Who Replaces Whom? Local versus Non-local Replacement in Social and Evolutionary Dynamics

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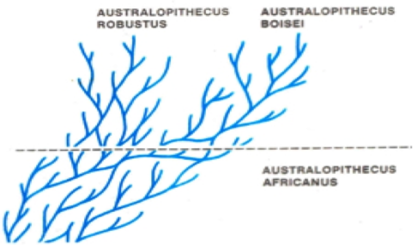
Outline

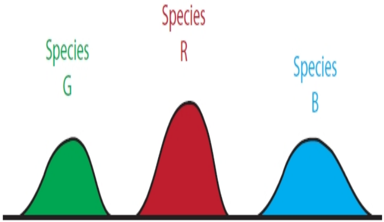
- Main concepts
- Research question
- Here we show that ...
- The agent-based model
- Probabilistic Analysis
- Discussion

Self-organization and Emergence

Complex Systems

- Typically, complex patterns **emerge** in a system of interacting individuals that participate in a **self-organizing** process.
- One of the **most typical patterns** is clustering: (biological) Speciation.





the emergence of multi-modal distributions

patterns of structured diversity

Adaptation *versus* Speciation

Artificial societies: simulations

Speciation and Adaptation appear as two opposing phenomena, not achieved by the same model.

Natural selection is neither necessary nor sufficient for the creation of Speciation.

- Natural selection
  1. the existence of an inhomogeneous impact on the individual dynamics.
  2. how global influences are considered when modeling Adaptation in an evolutionary process.
- Adaptation
  1. the improvement of some utility function (reproduction, profits, etc).
  2. finding strategies to better deal with the surrounding environment.
- Modeling Adaptation and Natural Selection
  1. Fitness Landscape models.
  2. Locally-interacting models: the exclusive result of local interactions.

Research question

The phenotype of living beings is not the only domain where patterns of structured diversity are observed. Phenomena include distributions of:

1. cultural behavior (opinion dynamics)

   R. Axelrod: how local convergence can generate global polarization.

2. languages and dialects
3. herd behavior in finance

Would the emergence of either adaptation or speciation be dependent on the constraints imposed on the interaction process?

Examples (from Biology) of possible constraints:

1. fitness landscapes
2. geographic barriers
3. assortative mating

Interaction Event

The system evolves from one time step to the other, by the following three components:

1. selection of agents (**S** **S**),
2. application of interaction rules (**I** **I**),
3. replacement of agents (**R** **R**).

- Any interaction event (mating, communication,...) $\rightarrow$ the sequential application of these three steps.
- Related studies: on synchronous updates, on non–overlapping (NOLG) and overlapping generations (OLG) in biology and economics.
    1. In OLG models, the population is updated after each single interaction event (and not after N events).
    2. The new state of an individual that is updated is **from then on** taken into account in the later iterations.

Here we show that

1. When the interaction is constrained (e.g., assortative mating)
   - important qualitative difference between OLG and NOLG models:
     1. speciation is observed in the former, but not in the latter case
     2. adaptation is favored by the latter and hindered by the former
2. The determinant role is played by **Locality** in replacement (the choice between local and non-local replacement) and **not** by the distinction between OLG and NOLG.
3. Even though locality also impacts selection and interaction mechanisms, it is on the replacement mode where relies the fundamental difference with respect to the conditions required for either adaptiveness or speciation.

In addition to the coincidence in time (synchronicity) there must be a coincidence in space (locality)

Adaptive Walks on Fitness Landscapes - S I R

Wright-Fisher model with non–overlapping generations

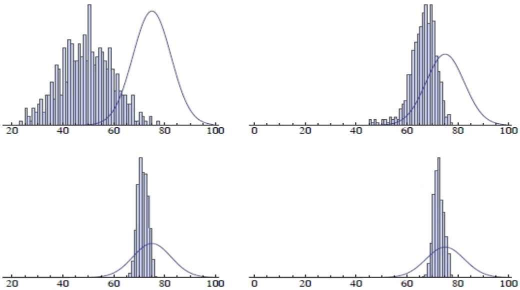
- N individuals in the original generation ($g = 0$) with sexual reproduction and constant population size.
- N mating events are performed until a new generation of N individuals is complete.
- The phenetic trait (locus) of the two chosen parent individuals are x_i and x_j, taking discrete values (from 0 to 99).
- Rules involved into the creation of a new individual (the mating event):
  1. selection of two individuals (i and j) with a probability proportional to their fitness ($F(x)$, x being the trait).
  2. application of recombination and mutation rules $x_{new} = (x_i + x_j)/2$
  3. replacement of an agent from the parent generation.

Mutations are implemented by adding a random value to x_{new}.

A single–peaked fitness function with a peak at trait 75

$$F(x) = \frac{1}{15} e^{-\frac{2}{225}(-75+x)^2} \sqrt{\frac{2}{\pi}} = \mathrm{N}(\mu, \sigma^2). \quad (1)$$

with $\mu = 75$ and $\sigma^2 = 7.5$. Due to mutations, the population maintains a certain amount of variation ($g = 0, 1, 2, 5$).

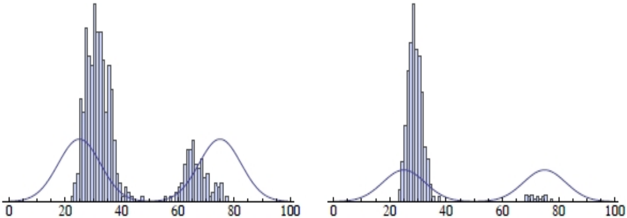


A two–peaked fitness function - S I R

Sympatric Speciation (no geographic constraints divide the population)

The fitness (that is, the probability of choosing an individual in state x) is defined by a mixture of two normal distributions $\mathrm{N}(25, 7.5)$ and $\mathrm{N}(75, 7.5)$

$$F(x) = \frac{e^{-\frac{2}{225}(-75+x)^2}}{15\sqrt{2\pi}} + \frac{e^{-\frac{2}{225}(-25+x)^2}}{15\sqrt{2\pi}}. \quad (2)$$



$$g = 0, 1, 2, 5$$

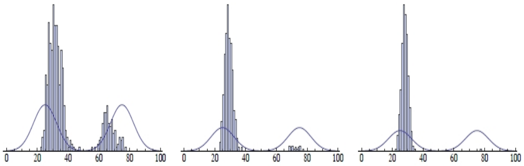
Disappearance of clustering is very fast, all the population concentrates at one of the peaks. Difficulties in generating a stable co–existence of species.

Assortative Mating - S I R

Individuals need to be similar in order to produce offsprings

Two chosen individuals i and j only produce an individual for the new generation if the their difference is small (here $|x_i - x_j| < 10$). Rules:

1. selection of 2 individuals with a probability proportional to their fitness,
2. application of recombination and mutation rules if the individuals are similar,
3. replacement of an agent from the parent generation using NOLG rule (asynchronous update).



The interbreeding of a pair of individuals from either peak is prohibited by the assortativity condition.

The introduction of interaction constraints leads to co–existence of clusters of individuals.
The rules used to model self–organization in opinion dynamics are very similar:

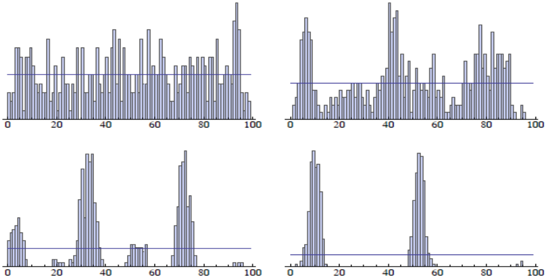
- selection of two individuals, *all with equal probability*.
- application of recombination and mutation rules *if the individuals are similar*,
- *update* of one parent agent *using* OLG rule (synchronous update).

1. Mutations, sometimes interpreted as cultural drift, are not always taken into account.
2. There are no global influences (fitness landscapes) $\longrightarrow$ the probability of selection is equal for all individuals.
3. The locally–interacting model (LI model) is implemented as a model of overlapping generations (OLG).

Cluster Formation in Population Genetics - S I R

Locally–interacting model with Assortative Mating

$N = 500$ individuals initially distributed uniformly over the traits 0...99.



- Update only takes place if the distance between two individuals ≤ 10.
- Initial inhomogeneities are reinforced during the process such that clusters of individuals are formed.
- The co–existence of "reproductively isolated" sub–populations is rather stable during long periods ($g = 1, 10, 40, 100$).

Overlapping versus Non–overlapping Generations

Difference between the LI model and the WF model → a crucial effect.
There are three potential sources of the different behavior:

1. There is uniform fitness in the LI model but a peaked landscape in the WF model.
2. The LI model is implemented as a model of OLG whereas the WF model implements NOLG.
3. In the LI model, the state change of an individual is modeled whereas the creation of a new individual is considered in the WF model.

Even adapting 1 and 2, the behavior of the model is in drastic contrast to the behavior of the LI scheme, being similar to the original WF model with NOLG.
The qualitative differences between the WF model and the LI model are neither due to different ways of dealing with generations (OLG versus NOLG) nor to the choices of different fitness landscapes.

Local versus Non–local Replacement

Will the new individual replace one of its parents or an arbitrary individual from the generation?
The two alternatives result in qualitatively different dynamical behaviors.

- *Local replacement:* new individual replaces one of its parents and
- *Non–local replacement:* an arbitrary individual is replaced by the new one.

NOLG models $\rightarrow$ non–local replacement $\rightarrow$ a child may replace someone distant from the "position" of the parents.

- Non–local replacement undermines the effects of assortative mating, because an individual with a trait x can effectively be replaced by an individual with trait y even if $|x - y| > 10$.

(Non–)Adaptiveness of Local Replacement S I R

- Modeling speciation in a model with a fixed population size requires that the update process operates with local replacement $\longrightarrow$ adaptiveness is lost $\longrightarrow$ the population is pushed away from the peak.
- Individuals close to the peak, though frequently chosen, are not replaced by individuals with low fitness (rarely chosen) so that the proportion of fit individuals does not increase.
- To the contrary, mutations tend to drive fittest individuals away from the peak. Hence, the mode of replacement in these two models with almost the same microscopic rules has a dramatic effect on the dynamics behavior.
- Cluster formation (or speciation) and adaptiveness are in the context of these models two opposing phenomena.

Probabilistic Analysis of a Minimal Model

- Allowed traits : the states left (L), right (R) and intermediate (M).
- Probabilities of transitions from one trait to the other $\longrightarrow$ Markov chains
- The transition structure of chains $\longrightarrow$ the dynamic mechanisms which different replacement modes give rise to.

The state of the new individual $\longrightarrow$ the recombination of the parent states.

$\alpha = 1 \longrightarrow$

	L	**M**	**R**
L	L	M	M
M	L	M	R
R	M	M	R

$\alpha_{LR} = \alpha_{RL} = 0 \longrightarrow$

	L	**M**	**R**
L	L	M	-
M	L	M	R
R	-	M	R

- An additional probability $\alpha \longrightarrow$ the recombination step is indeed performed once the respective trait combination is chosen. **Without** trait–dependent mating **constraints** or fitness differences $\alpha = 1$.
- Model assortative mating by setting $\alpha_{LR} = \alpha_{RL} = 0 \longrightarrow$ a pair of individuals in L and R are unable to produce offsprings.

Transition Rates

The counters: number of agents in each state

- After a mating event, the counters l, m, r are either unchanged or one of them increases while another one decreases by one.
- The probability that m increases while l decreases by one is P_l^m.
- $(l, m) \rightarrow (l-1, m+1)$ takes place if the states of the agent pair are either (L, R) or (L, M).
- The probability that a pair (L, R) is chosen is $\frac{lr}{N^2} = p_{LR}$.
- For (L, M), $p_{LM} = \frac{lm}{N^2}$.
- α_{LR} (α_{LM}): the probability that the combination, once chosen, gives indeed rise to a new individual: $Pr[LR \rightarrow M] = \alpha_{LR}\ p_{LR}$
- Then $P_l^m = \alpha_{LR}\frac{lr}{N^2} + \alpha_{LM}\frac{lm}{N^2} = \alpha_{LR}\ p_{LR} + \alpha_{LM}\ p_{LM}$
- For the other non–zero transitions in the local case

$$
\begin{aligned}
P_r^m &= \alpha_{RL}\ p_{RL} + \alpha_{RM}\ p_{RM} \\
P_m^l &= \alpha_{ML}\ p_{ML} \\
P_m^r &= \alpha_{MR}\ p_{MR}
\end{aligned}
$$

Non-local Replacement

The new–born individual replaces a **randomly chosen** agent.

The probability that **this** is an agent in state F is f/N (generic F).

For the replacement of a L–agent:

$$
\begin{aligned}
P_l^m &= \frac{l}{N}(\alpha_{LR}\ p_{LR} + \alpha_{RL}\ p_{RL} + \\
&+ \alpha_{LM}\ p_{LM} + \alpha_{RM}\ p_{RM} + \alpha_{MM}\ p_{MM}) \\
P_l^r &= \frac{l}{N}\left(\alpha_{RR}\ p_{RR} + \alpha_{MR}\ p_{MR}\right)
\end{aligned}
$$

For the replacement of an R–agent:

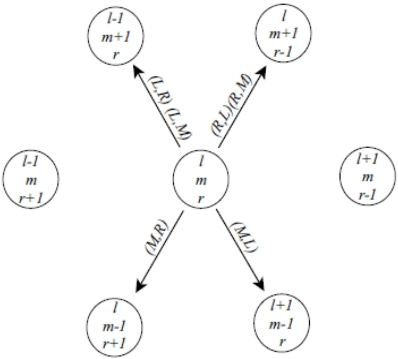
$$
\begin{aligned}
P_r^m &= \frac{r}{N}(\alpha_{LR}\ p_{LR} + \alpha_{RL}\ p_{RL} + \\
&+ \alpha_{LM}\ p_{LM} + \alpha_{RM}\ p_{RM} + \alpha_{MM}\ p_{MM}) \\
P_r^l &= \frac{r}{N}\left(\alpha_{LL}\ p_{LL} + \alpha_{ML}\ p_{ML}\right),
\end{aligned}
$$

and for replacement of an M–agent:

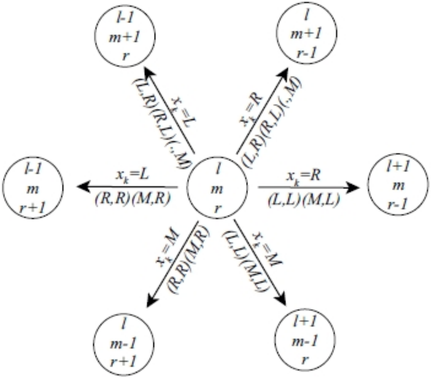
$$
\begin{aligned}
P_m^l &= \frac{m}{N}\left(\alpha_{LL}\ p_{LL} + \alpha_{ML}\ p_{ML}\right) \\
P_m^r &= \frac{m}{N}\left(\alpha_{RR}\ p_{RR} + \alpha_{MR}\ p_{MR}\right).
\end{aligned}
$$

Transition Rates

The counters: number of agents in each state



Assortative mating with local Replacement

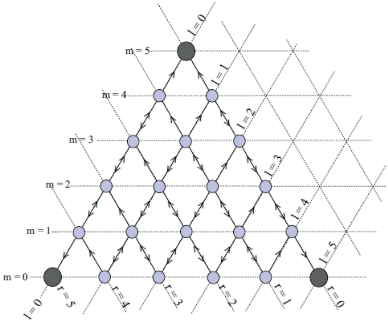


Assortative mating with non-local Replacement

Markov approach

For $N = 5$ each counter (l, r, m) can take values in between zero and five $\Rightarrow$ the triangular structure appears since $l + m + r = N$.

Larger gray atoms: absorbing states of the process
$\Rightarrow$ they can be reached by a transition, but once reached, there is no transition leaving them.
$\Rightarrow$ they characterize the final configurations of the process.
For both local and non–local replacement the absorbing states: 3 corners of the triangle grid with $l = N$ or $m = N$ or $r = N$.
Smaller light–blue states: transient atoms.

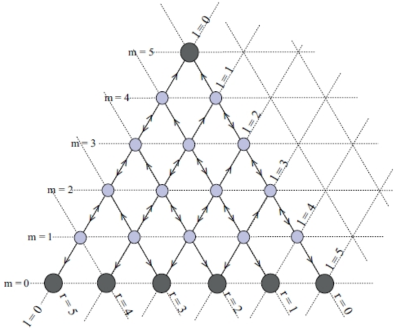


Random Mating/Unbounded Confidence

Assortative Mating with Local Replacement S I R

When $\alpha_{LR} = \alpha_{RL} = 0$ we prohibit mating between L– and R–agents.
For the local model, all the probabilities become zero if $m = 0$.
Assortative mating may lead to the stable co–existence of L– and R–agents.

- Local replacement preserves the effects of bounded confidence leading to speciation.
- Under this replacement mode, a newcomer agent takes the place of a similar one.
- Forbidden transitions contribute to the emergence of clusters.

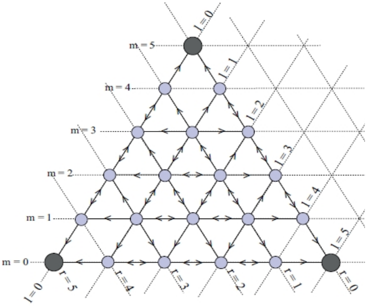


Assortative mating with Local Replacement

Assortative Mating with Random Replacement S I R

Even if $\alpha_{LR} = \alpha_{RL} = 0$ prohibits mating between L– and R–agents
Under non–local replacement, even if certain transitions are canceled there remain horizontal transitions leading away from the respective two–species configurations.
This explains why speciation cannot be observed in the simulations.

$\Rightarrow$ Random replacement sets aside the effects of bounded confidence leading to the merging of subpopulations and being an opposing force to speciation.
$\Rightarrow$ Under this replacement mode, a newcomer agent may take the place of a former-distant one.
$\Rightarrow$ Forbidden transitions turn out to be allowed so that the consequences at the macro level become the same of unbounded confidence.



Random Replacement

Discussion and Concluding Remarks

1. adaptiveness is favored by non–local replacement while it is difficult to achieve speciation.
2. opposed to this, under local replacement speciation becomes a natural result of assortative mating, but then the process is not convenient for approaching adaptive peaks in a fitness landscape.
3. evolution by natural selection and locally interacting dynamics do not appear as opposing one another.
4. the dynamical update rules used in the modeling of the microscopic interactions follow the same principles.

General Framework

Main mechanisms leading to the emergence of collective structures in adaptive and self-organizing complex systems

Selection	Interaction	Replacement	Outcome
1 peak	random	random	*convergence with Adaptation*
2 peaks	random	random	*convergence with Adaptation*
1 peak	Assortative	random	*convergence with Adaptation*
random	Assortative	Local	*speciation*
random	Assortative	random	*convergence*
1 peak	Assortative	Local	*convergence without Adaptation*
2 peaks	Assortative	Local	*convergence without Adaptation*
random	random	Local	*convergence*
random	random	random	*convergence*

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Thank you!