

# Laws of Adaptation

A course on biological evolution in eight lectures  
by Carlo Matessi

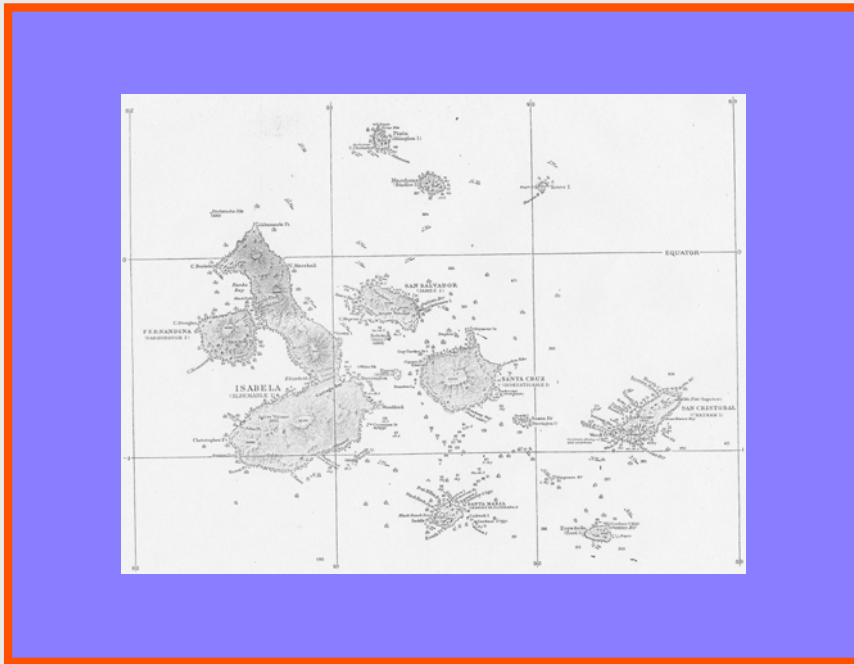
## Lecture 1

Demography, or the “short-term dynamics” point of view

Monday October 2, 13:00-14:00

## Charles Darwin in the Galapagos islands

- ❖ The Galapagos are volcanic islands, formed around 5 million years ago, situated in the Pacific ocean about 1000 Km west of Ecuador



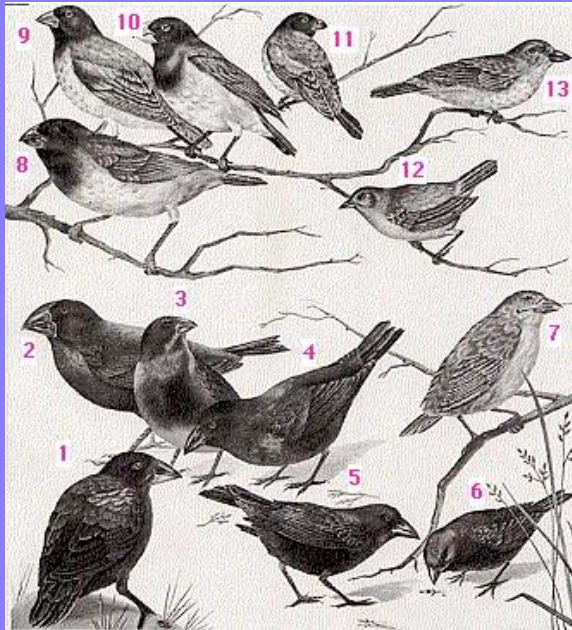
Map of the Galapagos  
downloaded from [www.du.edu/~ttyler](http://www.du.edu/~ttyler)



Geographical position of the Galapagos  
downloaded from [www.geol.umd.edu](http://www.geol.umd.edu)

- ❖ When Darwin, in his trip around the world as a naturalist on board the survey ship “Beagle”, visited them in 1835 was amazed by their surprisingly diverse fauna which –besides a giant tortoise and three species of iguanas, two terrestrial and one marine– included a very diversified group of finches

# The Galapagos finches



1. *Geospiza conirostris*
2. *Geospiza magnirostris*
3. *Geospiza fortis*
4. *Geospiza scandens*
5. *Geospiza difficilis*
6. *Geospiza fuliginosa*
7. *Cactospiza pallida*
8. *Platyspiza crassirostris*
9. *Camarhynchus pauper*
10. *Camarhynchus psittacula*
11. *Camarhynchus parvulus*
12. *Certhidia olivacea*
13. *Cactospiza heliobates*

The large species complex of Galapagos finches

From BSCS, Biological Science: Molecules to Man, Houghton Mifflin Co., 1963



The wide spectrum of bill sizes and shapes  
downloaded from [www.geolsoc.org.uk](http://www.geolsoc.org.uk)

- ❖ Several of these species inhabit distinct islands in the archipelago. None of these species exists in the mainland, where only one species is found that is distantly related to this complex. The diversity of bill sizes and shapes parallels an equally broad diversity of diet and habitat.

## Indications from Darwin's finches

- ❖ Characteristic features of living beings are modified in (geological) time: *biological evolution*
- ❖ Most changes occur in such a way to enable individuals to thrive in a given new environment and to exploit efficiently opportunities and resources specifically available in that environment: *adaptation*

## Adaptation

- ❖ Adaptation is manifested whenever structures or activities are distinctly adequate to achieve a specific end or to perform correctly a given duty.
- ❖ It is a distinctive property of living beings, where it is present under two aspects
  - Internal adaptation*: precise coordination and harmonious interaction between different parts of an organism at all levels of structure (molecular, subcellular, cellular, organs, systems of organs)
  - External adaptation*: tight correlation between characters of the organism and certain properties of the environment that are evidently important for its survival (e.g., food, shelter, etc.)

## Natural selection

- ❖ A process that can account for adaptive evolution of living beings
- ❖ It is necessarily active in any collection (population) of entities (individuals) where the following conditions are verified
  1. entities have a limited life-span but self-replicate (by acquiring and transforming energy and extraneous materials from the outside)
  2. self-replication is not exact, so that a limited amount of (transmissible) variation is present among replicates
  3. length of life-span and rates of self-replication depend on (transmissible) features of the entities
- ❖ These three conditions are characteristic of (define) life, so that any population of organisms is permanently undergoing natural selection
- ❖ The question is whether this specific process can account for the features and properties of biological diversity
- ❖ To answer this type of questions we need tools to construct, based on the concept of natural selection, theoretical predictions about specific biological phenomena

## Short term evolutionary dynamics

- ❖ Time scale: generation time  $t \in \{0, 1, \dots\}$
- ❖ Object: a population of interbreeding individuals
- ❖ Properties:  $K$  genetically transmissible types
  
- ❖  $X_\alpha(t)$  = proportion of adult individuals of type  $\alpha$  at time  $t$
- ❖  $Y_\alpha(t)$  = proportion of newborn individuals of type  $\alpha$  at time  $t$
- ❖  $w_\alpha$  = probability that newborn of type  $\alpha$  survive to reproduce
- ❖  $f_{\beta\gamma}(\alpha)$  = mean number of offspring of type  $\alpha$  born to pairs  $(\beta, \gamma)$
  
- ❖ Assume: infinite population; random mating

$$\begin{array}{ccc}
 \text{newborn} & \longrightarrow & \text{adults} \\
 Y_\alpha(t+1) = \frac{\sum_{\beta} \sum_{\gamma} X_\beta(t) X_\gamma(t) f_{\beta\gamma}(\alpha)}{\sum_{\delta} \sum_{\beta} \sum_{\gamma} X_\beta(t) X_\gamma(t) f_{\beta\gamma}(\delta)} & & X_\alpha(t+1) = \frac{w_\alpha Y_\alpha(t+1)}{\sum_{\beta} w_\beta Y_\beta(t+1)}
 \end{array}$$

$$\bar{w}(t) = \text{mean fitness} = \sum_{\alpha} \sum_{\beta} \sum_{\gamma} w_\alpha X_\beta(t) X_\gamma(t) f_{\beta\gamma}(\alpha)$$

## The case of one gene with $n$ variants

- ❖ Gene variants (alleles):  $\{A_1, \dots, A_n\}$
- ❖ Types (genotypes):  $\{A_1A_1, A_1A_2, \dots, A_nA_n\}$  – first allele is received from mother, second from father ;  $K = n^2$
- ❖  $X_{ij}(t)$ ,  $Y_{ij}(t)$  = proportion of  $A_iA_j$  among adults , newborn of generation  $t$
- ❖  $p_i(t)$ ,  $q_i(t)$  = frequency of allele  $A_i$  among adults , newborn

$$p_i(t) = \sum_j \frac{X_{ij} + X_{ji}}{2}, \quad q_i(t) = \sum_j \frac{Y_{ij} + Y_{ji}}{2}$$

- ❖ By the laws of genetics:

$$f_{ij|kl}(\mathbf{ik}) = f_{ij|kl}(\mathbf{il}) = f_{ij|kl}(\mathbf{jk}) = f_{ij|kl}(\mathbf{jl}) = F_{ij|kl}, \quad f_{ij|kl}(\alpha) = 0 \quad \forall \alpha \notin \{\mathbf{ik}, \mathbf{il}, \mathbf{jk}, \mathbf{jl}\}$$

- ❖ Assume:  $F_{ij|kl} = F/4 \quad \forall (ij | kl)$

$$Y_{ij}(t+1) = \frac{\frac{1}{4} \sum_k \sum_l (X_{ik}(t)X_{jl}(t) + X_{ik}(t)X_{lj}(t) + X_{ki}(t)X_{jl}(t) + X_{ki}(t)X_{lj}(t))}{\frac{1}{4} \sum_i \sum_j \sum_k \sum_l (X_{ik}(t)X_{jl}(t) + X_{ik}(t)X_{lj}(t) + X_{ki}(t)X_{jl}(t) + X_{ki}(t)X_{lj}(t))}$$

$$Y_{ij}(t+1) = \left( \sum_k \frac{X_{ik}(t) + X_{ki}(t)}{2} \right) \left( \sum_k \frac{X_{jk}(t) + X_{kj}(t)}{2} \right)$$

$$\therefore Y_{ij}(t+1) = p_i(t)p_j(t) \quad \forall (ij) \quad \text{and} \quad q_i(t+1) = p_i(t) \quad \forall i$$

- ❖ Gene frequencies are sufficient state variables and satisfy the following recurrence equations:

$$p_i(t+1) = p_i(t) \frac{\sum_j w_{ij} p_j(t)}{\sum_k \sum_j w_{kj} p_k(t) p_j(t)} = p_i(t) \frac{\bar{w}_i(t)}{\bar{w}(t)}, \quad \forall i = 1, \dots, n$$

$w_{ij} = w_{ji}$  = probability that newborn  $A_i A_j$  survive to reproduce

$$\bar{w}_i(t) = \sum_j w_{ij} p_j(t) = \text{mean fitness of allele } i$$

$$\bar{w}(t) = \sum_i \sum_j w_{ij} p_i(t) p_j(t) = \text{mean fitness}$$

- ❖ Any equilibrium point of the above recurrence equations must satisfy:

$$\text{either } \hat{p}_i = 0 \quad \text{or} \quad \bar{w}_i = \bar{w} \quad \forall i = 1, \dots, n$$



## Maximization of mean fitness (Fisher, 1930; Kingman 1961)

- ❖ Use a continuous time approximation by which the recurrence equations are transformed into differential equations
- ❖ Associate discrete generation indexes  $\{0, 1, \dots, t, t+1, \dots\}$  to equidistant points on a continuous time scale  $\tau \in [0, \infty)$ :

$$t \rightarrow \tau \quad , \quad t+k \rightarrow \tau + k\delta$$

- ❖ Moreover let:

$$w_{ij} = w + \delta v_{ij}$$

- ❖ Hence:

$$\bar{w}_i(t) = \bar{w}_i(\tau) = w + \delta \bar{v}_i(\tau) \quad , \quad \bar{w}(t) = \bar{w}(\tau) = w + \delta \bar{v}(\tau) \quad , \quad \bar{v}_i(\tau) = \sum_j v_{ij} p_j(\tau) \quad , \quad \bar{v}(\tau) = \sum_i \sum_j v_{ij} p_i(\tau) p_j(\tau)$$

- ❖ It follows that:

$$\frac{p_i(\tau + \delta) - p_i(\tau)}{\delta} = p_i(\tau) \frac{\bar{v}_i(\tau) - \bar{v}(\tau)}{w + \delta \bar{v}(\tau)} \quad \rightarrow \quad \frac{dp_i(\tau)}{d\tau} = p_i(\tau) \frac{\bar{v}_i(\tau) - \bar{v}(\tau)}{w} \quad \text{as } \delta \rightarrow 0$$

- ❖ Now we can take the time derivative of mean fitness:

$$\frac{d\bar{v}(\tau)}{d\tau} = 2 \sum_i \sum_j v_{ij} p_j(\tau) \frac{dp_i(\tau)}{d\tau} = 2 \sum_i \bar{v}_i(\tau) \frac{dp_i(\tau)}{d\tau} = \frac{2}{w} \sum_i p_i(\tau) \bar{v}_i(\tau) [\bar{v}_i(\tau) - \bar{v}(\tau)] = \frac{2}{w} \sum_i p_i(\tau) [\bar{v}_i(\tau) - \bar{v}(\tau)]^2 \geq 0$$

and equality obtains only at the equilibria of the system

- ❖ The mean fitness is a Liapunov function for the gene frequencies dynamics: it increase in time and its stationary points with respect to the gene frequencies coincide with the equilibria of the system. Hence it reaches a maximum when the population attains a stable equilibrium

## Competition for limited resources

- ❖ The population dynamics of a community of species competing for common, limited resources can be described by a system of “Lotka-Volterra” differential equations
- ❖ S species -  $N_\alpha(\tau)$  = number of individuals of species  $\alpha$  at time  $\tau$  (continuous time)

$$\frac{dN_\alpha(\tau)}{dt} = \rho_\alpha \left( C_\alpha - \sum_\beta B_{\alpha\beta} N_\beta(\tau) \right) N_\alpha(\tau) \quad ; \quad \rho_\alpha, C_\alpha > 0, B_{\alpha\beta} \geq 0 \quad \forall \alpha, \beta$$

$\rho_\alpha C_\alpha$  = intrinsic rate of increase of species  $\alpha$

$\frac{C_\alpha}{B_{\alpha\alpha}}$  = carrying capacity of species  $\alpha$

$\frac{B_{\alpha\beta}}{B_{\alpha\alpha}}$  = effect on species  $\alpha$  of competition with species  $\beta$

- ❖ Parameters  $C_\alpha$  and  $B_{\alpha\beta}$  have been given in Theoretical Ecology a “microscopic” interpretation:
- ❖ resources vary in a 1-dimensional spectrum identified by a variable  $z \in (-\infty, +\infty)$
- ❖ *production function*  $c(z) \geq 0 \quad \forall z$ : amount of resources of type  $z$  made available per unit time
- ❖ *utilization function*  $\phi_\alpha(z) \geq 0 \quad \forall z$ : harvesting, per unit time, unit resource and unit consumer, of resources type  $z$ , by consumers type  $\alpha$

$$C_\alpha = \int c(z) \phi_\alpha(z) dz \quad , \quad B_{\alpha\beta} = B_{\beta\alpha} = \int \phi_\alpha(z) \phi_\beta(z) dz$$

## Short-term evolution driven by competition

- ❖ The evolution of one, or more, species sharing limited resources, with respect to traits that affect their competitive ability can be represented in analogy with the “Lotka-Volterra” equations, by a slight extension of the “1-locus, discrete generations” evolutionary model considered sofar
- ❖  $S$  species; trait variation due to one gene in each species, with  $n_s$  alleles present in species  $s$

$$\{A_1^s, \dots, A_{n_s}^s\} = \text{alleles in species } s \in \{1, \dots, S\}$$

- ❖ Structure of the community

$$N_{ij}^s(t) = \text{number of newborn of species } s \text{ and genotype } A_i^s A_j^s \text{ at generation } t$$

- ❖ Sufficient state variables

$$N(t) = \sum_s \sum_{ij} N_{ij}^s(t) = \text{total number of newborn in the community at generation } t$$

$$u_s(t) = \frac{\sum_{ij} N_{ij}^s(t)}{N(t)} = \text{proportion of newborn of species } s \text{ at generation } t$$

$$p_i^s(t) = \frac{1}{2} \frac{\sum_j [N_{ij}^s(t) + N_{ji}^s(t)]}{\sum_{kl} N_{kl}^s(t)} = \text{frequency of allele } A_i^s \text{ among newborn of species } s \text{ at generation } t$$

## ❖ Demographic parameters

$$w_{ij}^s = \text{probability that newborn } A_i^s A_j^s \text{ survive to reproduce} = \frac{1}{\rho} + C_{ij}^s - \sum_t \sum_k \sum_l B_{ijkl}^{st} N_{kl}^t(t)$$

$\rho$  = number of offspring born to each adult irrespective of species and genotype

## ❖ notice that

$$C_{ij}^s = C_{ji}^s \quad , \quad B_{ijkl}^{st} = B_{jikl}^{st} \quad , \quad B_{ijkl}^{st} = B_{ijlk}^{st} \quad , \quad B_{ijkl}^{st} = B_{klij}^{ts}$$

## ❖ Recurrence equations

$$N(t+1) = N(t) + \rho N(t) [\bar{C}(t) - \bar{B}(t)N(t)]$$

$$u_s(t+1) = u_s(t) \frac{\frac{1}{\rho} + \bar{C}_s(t) - \bar{B}_s(t)N(t)}{\frac{1}{\rho} + \bar{C}(t) - \bar{B}(t)N(t)} \quad , \quad s = 1, \dots, S$$

$$p_i^s(t+1) = p_i^s(t) \frac{\frac{1}{\rho} + \bar{C}_i^s(t) - \bar{B}_i^s(t)N(t)}{\frac{1}{\rho} + \bar{C}_s(t) - \bar{B}_s(t)N(t)} \quad , \quad s = 1, \dots, S \quad , \quad i = 1, \dots, n_s$$

where

$$\bar{C}_i^s(t) = \sum_j p_j^s(t) C_{ij}^s \quad , \quad \bar{C}_s(t) = \sum_i p_i^s(t) \bar{C}_i^s(t) \quad , \quad \bar{C}(t) = \sum_s u_s(t) \bar{C}_s(t)$$

$$\bar{B}_i^s(t) = \sum_j \sum_t \sum_k \sum_l p_j^s(t) p_k^t(t) p_l^t(t) B_{ijkl}^{st} \quad , \quad \bar{B}_s(t) = \sum_i p_i^s(t) \bar{B}_i^s(t) \quad , \quad \bar{B}(t) = \sum_s u_s(t) \bar{B}_s(t)$$

# A quantity maximized by competition-driven evolution

(Matessi and Jayakar, 1981)

- ❖ Switch from discrete time  $t$  to continuous time  $\tau$  and approximate recurrence equations by differential equations

$$t + k \rightarrow \tau + k\delta \quad , \quad \rho = \delta r \quad , \quad \text{let } \delta \rightarrow 0$$

- ❖ the differential equations

$$\frac{dN(\tau)}{d\tau} = rN(\tau) [\bar{C}(\tau) - \bar{B}(\tau)N(\tau)]$$

$$\frac{du_s(\tau)}{d\tau} = ru_s(\tau) [\bar{C}_s(\tau) - \bar{B}_s(\tau)N(\tau) - \bar{C}(\tau) + \bar{B}(\tau)N(\tau)] \quad , \quad s = 1, \dots, S$$

$$\frac{dp_i^s(\tau)}{d\tau} = rp_i^s(\tau) [\bar{C}_i^s(\tau) - \bar{B}_i^s(\tau)N(\tau) - \bar{C}_s(\tau) + \bar{B}_s(\tau)N(\tau)] \quad , \quad s = 1, \dots, S \quad , \quad i = 1, \dots, n_s$$

- ❖ Equilibria must satisfy

$$\bar{C} - \bar{B}N = 0 \quad , \quad \text{assuming that the community can subsist at all}$$

$$\bar{C}_s - \bar{B}_sN = 0 \quad , \quad \text{for all species that are not extinct}$$

$$\bar{C}_i^s - \bar{B}_i^sN = 0 \quad , \quad \text{for all alleles that are not extinct, in non-extinct species}$$

- ❖ A Liapunov function for this system:

$$\Psi(\tau) = 2\bar{C}(\tau)N(\tau) - \bar{B}(\tau)N(\tau)^2$$

- ❖ In fact, as a function of time,  $\Psi$  is increasing because, as it can be shown,

$$\frac{d\Psi(\tau)}{d\tau} = 2rN[\bar{C} - \bar{B}N]^2 + 2rN \sum_s u_s [\bar{C}_s - \bar{B}_s N - \bar{C} + \bar{B}N]^2 + 4rN \sum_s \sum_i u_s p_i^s [\bar{C}_i^s - \bar{B}_i^s N - \bar{C}_s + \bar{B}_s N]^2 \geq 0$$

and equality only obtains at the equilibrium points of the system

- ❖ Moreover, the stationary points –internal and on the boundary– of  $\Psi$  with respect to the state variables  $\{N, u_s, p_i^s\}$  coincide with the equilibrium points of the system
- ❖ Hence  $\Psi$  is maximized in the course of competition-driven evolution

## The biological meaning of $\Psi$

- ❖ Use the “microscopic” interpretation of the interaction parameters:

$\{z : -\infty \leq z \leq +\infty\}$  : resource spectrum, the ensemble of resource types available in the environment

$c(z) \geq 0 \quad \forall z$  : production function, fixed for a given environment

$\phi_{ij}^s(z) \geq 0 \quad \forall z$  : utilization function of genotype  $A_i^s A_j^s$  in species  $s$ , the property that is subject to evolution

$$C_{ij}^s = \int c(z) \phi_{ij}^s(z) dz \quad , \quad B_{ijkl}^{st} = \int \phi_{ij}^s(z) \phi_{kl}^t(z) dz$$

$\phi(z, \tau) = \sum_s \sum_{ij} u_s(\tau) p_i^s(\tau) p_j^s(\tau) \phi_{ij}^s(z)$  : mean utilization function, changing in time

$$\bar{C}(\tau) = \int c(z) \phi(\tau, z) dz \quad , \quad \bar{B}(\tau) = \int \phi^2(\tau, z) dz \quad , \quad \Psi(\tau) = \int [2c(z) \phi(\tau, z) N(\tau) - \phi^2(\tau, z) N^2(\tau)] dz$$

- ❖ Define

$\Gamma(\tau) = \int [c(z) - \phi(\tau, z) N(\tau)]^2 dz$  : square deviation from habitat productivity of the community harvesting rate

so that

$$\Gamma(\tau) = \int c^2(z) dz - \Psi(\tau)$$

- ❖ Hence, the maximization of  $\Psi$  implies the minimization of  $\Gamma$ . Evolution maximizes the fit of the resource utilization pattern to the actual distribution of resources in the habitat.