Symbiotic Sympatric Speciation: Compliance with Interaction-driven Phenotype Differentiation from a Single Genotype

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experiment Akiko Kashiwagi, T. Yomo

(KK, T. Yomo; Proc. Roy. Soc. B, 267 (2000) 2367-2373;

KK; Population Ecology, 44 (2002) 71-85)

Sympatric Speciation: Difficult?

If slight genetic change leads to slight phenotype change

then distinct organisms compete each other for the same niche

Coexistence : difficult (unless neutral)

Most theory for (sympatric) speciation so far:

Search for a scheme that two groups are `effectively' isolated

* `minimize‘ interaction --- separation in space, in mating etc.

??? origin of mating preference???

?? robust speciation?? (two species; not necessary)

*   and/or almost neutral in some characteristics

?? character essential to survival ??

Recall underlying assumption in population genetics:

Selection by fitness=Function(Phenotype, environment)

but

assumption; Genotype ----> Phenotype: Single-Valued
determined uniquely

then Fitness=function(Genotype,environment)

→ individuals with little change in gene should compete under the same niche

Reconsider Genotype-Phenotype mapping

Consider seriously G -------[Development] → P;

** G-P relationship can be one to many

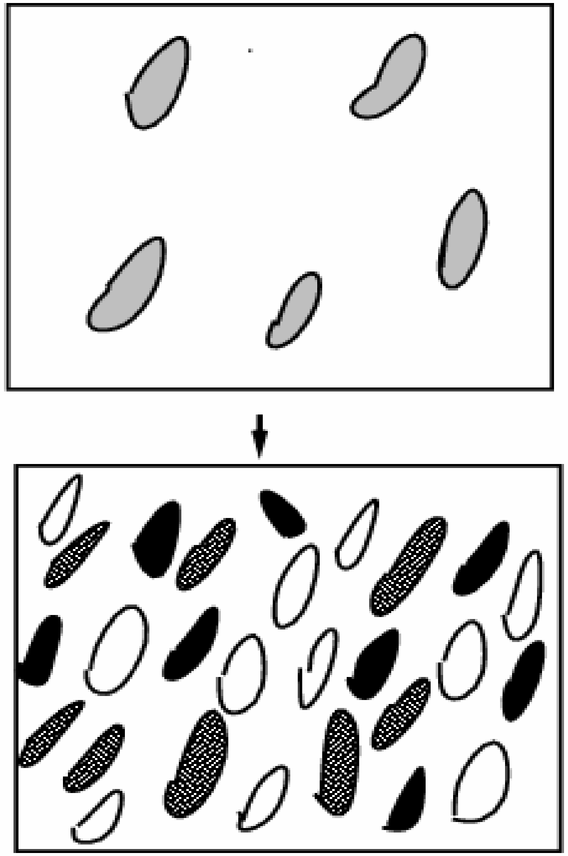
(1) Low penetrance (often in mutants?) (---observation)

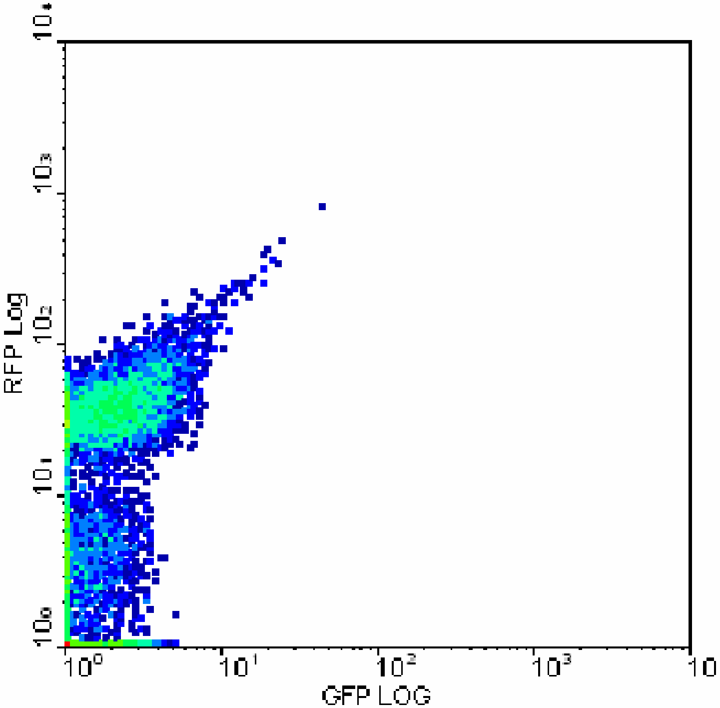
non-unique phenotypes (often in mutants)

(2) Interaction-induced differentiation in experiments

bacteria (E.coli) Shapiro, Yomo, …..

(3) Isologous diversification (---theory)





Measurement by fluoresecent proteins

Character of bacteria differentiate in a crowded condition

Isologous Diversification:

(adopted from cell differentiation model)

internal dynamics and interaction : development ⇄ phenotype

instability

distinct phenotypes

interaction-induced

$$\frac{dx^m}{dt} = f_m(x^1, x^2, .., x^k)$$

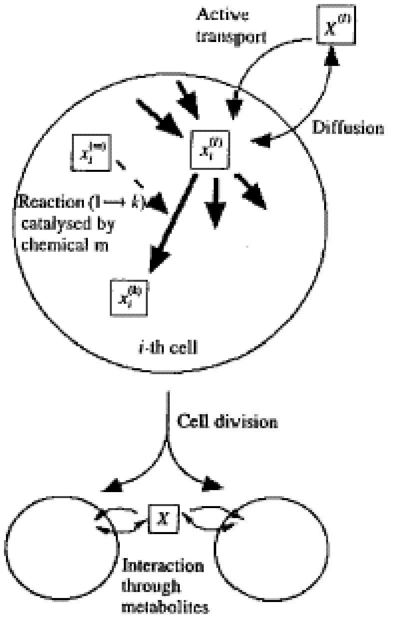
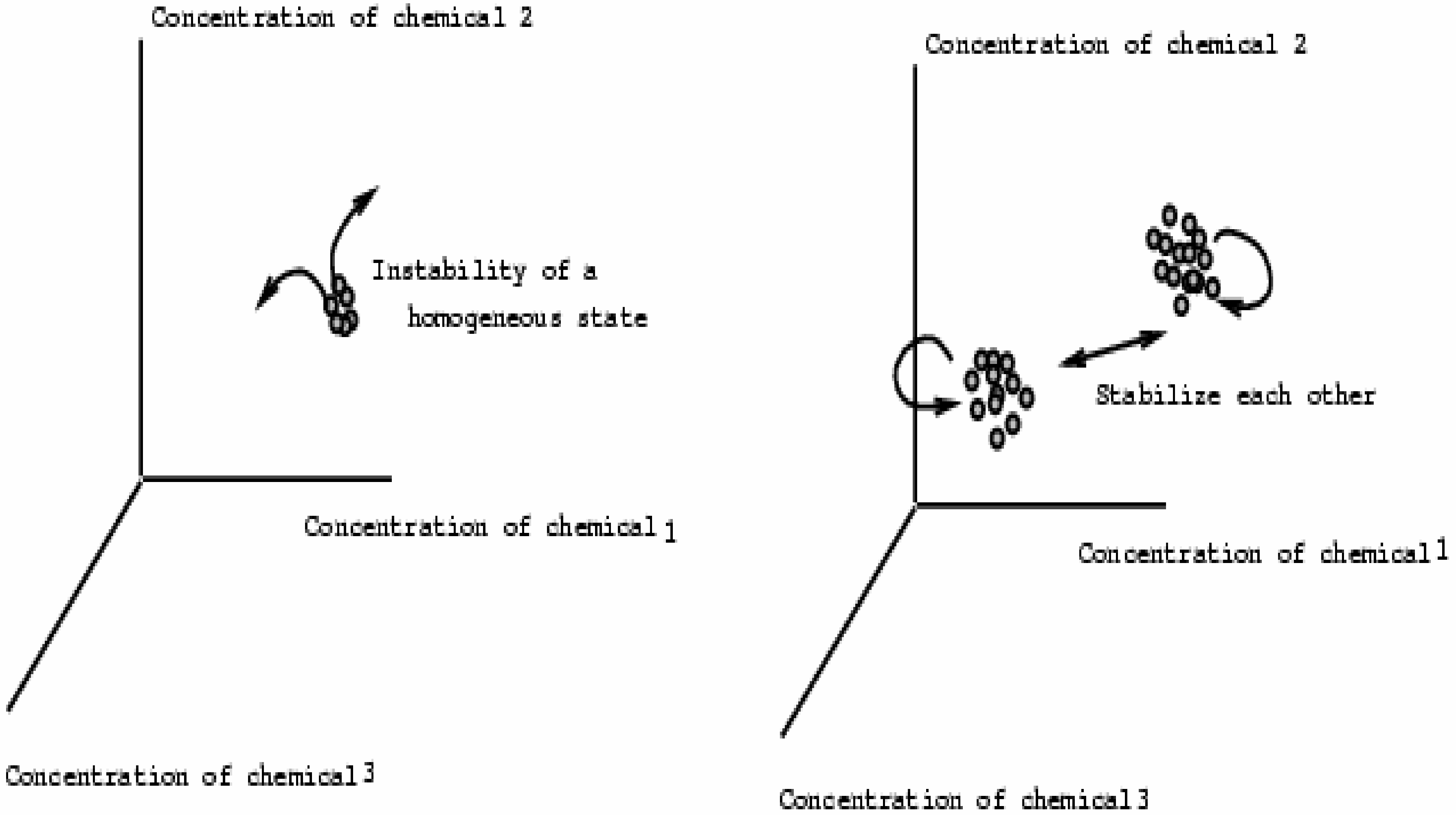


FIG. 1. Schematic representation of our model. See the appendix for the specific equation of each process.

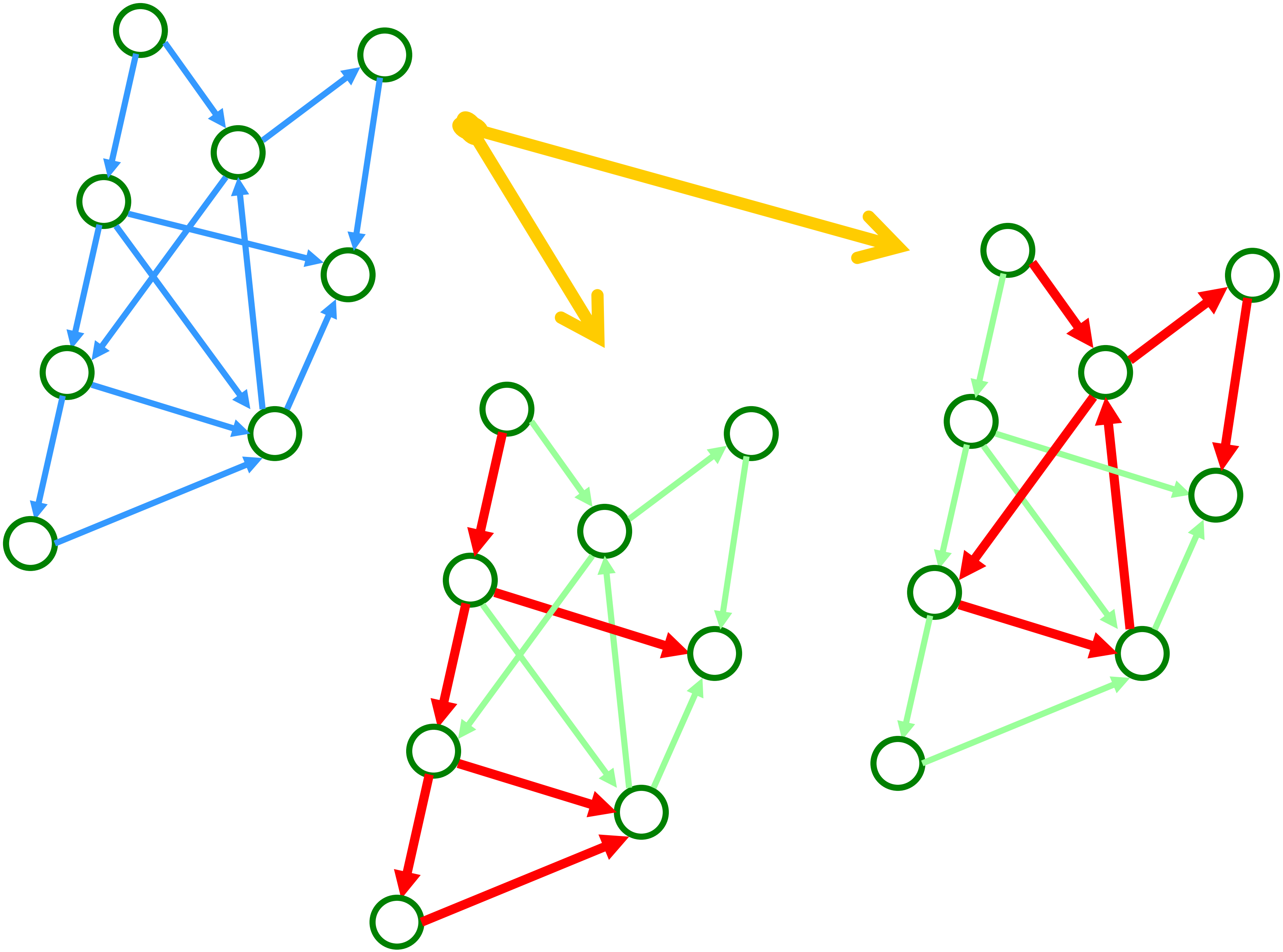
Example: chemical reaction network

specialize in the use of some path

→With the increase of the number



Distinct types are formed through instability in ‘developmental dynamics’ and interaction (both types are necessary)

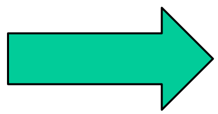


Model with Evolution :

Each unit Phenotype :: Variable X = $(X_1, X_2, .., X_k)$

Gene :: Parameter in the model e.g., reaction rate

$(g_1, g_2, ..., g_k)$

Parameter  Variable (dynamical systems)

X(t=0)→X(t)

Reproduction when maturity threshold condition (given by X) is satisfied

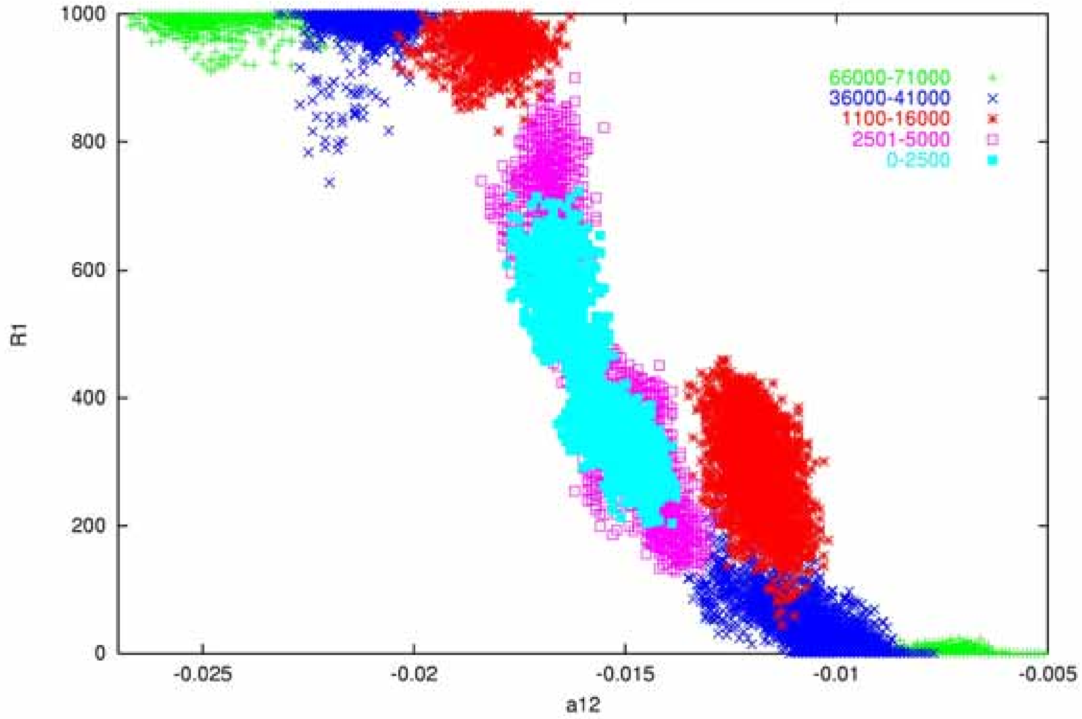
Mutation ---- small change in parameter in reproduction

Competition for survival:

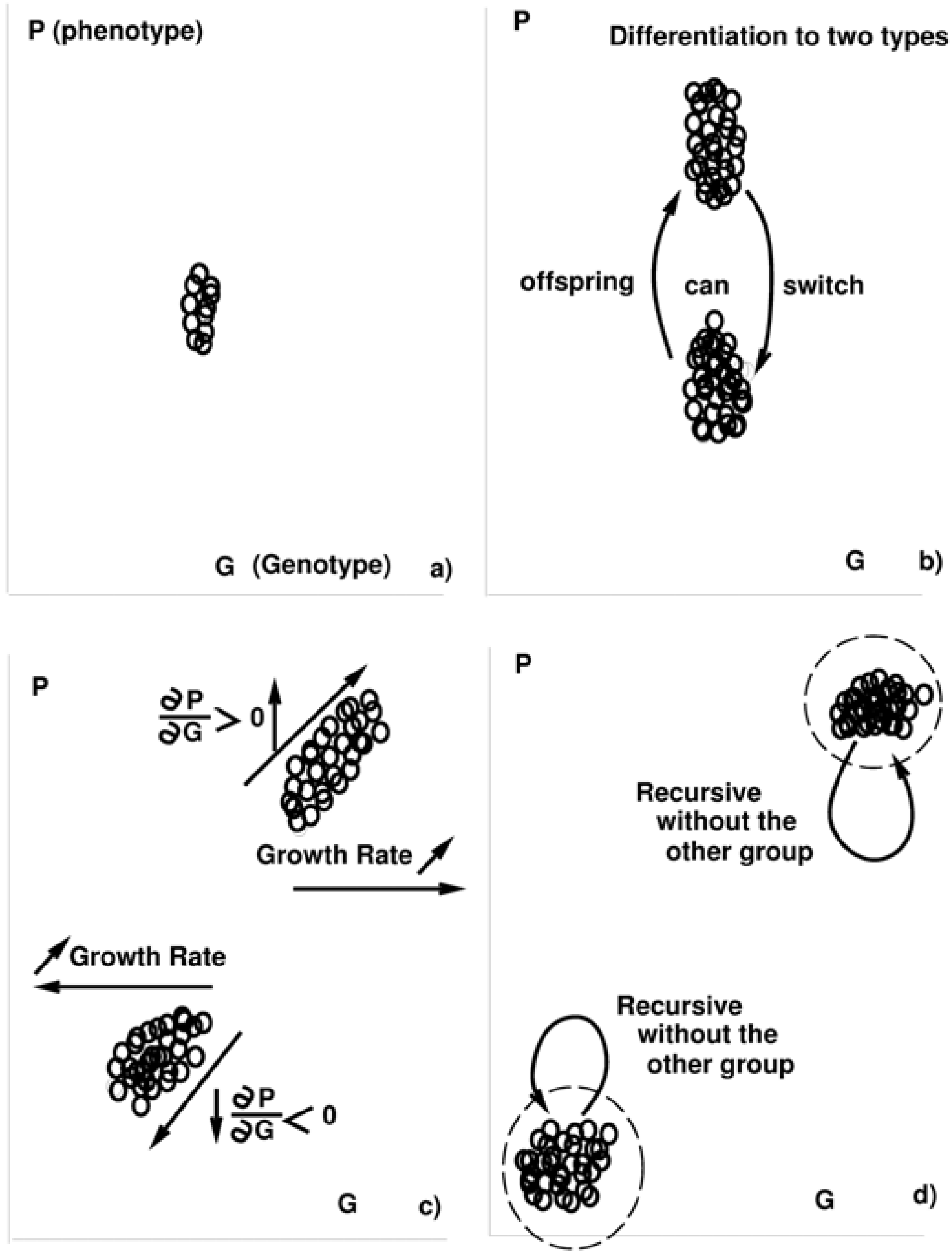
(remove some units (either randomly or under some condition))

Example of numerical simulation

Phenoptype(variable)



Gene (parameter)



P (phenotype)
G (Genotype)
a)
P
Differentiation to two types
offspring
can
switch
G
b)
P
$\frac{\partial P}{\partial G} > 0$
Growth Rate
Growth Rate
$\frac{\partial P}{\partial G} < 0$
G
c)
P
Recursive without the other group
Recursive without the other group
G
d)

Sympatric Speciation observed

(1) First interaction-induced phenotype differentiation;

homogeneous state is destabilized by the interaction

e.g., by the increase of population, decrease of resources

(2) Amplification of the difference through geno-pheno relation

Two groups form symbiotic relationship, and coevolve

(3) Genetic Fixation and Isolation of Differentiated Groups

consolidated to genotypes

(Example) chemical secreted out by one group are used as resources
for the other, and vice versa

create a niche each other and specialized in this created niche

Characteristics of the Symbiotic Sympatric Speciation

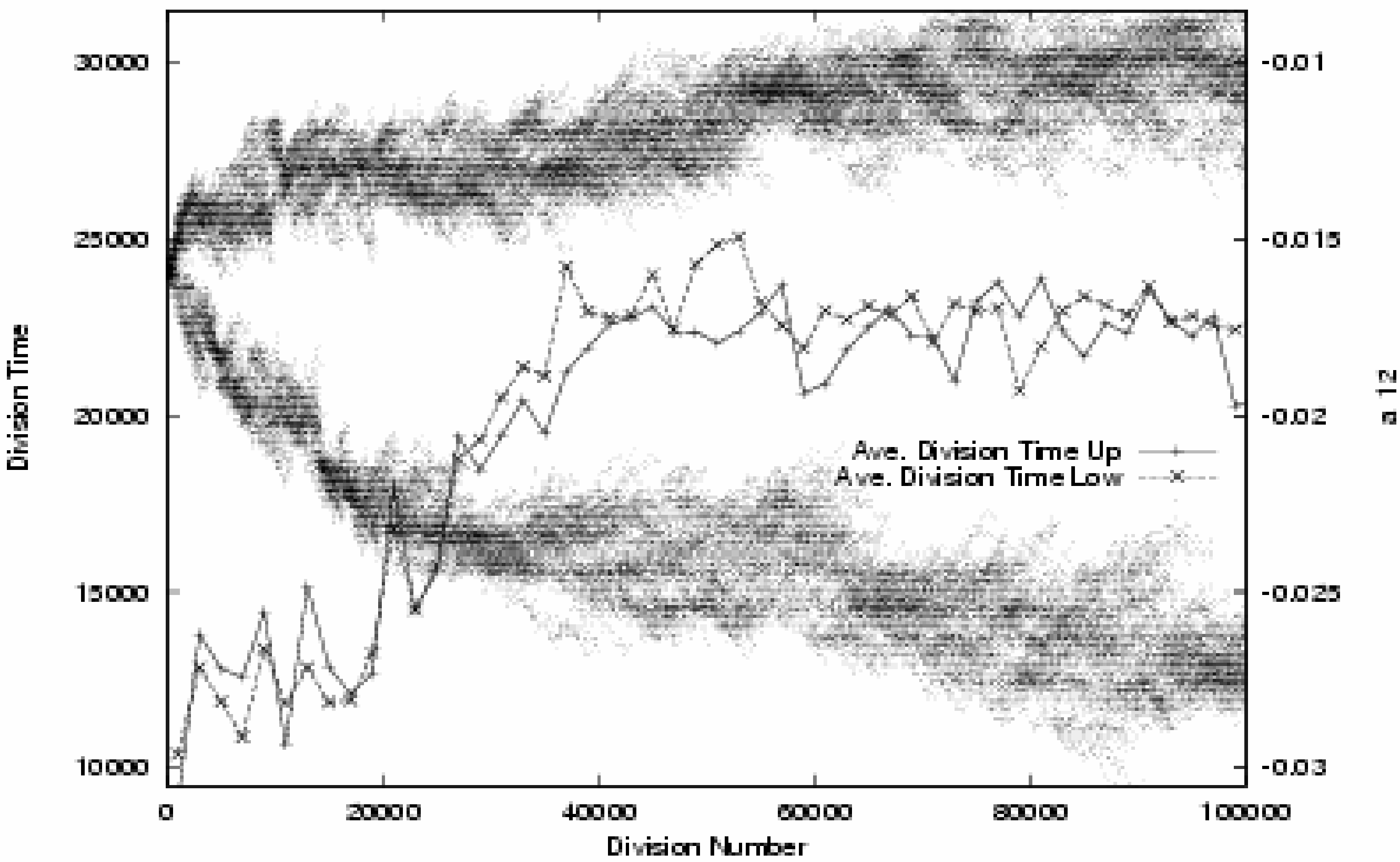
*Valid (possible) in the presence of strong interaction

*Robust speciation; two groups coevolve (fig)

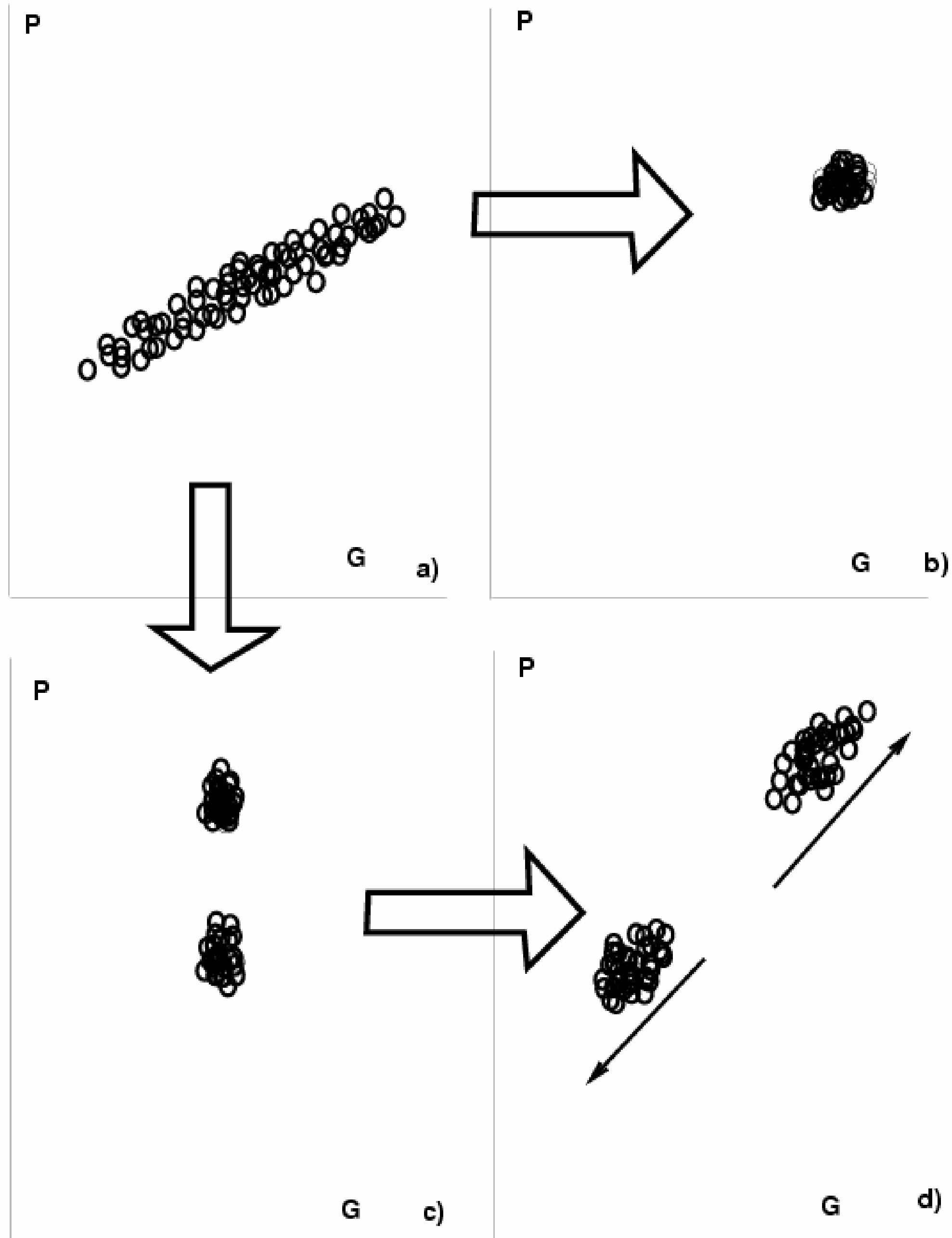
*Genetic separation always follows if there appears interaction-induced phenotypic differentiation (deterministic)

*Fast and deterministic in nature

*Relevance of the phenotypic differentiation, rather than genetic change, to genetic diversification



Division Time
Division Number
a_12
Ave. Division Time Up
Ave. Division Time Low
10000
15000
20000
25000
30000
0
20000
40000
60000
80000
100000
-0.01
-0.015
-0.02
-0.025
-0.03



P
G
a)
P
G
b)
P
G
c)
P
G
d)

Stable under sexual reproduction? i.e., stable against mixing of genes

Extension of the Model:

* two individuals satisfying maturity cond. mate randomly to have offspring

* offspring: mixed in genes (parameters) (and in loci)

i,j → m gm between g(i) and g(j)

Speciation observed Post-mating isolation

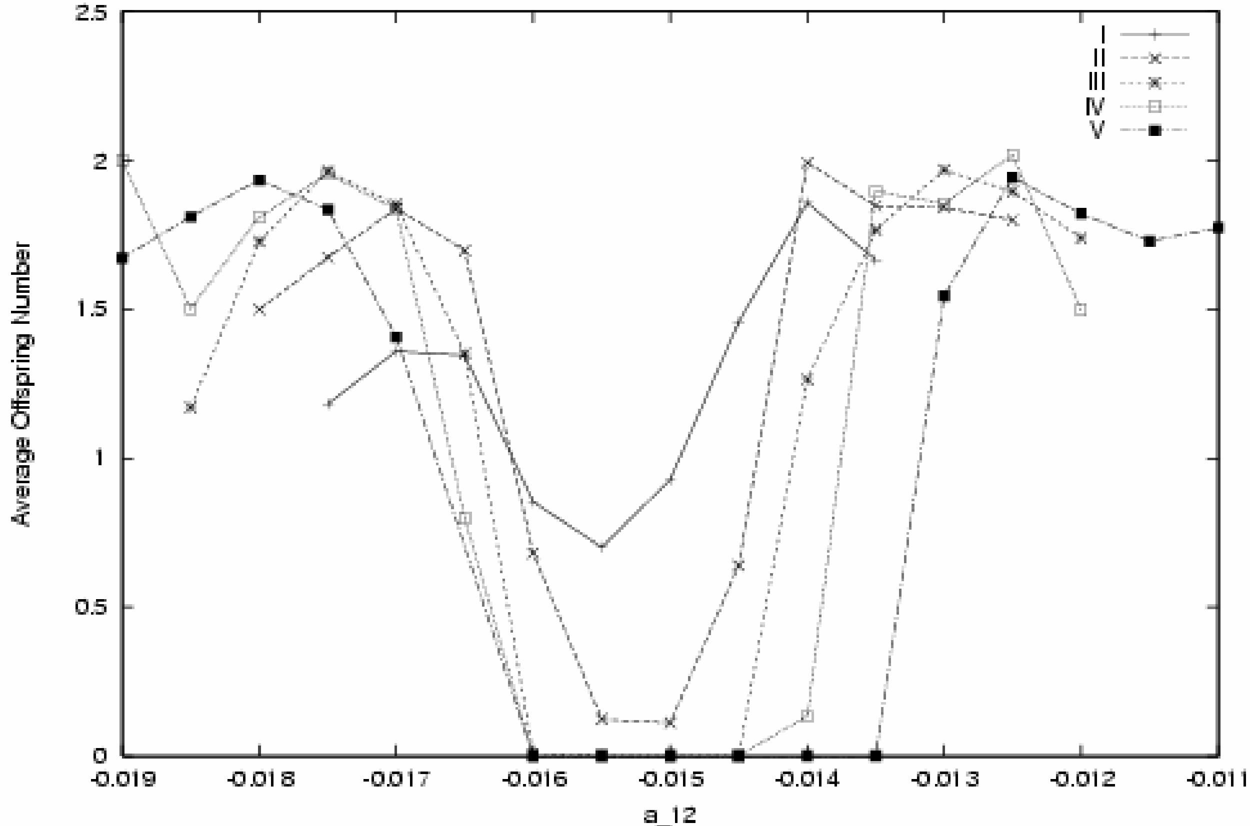
stable under mixing by sexual reproduction

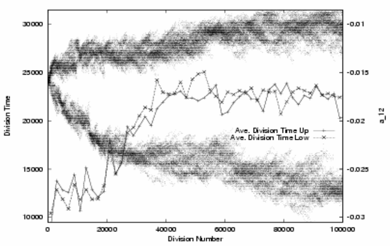
because symbiotic speciation is robust

…?still hybrid is formed…??

Stage

I→II→III→IV→V





Parameter

Completion of speciation

Although hybrid is formed, but they cannot leave offspring

interaction-induced phenotype differentiation

→ genetic change →

hybrid sterility (cf. definition of species)

→ Basis for mating preference

Evolution of mating preference

extend the model to include loci for mating preference parameters:

$$(\rho_1(i), \rho_2(i), \ldots, \rho_k(i)) \Leftrightarrow (X_1(i), X_2(i), \ldots, X_k(i))$$

if the other partner has $X_m(i) < \rho_m(j)$

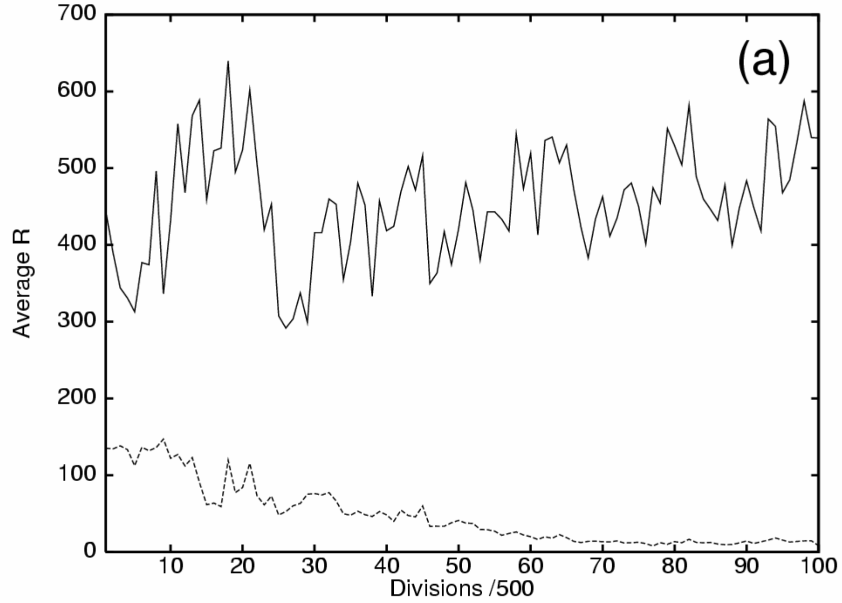
i denies the mating with j and vice versa

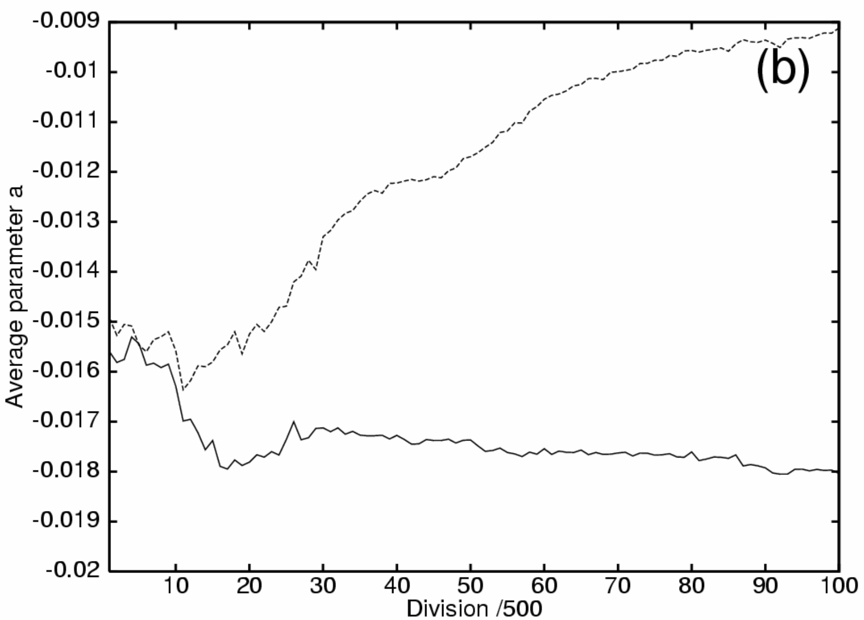
===> $\rho_m(j) < 0$ for all m, then no mating preference ;

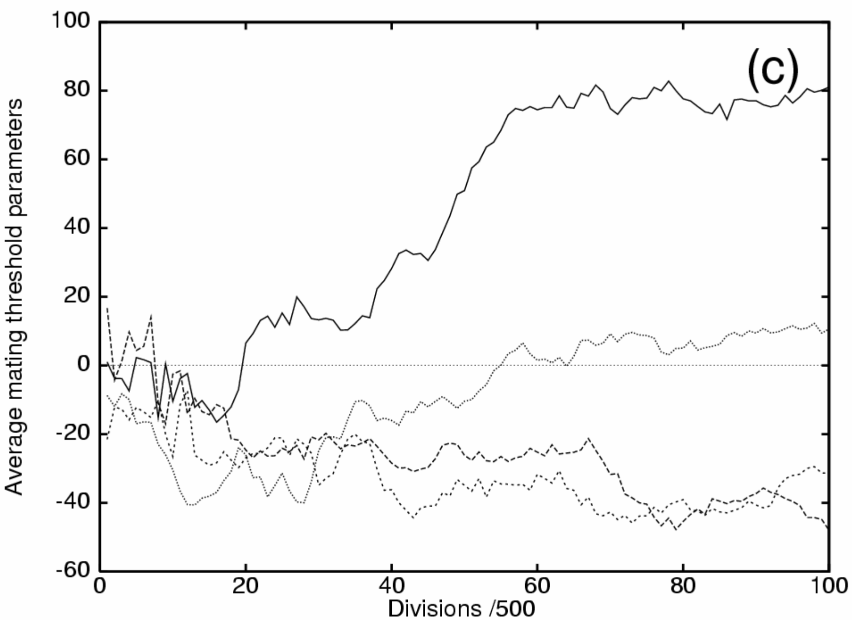
start from $\rho_m(j) < 0$ later $\rho_m(j) > 0$ for some m ==> evolution of mating preference

(postmating isolation first, premating isolation later)

* Coexistence of the two species is further stabilized by this

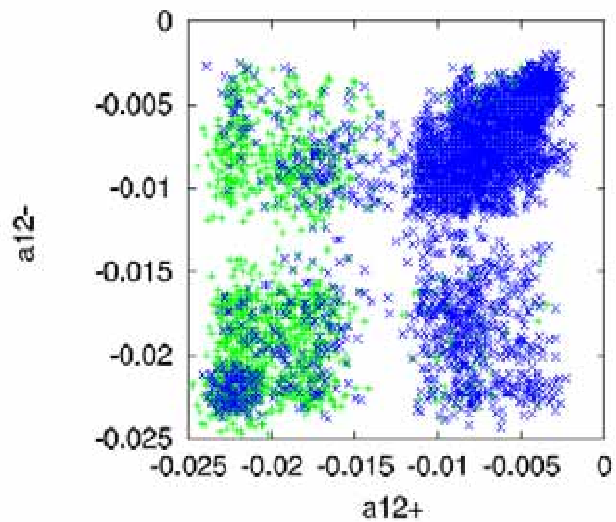

(a)
Average R
Divisions /500


(b)
Average parameter a
Division /500

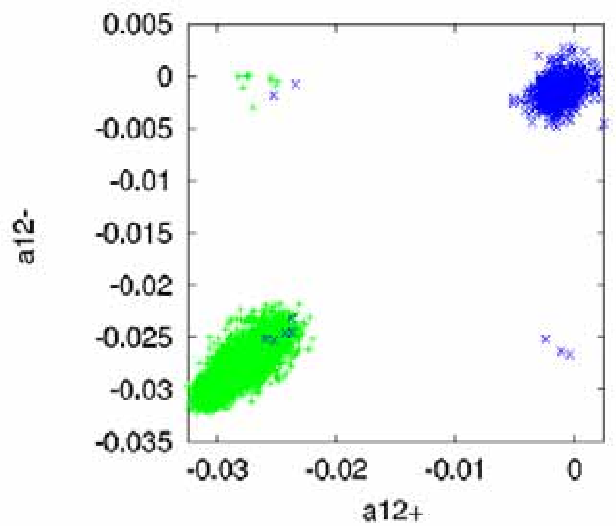

(c)
Average mating threshold parameters
Divisions /500

Two-allele case; correlation between two alleles is established??

Model with two alleles and random shuffling by mating



(a)



(b)

Speciation proceeds in the same way;

Later, correlation between two alleles are formed

Significance

* fast speciation process once the condition is satisfied

→ punctuated equilibrium; adaptive radiation

* relevance of competitive interaction to speciation

→ niche is created by each other (cf. Tilman)

• relevance of developmental plasticity (←→ the so-called phenotypic plasticity)

→ difference of tempo in evolution by species

• Degree of penetrance (why low penetrance is frequent in mutants)

* speciation in asexual and sexual reproduction: unified

Sympatric speciation can generally occur under strong interaction,

if the condition (for interaction-induced phenotype differentiation) is satisfied

Reversing the order:

phenotypic differentiation → genetic (cf Baldwin effect)
(→ postmating isolation → mating preference)
verifiable in the speciation in Cichlid??

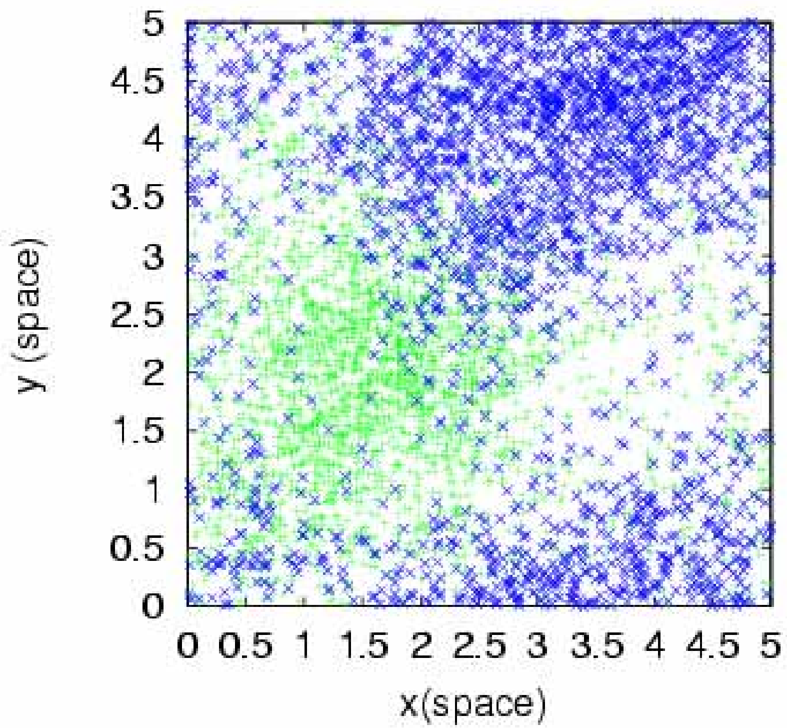
Doubting the conventional ordering???

Observed is `Correlation' A-B; but guess causal relationship A → B.

e.g., Allopatric speciation; spatial variation really cause?
(cf. the residence separation in city between rich/poor)

Sympatric speciation could be later consolidated spatially?

Two types, (blue and green) are speciated;
Later they start to be separated in space



Model with spatial location,
Slowly moving, mating within some range

Plasticity in phenotype from loose dynamics → interaction-induced phenotypic differentiation

Consolidated to Genes → Mating → Allele-correlation, Space..

Prove the above scenario?? From observation-- often remains a guess…

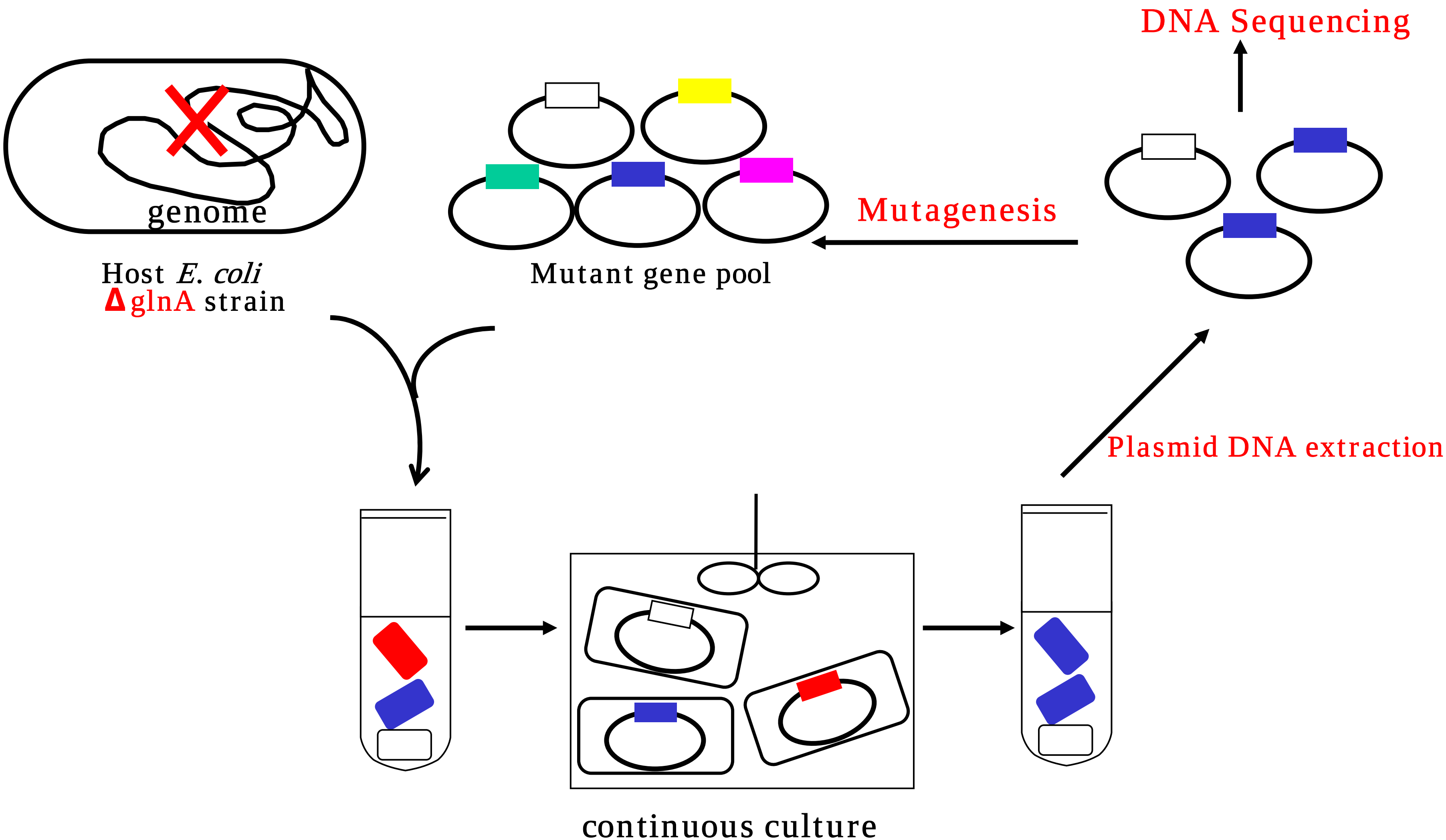
Real experiment wanted:

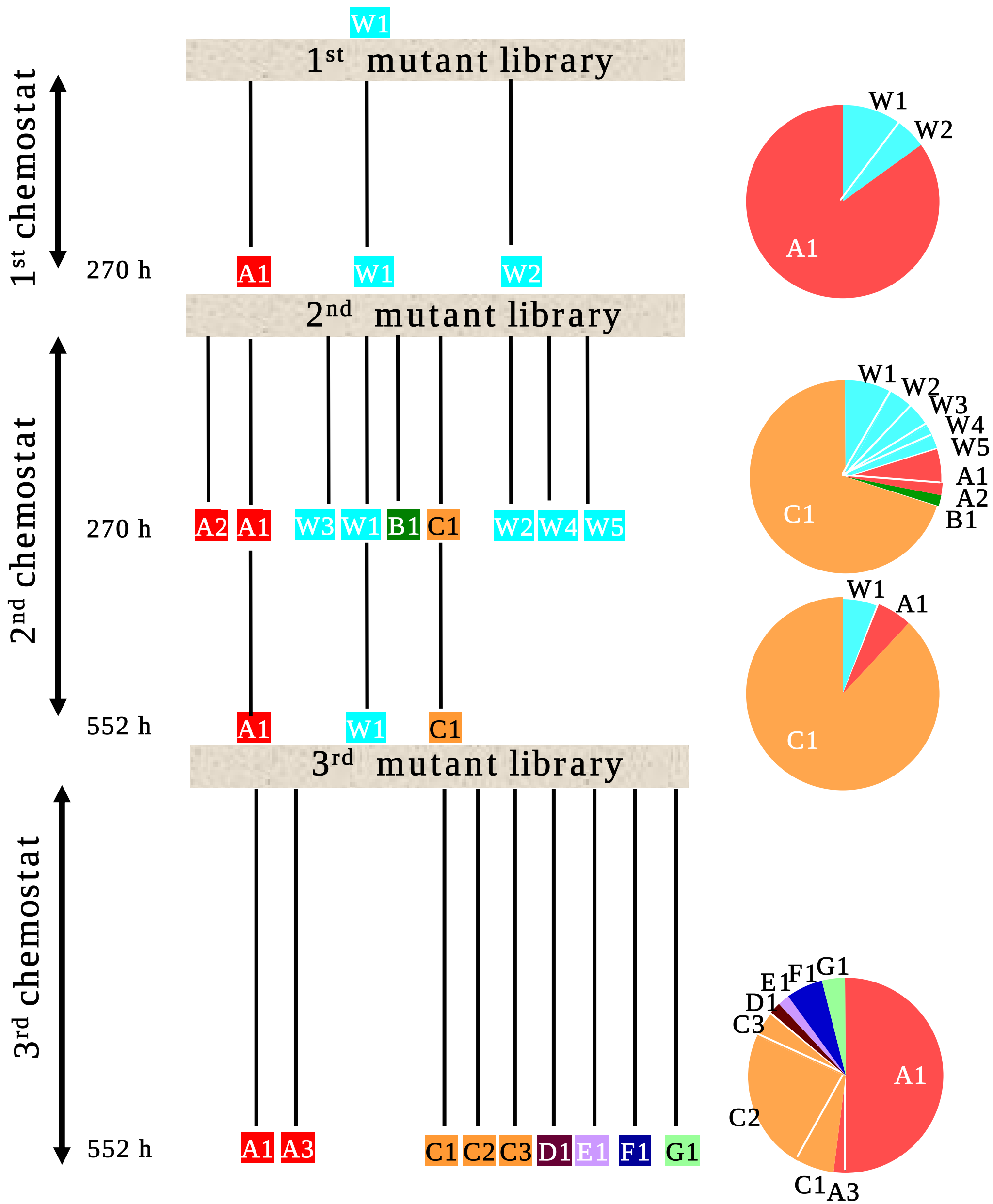
E Coli ; interaction-induced phenotypic differentiation observed

Evolution (Yomo's group)

genetic fixation --- not yet; but

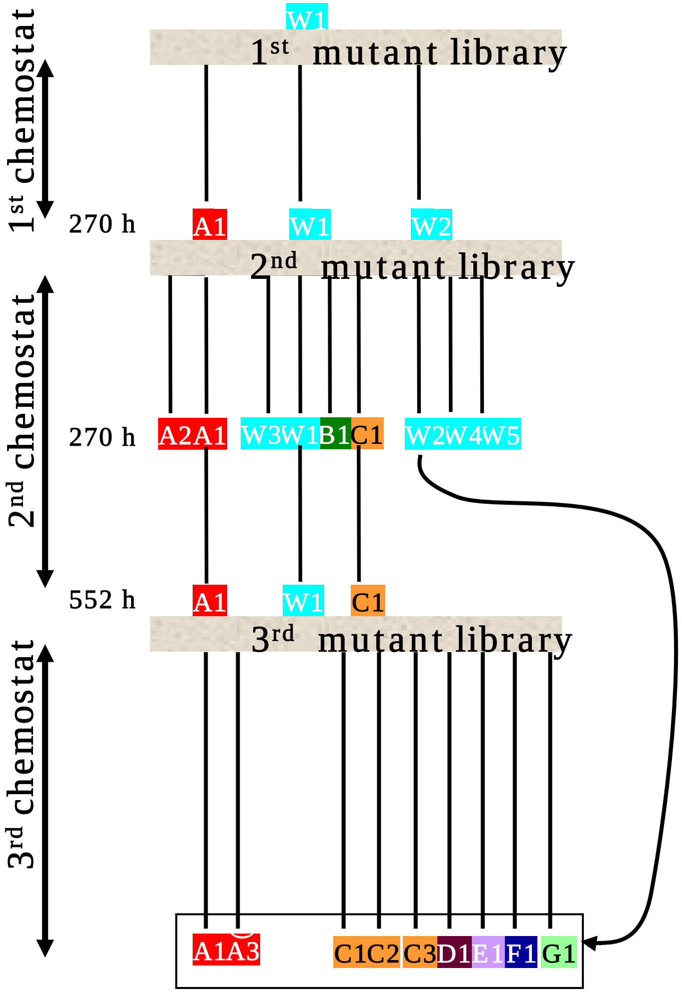
coexistence of diverse types by 'crowded' condition is confirmed


DNA Sequencing
genome
Host E. coli
ΔglnA strain
Mutant gene pool
Mutagenesis
Plasmid DNA extraction
continuous culture



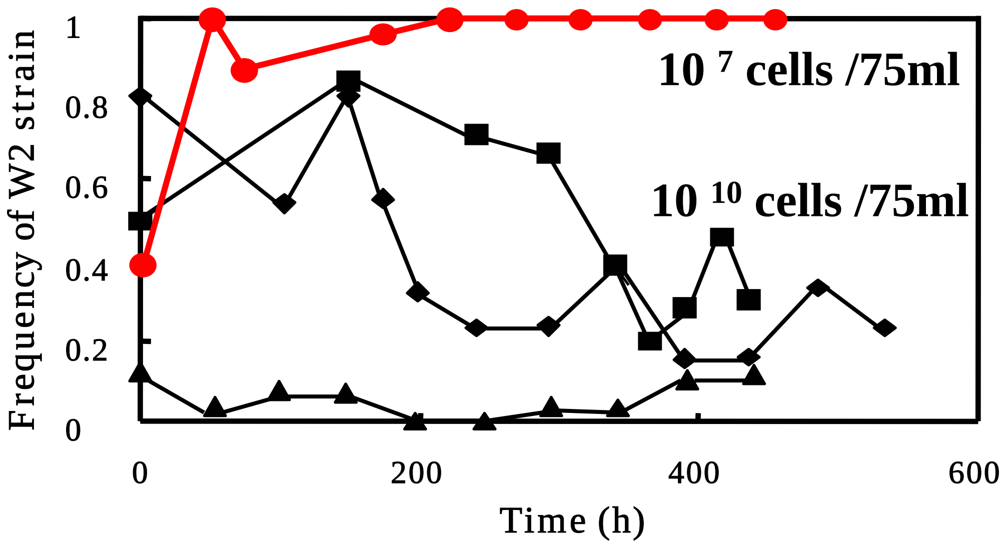
Coexistence of several types of E coli under identical enviroment

Does each mutant cell change its fitness through the cellular interaction?



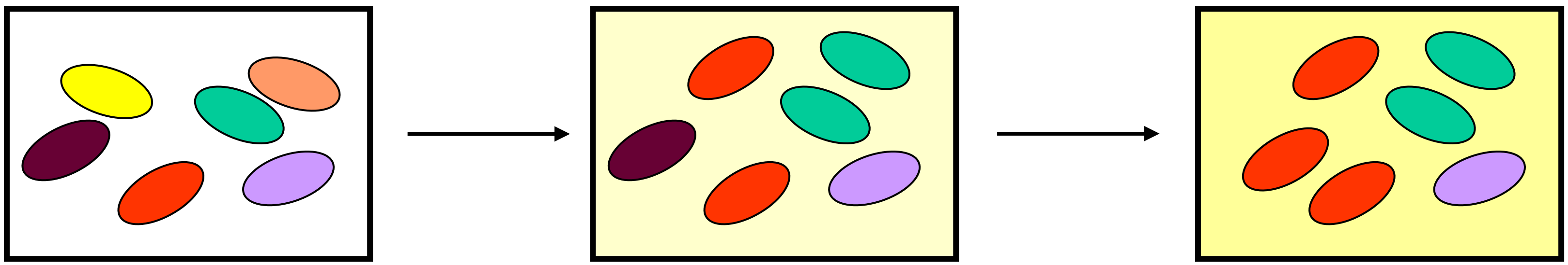
The fitness of W2 strain changes in accord to the changes of its surrounding members.

NOTE: second chemostat population and third chemostat one.

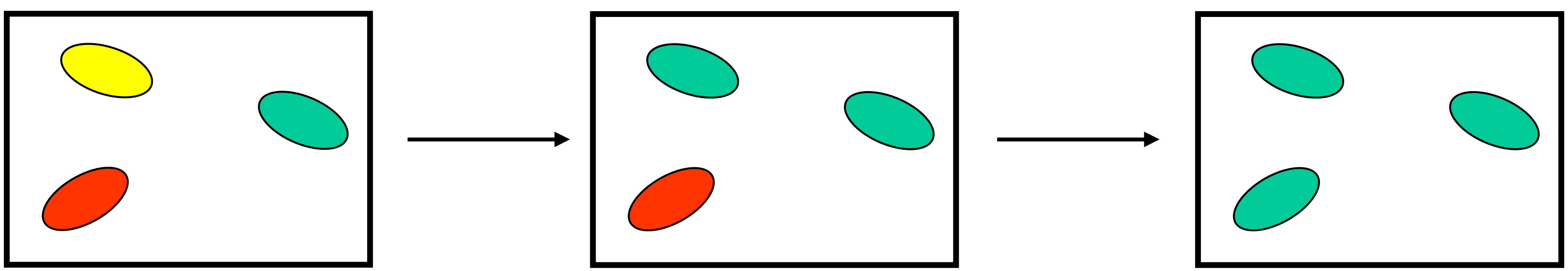


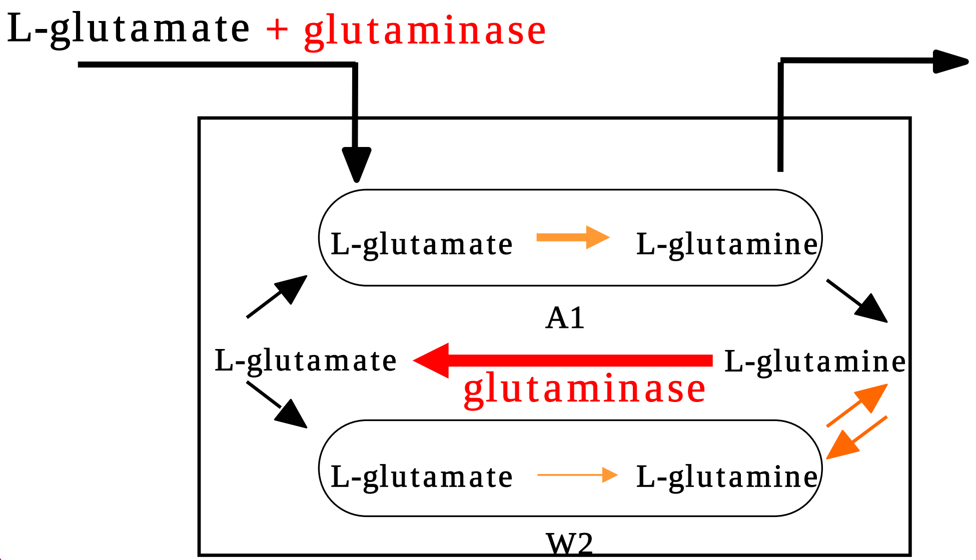
Crowded condition rendering sufficient interaction among the cells can cause fitness change and lead to the coexistence of closely-related mutants.

Crowded Condition



Diluted Condition



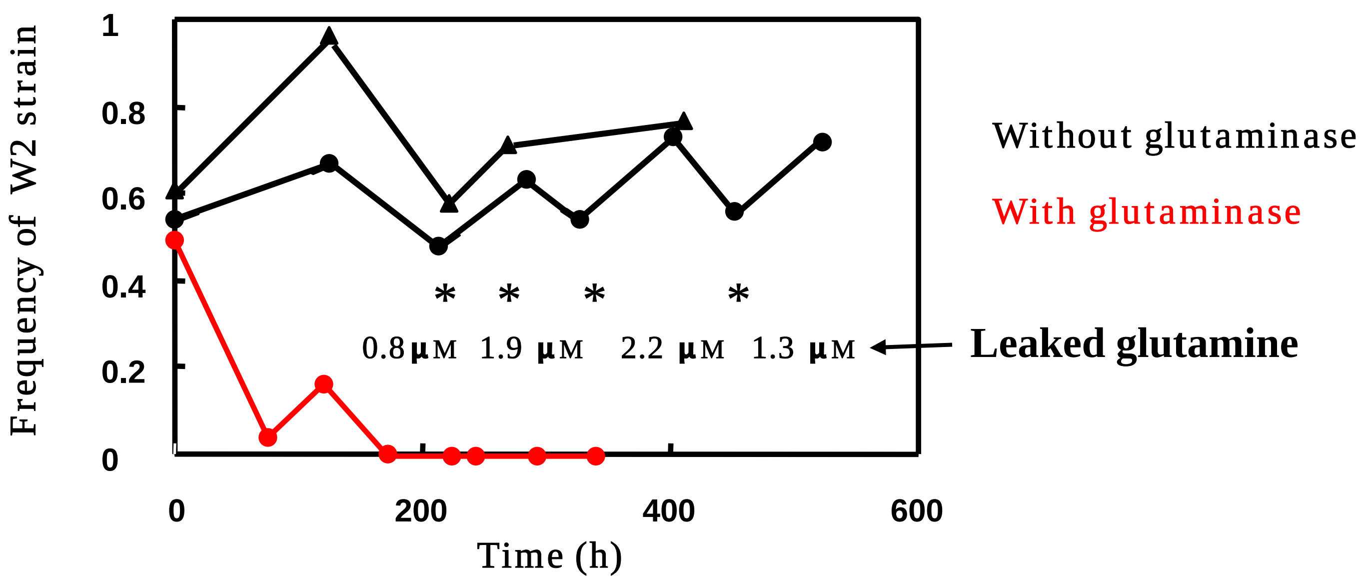


Continuous Culture

Question:

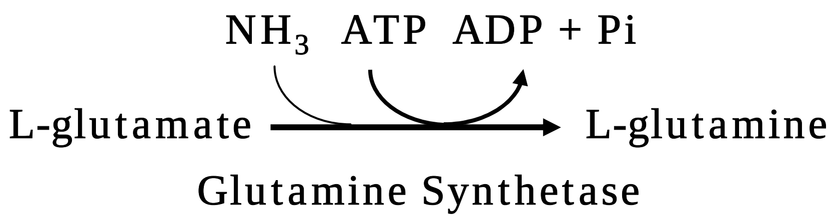
Is the coexistence temporal or reproducible?

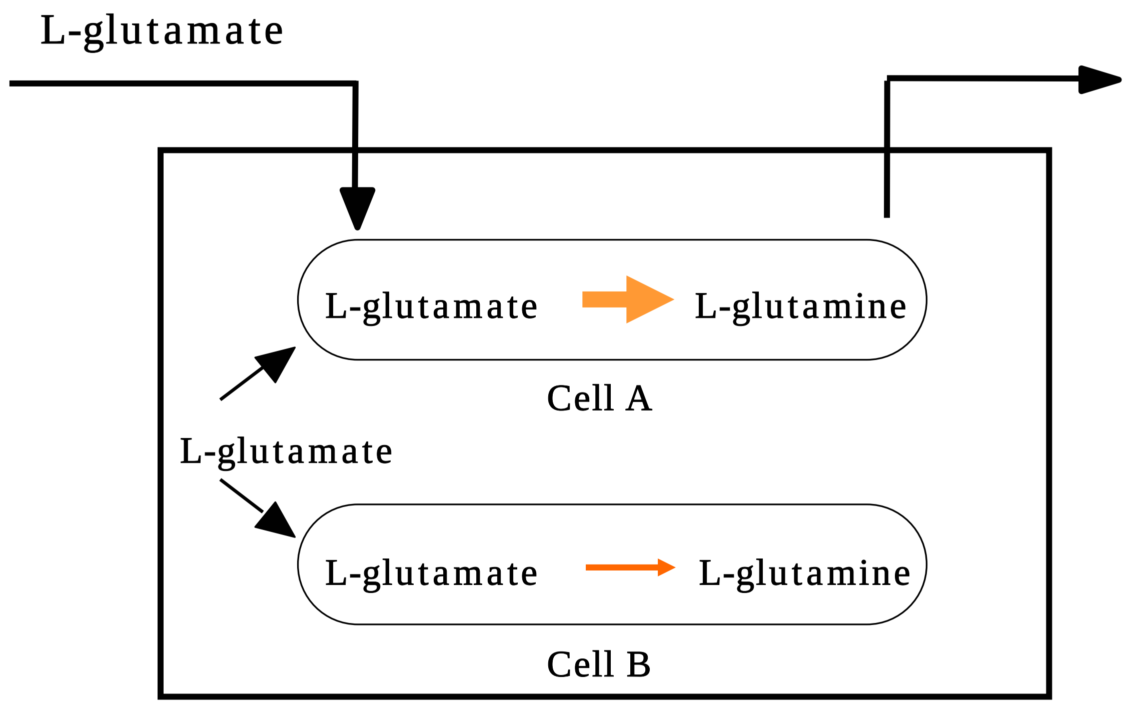
stochastic mechanisms does not explain the coexistence



The cellular interaction through the glutamine leaked into the medium is necessary for the state of coexistence.

How do cellular interactions affect molecular evolution to allow genetic diversity in a population?





Continuous Culture