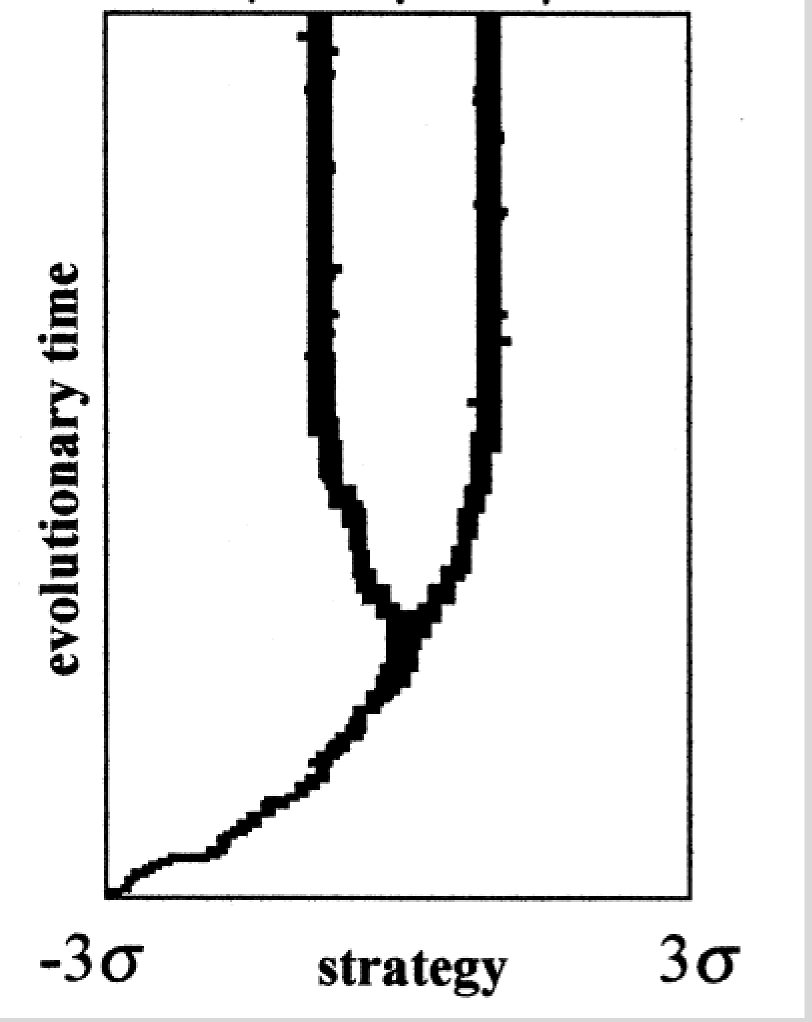
Else, no ESS

Game theory

Mixed strategies = combine different strategies with probabilities

Bishop-Cannings theorem

A mixed strategy is ESS implies that all its component strategies have the same payoff against the mixed strategy



ADAPTIVE DYNAMICS

Geritz et al. 1998 *Evol. Ecol.*

Adaptive dynamics

An extension of game theory to continuous trait values (≠ discrete in GT)

Assumptions:

✓ clonal reproduction

✓ rare mutations

✓ mutations of small effect

✓ resident at demographic equilibrium

✓ initially scarce mutant

Adaptive dynamics recipe

1. From a demographic model

$$\underbrace{\frac{\partial n}{\partial t}}_{\text{Increase in density of individuals with trait } y}(y,t) = rn(y,t)\left(1 - \frac{\overbrace{\int C(z,y)}^{\text{Interference competition between traits } z \text{ and } y}n(z,t)\,dz}{\underbrace{K(y)}_{\text{Carrying capacity for trait } y}}\right)$$

Dieckmann & Doebeli 1999

Adaptive dynamics recipe

1. From a demographic model

$$\frac{\partial n}{\partial t}(y,t) = rn(y,t)\left(1-\frac{\int C(z,y)n(z,t)dz}{K(y)}\right)$$

2. Find invasion criterion

Mutant trait Resident trait

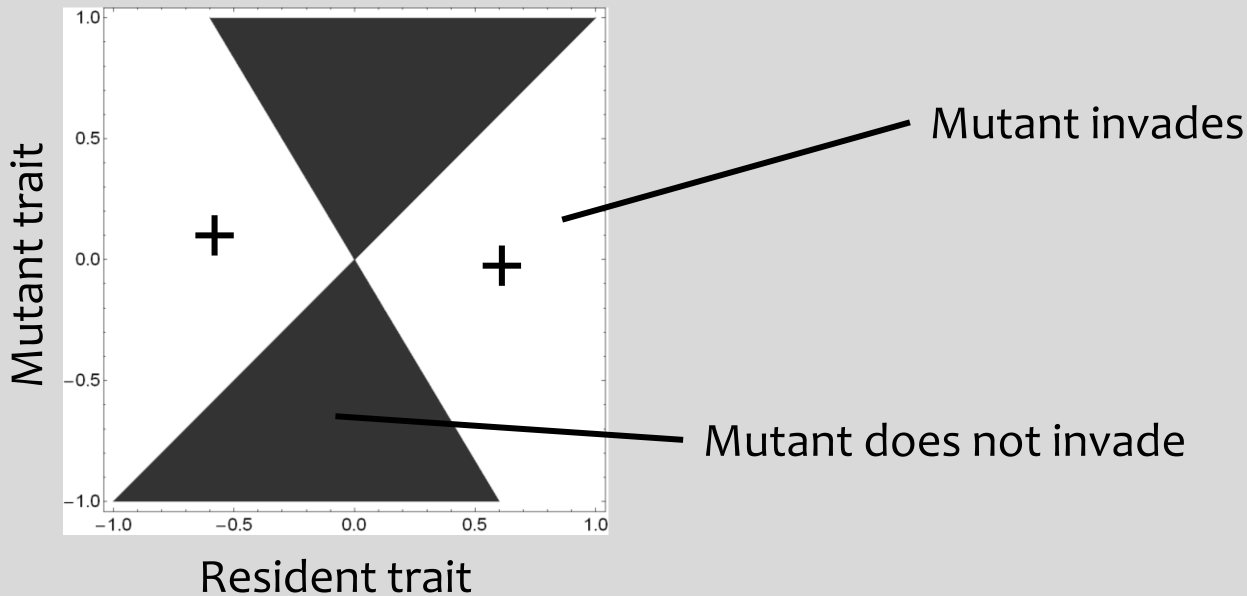
$$\underbrace{w(y,z)}_{\text{Rare mutant fitness}} = \frac{1}{n}\frac{\partial n}{\partial t}(y,t) = r\underbrace{\left(1-\frac{C(z,y)K(z)}{K(y)}\right)}_{\text{Assume } y \text{ does not exist in the whole population}}$$

Adaptive dynamics recipe

2. Find invasion criterion

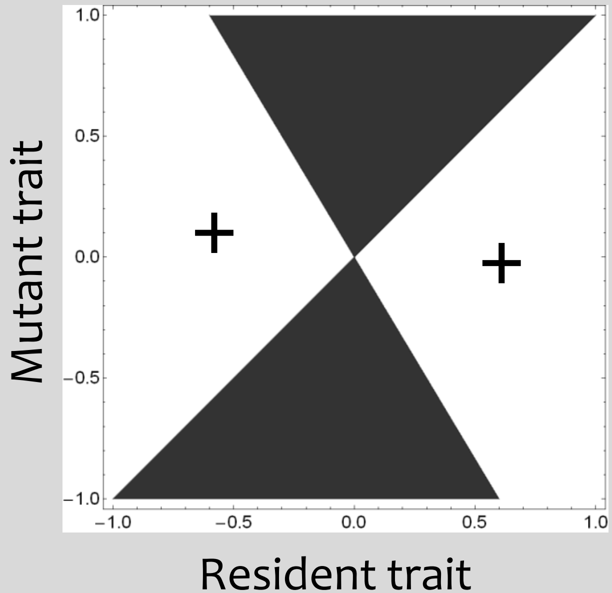
$$w(y,z) = \frac{1}{n}\frac{\partial n}{\partial t}(y,t) = r\left(1 - \frac{C(z,y)K(z)}{K(y)}\right)$$

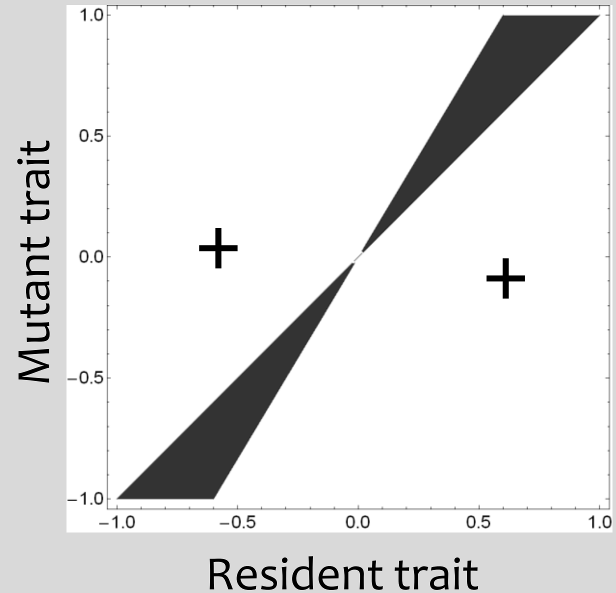
3. Look at the pairwise invasibility plot (PIP)



Adaptive dynamics recipe

3. Look at the pairwise invasibility plot (PIP)





4. Compute the selection gradient
5. Find singular strategies (where the gradient vanishes)
6. Assess stability properties

Adaptive dynamics recipe

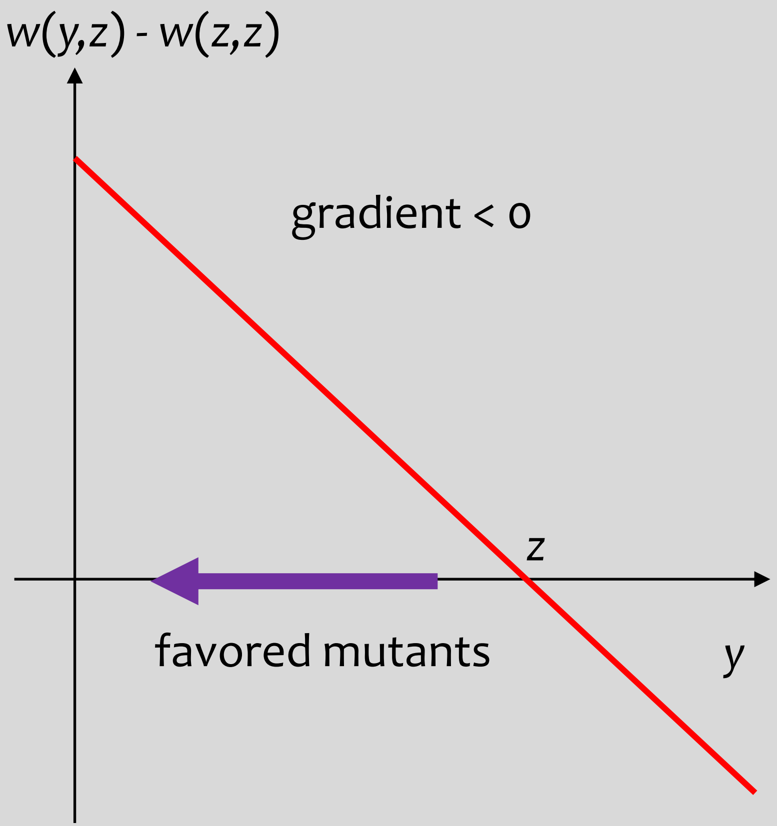
4. Compute the selection gradient

$$\underbrace{w(y,z)}_{\text{Fitness of a rare mutant}} \approx w(z,z) + (y-z)\underbrace{\partial_y w(z,z)}_{\text{Selection gradient}}$$

Adaptive dynamics recipe

4. Compute the selection gradient

$$w(y,z) \approx w(z,z) + (y-z)\partial_y w(z,z)$$



Adaptive dynamics recipe

4. Compute the selection gradient

$$w(y,z) \approx w(z,z) + (y-z)\partial_y w(z,z)$$

5. Find singular strategies

Equilibrium $\quad \partial_y w(z,z) = 0$

Adaptive dynamics recipe

4. Compute the selection gradient

$$w(y,z) \approx w(z,z) + \left(y - z\right)\partial_y w(z,z)$$

5. Find singular strategies

Equilibrium $\quad \partial_y w(z,z) = 0$

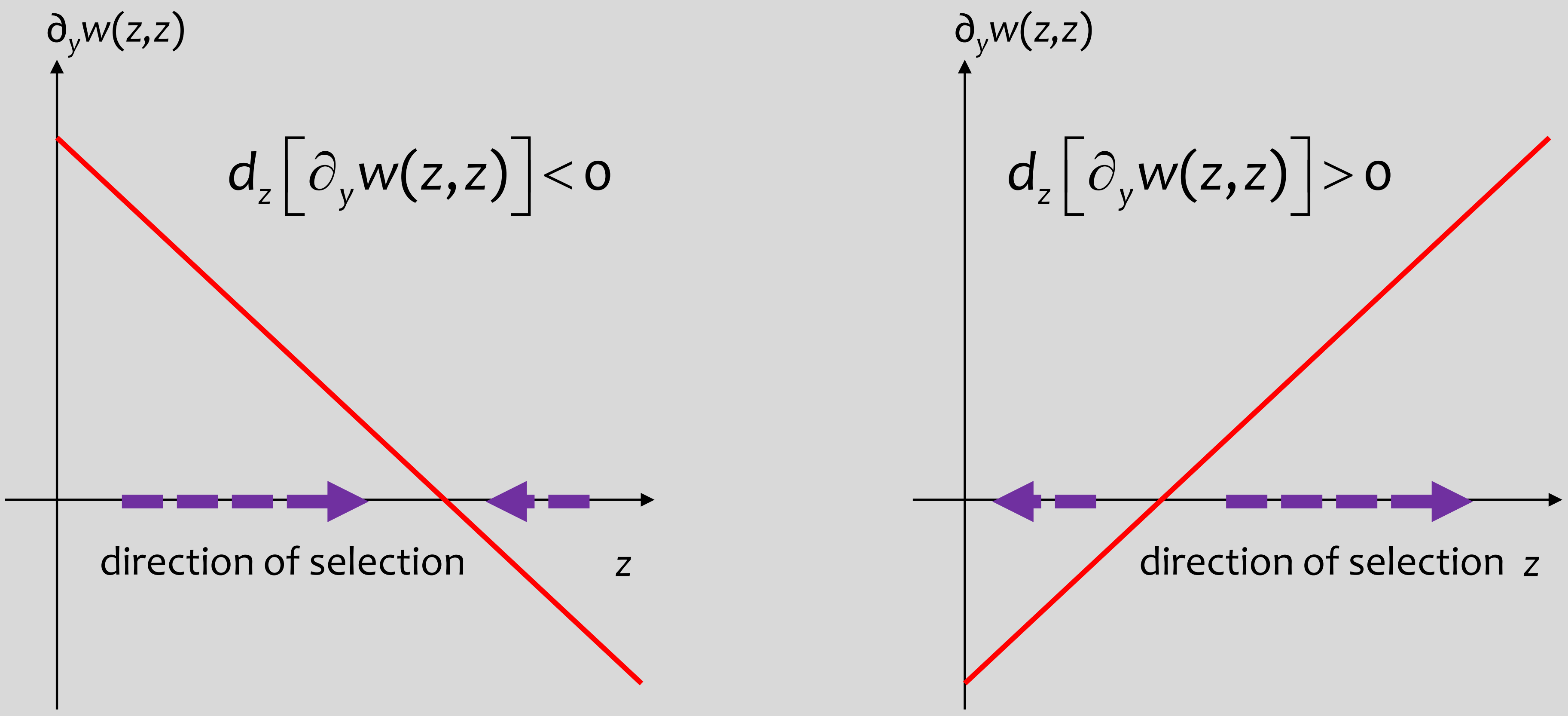
6. Assess stability properties

Convergence stable? $\quad d_z\left[\partial_y w(z,z)\right] < 0$

Adaptive dynamics recipe

6. Assess stability properties

Convergence stable? $d_z\left[\partial_y w(z,z)\right] < 0$



Adaptive dynamics recipe

6. Assess stability properties

Evolutionarily stable?

$$w(y,z) \approx w(z,z) + (y-z)\partial_y w(z,z) + \frac{1}{2}(y-z)^2 \underbrace{\partial_{y,y} w(z,z)}$$

Hessian / second-order derivative =
What happens next, once equilibrium is reached

Adaptive dynamics recipe

6. Assess stability properties

$\partial_{y,y} w(z,z) < 0$ = ESS

Evolutionarily stable?

$\partial_{y,y} w(z,z) > 0$ = branching

$$w(y,z) \approx w(z,z) + (y-z)\partial_y w(z,z) + \frac{1}{2}(y-z)^2 \underbrace{\partial_{y,y} w(z,z)}$$

Hessian / second-order derivative =
What happens next, once equilibrium is reached

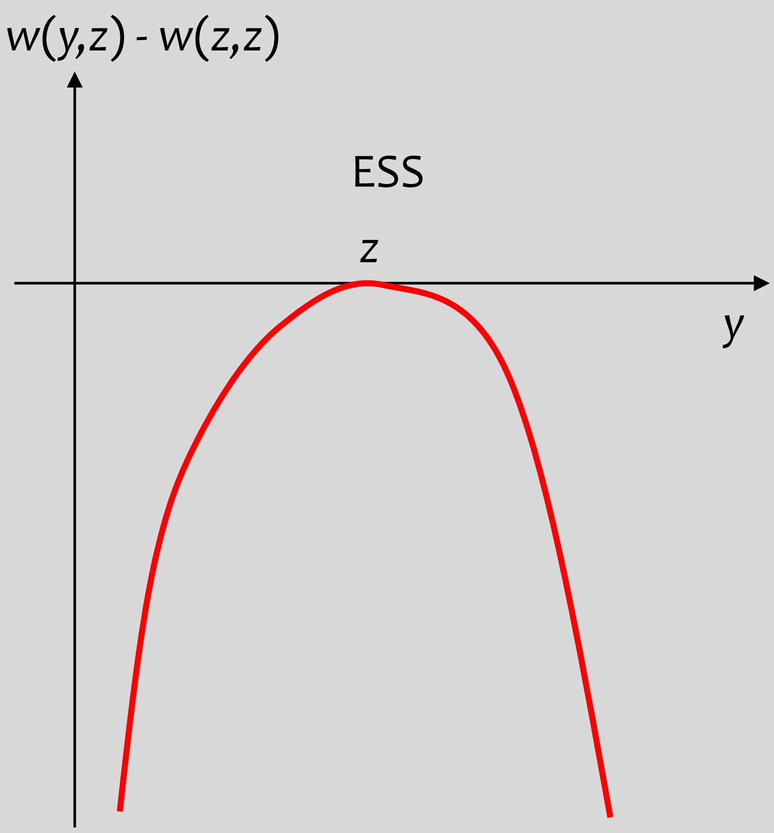
Adaptive dynamics recipe

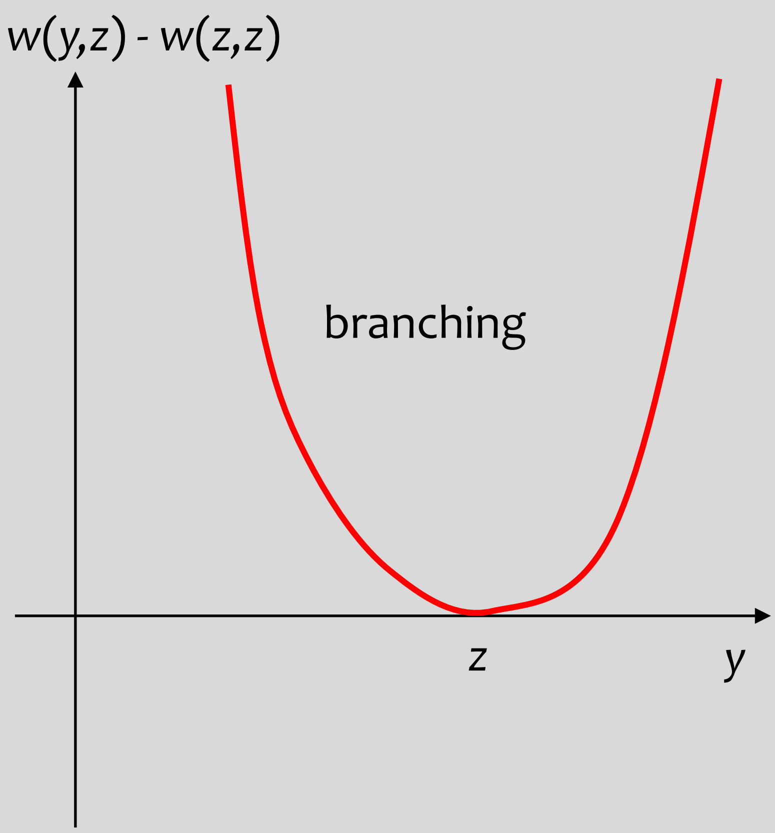
6. Assess stability properties

Evolutionarily stable?

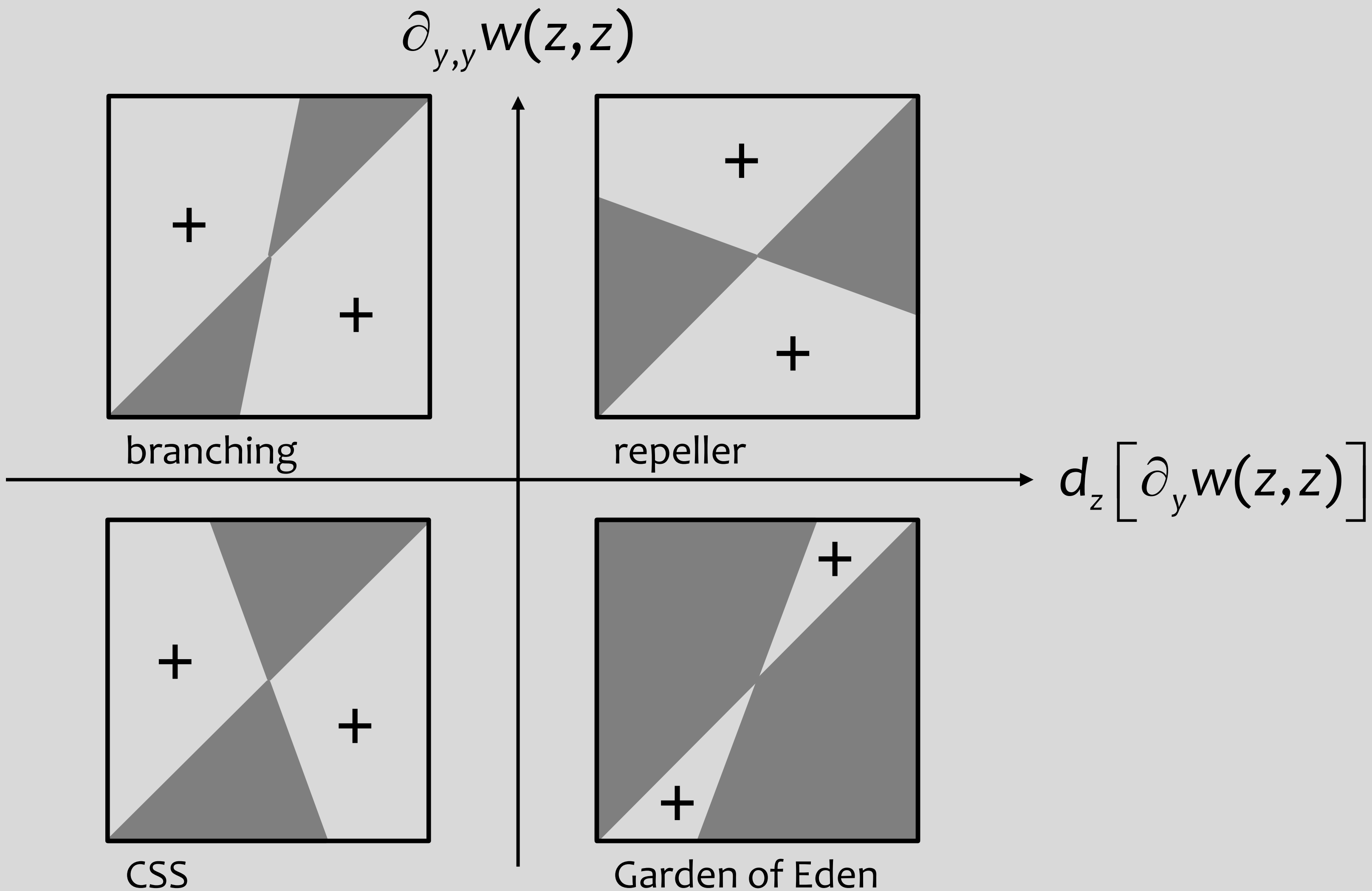
$\partial_{y,y} w(z,z) < 0$ = ESS

$\partial_{y,y} w(z,z) > 0$ = branching





Adaptive dynamics



QUANTITATIVE GENETICS

Quantitative genetics

In adaptive dynamics

Speed of trait evolution $\propto$ selection gradient

Quantitative genetics

In adaptive dynamics

Speed of trait evolution $\propto$ selection gradient

What is the proportionality factor?

Quantitative genetics

$$\frac{dn_i}{dt} = r_i(z_i)n_i \quad \Longrightarrow \quad \frac{d\bar{z}}{dt} = \mathrm{Cov}[r, z]$$

Quantitative genetics

$$\frac{dn_i}{dt} = r_i n_i$$

$$\frac{dn}{dt} = \sum_i \frac{dn_i}{dt} = \sum_i r_i n_i = \bar{r} n$$

Quantitative genetics

$$\frac{dn_i}{dt} = r_i n_i$$

$$\frac{dn}{dt} = \sum_i \frac{dn_i}{dt} = \sum_i r_i n_i = \bar{r} n$$

$$\frac{d}{dt}\left[n_i z_i\right] = z_i \frac{dn_i}{dt} = r_i z_i n_i$$

Quantitative genetics

$$\frac{dn_i}{dt} = r_i n_i$$

$$\frac{dn}{dt} = \sum_i \frac{dn_i}{dt} = \sum_i r_i n_i = \bar{r} n$$

$$\frac{d}{dt}\left[n_i z_i\right] = z_i \frac{dn_i}{dt} = r_i z_i n_i$$

$$n\frac{d\bar{z}}{dt} + \bar{z}\frac{dn}{dt} = \sum_i z_i \frac{dn_i}{dt} = \sum_i r_i z_i n_i = \overline{rz} n$$

Quantitative genetics

$$\frac{dn_i}{dt} = r_i n_i$$

$$\frac{dn}{dt} = \sum_i \frac{dn_i}{dt} = \sum_i r_i n_i = \bar{r} n$$

$$\frac{d}{dt}\left[n_i z_i\right] = z_i \frac{dn_i}{dt} = r_i z_i n_i$$

$$n\frac{d\bar{z}}{dt} + \bar{z}\frac{dn}{dt} = \sum_i z_i \frac{dn_i}{dt} = \sum_i r_i z_i n_i = \overline{rz} n$$

$$\frac{d\bar{z}}{dt} = \overline{rz} - \frac{\bar{z}}{n}\frac{dn}{dt} = \mathrm{Cov}\left[r, z\right]$$

Quantitative genetics

Price equation (in continuous time)

$$\frac{d\bar{z}}{dt} = \mathrm{Cov}[r, z]$$

Quantitative genetics

Price equation (in continuous time)

$$\frac{d\bar{z}}{dt} = \mathrm{Cov}\left[r, z\right]$$

Take *r* as trait (Fisher's fundamental theorem)

$$\frac{d\bar{r}}{dt} = \mathrm{Var}\left[r\right]$$

Quantitative genetics

Approximation by the selection gradient

$$\frac{d\bar{z}}{dt} \approx \underbrace{\frac{\partial r}{\partial z}}_{\text{Selection gradient}} . \underbrace{\mathrm{Var}[z]}_{\text{Genetic variance in trait values}}$$

Quantitative genetics

The effect of environmental noise

$$x_{ij} = z_i + e_{ij}$$

Expressed phenotype of individual *j* from strain *j*: x_{ij}

Genotypic effect: z_i

Environmental effect: e_{ij} (Gaussian noise)

Quantitative genetics

The effect of environmental noise

$$x_{ij} = z_i + e_{ij}$$

observed

determines trait dynamics

Expressed phenotype of individual *j* from strain *j*: x_{ij}

Genotypic effect: z_i

Environmental effect: e_{ij} (Gaussian noise)

Quantitative genetics

The breeder's equation

$$x = z + e$$

$$\hat{z} = \frac{Cov(z,x)}{Var(x)} x = \frac{G_z}{P_z} x$$

With uncorrelated environmental noise

Quantitative genetics

The breeder's equation

$$x = z + e$$

$$\hat{z} = \frac{Cov(z,x)}{Var(x)}x = \frac{G_z}{P_z}x$$

With uncorrelated environmental noise

$$R = h^2 S$$

$$S / P_z = \beta$$

$$R = \overline{x_{t+1}} - \overline{x_t}$$
$$= \overline{z_{t+1}} - \overline{z_t}$$

$$h^2 = \frac{G_z}{P_z} \quad S = Cov(w, x)$$

Quantitative genetics

Two main ideas from quantitative genetics (often mixed up):

- Response to selection depends on genetic variance (Price equation)

- What is selected is genotype; what is observed is phenotype, thus the emergence of h^2 in response to selection

Pros & cons

	Pros	Cons
Game theory	▪ handles dynamics of multiple strategies ▪ simple and testable	▪ no strategy dynamics due to mutation ▪ no explicit env. feedback
Adaptive dynamics	▪ explicit env. feedback ▪ criterion for branching	▪ no standing variance ▪ poorly modeled mutation ▪ over-interpretation of branching
Quantitative genetics	▪ deals with the distribution of trait values ▪ readily testable predictions	▪what to do about the evolution of trait moments of order > 1? ▪ no env. feedback at all

Thank you for your attention!

Further reading

Game theory

Akçay E. & Roughgarden J. (2010). The evolution of payoff matrices: providing incentives to cooperate. *Proc R Soc Lond B Biol Sci, 278.*

Bishop D.T. & Cannings C. (1976). Models of animal conflict. *Adv Appl Proba, 8, 616-621.*

Bishop D.T. & Cannings C. (1978). A generalized war of attrition. *J Theor Biol, 70, 85-124.*

Maynard Smith J. & Price G.R. (1973). The logic of animal conflict. *Nature, 246, 15-18.*

Nash Jr J.F. (1950). The bargaining problem. *Econometrica, 155-162.*

Nowak M. & Sigmund K. (1990). The evolution of stochastic strategies in the prisoner's dilemma. *Acta Appl Math, 20, 247-265.*

Nowak M.A. & Sigmund K. (2004). Evolutionary dynamics of biological games. *Science, 303, 793-799.*

Schuster P. & Sigmund K. (1983). Replicator dynamics. *J Theor Biol, 100, 533-538.*

Sinervo B. & Lively C.M. (1996). The rock-paper-scissors game and the evolution of alternative male strategies. *Nature, 380, 240-243.*

Further reading

Adaptive dynamics

Champagnat N. (2006). A microscopic interpretation for adaptive dynamics trait substitution sequence models. *Stochastic Processes and their Applications, 116, 1127-1160.*

Champagnat N., Ferrière R. & Ben Arous G. (2002). The canonical equation of adaptive dynamics: a mathematical view. *Selection, 2, 73-83.*

Dieckmann U. & Doebeli M. (1999). On the origin of species by sympatric speciation. *Nature, 400, 354-357.*

Dieckmann U. & Law R. (1996). The dynamical theory of coevolution: A derivation from stochastic ecological processes. *J Math Biol, 34, 579-612.*

Eshel I. (1983). Evolutionary and continuous stability. *J Theor Biol, 103, 99-111.*

Geritz S.A.H., Kisdi E., Meszena G. & Metz J.A.J. (1998). Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evol Ecol, 12, 35-57.*

Hofbauer J. & Sigmund K. (1990). Adaptive dynamics and evolutionary stability. *Appl Math Lett, 3, 75-79.*

Further reading

Quantitative genetics

Arnold S.J. (1992). Constraints on phenotypic evolution. *Am Nat, 140, S85-S107.*

Bulmer M.G. (1989). Maintenance of genetic variability by mutation–selection balance: a child's guide through the jungle. *Genome, 31, 761-767.*

Bürger R. & Lynch M. (1995). Evolution and extinction in a changing environment: a quantitative genetic analysis. *Evolution, 49, 151-163.*

Chevin L.-M. (2013). Genetic constraints on adaptation to a changing environment. *Evolution, 67, 708-721.*

Falconer D.S. & Mackay T.F.C. (1996). *Introduction to quantitative genetics. 4th edn.*

Frank S.A. (1995). George Price's contributions to evolutionary genetics. *J Theor Biol, 175, 373-388.*

Lande R. (1979). Quantitative genetic analysis of multivariate evolution, applied to brain: body size allometry. *Evolution, 33, 402-416.*

Lande R. (1980). The genetic covariance between characters maintained by pleiotropic mutations. *Genetics, 94, 203-215.*

Lynch M. & Walsh B. (1998). *Genetics and analysis of quantitative traits.* Sinauer (Sunderland, Mass.).

Slatkin M. (1980). Ecological character displacement. *Ecology, 61, 163-177.*

Turelli M. & Barton N.H. (1994). Genetic and statistical analyses of strong selection on polygenic traits: what, me normal? *Genetics, 138, 913-941.*