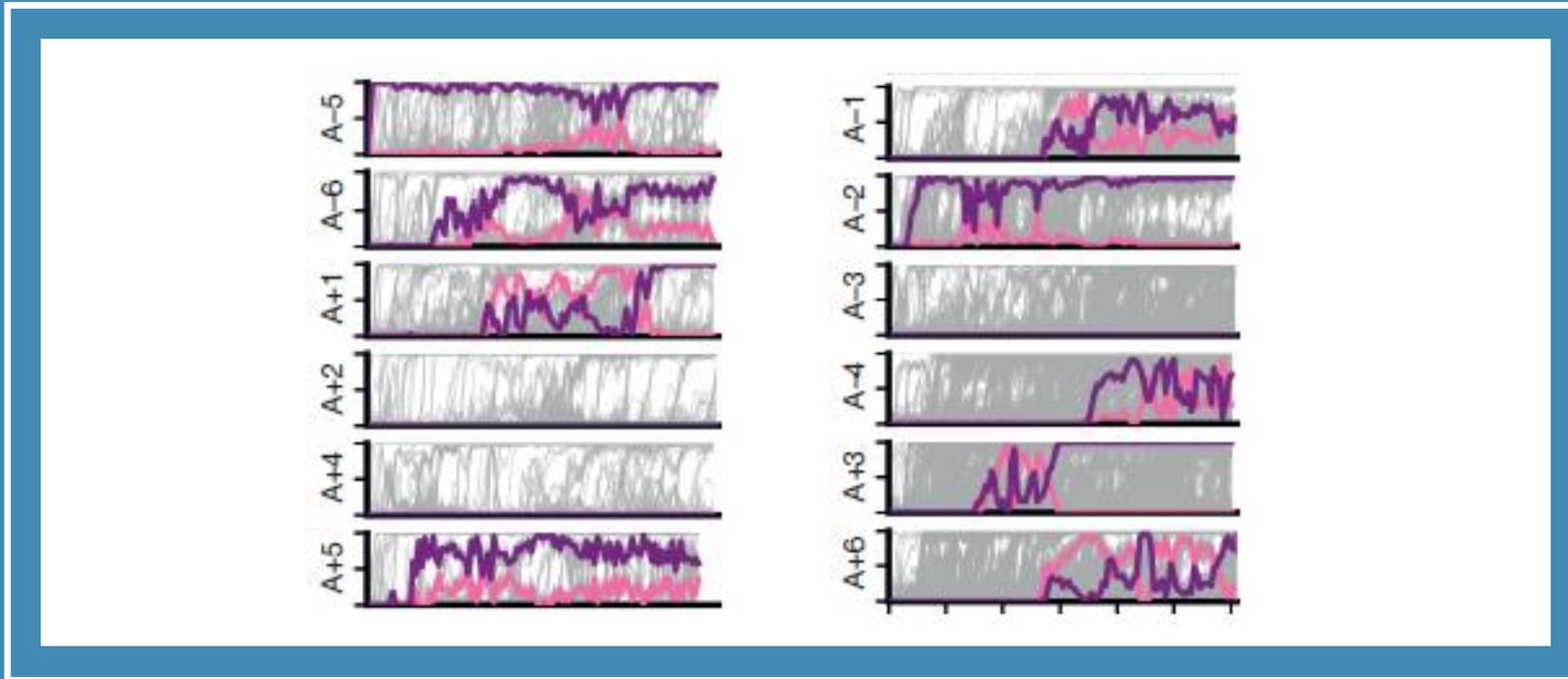


CONDITIONS FOR EVOLUTION BY
NATURAL SELECTION AND NICHE
CONSTRUCTION

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THE DYNAMICS OF MOLECULAR EVOLUTION OVER 60,000 GENERATIONS

Good, B. H., McDonald, M. J., Barrick, J. E., Lenski, R. E., & Desai, M. M. (2017).
The dynamics of molecular evolution over 60,000 generations. *Nature*, 551(7678), 45.

UNPREDICTABILITY?

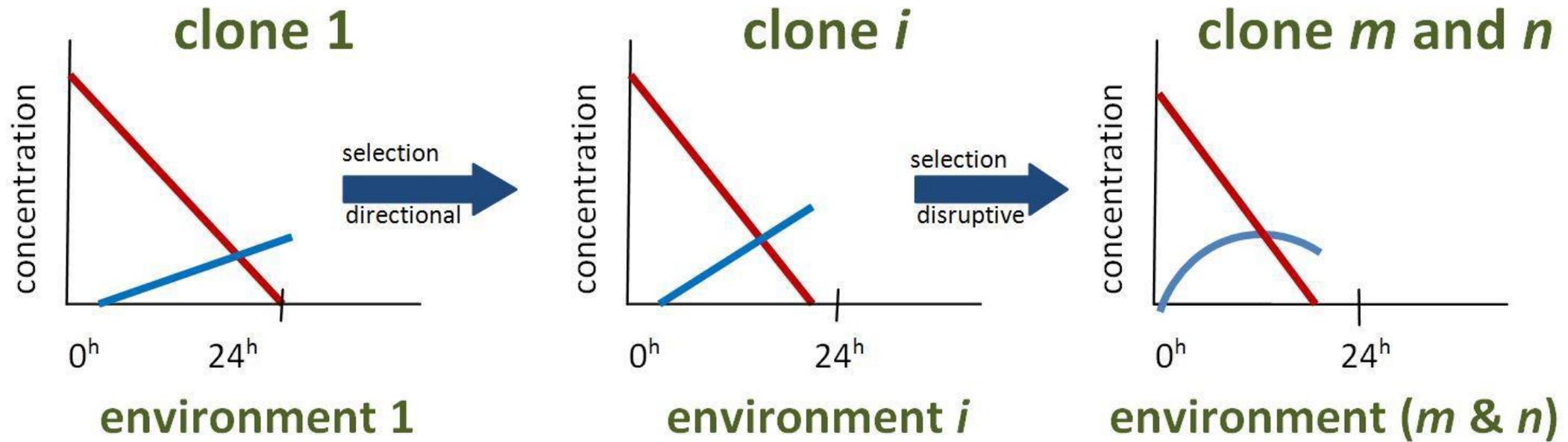
Steady accumulation of mutations

Non-stop selection, many exclusions and fixations

Diversification in homogeneous environments

Quasi-stable coexistence in spite of changing genetic composition

NO!



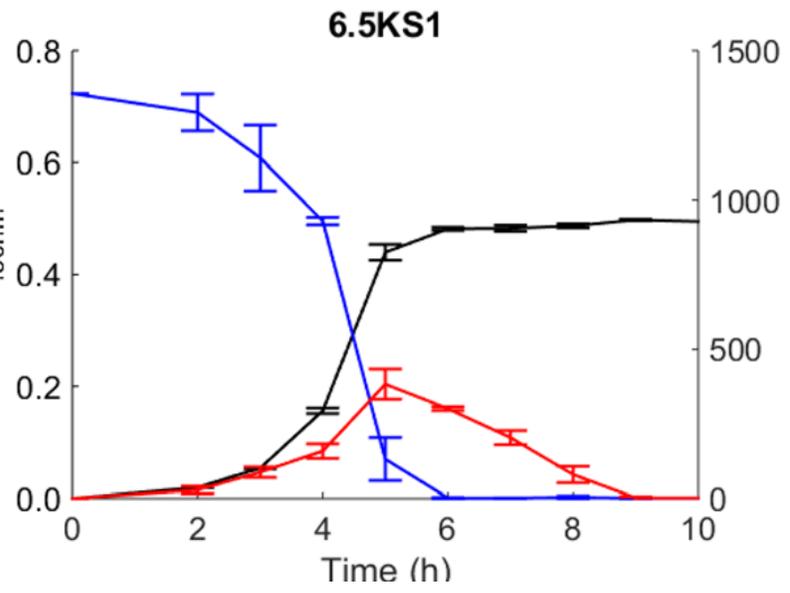
regulating variables:



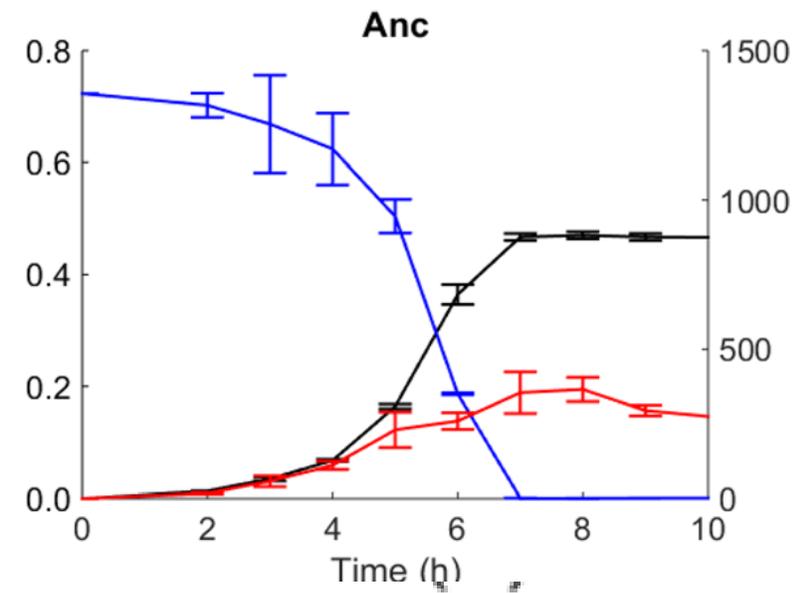
COMPETITION FOR RESOURCES,
SELECTION, NICHE CONSTRUCTION

3

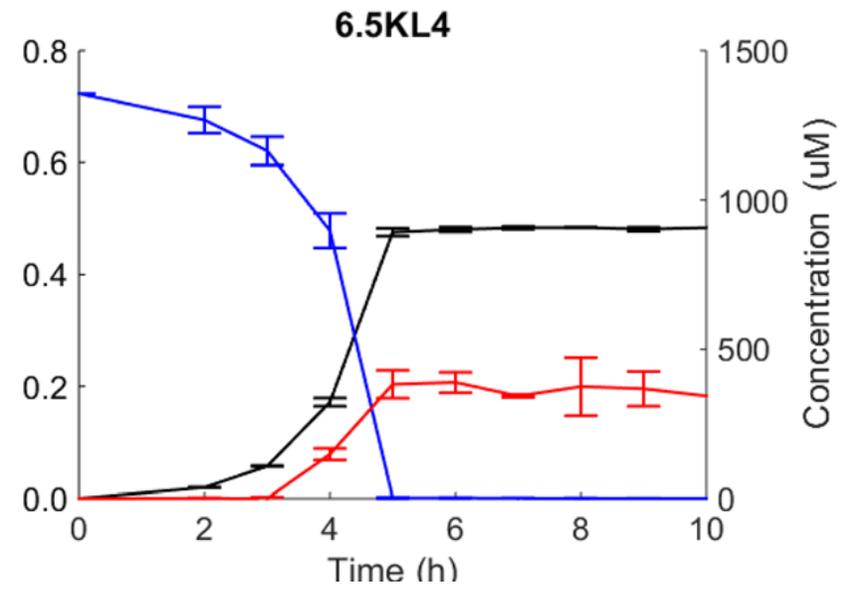
GLUCOSE-ACETATE CONSUMER



ANCESTRAL CLONE



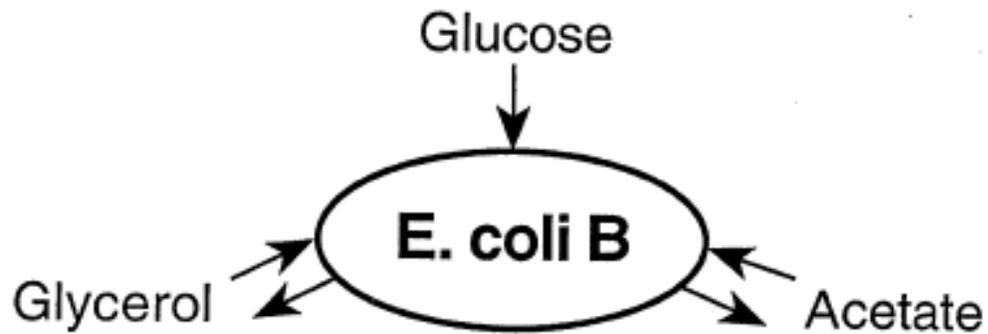
GLUCOSE-CONSUMER CLONE



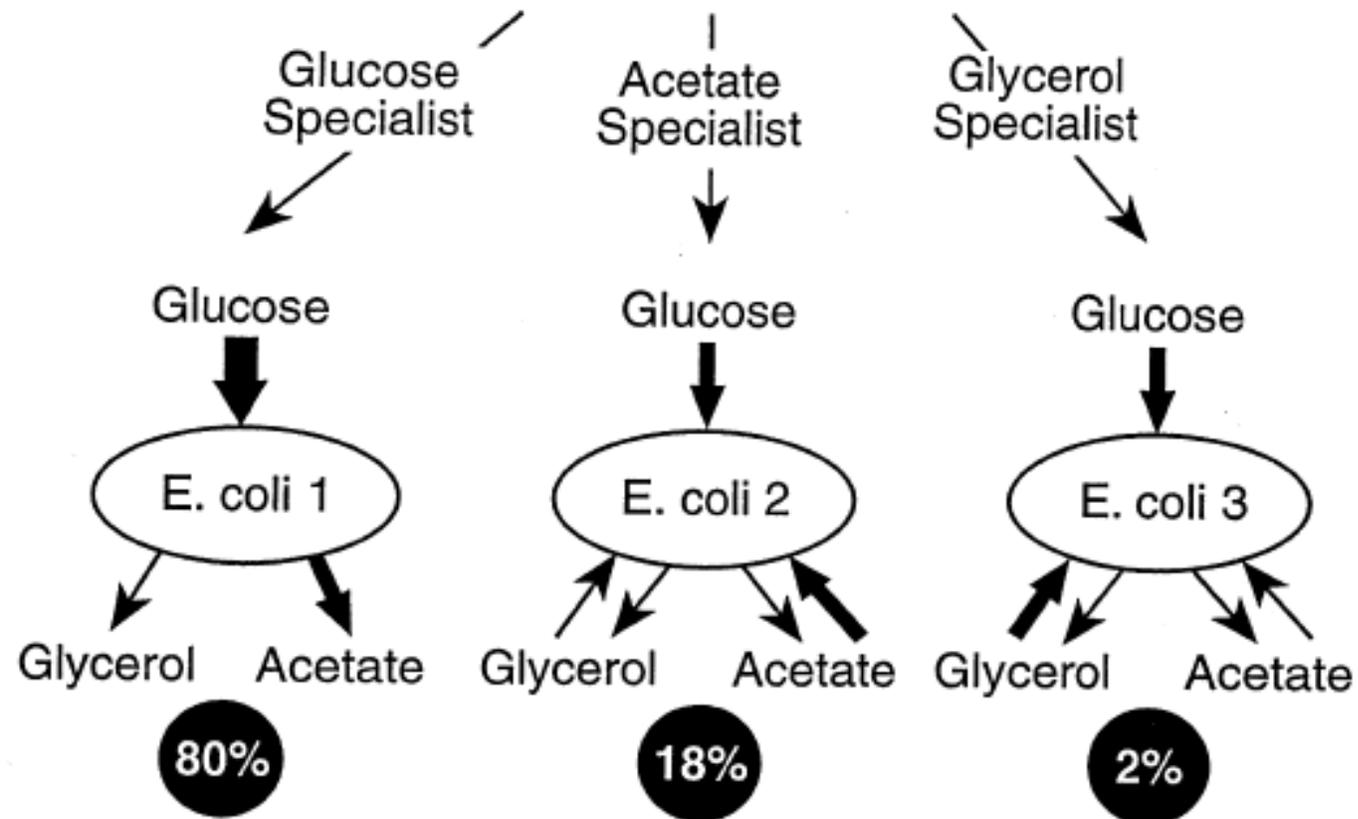
— Population density — Glucose — Acetate

EXPERIMENTAL RESULTS

Großkopf, Tobias, et al. "Metabolic modelling in a dynamic evolutionary framework predicts adaptive diversification of bacteria in a long-term evolution experiment." *BMC evolutionary biology* 16.1 (2016): 163.



800 Generations Later



THREE RESOURCES –
THREE NICHES

Is cross-feeding the
exception or the rule?

Helling et. al. 1987
Rosenzweig et.al. 1994
Dykhuizen 1998

RESEARCH ARTICLE

An enormous potential for niche construction through bacterial cross-feeding in a homogeneous environment

Magdalena San Roman^{1,2}, Andreas Wagner^{1,2,3*}

Growth on glucose can create multiple additional carbon-source niches

Niche construction by providing additional resources due to glucose can metabolic constraints must be common in microbial communities

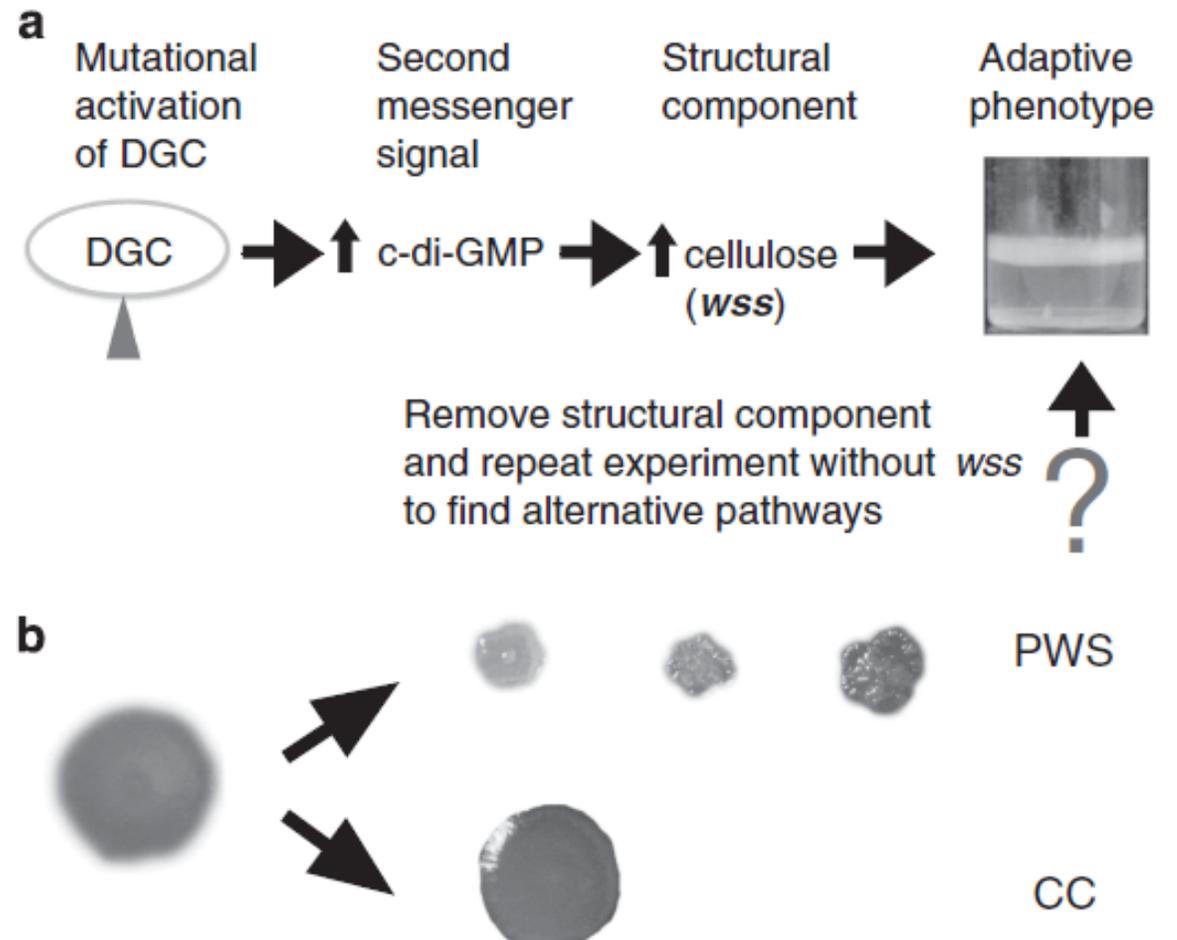
The potential for metabolic niche construction is not a peculiarity of *E. coli* metabolism



COMPETITION FOR SPACE AND
NICHE CONSTRUCTION



MANY DIFFERENT
MUTATIONS MAY
PRODUCE THE MAT
FORMING CLONE



Lind, P. A., Farr, A. D., & Rainey, P. B. (2017). Evolutionary convergence in experimental *Pseudomonas* populations. *The ISME journal*, 11(3), 589.

COMMON FEATURES

Evolution by
competition

Regulating factors are
known: nutrients; sites
with different O₂
concentrations

The selecting
environment=levels of
the regulating variables
change with evolution

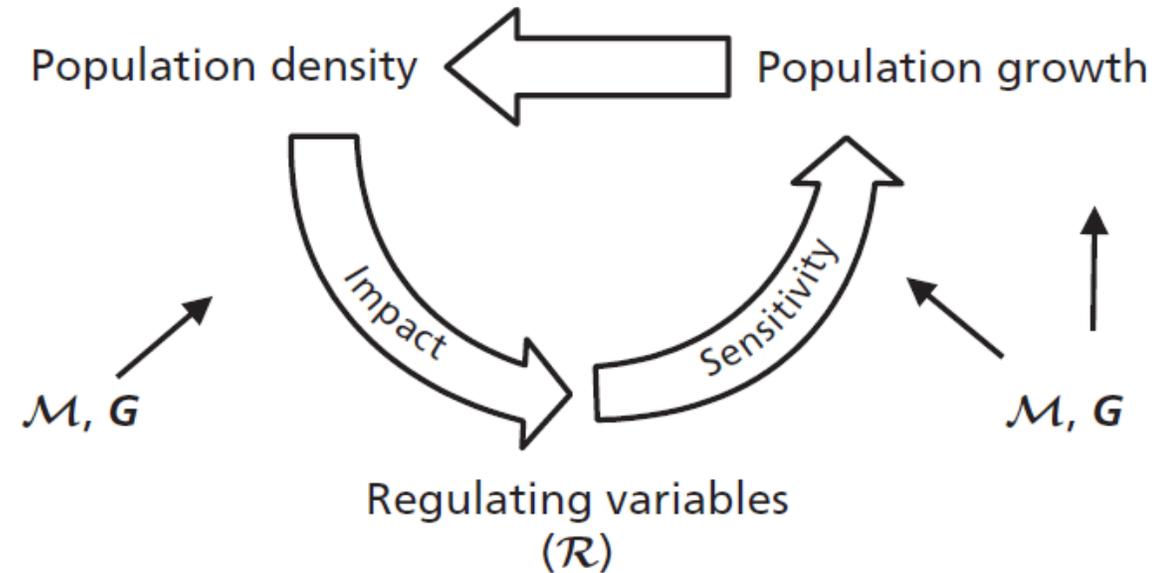
Repeatable and
predictable
diversification

Many different
mutations may have
the same effect

Negative feed-back

POPULATION REGULATION
explicit description

Explicit description is essential for
mechanistic modeling and understanding.



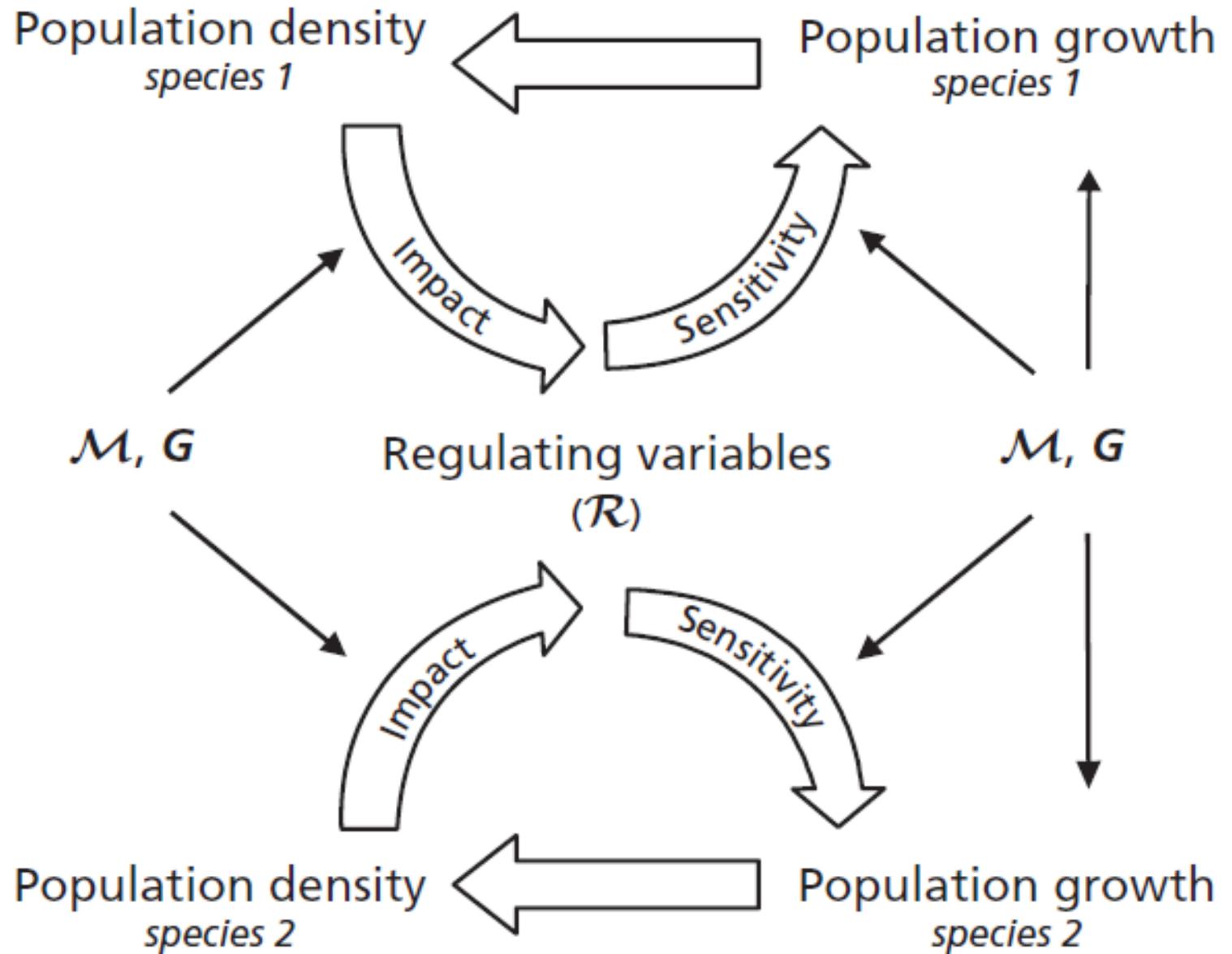
ENVIRONMENT:

\mathcal{R} : Regulating variables: resources or natural enemies

\mathcal{M} : modifying variables, \mathbf{G} : genes

INTERACTIONS BETWEEN POPULATIONS

via resources or natural enemies
or direct interactions

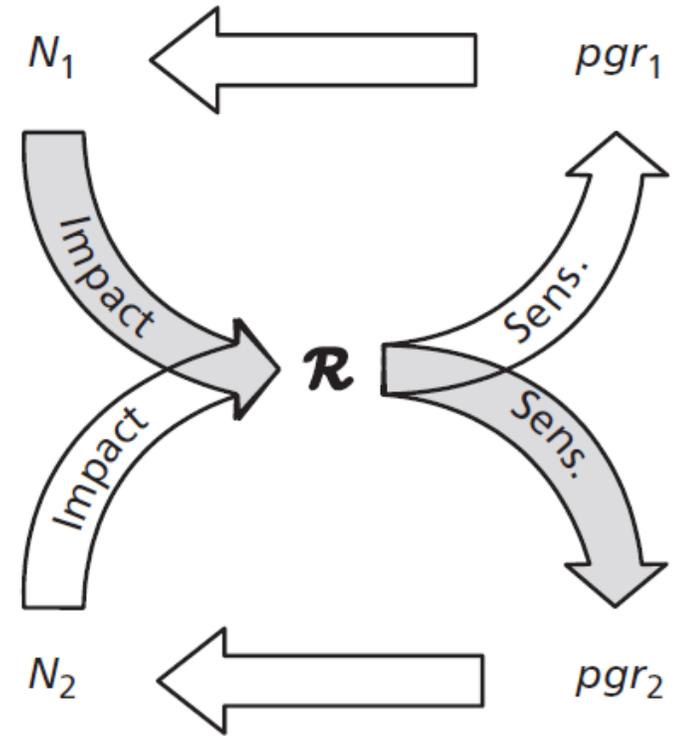


CONDITION FOR ROBUST COEXISTENCE

Principle of Robust Coexistence:

In a community of non-equivalent reproductive units regulated by more than a single regulating agent or factor robust coexistence is possible. The larger the difference between the competing reproductive units in their way of growth regulation, the more robust their coexistence is.

DIFFERENT REGULATION = DIFFERENT NICHES
┆ Coexistence



01

Impact on the environment is a necessity.

02

Any adaptive evolution affects the equilibrium level of the regulating variables.

03

Feed-back loops regulating pop. growth have to be considered.

04

Facilitation may provide food to eat or place to live: positive feed-backs and new regulating variables.

NICHE CONSTRUCTION

EXTENDED CORE THEORY

A1: Organisms reproduce. Genes, clonal identity and species identity are units of replication.

A2: The capacity of any region to support any population of reproducing individuals is finite.

A3: Replication is imprecise thus new reproductive units (gene-kinds and clonal-types) are constantly emerging.

A4: Variation of individual traits are usually cross-constrained, and the components of fitness are generically traded off.

A5: Some mutations affect survival or reproduction of the organism thus produce non-equivalent reproductive units.

EXTENDED CORE THEORY

Reproduction

A1: Organisms reproduce. Genes, clonal identity and species identity are units of replication.

A2: The capacity of any region to support any population of reproducing individuals is finite.

Struggle for existence

Inherited variation

A3: Replication is imprecise thus new reproductive units (gene-kinds and clonal-types) are constantly emerging.

A4: Variation of individual traits are usually cross-constrained, and the components of fitness are generically traded off. Not all components of fitness of a reproductive unit can change independently.

Trade offs, constraint

Natural selection

A5: Some mutations affect survival or reproduction of the organism thus produce non-equivalent reproductive units.

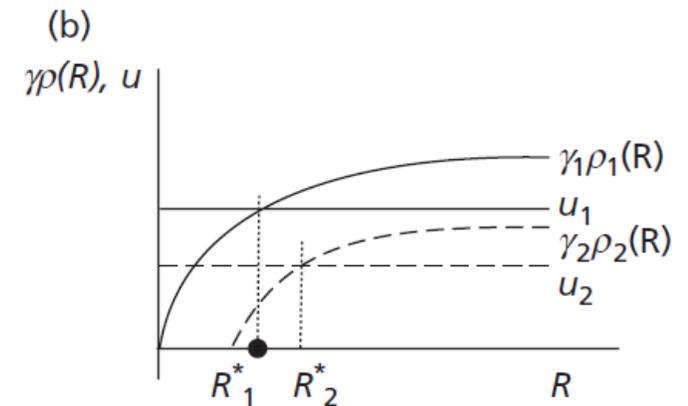
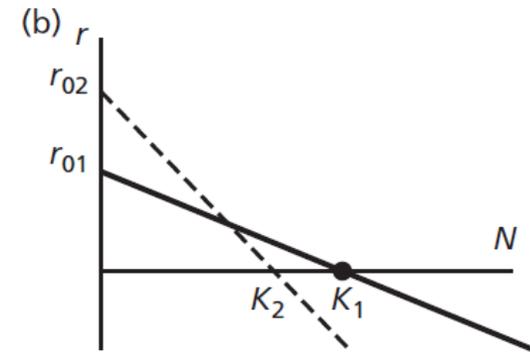
Lewontin

Darwin, ecology, developmental biology

SURVIVAL OF THE FITTEST=COMPETITIVE EXCLUSION

In a community of non-equivalent reproductive units regulated by a single common agent or factor one variety excludes all the other ones. The winner is the one whose fitness is the highest at the extremum value of the regulating agent or factor.

└ K-maximization, R^* -rule, P^* -rule



INFERENCES

- ❖ Reciprocal causation is a necessity.
- ❖ Evolution has got direction.
- ❖ It is predictable in a certain extent.
- ❖ Genes get out of focus automatically.
- ❖ Developmental bias, tradeoffs and population regulation have to be determined in order to understand the evolution of stable structures.

Reproduction

- Capacity for exponential growth

Finite world

- Regulated population growth

Finite population size

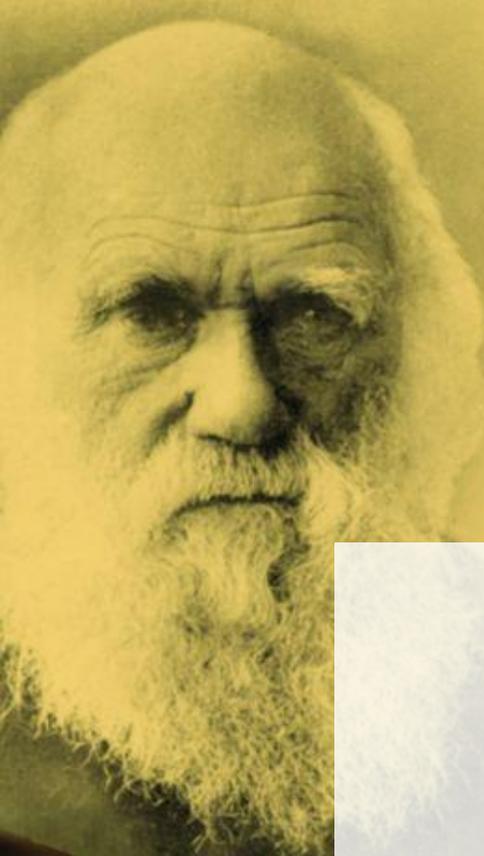
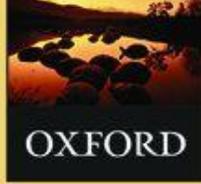
- Extinction by chance

Constraints

- Developmental bias on emergent variation

Differential survival

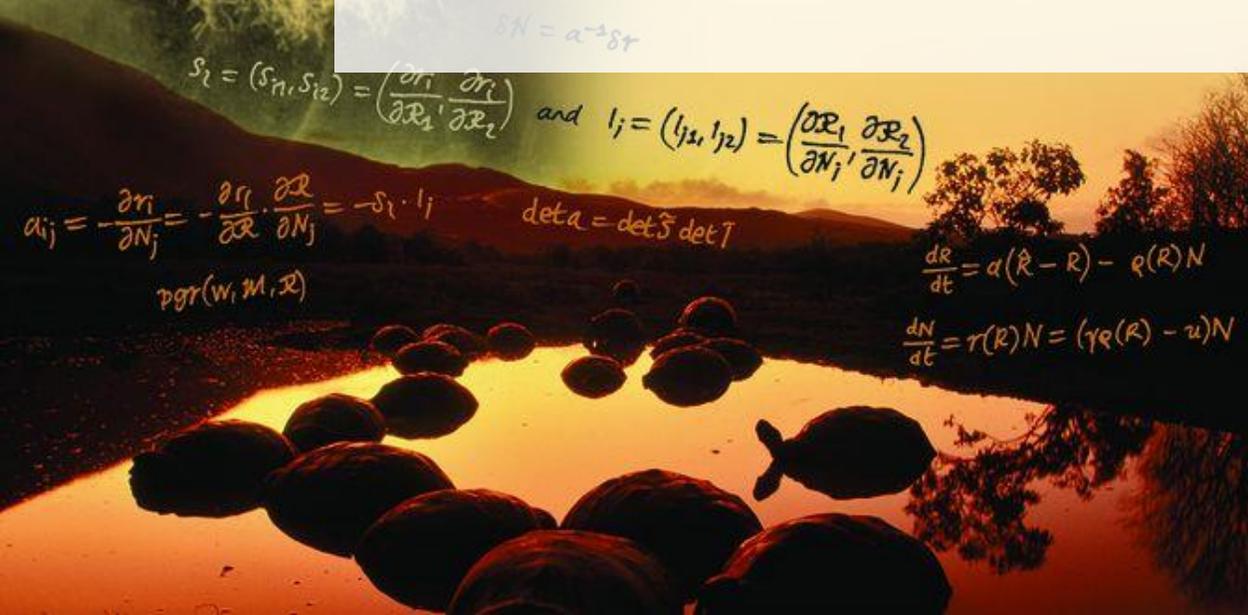
- Competitive exclusion
- Robust coexistence



THEORY-BASED ECOLOGY

A Darwinian approach

tbe.elte.hu



Axioms (A) and theorems (T) of a Darwinian theory of diversification.

A1: Organisms reproduce. They replicate their genes and their offspring inherit their genome and their clonal identity in case of asexual reproduction as well as their genes and species identity in case of sexual reproduction. Genes, clonal identity and species identity are units of replication.

T1: Principle of Exponential Growth: Population size of reproductive units increase/decrease exponentially in lack of feed-backs between per capita population growth rate (*pgr*) and population size.

A2: The capacity of any region to support any reproducing population is finite.

T2: Population sizes of reproductive units either varies between limits or the populations go extinct.

T3: Principle of Finiteness: Stochastic changes in population sizes are unavoidable due to finite population size.

T4: Principle of Regulated Population Growth: Long-run *pgr* (fitness) of any established population within a region must be exactly zero (continuous measure) or 1 (discrete measure). As the probability that a continuous random variable takes on any specific value is zero, the growth rates of the populations