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From Behavioural to Population Level: Growth and Competition

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Abstract—The aim of this work is to build models of population dynamics for growth and competition interaction by starting with detailed models at the individual level. At the individual level, we start with detailed models where the growth is described by linear terms. By considering individual interferences and by using aggregation methods, we show that the population level, different growth equation can emerge. We present an example of the emergence of logistic growth and an example of the emergence of logistic growth with Allee effect. Furthermore, in the case of two populations, we show that individual interferences can lead at the population level, to a model which has the same qualitative dynamics behaviour as the Lotka-Volterra competition model. Finally, we show that our model brings to light the effects of spatial heterogeneity on competition models. First, we find the stabilizing effects but also we show that destabilizing effects can occur.

Keywords—Aggregation emergence, Logistic growth, Allee effect, Intraspecific and interspecific competition.

INTRODUCTION

In 1798, Malthus proposed a simple model for the growth of a population. This model is a linear differential equation

$$\frac{dn}{dt} = rn,$$

where r is the growth rate of the population and n is its density. This model is generally unrealistic. However, the total world population from the 17^{th} to 21^{st} centuries follows nearly, the prediction of this model [1]. In fact, it gives a good approximation when there are no limitant factors [2]. In 1938, Verhulst proposed a model with a saturating term, due to the fact that when the population becomes too large, resources per individual become insufficient. This model, called the *logistic growth model* is the following:

$$\frac{dn}{dt} = rn\left(1 - \frac{n}{K}\right),$$

where K is the carrying capacity of the environment. If the population density is small, the growth is almost exponential but it cannot cross over the carrying capacity K. The self-limitation is the result of the intraspecific competition. For example, when the population density is large, the individuals have to compete to obtain some food. The previous model is established at the population level: it describes the total population dynamics. However, the competition takes place at the individual level.

In the first part of this work, we consider one population subdivided into subpopulations, such that each subpopulation corresponds to a kind of activity. Each individual can do many activities in a day. Some activities are favourable to the growth, but other activities are unfavourable. We

Typeset by $\mathcal{A}_{\mathcal{M}}\mathcal{S}$-TEX start with a model in which each subpopulation follows the Malthus law: we consider a positive growth rate for the favourable activities and a negative growth rate for the unfavourable activities. We show that the competition at the individual level leads to a population model which has the same qualitative behaviour as the logistic model [3]. We also present an example where the model at the population model exhibits an Allee Effect, i.e., when the population density is initially below a threshold size, it tends to zero.

In the second part, we consider two populations. We still use aggregation method in order to obtain a competition-like model at the population level. We check that the obtained model has the same qualitative behaviour as the Lotka-Volterra competition model [3].

In the third part, we show that the method used previously is useful for the study of a competition model in a heterogeneous environment. We consider two examples of competition models with two patches. In a first example, we assume that one species in competition gets extinct when there is no migration. We show that the competition at the population level can lead to the coexistence, that is, we check that a positive equilibrium exists for both species, when the migrations occur. We speak about the stabilizing effect of the spatial heterogeneity. In a second example, we assume that both species can coexist on each patch separately (when there is no migration). We show analytically that the migrations can lead to the destruction of one species: this is the destabilizing effect of the migrations.

GROWTH OF A POPULATION

We consider a population in which individuals can have two classes of activities: there are activities which are favourable to the growth (feeding, reproducing, ...) and those which are unfavourable to the growth (fighting, ...). Each individual can have all kinds of activities in the day: it can rest, reproduce, fight for food, and so on. We assume that if all individuals have "good" activities, then the population grows exponentially. However, if all the individuals have "bad" activities, then the population decays exponentially.

With these assumptions, we consider the following model:

$$\begin{aligned} \frac{dn_1}{d\tau} &= k_{12}n_2 - k_{21}n_1 + \varepsilon r_1 n_1, \\ \frac{dn_2}{d\tau} &= k_{21}n_1 - k_{12}n_2 - \varepsilon d_2 n_2, \end{aligned} \tag{S}$$

where k_{ij} is the change rate from activity j to activity i. Activity 1 is assumed to be favourable to the growth although activity 2 is assumed to be unfavourable. r_1 is the growth rate for the individuals in activity 1 and d_2 is the decay rate for the individuals in activity 2. ε is a small parameter ($\varepsilon \ll 1$) which means that the activities changes are fast with respect to the growth: each individual changes its activities many time in a day but the population growth is in the order of the week for example.

In order to aggregate this model and to obtain the dynamics of the whole population, we need to calculate the fast equilibrium, that is, the equilibrium of the fast part of (S), obtained by putting $\varepsilon = 0$ in (S). The equilibrium of the fast part is then obtained by solving the following system of equations:

$$\begin{aligned} k_{12}n_2 - k_{21}n_1 &= 0, \\ n_1 + n_2 &= n, \end{aligned}$$

where n is the total population density. It is clear that n is constant when $\varepsilon = 0$ because its derivative with respect to the time τ is null. As a consequence, in the last system, we can replace the fast variable n_2 by $n - n_1$ and we obtain the solutions as follows:

$$\begin{aligned} n_1^* &= \frac{k_{12}n}{k_{12} + k_{21}}, \\ n_2^* &= \frac{k_{21}n}{k_{12} + k_{21}}. \end{aligned}$$

By putting $\nu_i = n_i/n$ (ν_i are called the frequencies), the population dynamics is given by the following formula:

$$\frac{dn}{dt} = (r_1\nu_1 - d_2\nu_2)n,$$

where $t = \varepsilon\tau$. The aggregation method, based on a Center Manifold Theorem [4–6], consists in replacing the fast variables by their equilibrium values.

Random Activities Changes: Malthus Law

Let us assume that the activities changes are random, that is, we assume the change rates k_{ij} are constant. In this case, the fast variables ν_i reach constant values ν_i^* given by

$$\nu_1^* = \frac{k_{12}}{k_{12}+k_{21}} = C^{te},$$
$$\nu_2^* = \frac{k_{21}}{k_{12}+k_{21}} = C^{te}.$$

By replacing these variables by their equilibrium values, we obtain the following aggregated model:

$$\frac{dn}{dt} = rn + O(\varepsilon),$$

where

$$r = \frac{r_1k_{12} - d_2k_{21}}{k_{12}+k_{21}}.$$

The aggregated model is then formally the same as the model used for the subpopulations: the growth term is linear. If $r > 0$, then the population density increases while if $r < 0$, then the population density decreases. Note that in both cases, we can neglect the perturbation term if ε is small enough because the dynamics is structurally stable. It is not the case if $r = 0$, which is a particular case: we do not discuss this problem in this article. However, it is possible to calculate the perturbation term if necessary [3,5,7].

In the case of random activities changes, the aggregated model is not different from the individual models: there is not emergence of individuals properties at the population level.

Density-Dependent Activities Changes: Intraspecific Competition

Now, let us assume that when the population density is large, the individuals spend more time in fighting for food, for example. In other words, we suppose that in the case of large population density, the individuals tend to spend the most of their time in the activity 2. The changes activities rates are the following:

$$k_{12} = \alpha,$$
$$k_{21} = \beta n.$$

Then, the frequencies tend fastly to the following equilibria:

$$\nu_1^* = \frac{\alpha}{\alpha+\beta n},$$
$$\nu_2^* = \frac{\beta n}{\alpha+\beta n}.$$

As a consequence, the aggregated model is given by

$$\frac{dn}{dt} = r(n)n\left(1 - \frac{n}{K}\right),$$

where

$$r(n) = \frac{r_1\alpha}{\alpha + \beta n} \quad \text{and} \quad K = \frac{r_1\alpha}{\beta n}.$$

One can easily check that this model presents the same dynamics as the logistic model: it is a logistic-like model. In this case, we observe an emergence of the individuals competition behaviour in the population model. It is a simple example which permits to see that the aggregation method is useful for building complex models by starting with a simpler one at a more detailed scale.

Considering spatial migrations between a "good" patch 1 and a "bad" patch 2, it should be interesting to obtain the previous result by using migration rates which only depend on local densities. For example:

$$\begin{aligned} k_{12} &= \alpha, \\ k_{21} &= \beta n_1. \end{aligned} \tag{S$_1$}$$

This means that the individuals in patch 1 migrate with respect to the density on patch 1 and not with respect to the total density. It is not the case when we consider activities, because in this case, each individual can interact with all the other ones. In example (S_1), the individuals have a repulsive behaviour when they are on the good patch, which can be, for example, the patch where resources are located. The larger the density on this patch, the larger the migration towards the bad patch.

The migration rates given by (S_1) lead to the following equilibrium frequencies:

$$\begin{aligned} \nu_1^* &= \frac{-\alpha + (\alpha^2 + 4\alpha\beta n)^{1/2}}{2\beta n}, \\ \nu_2^* &= 1 - \nu_1^*. \end{aligned}$$

Consequently, the corresponding aggregated model is

$$\frac{dn}{dt} = r(n)n\left(1 - \frac{n}{K}\right),$$

where

$$r(n) = \frac{2r_1\alpha(r_1 + d_2)}{2d_2\beta n + (r_1 + d_2)(\alpha + \alpha^2 + 4\alpha\beta n))} \quad \text{and} \quad K = \frac{r_1\alpha(r_1 + d_2)}{\beta d_2^2}.$$

Once again, we conclude that the competitive behaviour at the individual level is transferred to the population level. We obtain a population model which has the same qualitative dynamics behaviour as the logistic model.

In both examples (total and local dependent migration rates), we are able to express the global parameters $r(n)$ and K with respect to the local parameters $(r_1, d_2, \dots)$. This means that the aggregation method permits one to link the individual level with the population level.

Allee Effect

Another interesting and simple example is obtained by considering an individual scenario which leads to the Allee effect [8]. This effect corresponds to the extinction of a species when its density is too small (see [2,8] for ecological examples). We can assume, for example, that when the individuals are rare, they spend most of their time in searching a partner for reproducing. We make the following assumptions. There are three activities: activity 1 is searching a partner for reproducing, activity 2 is feeding or reproducing, activity 3 is fighting for food. The first and the third activities are unfavourable to growth while the second one is favourable. Furthermore, we assume that if the population density decreases, the individuals spend more time in activity 1 and if the population density increases, the individuals spent more time in activity 3. We propose the following model:

$$\begin{aligned}
\frac{dn_1}{d\tau} &= k_{12}n_2 - k_{21}n_1 - \varepsilon d_1 n_1, \\
\frac{dn_2}{d\tau} &= k_{21}n_1 + k_{23}n_3 - (k_{12} + k_{32})n_2 + \varepsilon r_2 n_2, \\
\frac{dn_3}{d\tau} &= k_{32}n_2 - k_{23}n_3 - \varepsilon d_3 n_3,
\end{aligned} \tag{S$_2$}$$

with

$$\begin{aligned}
k_{12} &= \alpha, & k_{21} &= \beta n, \\
k_{23} &= \gamma, & k_{32} &= \delta n.
\end{aligned}$$

With these parameters k_{ij}, the equilibrium frequencies are given by

$$\begin{aligned}
\nu_1^* &= \frac{\alpha\gamma}{\alpha\gamma + \beta\gamma n + \beta\delta n^2}, \\
\nu_2^* &= \frac{\beta\gamma n}{\alpha\gamma + \beta\gamma n + \beta\delta n^2}, \\
\nu_3^* &= \frac{\beta\delta n^2}{\alpha\gamma + \beta\gamma n + \beta\delta n^2}.
\end{aligned}$$

Finally, we can check that, if $(\beta\gamma r_2)^2 > 4\alpha\beta\gamma\delta\, d_1\, d_3$, then the aggregated model is

$$\frac{dn}{dt} = r(n)(K - n)(n - A),$$

where

$$\begin{aligned}
t &= \varepsilon\tau, \\
A &= \frac{\beta\gamma r_2 - ((\beta\gamma r_2)^2 - 4\alpha\beta\gamma\delta\, d_1\, d_3)^{1/2}}{2\beta\delta d_3} > 0, \\
B &= \frac{\beta\gamma r_2 + ((\beta\gamma r_2)^2 - 4\alpha\beta\gamma\delta\, d_1\, d_3)^{1/2}}{2\beta\delta d_3} > A.
\end{aligned}$$

It follows that the population dynamics presents three equilibria: 0, A, and K. If the population density is less than the threshold density A, then the population becomes extinct. If the population density is more than the threshold density A, then the population dynamics is the same as the logistic one. A similar model is presented in most of modelisation books in population dynamics (refer to [9], for example). Once again, by using the aggregation method, we show now that the individual behaviour is transferred at the population level.

In the next part, we are interested in the interaction between two populations and more precisely by the competition between two species.

COMPETITION BETWEEN TWO POPULATIONS

From Malthus Law to Interspecific Competition

In this section, we consider two populations, each of them is subdivided into two subpopulations corresponding to two activities: feeding and reproducing (activity 1) on one hand and fighting for food (activity 2) on the other hand. The larger population density is, the more the individuals have to fight for food. We still assume that in each subpopulation, the Malthus law is available. We propose, thus, the following model:

$$\begin{aligned}
\frac{dn_1^1}{d\tau} &= k_{12}^1 n_2^1 - k_{21}^1 n_1^1 + r_1^1 n_1^1, \\
\frac{dn_2^1}{d\tau} &= k_{21}^1 n_1^1 - k_{12}^1 n_2^1 - d_2^1 n_2^1, \\
\frac{dn_1^2}{d\tau} &= k_{12}^2 n_2^2 - k_{21}^1 n_1^2 + r_1^2 n_1^2, \\
\frac{dn_2^2}{d\tau} &= k_{21}^2 n_1^2 - k_{12}^2 n_2^2 - d_2^2 n_2^2,
\end{aligned}$$

where n_i^α is the density of population α in activity i. Let $n^\alpha = n_1^\alpha + n_2^\alpha$ be the total density of population α. We consider the activities changes rates given by

$$\begin{aligned}
k_{12}^1 &= C^{te}, & k_{21}^1 &= \alpha n^1 + \beta n^2, \\
k_{12}^2 &= C^{te}, & k_{21}^2 &= \gamma n^1 + \delta n^2.
\end{aligned}$$

The meaning of these parameters k_{ij}^α is that when the density of a population increases, then the intraspecific and the interspecific individual competitions increases, forcing the individuals to spend more time in "bad" activities. We obtain, thus, the following equilibrium frequencies:

$$\begin{aligned}
\nu_1^{1*} &= \frac{k_{12}^1}{k_{12}^1 + \alpha n^1 + \beta n^2}, & \nu_2^{1*} &= \frac{\alpha n^1 + \beta n^2}{k_{12}^1 + \alpha n^1 + \beta n^2}, \\
\nu_1^{2*} &= \frac{k_{12}^2}{k_{12}^2 + \gamma n^1 + \delta n^2}, & \nu_2^{2*} &= \frac{\gamma n^1 + \delta n^2}{k_{12}^2 + \gamma n^1 + \delta n^2}.
\end{aligned}$$

We can now easily check that the aggregated model is

$$\begin{aligned}
\frac{dn^1}{dt} &= \frac{n^1}{k_{12}^1 + \alpha n^1 + \beta n^2} \left(r_1^1 k_{12}^1 - \alpha r_2^1 n^1 - \beta r_2^1 n^2 \right), \\
\frac{dn^2}{dt} &= \frac{n^2}{k_{12}^2 + \gamma n^1 + \delta n^2} \left(r_1^2 k_{12}^2 - \gamma r_2^2 n^1 - \delta r_2^2 n^2 \right).
\end{aligned}$$

These equations can be rearranged in the following way:

$$\begin{aligned}
\frac{dx}{dt} &= \frac{r_1^1 x}{1 + \bar{\alpha} x + \bar{\beta} y} (1 - x - c_{12} y), \\
\frac{dy}{dt} &= \frac{r_1^2 x}{1 + \bar{\gamma} x + \bar{\delta} y} (1 - y - c_{21} x),
\end{aligned}$$

where

$$x = \frac{k_{12}^1 r_1^1}{\alpha d_2^1} n^1 \quad \text{and} \quad y = \frac{k_{12}^2 r_1^2}{\delta d_2^2} n^2,$$

$$\bar{\alpha} = \frac{\alpha^2 d_2^1}{(k_{12}^1)^2 r_1^1}, \qquad \bar{\beta} = \frac{\beta \delta d_2^2}{k_{12}^1 k_{12}^2 r_1^2}, \qquad \bar{\gamma} = \frac{\alpha \gamma d_2^1}{k_{12}^1 k_{12}^2 r_1^1}, \qquad \bar{\delta} = \frac{\delta^2 d_2^2}{(k_{12}^2)^2 r_1^2},$$

$$c_{12} = \frac{\beta \delta d_2^1 d_2^2}{k_{12}^1 k_{12}^2 r_1^1 r_1^2} \quad \text{and} \quad c_{21} = \frac{\alpha \gamma d_1^1 d_2^2}{k_{12}^1 k_{12}^2 r_1^1 r_1^2}.$$

The dynamics of this model is the same as the dynamics of the Lotka-Volterra competition model (see the next section).

Lotka-Volterra Competition Model in a Heterogeneous Environment

In this section, we are interested in the effect of the spatial heterogeneity of the environment on the result of competition between two species. We consider a competition model on two patches. Furthermore, we assume that both species can migrate randomly between both patches and these migrations are fast. We use the aggregation method and we obtain a simple model for the global dynamics. The result of the dynamics (coexistence or exclusion) depends on the migrations. In a first step, we briefly recall the dynamics of the Lotka-Volterra competition model. In the second step, we show that the migration may stabilize the system. The third step is devoted to a case of destabilization due to the migration. In all cases, we give the analytical conditions on the migration rates which lead to the expected dynamics (coexistence or exclusion).

The Lotka-Volterra competition model is the following:

$$\frac{dn^1}{dt} = r_1 n^1 \left(1 - \frac{n^1}{K_1} - \frac{b_1 n^2}{K_1}\right),$$
$$\frac{dn^2}{dt} = r_2 n^2 \left(1 - \frac{n^2}{K_2} - \frac{b_2 n^1}{K_2}\right).$$

Let $x = n^1/K_1$ and $y = n^2/K_2$. We can rearrange the previous model in the following form:

$$\frac{dx}{dt} = r_1 x(1 - x - c_{12}y),$$
$$\frac{dy}{dt} = r_2 y(1 - y - c_{21}x),$$

where

$$c_{ij} = \frac{b_i K_j}{K_i}.$$

There are four cases as follows.

- If $c_{12} < 1$ and $c_{21} < 1$: the interspecific competition exerted on both species is weak. There is a stable equilibrium in the positive orthant and we conclude that both species coexist.
- If $c_{12} < 1$ and $c_{21} > 1$: the interspecific competition exerted on the species 1 is weak, while the interspecific competition exerted on the species 2 is strong. The species 2 disappears.
- If $c_{12} > 1$ and $c_{21} < 1$: the interspecific competition exerted on the species 2 is weak, while the interspecific competition exerted on the species 1 is strong. The species 1 disappears.
- If $c_{12} > 1$ and $c_{21} > 1$: the interspecific competition exerted on both species is strong. There is an equilibrium in the positive orthant which is a saddle. We conclude that one of both species disappears, depending on the initial conditions.

Note that the dynamics of our model in the previous section is the same as the dynamics described above.

We consider now a two patches competition model:

$$\frac{dn_1^1}{d\tau} = k_{12}^1 n_2^1 - k_{21}^1 n_1^1 + \varepsilon r^1 n_1^1 \left(1 - \frac{n_1^1}{K_1^1} - \frac{b_1^1 n_1^2}{K_1^1}\right),$$
$$\frac{dn_2^1}{d\tau} = k_{21}^1 n_1^1 - k_{12}^1 n_2^1 + \varepsilon r^1 n_2^1 \left(1 - \frac{n_2^1}{K_2^1} - \frac{b_2^1 n_2^2}{K_2^1}\right),$$
$$\frac{dn_1^2}{d\tau} = k_{12}^2 n_2^2 - k_{21}^2 n_1^2 + \varepsilon r^2 n_1^2 \left(1 - \frac{n_1^2}{K_1^2} - \frac{b_1^2 n_1^1}{K_1^2}\right),$$
$$\frac{dn_2^2}{d\tau} = k_{21}^2 n_1^2 - k_{12}^2 n_2^2 + \varepsilon r^2 n_2^2 \left(1 - \frac{n_2^2}{K_2^2} - \frac{b_2^2 n_2^1}{K_2^2}\right),$$

where the notations are the same as those used in the previous sections. k_{ij}^{α} is the migration rate of species α from patch j to patch i. By considering the new variables and parameters

$$x_i = \frac{n_i^1}{K_i^1}, \quad y_i = \frac{n_i^2}{K_i^2}, \quad \text{and } c_i^{\alpha\beta} = \frac{b_i^{\alpha} K_i^{\beta}}{K_i^{\alpha}},$$

the previous model can be rearranged in the following form:

$$\begin{aligned}
\frac{dx_1}{d\tau} &= k_{12}^1 x_2 - k_{21}^1 x_1 + \varepsilon r^1 x_1 \left(1 - x_1 - c_1^{12} y_1\right), \\
\frac{dx_2}{d\tau} &= k_{21}^1 x_1 - k_{12}^1 x_2 + \varepsilon r^1 x_2 \left(1 - x_2 - c_2^{12} y_2\right), \\
\frac{dy_1}{d\tau} &= k_{12}^2 y_2 - k_{21}^2 y_1 + \varepsilon r^2 y_1 \left(1 - y_1 - c_1^{21} x_1\right), \\
\frac{dy_2}{d\tau} &= k_{21}^2 y_1 - k_{12}^2 y_2 + \varepsilon r^2 y_2 \left(1 - y_2 - c_2^{21} x_2\right).
\end{aligned}$$

Now, we use the aggregation method. It leads to the following aggregated model:

$$\begin{aligned}
\frac{dn^1}{dt} &= r^1 n^1 \left(1 - \frac{n^1}{K^1} - \frac{b^1 n^2}{K^1}\right), \\
\frac{dn^2}{dt} &= r^2 n^2 \left(1 - \frac{n^2}{K^2} - \frac{b^2 n^1}{K^2}\right),
\end{aligned}$$

where $t = \varepsilon r$ and

$$\begin{aligned}
\frac{1}{K^1} &= \frac{(k_{12}^1)^2 + (k_{21}^1)^2}{(k_{12}^1 + k_{21}^1)^2}, \\
\frac{1}{K^2} &= \frac{(k_{12}^2)^2 + (k_{21}^2)^2}{(k_{12}^2 + k_{21}^2)^2}, \\
\frac{b^1}{K^1} &= \frac{c_1^{12} k_{12}^1 k_{12}^2 + c_2^{12} k_{21}^1 k_{21}^2}{(k_{12}^1 + k_{21}^1)(k_{12}^2 + k_{21}^2)}, \\
\frac{b^2}{K^2} &= \frac{c_1^{21} k_{12}^1 k_{12}^2 + c_2^{21} k_{21}^1 k_{21}^2}{(k_{12}^1 + k_{21}^1)(k_{12}^2 + k_{21}^2)}.
\end{aligned}$$

Note that the aggregated model is a Lotka-Volterra competition mode. By considering again $x = n^1/K^1$, $y = n^2/K^2$, and $c_{ij} = b^i K^j / K^i$, we obtain the simplified form of that model.

Let us assume that the parameters on both patches are such that the species 1 disappears on each of them separately. That is, we assume that: c_1^{12} and c_2^{12} are greater than 1, while c_1^{21} and c_2^{21} are less than 1. In other terms, if both species are only on patch 1 (without migration), then the species 1 disappears. This result is still true on patch 2 without migration. However, migrations may lead to the coexistence because both species can then share the space. Indeed, let us consider the following parameters values:

$$\begin{aligned}
&k_{12}^1 = 0.9, \quad && k_{21}^1 = 0.1, \quad && k_{12}^2 = 0.1, \quad && k_{21}^2 = 0.9, \\
&c_1^{12} = 1.2, && c_2^{12} = 1.1, && c_1^{21} = 0.5, && c_2^{21} = 0.6.
\end{aligned}$$

A simple calculation shows that

$$c_{12} \simeq 0.252 < 1 \quad \text{and} \quad c_{21} \simeq 0.121 < 1.$$

Then we can conclude that the migration process leads to the stabilization of the ecological system. The coexistence is the result of the migrations.

There is another interesting consequence of the migrations. Let us assume now that, without migration, the coexistence occurs on each patch separately. It means that all the parameters c_1^{12}, c_2^{12}, c_1^{21}, and c_2^{21} are less than 1. The migrations may lead to the extinction on one both species. We give here a numerical example:

$$k_{12}^1 = 3, \qquad k_{21}^1 = 1, \qquad k_{12}^2 = 0.9, \qquad k_{21}^2 = 0.1,$$
$$c_1^{12} = 0.1, \qquad c_2^{12} = 0.2, \qquad c_1^{21} = 0.9, \qquad c_2^{21} = 0.9.$$

A simple calculation shows that

$$c_{12} \simeq 0.088 < 1 \quad \text{and} \quad c_{21} \simeq 1.575 > 1.$$

In this example, species 2 will disappear. We conclude that the migrations can in some cases destabilize the ecological system. Both species could coexist if migrations are prohibited. However, in a natural environment, these populations cannot coexist, one of them becomes extinct.

CONCLUSION

In ecology, the spatial heterogeneity and the individual behaviour are known to play an important role in the populations dynamics. In modelization, taking into account these constraints leads to consider large systems which are not simple to deal with. As a consequence, the aggregation methods are very useful for simplifying the models. Furthermore, the aggregated models often present new properties. It is interesting to understand how the spatial heterogeneity or the individual behaviour emerge at the population level.

In this article, we show that simple individual behaviours in a population where the Malthus law is locally applied, make emerge more complex dynamics as logistic-like growth, Allee effect, and so on. Moreover, individual interactions between individuals of different species make emerge competition models.

In the last section, we studied the effect of random migration on the Lotka-Volterra competition model. The aggregated model is still a Lotka-Volterra model: there is no functional emergence. However, the dynamics of the aggregated model can be different as the dynamics in the different spatial patches: in this case, there is dynamics emergence. We can quantify the effects of competition on the population dynamics by measuring the competition at the individual level for instance.

In this article, we were interested by the effects of individual dynamics on the population dynamics. A future work is devoted to the opposite way: how the population dynamics influences the individual behaviour.

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