

# Minicourse: Multiscale behaviour in selection-mutation systems

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Part 5: Emergence and fixation on a infinite geographic space  $\Omega_N$  in the  $N \rightarrow \infty$  limit

- 1 Hierarchical mean-field limit and renormalization
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# A Sequence of Space and Time Scales

## Step 1 (*Times Scales*)

Define three types of time scales for the  $j$ -th step in the transition, i.e. for  $j$ -equilibration,  $(j+1)$ -fixation and  $(j+1)$ -equilibration by considering for each  $j$  :

$$T(N)N^j : T(N) \uparrow \infty, \text{ with } \frac{T(N)}{\log N} \rightarrow 0, \text{ as } N \rightarrow \infty \quad (0.1)$$

$$S(N)N^j : S(N) \uparrow \infty, S(N)N^{-1} \rightarrow 0 \text{ as } N \rightarrow \infty, \text{ with} \quad (0.2)$$

$$\liminf_{N \rightarrow \infty} \frac{S(N)}{\log N} \text{ sufficiently large,}$$

$$sN^{j+1} \text{ with } s \in (0, \infty). \quad (0.3)$$

## Step 2 (*Space scales and corresponding characteristic functionals*)

We introduce a sequence indexed by  $k \in \mathbb{N}_0$ , of *spatial rescalings* (with scaling parameter  $N$ ) of the spatial system as follows.

Define now the **block averages** over  $k$ -balls of the process  $X(t) = (x_\xi(t))_{\xi \in \Omega_N}$ , as

$$x_{\xi,k}(t) = N^{-k} \sum_{d(\xi',\xi) \leq k} x_{\xi'}(t), \quad \xi \in \Omega_N. \quad (0.4)$$

$$x_{\xi,k}(t) \in \mathcal{P}(\cup_j E\ell) \quad (0.5)$$

Furthermore we define the **level- $k$  empirical measure** for the level- $(k-1)$  averages:

$$\Xi_{\xi,k}^N(t) = \frac{1}{N} \sum_{\xi' \in \Omega_N^{k-1}, d_{k-1}(\xi, \xi') \leq 1} \delta_{x_{\xi',k-1}(t)}, \quad \xi \in \Omega_N^{(k-1)}. \quad (0.6)$$

$$\Xi_{\xi,k}(t) \in \mathcal{P}(\mathcal{P}(\cup_j E_\ell)) \quad (0.7)$$

### Step 3 (Renormalization via multiple time-space scales)

Definition (Renormalized system of index  $(j, k)$  and scaling parameter  $N$ )

Fix  $N \geq 2$ . Then we look at the following  $\mathbb{N}_0^2$ -indexed collection of *space-time rescaled systems* (we display now the dependence of  $X(t)$  on  $N$  by writing  $X^N(t) = ((x_\xi^N(t))_{\xi \in \Omega_N})$ ):

$$\left\{ \left\{ (x_{\xi,k}^N(U(N)N^j + tN^k))_{t \geq 0}, \quad \xi \in \Omega_N \right\}, \quad j, k \in \mathbb{N} \right\}, \quad (0.8)$$

with  $U$  being either  $S$ ,  $T$  or  $sN$  from (0.1) - (0.3).

This collection induces for every  $(j, k)$  and  $U$  as above a random field (since the field is constant in  $k$ -balls for the original index set  $\Omega_N$ )

$$\left\{ (x_{\xi,k}^N(U(N)N^j + tN^k))_{t \geq 0}, \quad \xi \in \Omega_N^{(k)} \right\}. \quad (0.9)$$

This recipe defines in each of the *three sets of time scales* for every index  $(j, k) \in \mathbb{N}_0^2$  and every value of the scaling parameter  $N$  a *new renormalized system* again indexed by locations  $\xi$ .



#### Step 4 (*Droplet description of fitter types*)

Next we have in order to understand the transitions between the different regimes to provide for the  $j$ -th step a precise description of the (very small) mass of the types in  $E_{j+1}$  in times of order  $N^j$ . This is referred to as droplet formation.

$$\widehat{x}_{1,j}(t) = \sum_{d_j(\xi,0) \leq 1} x_{\xi,j}(t), \quad \xi \in \Omega_N^{(j)}, \quad t \in [0, \text{Const} \cdot N^j \log N]. \quad (0.10)$$

Assign to every  $j$ -block within the  $(j + 1)$ -block which we consider and which is characterized by  $\ell \in \{0, 1, 2, \dots, N\}$  the  $j$ -th digit in  $\xi \in \Omega_N$  a label  $a_j(\ell)$ , so that for each  $j$  we get a collection

$$a_j(\ell) \quad , \quad \ell \in \mathbb{N}, \quad (0.11)$$

which are i.i.d. uniformly  $[0, 1]$ -distributed. Then consider for the  $j$ -th transition step the *atomic measure-valued process* defined as

$$\mathcal{J}_{j,t}^N = \sum_{\ell} \sum_{i \in E_{j+1}} x_{\xi(\ell),j}^N(tN^j)(\{i\})[\delta_{a_j(\ell)} \otimes \delta_{\{i\}}] \in \mathcal{P}([0, 1] \times E_{j+1}), \quad (0.12)$$

where  $\xi(\ell) = (0, \dots, \ell, 0, \dots)$ ,  $\ell \in \{0, 1, 2, 3, \dots\}$  with  $\ell$  on the  $j$ -th position.

### Definition (Renormalized droplets of index $j$ )

The collection of renormalized droplets at time-space scale  $(j, j)$  is given by the processes

$$\{(\mathcal{J}_{j,t}^N)_{t \geq 0}, \quad j \in \mathbb{N}\}. \quad (0.13)$$

## Step 5 (*Quasi-equilibria*)

In the *hierarchical mean-field limit of  $N \rightarrow \infty$* , the limiting object (certain nonlinear Markov processes) will allow us to describe asymptotically the various states (quasi-equilibria) through which the system passes on its way to the final equilibrium as time tends to infinity.

The *quasi-equilibrium* is defined as the equilibrium of a limiting dynamics and hence becomes a precise mathematical meaning.

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# Five Phases of Transition

**Phase 0:** Approach to *quasi-equilibrium of  $E_j$ -population*; germs for  $E_{j+1}$ -droplets.

(i) At the time  $T(N)N^j$  a *level- $j$  quasi-equilibrium* concentrated on  $E_j$ -types arises in the limit  $N \rightarrow \infty$  as equilibrium of a limiting dynamic derived from the selection-mutation-migration mechanism for the averages in  $k$ -blocks within a tagged  $j$ -block for  $k \leq j$ . The quasi-equilibrium of this tagged  $j$ -block is described by a *nonlinear McKean - Vlasov equation* with selection, mutation for the *limiting empirical measure*  $\Xi_{\xi,j}^N$ .

(ii) However on a **sparse set in space**, a subset of the **tagged  $(j + 1)$ -block** and consisting of  **$j$ -blocks** but whose number is  $o(N)$  (as  $N \rightarrow \infty$ ), these blocks are already dominated by fitter  $E_{j+1}$ -types which appeared through rare mutation and the subsequent selection-migration dynamic. These sparse subsets are called **droplets** which we described by  $(\mathcal{J}_{j,t}^N)_{t \geq 0}$ .

### Phase 1: *Emergence* of $E_{j+1}$ -types

The *emergence* of level- $(j + 1)$  types in the tagged  $j$ -block (i.e. a fixed threshold of type  $E_{j+1}$ -mass is reached with positive probability as  $N \rightarrow \infty$ ) occurs at times

$$T_j N^j + C N^j \log N = N^j (T_j + C \log N) \quad (0.14)$$

for some *constant*  $C$  and a positive *random variable*  $T_j$  with values in  $\mathbb{R}$ . Both  $C$  and  $\mathcal{L}[T_j]$  we determine via the dual process.

The time above has two distinct components.

- ① The (large) part  $CN^j \log N$  in (0.14) describes what occurs between time  $T_j N^j$  and the time  $CN^j \log N + T_j N^j$ , the time interval at which time some **fixed positive intensity  $\varepsilon$  of the new type can be established** following a deterministic evolution starting from a large number of germs of the  $E_{j+1}$ -type which have developed by time  $T(N)$ .
- ② The **second part  $T_j$**  arises if we wait in the *beginning*, i.e. times in  $[0, T_j N^j]$ , for a **droplet** of the rare mutants consisting of a finite random number of  $j$ -blocks. **This initial randomness remains visible in the system after the much larger time  $C \log N$  has passed.**



## Phase 2: *Fixation* of $E_{j+1}$ -types

The *fixation* (or *take-over*) of the tagged  $j$ -block or the  $(j+1)$ -blockaverage by  $E_{j+1}$ -types occurs rather fast compared to phase 1 and is captured considering the time scale

$$(T_j N^j + C N^j \log N) + t N^j \quad \text{for varying } t \in \mathbb{R}, (= N^j (T_j + C \log N + t)). \quad (0.15)$$

- ① The **limiting dynamic** of the  $(j + 1)$ -**block empirical measure**  $\Xi_{0,j}^N$  is a **nonlinear McKean - Vlasov process** leading from a state-concentrated almost completely on  $E_j$  as  $t \rightarrow \infty$  to fixation on  $E_{j+1}$ .
- ② We find for a tagged  $j$ -blockaverage in the limit  $N \rightarrow \infty$  an evolution, which is described by an **entrance law of a Markov process in a random medium**, the latter describing the independent feeding in of the rare mutants from somewhere in the  $(j + 1)$ -block.
- ③ In order to track the genealogy and spatial spread of the mutant types in that phase we will use the **historical process** and corresponding to it as a dual object a **spatial coalescent**.

### Phase 3: *Neutral evolution* of $E_{j+1}$ -types

After fixation a friendly (*neutral*) *coexistence* of all the  $E_{j+1}$ -types develops. Namely at the time scale  $S(N)N^j$  the invasion and complete fixation of a region of radius  $j + 1$  on mutants of  $E_{j+1}$ -type has occurred. As time varies from  $S(N)N^j$  to  $S(N)N^j + t_N N^j$  with  $t_N \uparrow +\infty$  and  $0 \leq t_N = o(N)$  an *intermediate "neutral" quasi-equilibrium* with *immigration-emigration* on  $E_{j+1}$ -types develops in the tagged  $j$ -block.



*Role of migration process in neutral quasi-equilibrium* - the spatial distribution on the  $E_{j+1}$ -types within the  $j$ -block depends on the  $\{c_\ell : \ell < j\}$ .

$\{x_{\xi,k}^N(U(N)N^j)\}_{k=j,j-1,\dots,0}$  converges to a Markov chain with state space  $\mathcal{P}(E_{j+1})$  [DGV95], which exhibits *coexistence* or *clustering*.

**Phase 4:** Approach to *quasi-equilibrium of  $E_{j+1}$  population*

Finally in times of order  $N^{j+1}$ , i.e. much later as we evolved in phase 3, the selection among the types of level  $j + 1$  starts to act and migration connects the  $N$  different  $j$ -blocks within distance  $j + 1$  and one observes in time scale  $tN^{j+1}$  a limiting dynamic for the  $(j + 1)$ -blockaverages.

Later by time  $T(N)N^{j+1}$  convergence to a *mutation-selection quasi-equilibrium concentrated now on level  $(j + 1)$ -types* in the average over the  $(j + 1)$ -block occurs.

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