200 ANNI DI DARWIN

Facoltà di Scienze Matemtiche Fisiche e Naturali
Università del Salento

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DARWIN:

WHICH MATHEMATICS?

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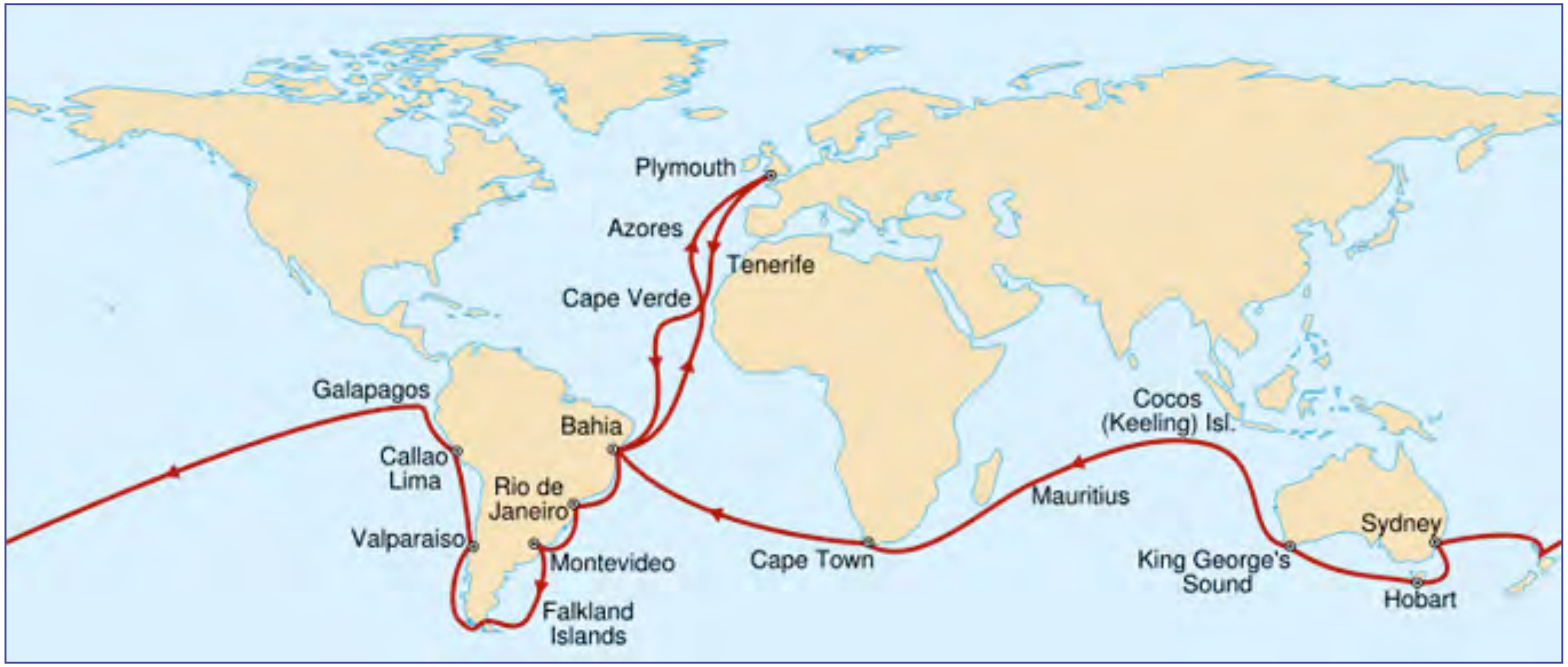
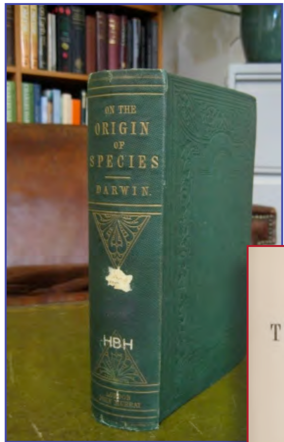
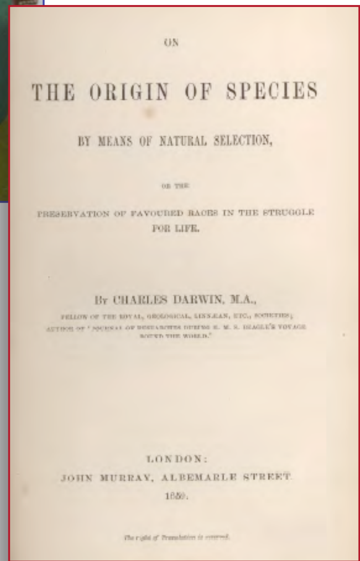
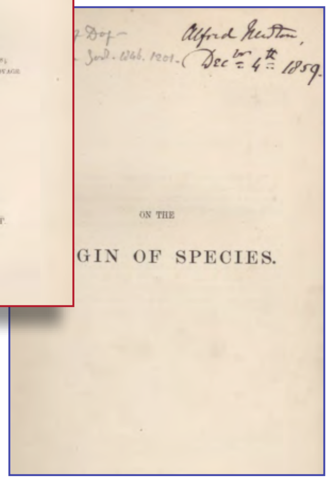
DARWIN: SCIENTIST AND VOYAGER



DARWIN AND THE ORIGIN OF THE SPECIES







DARWIN AND THE ORIGIN OF THE SPECIES

DARWIN AND THE NATURAL SELECTION

CHAPTER IV

NATURAL SELECTION; OR THE SURVIVAL OF THE FITTEST

HOW will the struggle for existence, briefly discussed in the last chapter, act in regard to variation? Can the principle of selection, which we have seen is so potent in the hands of man, apply under nature? I think we shall see that it can act most efficiently. Let the endless

changes of conditions might and do occur under nature. Let it also be borne in mind how infinitely complex and close-fitting are the mutual relations of all organic beings to each other and to their physical conditions of life; and conse-

DARWIN AND THE NATURAL SELECTION

ous would be rigidly destroyed. This preservation of favourable individual differences and variations, and the destruction of those which are injurious, I have called Natural Selection, or the Survival of the Fittest. Variations neither useful nor injurious would not be affected by natural selection, and would be left either a fluctuating element, as perhaps we see in certain polymorphic species, or would ultimately become fixed, owing to the nature of the organism and the nature of the conditions.

Charles Darwin, laid down his great theory of evolution and the origin of species without making use of a single equation.

IS A "MATHEMATICS OF EVOLUTION" POSSIBLE?

IS A "MATHEMATICS OF EVOLUTION" POSSIBLE?

OBSERVATION

DESCRIPTION

BIOLOGY

GENERALIZATION

CLASSIFICATION

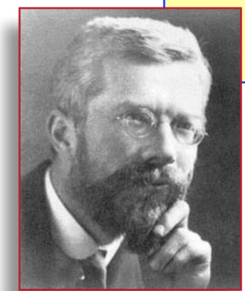
XX century:
MATHEMATICS INSPIRED BY BIOLOGY

- cell kinetics
- population ecology
- epidemiology
- population genetics

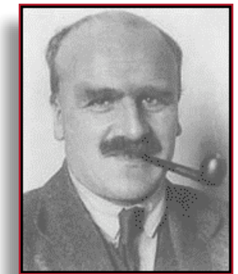
POPULATION GENETICS OF ADAPTATION

In the case of population genetics, the formal approach was introduced already in XIX century by Gregor Mendel, who applied his knowledge of probability theory to the problem of inheritance.

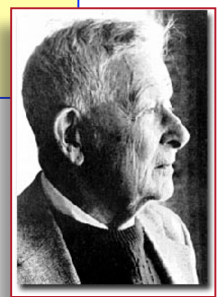
The mathematics of heredity was then taken up and developed by…….
Fisher, Haldane, and Wright.



R.A. Fisher



J. B. S. Haldane



S.G. Wright

POPULATION GENETICS OF ADAPTATION

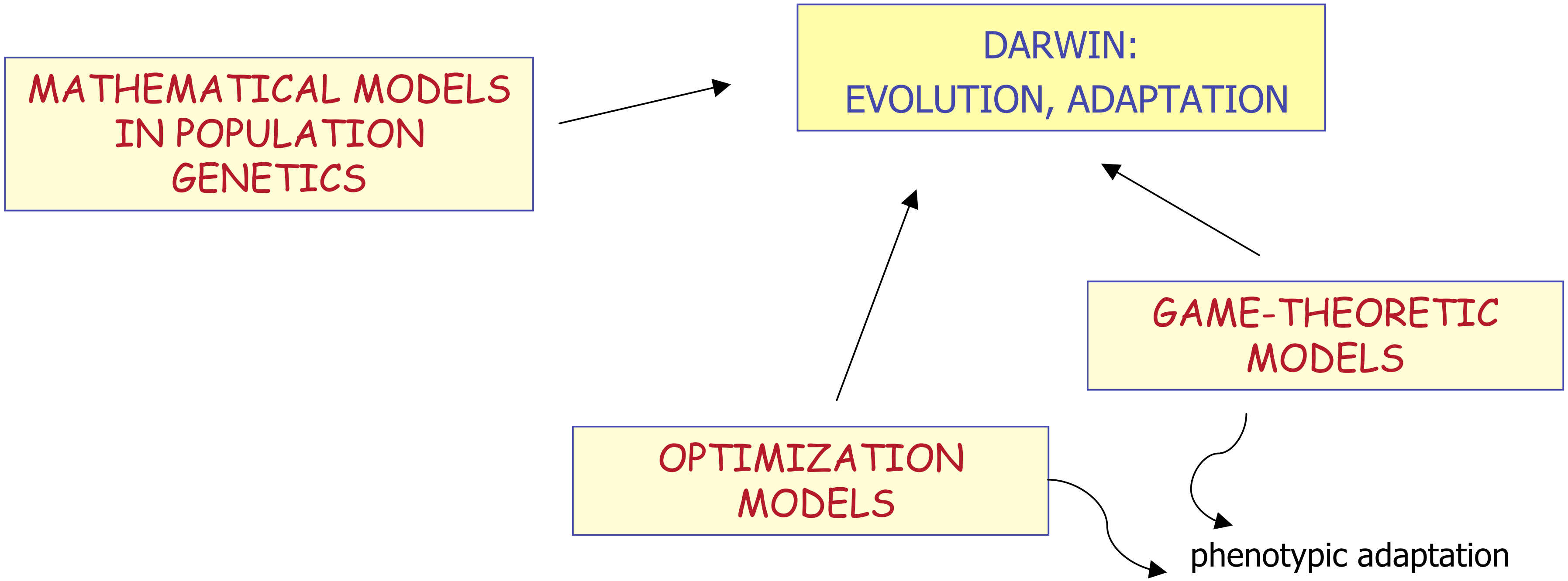
They used mathematical models to generate a synthesis between Mendelian genetics and Darwinian evolution, opening the way toward contemporary models of evolutionary population genetics

DARWIN:
EVOLUTION, ADAPTATION

MATHEMATICAL MODELS IN POPULATION GENETICS

IS THE ONLY POSSIBLE APPROACH?

A GLANCE ON POSSIBLE APPROACHES……



Aim: explain adaptation by considering how fitness varies as a function of phenotypic performance in a given environment.

OPTIMALITY MODELS

OPTIMALITY APPROACH ⇨ typicall ignore the details of how the genotype of an organism gives rise to its phenotype and simply seek to characterize the phenotype that yields the highest fitness.

The specification of a fitness function is required and the underlying assumption is that natural selection proceeds so as to maximize this function

"fitness": can be thought as the long-term per capita population growth rate of a strategy when it appears as a rare mutant in a given resident population.

Optimisation theory as straightforward formalisation of Darwin's idea of natural selection as the

'preservation of favourable variations and the rejection of injurious variations' (Darwin, 1859).

GAME-THEORETIC MODELLING

GAME-THEORETIC APPROACH

Optimization models assume that the fitness of an individual depends only on that individual's phenotype

But an individual's fitness is determined by the phenotypes of other individuals in the population as well.

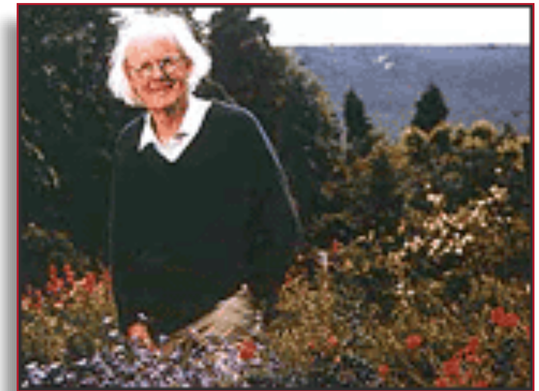
Need for incorporating frequency-dependent selection into evolutionary models.

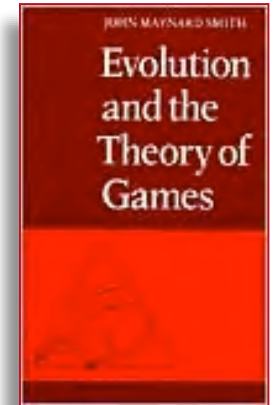
The introduction of game-theoretic ideas addressed this complexity

GAME-THEORETIC MODELLING OF ADAPTATION

GAME-THEORETIC APPROACH → EVOLUTIONARY BIOLOGY

John Maynard Smith developed novel ways of modelling phenotypic evolution





'This book is about a method of modelling evolution, rather than about any specific problem to which the method can be applied'.

GAME-THEORETIC MODELLING OF ADAPTATION

EVOLUTIONARY GAME-THEORY

development of novel interpretive concepts

importation into biology of mathematical methods.

game theory analyzes complex situations in which the best strategy of one player depends on the actions of another.

game theory

For Maynard Smith, these methods could provide a novel way of understanding biological structures and behaviours, and the diversity of life itself

GAME-THEORETIC MODELLING OF ADAPTATION

Applying game theory to animal behavior, he found that although variation exists, natural selection tends to maintain a balance between different characteristics within a species.

This balance is called the *"Evolutionary Stable Strategy."*

A FAMOUS EXAMPLE: THE HAWKS AND THE DOVES

GAME-THEORETIC MODELLING OF ADAPTATION

THE HAWKS AND THE DOVES

The old idea had been that selection inevitably favors organisms to act aggressively. Maynard Smith showed that this isn't necessarily true and that selection may actually favor both aggressive and non-aggressive behaviors.

Through application of game theory, Maynard Smith showed that there is a particular ratio of hawks to doves that forms what he called an "evolutionary stable strategy" for the species.

GAME-THEORETIC MODELLING OF ADAPTATION

EVOLUTIONARY GAME-THEORY

development of novel interpretative concepts

ESS

EVOLUTIONARY ATTAINABILITY

An evolutionarily stable strategy (ESS) is characterised by the condition that if all individuals choose this strategy, then no other strategy can spread in the population (Maynard Smith, 1982).

Evolutionary attainability introduces possible dynamical trajectories for a given equilibrium.

GAME-THEORETIC MODELLING OF ADAPTATION

EVOLUTIONARY GAME-THEORY

DEVELOPMENT OF NOVEL INTERPRETATIVE CONCEPTS

MATHEMATICAL METHODS

WHAT KIND OF MODELLING?

THOUGHTS ON THE METHOD....

THOUGHTS ON THE "METHOD"....

"STRUCTURAL CONCEPTION" OF SCIENTIFIC UNDERSTANDING

The underlying assumption is that structure determines behaviour

Understanding the behaviour of the system involves understanding how the behaviour is determined by the relations that hold between the parts.

Tipically the behaviour is described mathematically, by means of a differential equation, but understanding the equation is not enough.

THOUGHTS ON THE "METHOD"....

> If I claim to understand the behaviour of some system, I mean rather more than that I understand the mathematical description of it. I mean that I can in some way analyse it and play with it in my head, imagining how it would behave in various circumstances. For want of an alternative, this ability can be described as having a 'physical intuition' about a system. (Maynard Smith 1989, p. 227)

"Physical intuition" is complementary to the mathematical analysis of the system.

"Analysing a system and playing with it in one's head" means building theoretical scenarios – models – in which one investigates how the system behaves under different idealising assumptions.

HOW TO MODEL ADAPTATION?

Focus on structural features which may be represented through models and equations.

AND WHAT ABOUT…… MODELLING ADAPTATION?

Locating actual phenotypes in a space of biological possibilities, constructing a fitness function modulo a given environment and exploring the resulting evolutionary dynamics.

AND WHICH KIND OF FORMALIZATION ……

ADAPTIVE DYNAMICS: A UNIFYING PERSPECTIVE

The theory of adaptive dynamics offers a unifying framework in which optimisation models and matrix games represent two special cases.

In order to study the generic patterns of evolution driven by frequency-dependent selection, the fitness of a mutant strategy $\boldsymbol{y}$ in a resident population with strategy $\boldsymbol{x}$, $s_{\boldsymbol{x}}(\boldsymbol{y})$, must not be constrained to any particular form.

What $s_{\boldsymbol{x}}(\boldsymbol{y})$ looks like depends on the biological problem at hand.

ADAPTIVE DYNAMICS: A UNIFYING PERSPECTIVE

Assumptions: $s_{\boldsymbol{x}}(\boldsymbol{y})$ is known; defined in such a manner that mutants with positive values of $s_{\boldsymbol{x}}(\boldsymbol{y})$ can grow and invade; whereas mutants with negative values of $s_{\boldsymbol{x}}(\boldsymbol{y})$ die out in a resident population of strategy $\boldsymbol{x}$.

For a resident strategy $\boldsymbol{x^*}$, the generic condition of evolutionary stability is

$$s_{\boldsymbol{x^*}}(\boldsymbol{y}) < s_{\boldsymbol{x^*}}(\boldsymbol{x^*}) = 0 \text{ for all } \boldsymbol{y} \neq \boldsymbol{x^*},$$

i.e. that no mutant has a fitness advantage when it interacts with the resident only.

In order to model the evolutionary process in the framework of adaptive dynamics, one assumes that mutations are of small phenotypic effect so that a mutant $\boldsymbol{y}$ is always similar to its ancestor $\boldsymbol{x}$.

ADAPTIVE DYNAMICS: A UNIFYING PERSPECTIVE

The population makes a small evolutionary step each time a mutant successfully invades and replaces the former resident

A sequence of these small steps constitutes a stochastic evolutionary path that can be approximated by the deterministic trajectory described by the so-called canonical equation of adaptive dynamics,

$$\frac{d\mathbf{x}}{dt} = \frac{1}{2}\alpha u(\mathbf{x}) N(\mathbf{x}) \mathbf{C}(\mathbf{x}) \left.\frac{\partial s_{\mathbf{x}}(\mathbf{y})}{\partial \mathbf{y}}\right|_{\mathbf{y}=\mathbf{x}}$$

ADAPTIVE DYNAMICS: A UNIFYING PERSPECTIVE

$$\frac{d\mathbf{x}}{dt} = \frac{1}{2}\alpha u(\mathbf{x})N(\mathbf{x})\mathbf{C}(\mathbf{x})\left.\frac{\partial s_{\mathbf{x}}(\mathbf{y})}{\partial \mathbf{y}}\right|_{\mathbf{y}=\mathbf{x}}$$

u denotes the probability of a mutation per birth event

The constant **α** depends on details of the individual-based demography of the evolving population.

N (x) is the equilibrium size of the resident population for strategy ***x***.

The factor **½** indicates that one half of the nearby mutants of a strategy are deleterious and thus cannot contribute to the evolutionary change

C is the variance-covariance matrix of the mutation distribution. It characterises the expected size of mutational steps in different components of ***x*** as well as their potential correlations.

ADAPTIVE DYNAMICS: A UNIFYING PERSPECTIVE

$$\frac{d\mathbf{x}}{dt} = \frac{1}{2}\alpha u(\mathbf{x})N(\mathbf{x})\mathbf{C}(\mathbf{x})\frac{\partial s_{\mathbf{x}}(\mathbf{y})}{\partial \mathbf{y}}\bigg|_{\mathbf{y}=\mathbf{x}}$$

Finally, the fitness gradient

$$\frac{\partial s_{\mathbf{x}}(\mathbf{y})}{\partial \mathbf{y}}\bigg|_{\mathbf{y}=\mathbf{x}}$$

describes the force of selection

For a resident strategy ***x***, this gradient determines the direction as well as scales the speed of evolutionary change.

WHICH KIND OF ANSWER?

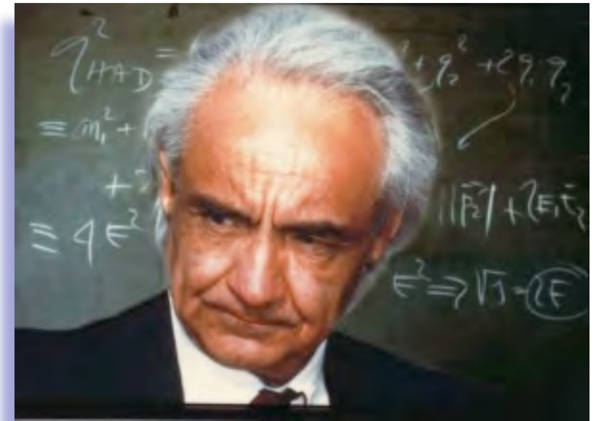
IS A "MATHEMATICS OF EVOLUTION" POSSIBLE?

- ✓ Yes. The development of a general and coherent framework for adaptive evolution modelling is still far from being complete

IS THE "EQUATION OF OF EVOLUTION" POSSIBLE?

- ✓ some very "different" points of view……

WHICH KIND OF ANSWER?



Antonino Zichichi

Piergiorgio Odifreddi

WHICH KIND OF ANSWER?

$$\frac{d\mathbf{x}}{dt} = \frac{1}{2}\alpha u(\mathbf{x})N(\mathbf{x})\mathbf{C}(\mathbf{x})\left.\frac{\partial s_{\mathbf{x}}(\mathbf{y})}{\partial \mathbf{y}}\right|_{\mathbf{y}=\mathbf{x}}$$

MAY A SET OF EQUATIONS EMBRACE ALL THE FASCINATING VARIETY AND THE UNIQUE DIVERSITY OF THE LIVING WORLD?

WHICH KIND OF ANSWER ?

$$\frac{d\mathbf{x}}{dt} = \frac{1}{2}\alpha u(\mathbf{x}) N(\mathbf{x}) \mathbf{C}(\mathbf{x}) \frac{\partial s_{\mathbf{x}}(\mathbf{y})}{\partial \mathbf{y}}\bigg|_{\mathbf{y}=\mathbf{x}}$$

However mathematical models, for the distinctive kind of structural understandig they provide, may be considered a useful tools also in the field of evolutionary adaptation.

In this context, mathematical models may be 'aids for understanding adaptive scenarios, rather than precise predictions about the outcome of evolutionary processes in specific systems.' (Peter Abrams)