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

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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 \( \text{fitness} = \text{Function(Phenotype, environment)} \)

but

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

then \( \text{Fitness} = \text{function(Genotype,environment)} \)

individuals with little change in gene should compete under the same niche
Reconsider Genotype-Phenotype mapping

Consider seriously \( G \rightarrow [\text{Development}] \rightarrow P \);

** 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)
Character of bacteria differentiate in a crowded condition

Measurement by fluorescent proteins
Isologous Diversification:

(adopted from cell differentiation model)

internal dynamics and interaction: development ⇔ phenotype

instability

distinct phenotypes

interaction-induced

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 $\rightarrow$ Variable (dynamical systems) $X(t=0) \rightarrow X(t)$

**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

Phenotype (variable)
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
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)

\[ i_j \rightarrow m \quad g_m \text{ between } g(i) \text{ and } g(j) \]

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

\[\Rightarrow \rho_m(j) < 0\]  for all m, then no mating preference ;

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

(postmating isolation first, premating isolation later)

* Coexistence of the two species is further stabilized by this
Two-allele case; correlation between two alleles is established?

Model with two alleles and random shuffling by mating

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 $\rightarrow$ genetic (cf Baldwin effect)
($\rightarrow$ postmating isolation $\rightarrow$ mating preference)

verifiable in the speciation in Cichlid??

Doubting the conventional ordering???

Observed is `Correlation' A-B; but guess causal relationship A $\rightarrow$ 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 $\rightarrow$ interaction-induced phenotypic differentiation

Consolidated to Genes $\rightarrow$ Mating $\rightarrow$ 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

coeexistence of diverse types by ‘crowded’ condition is confirmed
Host *E. coli* strain

Mutant gene pool

Mutagenesis

DNA Sequencing

Plasmid DNA extraction

continuous culture
Coexistence of several types of E. coli under identical environment
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.
Question: Is the coexistence temporal or reproducible?  

Without glutaminase  

With glutaminase  

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?

Glutamine Synthetase

\[ \text{NH}_3 + \text{ATP} \rightarrow \text{ADP} + \text{Pi} + \text{L-glutamine} \]

Cell A

L-glutamate \(\rightarrow\) L-glutamine

Cell B

L-glutamate \(\rightarrow\) L-glutamine

Continuous Culture