

One-dimensional dynamical systems, and selection at a single haploid locus

General solutions

- In simple cases, we can find a general solution to a dynamical system.
- For example, discrete exponential growth, $N(t+1) = R N(t)$ has the general solution $N(t) = R^t N(0)$
- continuous exponential growth $dN(t)/dt = r N(t)$ the general solution $N(t) = e^{rt} N(0)$
- and continuous logistic growth $dN/dt = r N(1 - N/K)$ the general solution

$$N(t) = \frac{K N(0) e^{rt}}{k + N(0)(e^{rt} - 1)}$$

Equilibria

- In most cases, obtaining a general solution is not possible.
- We can still learn a lot about the system by analyzing its equilibria and their stability.
- An equilibrium or fixed-point is defined by one of the following conditions:

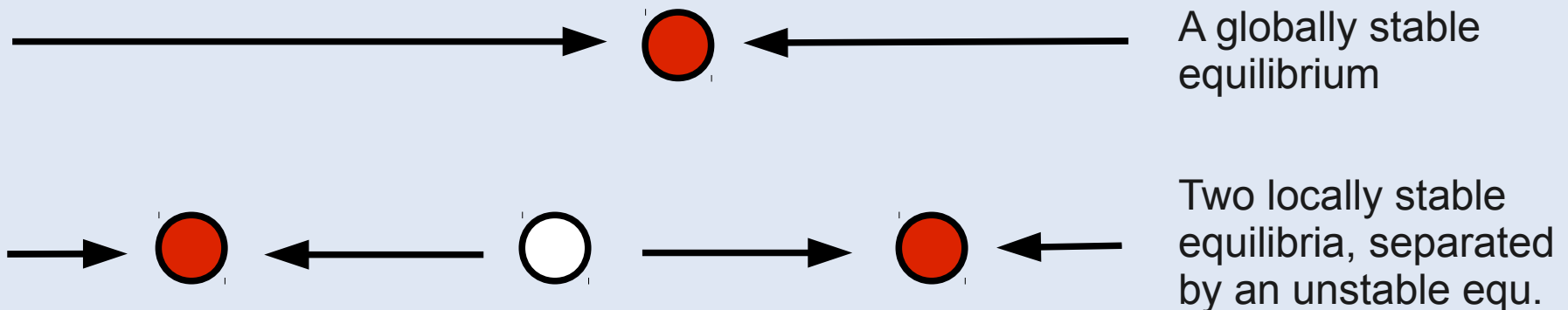
$$x(t+1) = x(t)$$

$$\Delta x = 0$$

$$dx/dt = 0$$

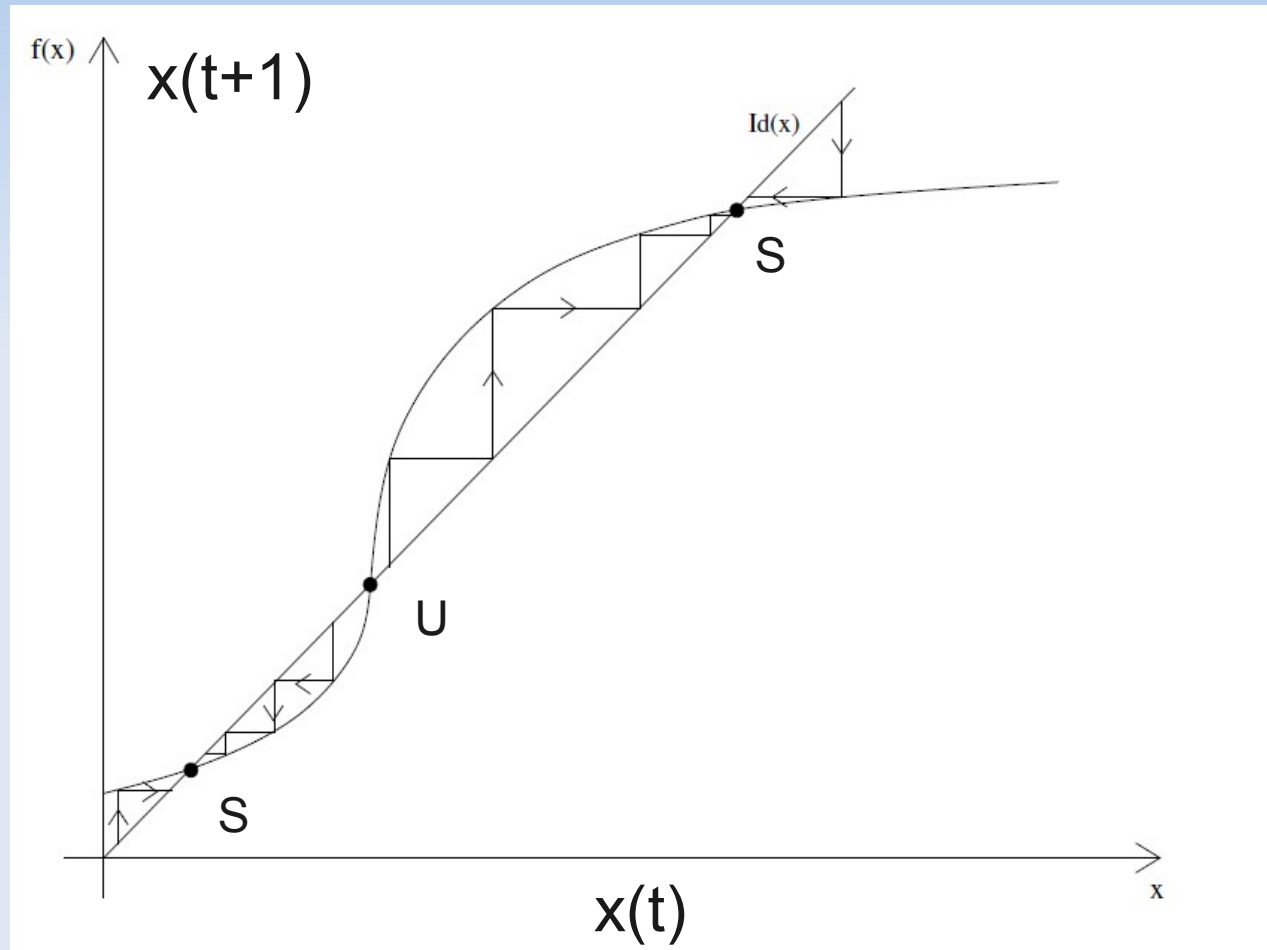
Stability

- An equilibrium is **locally stable** if a system near the equilibrium approaches it.
- An equilibrium is **globally stable** if a system approaches it from all initial conditions.
- An equilibrium is **unstable**, if a system near the equilibrium moves away from it.

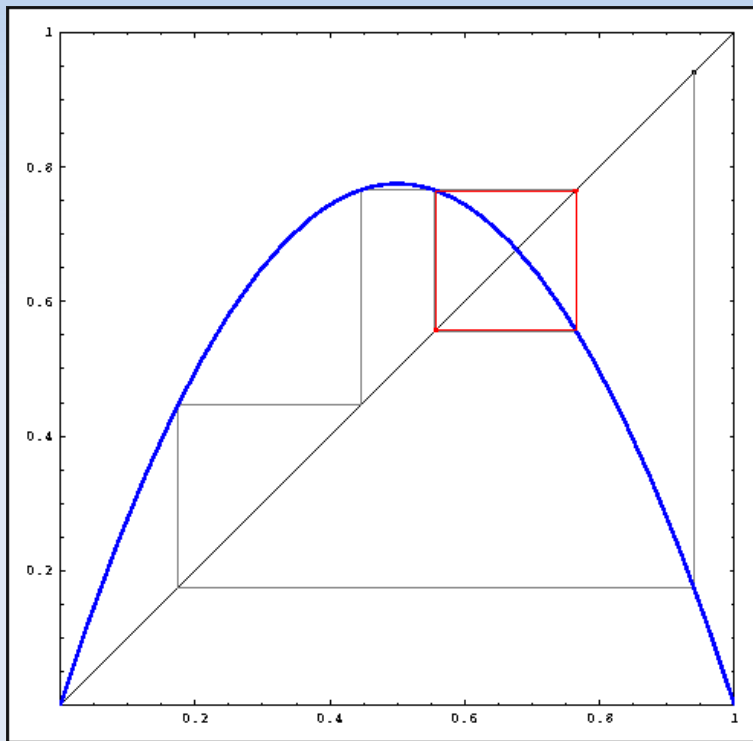


- The set of initial conditions leading to a particular equilibrium is called its **domain (or basin) of attraction**.

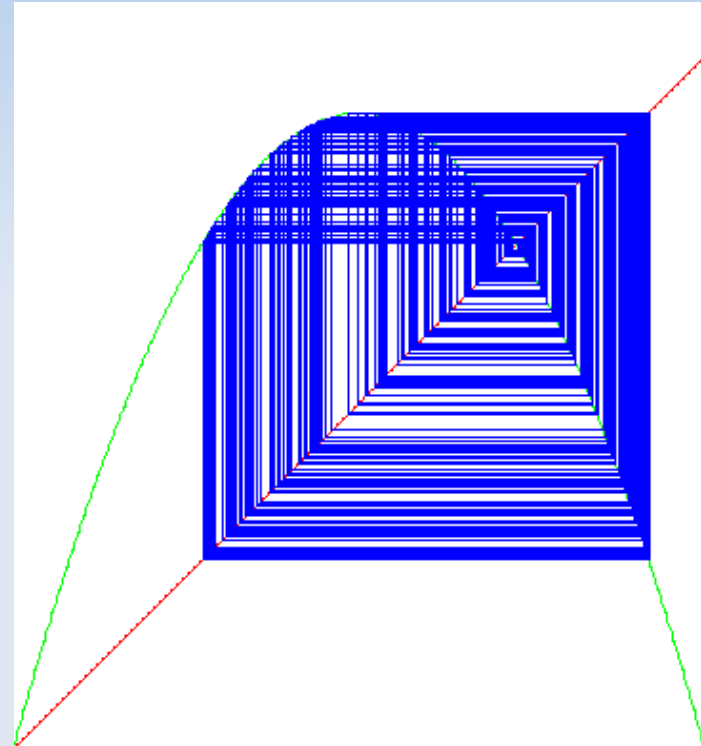
Cobwebbing



The logistic map revisited



Stable 2-cycle



Chaos

Check out http://en.wikipedia.org/wiki/Cobweb_plot for an animated plot.

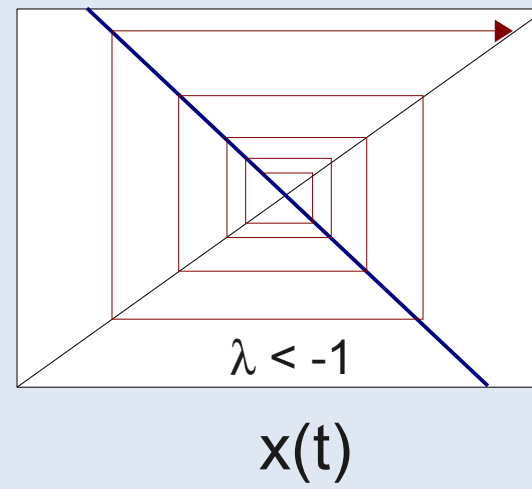
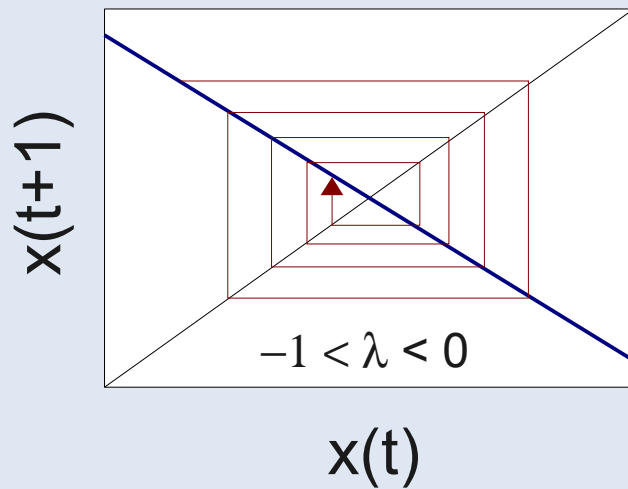
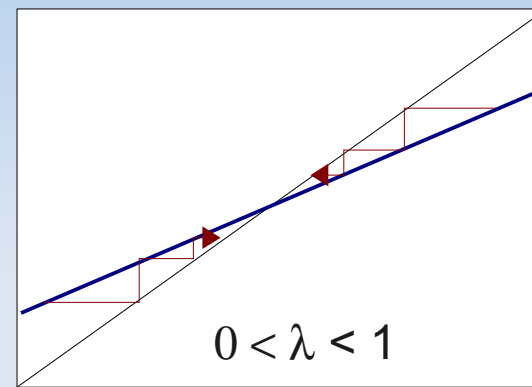
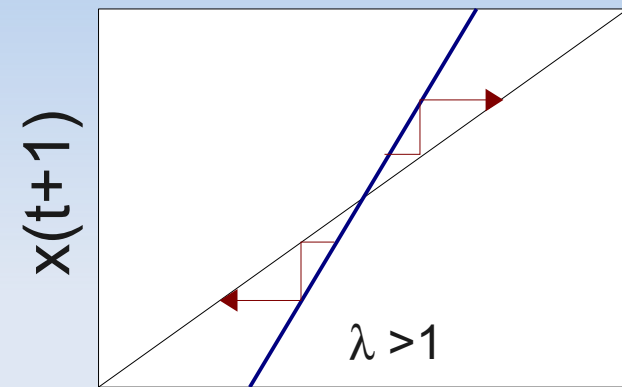
Local stability analysis

- Close to an equilibrium, we can approximate the function $x(t+1)$ by a straight line, that is, its tangent. (This is an example of a Taylor approximation.)
- Let λ be the slope of $x(t+1)$ at equilibrium.
- Then the dynamics of the difference from the equilibrium can be approximated by a linear system:

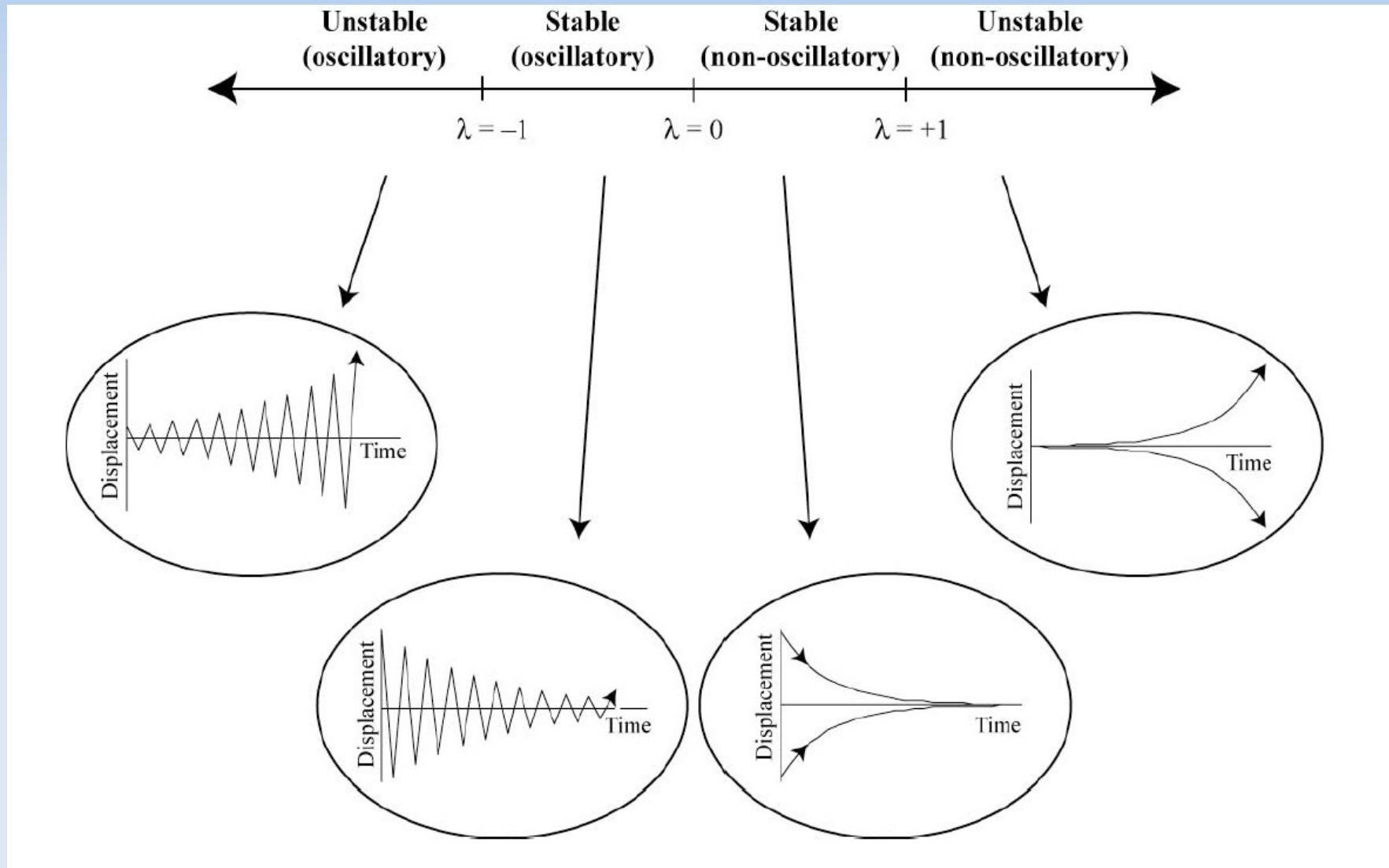
$$\begin{aligned}\epsilon(t+1) &\approx \lambda \epsilon(t) \\ \epsilon(t) &= \lambda^t \epsilon(0)\end{aligned}$$

- Thus, the equilibrium is approached if $|\lambda| < 1$.
- For negative λ , the approach is cyclic.

Local stability analysis

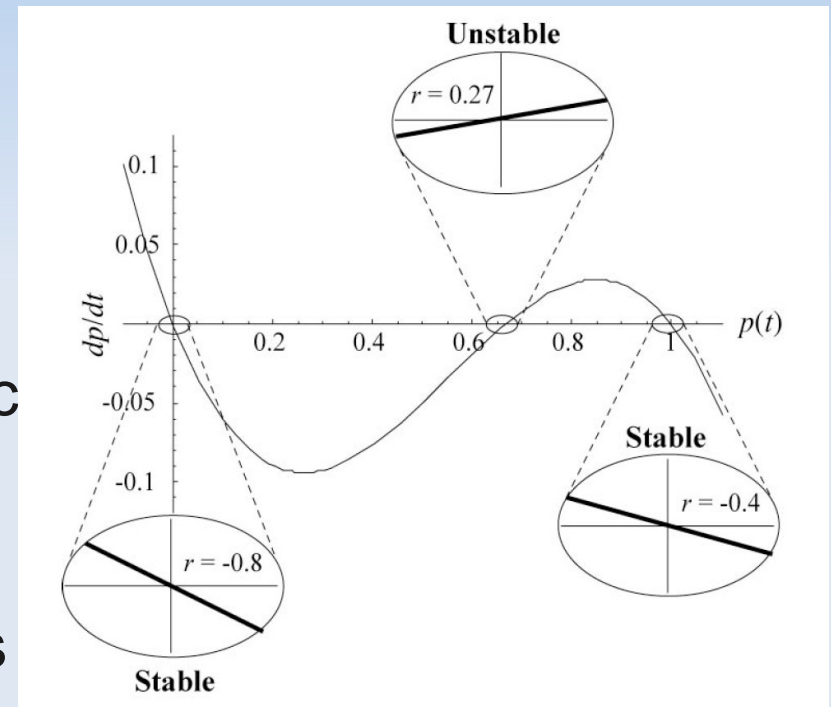


Local stability analysis



Local stability analysis in continuous time

- In continuous time, the equilibrium condition is $dx/dt = 0$.
- Let r be the slope of dx/dt at an equilibrium.
- The equilibrium is locally stable if $r < 0$, and unstable otherwise. Cyclic dynamics are not possible with only a single variable.
- Later, we will see how the principles of stability analysis (in both discrete and continuous time) can be generalized to systems with more than one variable.



Population genetics

- Population genetics is the study of **allele frequency distribution and change** under the influence of the four main evolutionary processes: natural selection, genetic drift, mutation and gene flow.
- Note that evolution is often defined as a change in allele frequencies.
- To model **selection**, we will assign fitness values to genotypes.
- **Fitness** can be defined as the expected contribution of a genotype to the next generation.
- We can distinguish **absolute fitness** (e.g., survival probability times life-time reproductive success) and **relative fitness** (absolute fitness divided by the population **mean fitness**). Evolutionary change always depends on relative fitness.

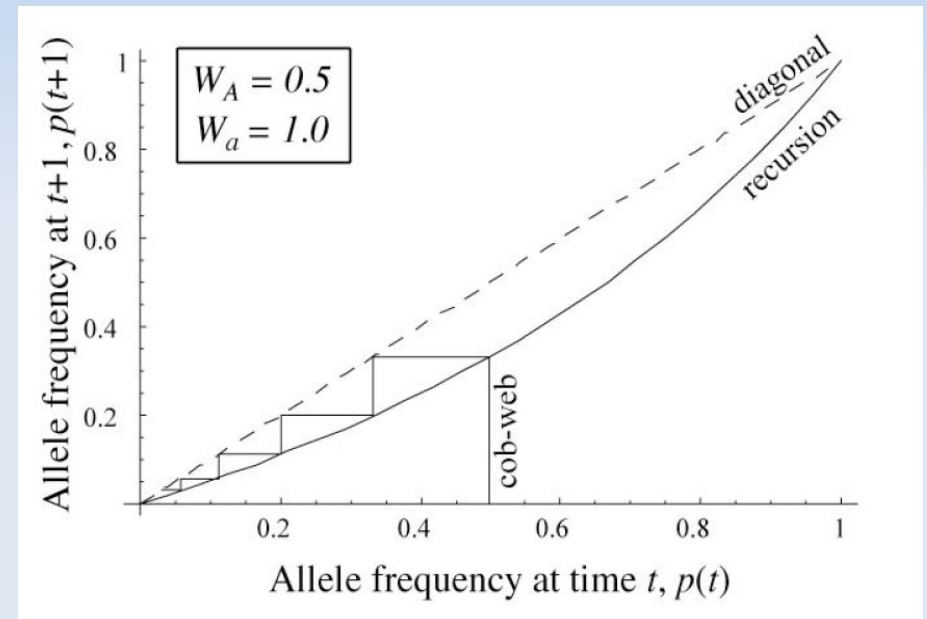
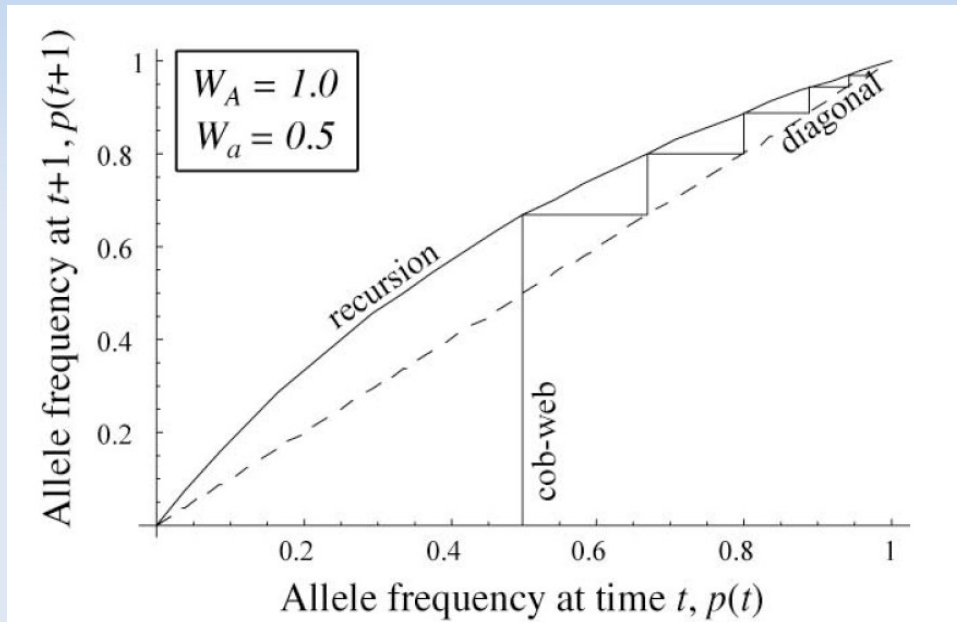
Selection at a haploid locus

- Let there be a haploid locus with alleles A and a , with p being the frequency of A .
- Let the fitness values of the two alleles be W_A and W_a , resp.
- The **mean fitness** of the population is $\bar{W} = p W_A + (1 - p) W_a$.
- After one generation of selection, the frequency of A has changed to

$$p' = \frac{W_A p}{\bar{W}}$$

- This equation has two equilibria: $p = 0$ and $p = 1$.
- If $W_A > W_a$ then $p = 1$ is stable and $p = 0$ unstable.
- If $W_A < W_a$ then $p = 0$ is stable and $p = 1$ unstable.
- If $W_A = W_a$ then the two alleles are neutral, and each value of p is a **neutrally stable** equilibrium.

Cobwebbing diagrams for haploid selection



General solution for haploid selection

- We can solve the haploid recursion equation $p' = W_A p / \bar{W}$ by looking at the ratio $f = p / (1 - p)$:

- We find

$$f' = \frac{p'}{1 - p'} = \frac{W_A p}{W_a (1 - p)} = \frac{W_A}{W_a} f$$

- Thus, the ratio of the two allele frequencies changes exponentially,

$$f(t) = (W_A / W_a)^t f(0).$$

- Substituting back leads to

$$p(t) = \frac{W_A^t p(0)}{W_A^t p(0) + W_a^t (1 - p(0))}$$

Time-dependent selection

- The preceding analysis also works if the fitness values change over time.

- We then get
$$f(t) = f(0) \prod_{\tau=0}^{t-1} \frac{W_A(\tau)}{W_a(\tau)}$$

- This can be written in terms of the **geometric mean fitness**

$$\bar{W}^g = \left(\prod_{\tau=0}^{t-1} W_A(\tau) \right)^{1/t}$$

yielding

$$f(t) = \frac{(\bar{W}_A^g)^t}{(\bar{W}_a^g)^t} f(0)$$

- Thus, the allele with higher geometric mean fitness wins.

Haploid selection in continuous time

- Defining the **selection coefficient** for A as

$$s = \frac{W_A - W_a}{W_a} = \frac{W_A}{W_a} - 1$$

the continuous-time version of the haploid selection model becomes

$$\frac{dp}{dt} = sp(1-p)$$

- This is a special case of the continuous logistic equation, and has the general solution

$$p(t) = \frac{e^{st} p(0)}{1 - p(0) + e^{st} p(0)}$$