



## Emergence of Population Growth Models: Fast Migration and Slow Growth

PIERRE AUGER<sup>†</sup> AND JEAN-CHRISTOPHE POGGIALE<sup>‡</sup>

<sup>†</sup> *UMR CNRS 5558, Université Claude Bernard Lyon-1, 43 Boulevard du 11 Novembre 1918, 69622 Villeurbanne cedex, and* <sup>‡</sup> *COM Luminy, Case 901, 13288 Marseille Cedex 9, France*

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We present aggregation and emergence methods in large-scale dynamical systems with different timescales. Aggregation corresponds to the reduction of the dimension of a dynamical system which is replaced by a smaller model for a small number of global variables at a slow timescale. We study the couplings between fast and slow dynamics leading to the emergence of global properties in the aggregated model. First, we study the case of a single population in a patchy environment. Growth rates are assumed to be linear on each patch. Individuals can migrate from one patch to another at a fast timescale. We choose different density dependent migration processes. In each case, we use aggregation methods to obtain the corresponding growth equation for the total density of the population at a slow timescale. We look for particular density dependent migration processes leading to an aggregated logistic-like equation. Second, we study the case of two interacting populations. A particular choice of density dependent migrations leads to an aggregated competition model.

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### Introduction

Modelling biological systems implies dealing with systems involving a large number of variables. Indeed, communities are sets of several interacting populations. Many individuals of different ages or in different physiological stages belong to these populations. These individuals carry out several activities during the day and visit different sites. Thus, populations are divided into various sub-populations corresponding to ages, stages, individual states or activities, phenotypes, genotypes, spatial patches etc. Modelling ecological communities, we are faced with complexity, in particular due to the structure of populations. The complexity of biological systems is partly the result of the large number of components involved in the dynamics.

Facing this complexity, several approaches are

possible. A first possibility is to try and manage this complexity. This means building a mathematical model which describes the biological system in detail. This leads to a family of models involving a large number of equations and of coupled variables. The complexity of the real system is included in the model. However, few mathematical results are usually available for these large models which are difficult to handle. In many cases, one uses computer simulations to look for particular solutions.

In a second type of model, most details are ignored. For example, many models of ecological communities deal only with a few variables. The structure of the populations are neglected. Populations are considered as entities and are described by a single variable, for example the total population or density. This simplification implies that the internal structure of the population does not have an important effect on its dynamics and that it can be neglected. It is an approximation of the total system by a reduced system. However, in many cases, the simplified model

<sup>†</sup> Author to whom correspondence should be addressed.

is defined and used and very few arguments are given to justify the approximations and the simplifications which are needed to obtain this model.

Our approach goes half way between the two types of methods. Indeed, we start with a model which includes many subpopulations and details. In this way, we take into account the complexity of the initial model. However, we use methods for simplifying and reducing the dimensions of this large-scale model. In order to succeed with this simplification, we focus on particular dynamical systems involving two timescales. Two main aspects seem important. The first concerns aggregation or reduction methods, (Iwasa *et al.*, 1987, 1989; Gard, 1988; Gardner *et al.*, 1982). The second concerns the emergence of global properties in the aggregated model.

The existence of different timescales makes it possible to use perturbation methods to aggregate systems of ODE's which are composed of fast and slow parts. Perturbation methods allow us to aggregate large systems into a smaller system which is described by a few global variables. The center manifold theorem can be used for aggregation, (Fenichel, 1971). For details, we refer to Auger & Roussarie (1994), see also our previous contributions (Auger, 1983, 1985, 1989, 1992, 1993; Auger & Benoît, 1993). In the present paper, a fast model describing migration on spatial patches is coupled to a slow growth model on each patch. Our aim is to show that different scenarios for the fast migration can lead to different growth models.

### Growth of Single Population in a Two-patch Environment

#### THE MODEL

##### *Presentation of the micro-model*

We consider a single population of total density  $n(t)$ . This population is subdivided into subpopulations  $n_i(t)$ ,  $i = 1, N$  where  $N$  is the number of subpopulations. For example, individuals can move on to different spatial patches or can be in different states. The state vector is the following  $(n_1(t), n_2(t), \dots, n_N(t))$ . The following microsystem describes the growth of the subpopulations:

$$\varepsilon \frac{dn_i}{dt} = \sum_j k_{ij}n_j - \sum_k k_{ki}n_i + \varepsilon g_i(n_1, n_2, \dots, n_N), \quad (1)$$

$k_{ij}$  is the rate of state change from state  $j$  to state  $i$  per unit time,  $g_i$  is a function of subpopulations and describes the growth of the subpopulations.  $\varepsilon$  is a

small parameter ( $\varepsilon \ll 1$ ). The change of states takes place at a fast timescale and the growth at a slow timescale. The simplest case assumes linear growth for subpopulations, i.e. linear  $g$ -functions so that microsystem (1) becomes:

$$\varepsilon \frac{dn_i}{dt} = \sum_j k_{ij}n_j - \sum_k k_{ki}n_i + \varepsilon r_i n_i. \quad (2)$$

In the case of two states only (for example two spatial patches), system (2) reduces to two equations (3):

$$\begin{aligned} \varepsilon \frac{dn_1}{dt} &= k_{12}n_2 - k_{21}n_1 + \varepsilon r_1 n_1, \\ \varepsilon \frac{dn_2}{dt} &= k_{21}n_1 - k_{12}n_2 + \varepsilon r_2 n_2. \end{aligned} \quad (3)$$

Figure 1 presents a diagram of this simple two-patch system in which individuals can migrate from patch 1 to patch 2 and vice versa at a fast timescale.

##### *The aggregated model*

It must be noted that the fast part is conservative, i.e.  $n(t) = n_1(t) + n_2(t)$  is invariant for the migration process. In order to aggregate this equation into a single equation for the whole density  $n$ , perturbation methods can be used (Hoppensteadt, 1966; Nayfeh, 1973; Tihonov, 1948). It is necessary to look for the equilibrium of the fast part. This equilibrium corresponds to  $\varepsilon = 0$  in system (3):

$$k_{12}n_2 - k_{21}n_1 = 0. \quad (4)$$

When  $k$ -parameters are constant or functions of  $n$ , the fast equilibrium can be characterized by the equilibrium patch proportions of frequencies noted  $v_1^* = n_1/n$  and  $v_2^* = n_2/n$ .

$$v_1^* = \frac{k_{12}}{k_{12} + k_{21}} \quad \text{and} \quad v_2^* = \frac{k_{21}}{k_{12} + k_{21}}, \quad (5)$$

where the asterisk denotes the equilibrium. It is then

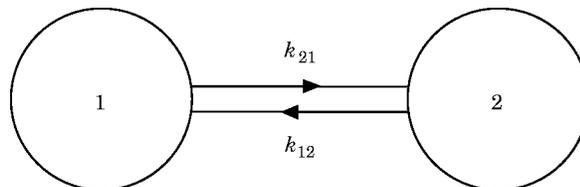


FIG. 1. Individuals can go on two patches.  $k_{12}$  and  $k_{21}$  are the migration rates which take place at a fast timescale.

possible to aggregate model (3) into a single equation for  $n$ :

$$\frac{dn}{dt} = rn + O(\varepsilon), \quad (6)$$

with

$$r = r_1 v_1^* + r_2 v_2^*.$$

#### CONSTANT MIGRATION RATES

The simplest case occurs when the migration rates  $k_{12}$  and  $k_{21}$  are constant. In this case, the overall growth rate  $r$  is also constant leading to an exponential growth model for the total population  $n(t)$  for a sufficiently small  $\varepsilon$ . One can imagine two patches, a favorable patch 1 ( $r > 0$ ) and an unfavorable patch 2 ( $r < 0$ ). Now, we note  $-r_2$  for the growth rate of the unfavorable patch 2 with  $r_2 > 0$ . If the total population lives on patch 1 ( $v_1^* = 1$  and  $v_2^* = 0$ ), the population increases exponentially. If the total population lives on patch 2 ( $v_1^* = 0$  and  $v_2^* = 1$ ), the population is decaying. An interesting case occurs when the equilibrium subpopulations are shared between the two patches. This occurs when (7) holds:

$$\begin{aligned} r_1 v_1^* - r_2 v_2^* &= 0, \\ v_1^* + v_2^* &= 1. \end{aligned} \quad (7)$$

Solutions of (7) are the following:

$$v_1^* = \frac{r_2}{r_1 + r_2}, \quad v_2^* = \frac{r_1}{r_1 + r_2}. \quad (8)$$

When patch frequencies take these particular values, (6) becomes:

$$\frac{dn}{dt} = O(\varepsilon). \quad (9)$$

We need to calculate the first order term with respect to  $\varepsilon$ , see Auger & Roussarie (1994) for more details. The calculation gives the following global system:

$$\frac{dn}{dt} = \varepsilon \left( \frac{r_1 r_2}{k_{12} + k_{21}} \right) n + O(\varepsilon^2). \quad (10)$$

This shows that it is not possible to have a constant sized population with constant migration rates and linear growth terms on each patch. The next section will consider density-dependent migrations.

#### DENSITY DEPENDENT MIGRATION RATES

In this section, we shall investigate the effect of density dependence on the growth of a single

population. Two cases can occur. First, the migration rates depend on the total density (total density dependence). Second, the migration rates depend on the local density (local density dependence). In this article, two patches are considered, a source ( $r > 0$ ) and a sink ( $r < 0$ ), (Pulliam, 1988). The source is a patch on which food can be found and which it is necessary to visit to get resources. For example, the sink is a refuge where individuals rest but cannot grow. It is assumed that each day animals must leave their refuge to go to the source patch in order to get resources. Thus, in our approach, the patches are close to each other. It makes sense to consider that the individuals react with respect to the total density. In other cases, individuals can react with respect to the local density on a particular patch where they are. The next section studies an example of total density and the following section an example of local density.

#### *Logistic type growth in the case of total density dependence*

Let us consider the previous example of two patches, a favorable patch 1 ( $r_1 > 0$ ) and an unfavorable patch 2 ( $-r_2 < 0$ ). Furthermore, we assume that migration from patch 1 to patch 2 is favoured at large densities. Individuals leave patch 1 and go to patch 2 when the total population is large:

$$k_{21} = \alpha n \quad \text{and} \quad k_{12} = \text{constant}. \quad (11)$$

More general relationships would assume that migration rates depend on patch subpopulations  $n_1$  and  $n_2$  rather than on the total density  $n$ . However, assuming fast migrations implies that individuals often change patches and, thus can make an estimate of the total population to which they belong. Under assumption (9), equilibrium patch frequencies can be calculated:

$$v_1^* = \frac{k_{12}}{k_{12} + \alpha n} \quad \text{and} \quad v_2^* = \frac{\alpha n}{k_{12} + \alpha n}. \quad (12)$$

These patch frequencies are density dependent. At small densities, individuals live on the favorable patch 1. At large densities, they migrate to the unfavorable patch 2. The aggregated model for the total population is given by eqn (6). In this case, one obtains the following equation:

$$\frac{dn}{dt} = \frac{1}{k_{12} + \alpha n} (r_1 k_{12} - r_2 \alpha n) n. \quad (13)$$

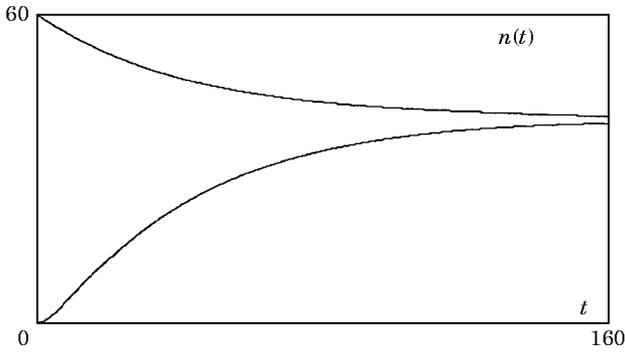


FIG. 2.  $\beta = 1$ ,  $r_1 = 1$ ,  $K = 40$ . Computer simulation of the logistic-like model with two initial conditions.

This equation can be rearranged in a simpler way:

$$\frac{dn}{dt} = \frac{r_1}{1 + \beta n} \left(1 - \frac{n}{K}\right)n, \quad (14)$$

where

$$\beta = \frac{\alpha}{k_{12}} \quad \text{and} \quad K = \frac{r_1 k_{12}}{\alpha r_2}.$$

Equation (14) has two steady states 0 and  $K$ . 0 is unstable and  $K$  is stable. The qualitative behavior of the equation is similar to a logistic or a Gompertz equation, (Edelstein-Keshet, 1988; Murray, 1989). Interpretation is as follows: When the density  $n$  increases, there is overcrowding on patch 1 and the response of the population is migration towards an unfavorable patch 2. This has the effect of stabilizing the population which tends to a constant density  $K$ . This regulation of the population was brought to light by Pulliam (1988) in terms of sinks (unfavorable habitats) and sources (favorable habitats). Our example also shows, by use of a mathematical model, that spatial heterogeneity coupled with density dependence has an important effect on the overall growth of the population and furthermore it can stabilize the population size. Host-parasitoid models in a discrete set of patches (Hassell *et al.*, 1992) have shown similar results. The Nicholson–Bailey model for a single patch is unstable. Computer simulations in a multi-patch system have shown that as soon as the size of the array of patches becomes large enough, the probability of extinction tends to zero.

Figure 2 presents a Runge–Kutta computer simulation of our logistic-like model (14), the total model of two equations. Solutions exhibit a logistic-like shape with a carrying capacity here equal to  $K = 40$ .

### Logistic type growth in the case of local density dependence

Let us study a local density dependence example still having two patches. Such as in the previous case, we assume that migration from patch 1 to patch 2 is favored at large densities on patch 1:

$$k_{21} = \alpha n_1 \quad \text{and} \quad k_{12} = \beta = \text{constant}. \quad (15)$$

Under assumption (15), equilibrium patch frequencies can be calculated:

$$v_1^* = \frac{-\beta + (\beta^2 + 4\alpha\beta n)^{1/2}}{2\alpha n} \quad \text{and} \quad v_2^* = 1 - v_1^*. \quad (16)$$

It can be checked that the frequencies remain within the interval  $[0, 1]$ . It is necessary to compute the equilibrium patch frequencies by looking at the fixed points of the fast system. As the total density is an invariant for the fast system, the equilibrium frequencies (16) depend on  $n$  (see Appendix).  $v_1^*(n)$  tends to one when  $n$  tends to zero and it tends to zero at large total densities. The aggregated model for the total population is given by eqn (17). In this case, a computation leads to the next aggregated equation:

$$\frac{dn}{dt} = \frac{2r_1 n}{1 + \frac{r_2 n}{\gamma} + \left(1 + \frac{4\alpha n}{\beta}\right)^{1/2}} \left(1 - \frac{n}{K}\right) \quad (17)$$

where

$$\gamma = \frac{\beta(r_1 + r_2)}{\alpha} \quad \text{and} \quad K = \frac{2r_1 \gamma^2}{(r_2)^2}.$$

Equation (17) also has two equilibrium points 0 and  $K$ . 0 is unstable and  $K$  is stable. The qualitative behavior of this equation is similar to a logistic equation.

### Growth or decay

Let us consider the following growth equation:

$$\frac{dn}{dt} = r(M - n)(n - K)n, \quad (18)$$

where  $0 < M < K$ . There are three steady states, 0,  $M$  and  $K$ . 0 is stable,  $M$  is unstable and  $K$  is stable (Edelstein–Keshet, 1988).  $M$  corresponds to a threshold population size. When the initial population is smaller than  $M$ , the population tends to zero. When the initial condition is larger than  $M$ , it tends to the carrying capacity  $K$ . Let us try to find particular fast migration systems leading to a similar

threshold effect. Let us make the following choice for migration rates:

If  $n < M$

$$k_{21} = \text{constant} \quad \text{and} \quad k_{12} = \alpha n,$$

If  $n > M$

$$k_{21} = \delta n \quad \text{and} \quad k_{12} = \text{constant}. \quad (19)$$

At low density, while  $n$  increases, migration from patch 2 to 1 also increases. At large densities, the inverse happens. Under these assumptions, the equation for the growth of the overall population can be divided into two parts:

If  $n < M$

$$\frac{dn}{dt} = \frac{r_2}{1 + \beta n} \left( \frac{n}{M} - 1 \right) n,$$

If  $n > M$

$$\frac{dn}{dt} = \frac{r_1}{1 + \gamma n} \left( 1 - \frac{n}{K} \right) n, \quad (20)$$

where

$$\beta = \frac{\alpha}{k_{21}}, \quad M = \frac{r_2 k_{21}}{\alpha r_1}, \quad \gamma = \frac{\delta}{k_{12}} \quad \text{and} \quad K = \frac{r_1 k_{12}}{\delta r_2}.$$

Here,  $M$  is defined by the previous relationship. For an initial population  $n(0)$  smaller than  $M$ , the first eqn (20) holds (0 is stable and  $M$  is unstable), the population decays to 0. For an initial population larger than  $M$ , the second eqn (20) holds, (0 is unstable,  $K$  is stable), the population tends to the carrying capacity  $K$ . The qualitative behavior is similar to the allee effect. Below a certain threshold, the population cannot grow. Figure 3 presents a Runge–Kutta computer simulation of eqn (20).

One could also apply the previous method to more patches. Aggregation methods could be applied leading to important reduction of the dimension of the initial system.

#### *Emergence: two possibilities*

Conclusions drawn in this section are that we can make population growth models of different kinds emerge. The method can work in two opposing ways:

(i) A fast migration nonlinear model is chosen (or assumed). Our method makes the corresponding slow population growth model emerge. The solution is unique. In this section, we have performed this way.

(ii) A slow population growth model is assumed and one can look for a fast model which allows us to aggregate it. The solution is generally not unique, i.e. several fast processes can be suitable.

Now, we shall consider the case of two interacting populations with migrations on spatial patches.

### **Structured Populations and Interspecific Competition**

In the classical Lotka–Volterra competition model, the competition between two populations for the same food source can lead to processes of coexistence or of mutual exclusion (Edelstein–Keshet, 1988; Gause, 1934; Murray, 1989). Most models of competition do not take into account the structures of the populations, for example on spatial patches. The two populations are described as entities and the model is built of two ordinary differential equations. First of all, let us recall the main results of the Lotka–Volterra model.

#### THE LOTKA–VOLTERRA COMPETITION MODEL

Let  $n_1$  and  $n_2$  be the populations of two competing species 1 and 2 for the same food source. In the Lotka–Volterra competition model, the competition process is described by a set of two ordinary differential equations:

$$\begin{aligned} \frac{dn_1}{dt} &= r_1 n_1 [1 - n_1/K_1 - b_{12} n_2/K_1], \\ \frac{dn_2}{dt} &= r_2 n_2 [1 - n_2/K_2 - b_{21} n_1/K_2], \end{aligned} \quad (21)$$

where  $r_1, r_2$  are the linear growth rates,  $K_1, K_2$  are the carrying capacities respectively for species 1 and 2.  $b_{12}$  and  $b_{21}$  are parameters relative to the competition effects between the two species. The parameters are positive. It is usual to rewrite the model using new variables (non-dimensionalisation):

$$\begin{aligned} \frac{du_1}{d\tau} &= u_1 [1 - u_1 - a_{12} u_2], \\ \frac{du_2}{d\tau} &= \rho u_2 [1 - u_2 - a_{21} u_1], \end{aligned} \quad (22)$$

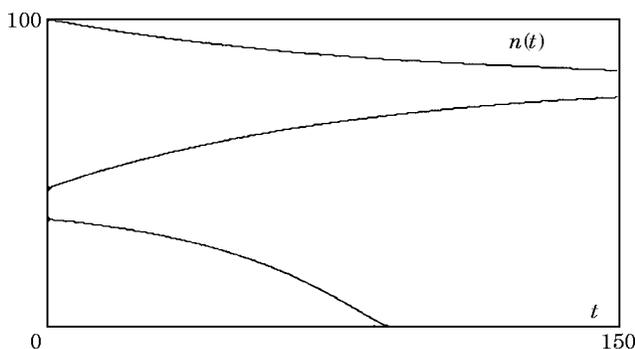


FIG. 3.  $\beta = \gamma = 1$ ,  $r_1 = r_2 = 1$ ,  $M = 40$ ,  $K = 80$ . Computer simulation of the logistic-like model with threshold.

where

$$u_i = \frac{n_i}{K_i}, \quad \rho = \frac{r_1}{r_2}, \quad \tau = r_1 t \quad \text{and} \quad a_{ij} = b_{ij} \frac{K_j}{K_i}.$$

In this new form, the  $u$ -population variables are normalized between 0 and 1 corresponding to the interval  $[0, K]$  for real populations. There are four possible steady-state points, the trivial point  $(0, 0)$ , the exclusion points  $(0, 1)$ ,  $(1, 0)$  and the coexistence point  $(u_1^*, u_2^*)$  with:

$$u_1^* = \frac{1 - a_{12}}{1 - a_{12}a_{21}} \quad \text{and} \quad u_2^* = \frac{1 - a_{21}}{1 - a_{12}a_{21}}, \quad (23)$$

$(0, 0)$  is always unstable. The stability of the other steady-state points depends on the two important parameters  $a_{12}$  and  $a_{21}$ . A linear stability analysis shows that:

*Coexistence:* when  $a_{12}$  and  $a_{21}$  are both smaller than 1,  $(u_1^*, u_2^*)$  is located in the positive orthant and is the only stable point.

*Exclusion:* when one of the two parameters  $a_{12}$  or  $a_{21}$  is larger than one, either  $(1, 0)$  is stable and  $(0, 1)$  is unstable or vice versa or still both are stable. In these cases, one of the two populations becomes extinct:

If  $a_{12} < 1$  and  $a_{21} > 1$ , population 2 becomes extinct

If  $a_{12} > 1$  and  $a_{21} < 1$ , population 1 becomes extinct.

If  $a_{12} > 1$  and  $a_{21} > 1$ , either population 1 or population 2 becomes extinct depending on the initial position with respect to a separatrix.

#### AGGREGATING THE LOTKA-VOLTERRA-LIKE COMPETITION MODEL

Consider two populations subdivided into two patch sub-populations. Let  $n_1^1(t)$  and  $n_2^1(t)$  be population densities 1 respectively on patch 1 and 2 at time  $t$ .  $n_1^2(t)$  and  $n_2^2(t)$  are the same for population 2. First of all, similar to the case of a single species, we assume a favorable patch 1 ( $r_1^1 > 0$  and  $r_2^1 > 0$ ) and an unfavorable patch 2 ( $-r_1^2 < 0$  and  $-r_2^2 < 0$ ). Let us consider the following equations:

$$\begin{aligned} \varepsilon \frac{dn_1^1}{dt} &= k_{12}^1 n_2^1 - k_{21}^1 n_1^1 + \varepsilon r_1^1 n_1^1, \\ \varepsilon \frac{dn_2^1}{dt} &= k_{21}^1 n_1^1 - k_{12}^1 n_2^1 - \varepsilon r_2^1 n_2^1, \end{aligned}$$

$$\begin{aligned} \varepsilon \frac{dn_1^2}{dt} &= k_{12}^2 n_2^2 - k_{21}^2 n_1^2 + \varepsilon r_1^2 n_1^2, \\ \varepsilon \frac{dn_2^2}{dt} &= k_{21}^2 n_1^2 - k_{12}^2 n_2^2 - \varepsilon r_2^2 n_2^2. \end{aligned} \quad (24)$$

$k_{ik}^\alpha$  is a migration rate from patch  $k$  to patch  $i$  for population  $\alpha$ . The growth rate of population  $\alpha$  on patch  $i$  is written  $r_i^\alpha$ . The fast parts are conservative, i.e.  $n^1(t) = n_1^1(t) + n_2^1(t)$  and  $n^2(t) = n_1^2(t) + n_2^2(t)$  are invariant for the migration process. The equilibrium of the fast part corresponds to  $\varepsilon = 0$ . Equilibrium patch proportions or frequencies written  $v_k^{\alpha*} = n_k^\alpha / n^\alpha$  are the following:

$$v_1^{\alpha*} = \frac{k_{12}^\alpha}{k_{12}^\alpha + k_{21}^\alpha} \quad \text{and} \quad v_2^{\alpha*} = \frac{k_{21}^\alpha}{k_{12}^\alpha + k_{21}^\alpha}. \quad (25)$$

The aggregated model is then composed of the two following equations:

$$\frac{dn^1}{dt} = r^1 n^1, \quad \frac{dn^2}{dt} = r^2 n^2, \quad (26)$$

with

$$r^1 = r_1^1 v_1^{1*} - r_2^1 v_2^{1*} \quad \text{and} \quad r^2 = r_1^2 v_1^{2*} - r_2^2 v_2^{2*}.$$

In the density independent case, both populations follow an exponential growth curve because the overall growth rates  $r^1$  and  $r^2$  are constant. Now, similar to the case of a single population, let us consider a density dependent case where the migration rates are assumed as follows:

$$\begin{aligned} k_{21}^1 &= \alpha n^1 + \beta n^2 \quad \text{and} \quad k_{12}^1 = \text{constant}, \\ k_{21}^2 &= \gamma n^1 + \delta n^2 \quad \text{and} \quad k_{12}^2 = \text{constant}, \end{aligned} \quad (27)$$

where  $\alpha, \beta, \gamma, \delta$  are positive constant. At large densities, individuals of both species migrate increasingly from the favorable patch 1 to the unfavorable patch 2. Equilibrium patch frequencies are:

$$\begin{aligned} v_1^{1*} &= \frac{k_{12}^1}{k_{12}^1 + \alpha n^1 + \beta n^2} \quad \text{and} \quad v_2^{1*} = \frac{\alpha n^1 + \beta n^2}{k_{12}^1 + \alpha n^1 + \beta n^2}, \\ v_1^{2*} &= \frac{k_{12}^2}{k_{12}^2 + \gamma n^1 + \delta n^2} \quad \text{and} \quad v_2^{2*} = \frac{\gamma n^1 + \delta n^2}{k_{12}^2 + \gamma n^1 + \delta n^2}. \end{aligned} \quad (28)$$

The aggregated model for the total densities is given by eqns (29):

$$\begin{aligned} \frac{dn^1}{dt} &= \frac{1}{k_{12}^1 + \alpha n^1 + \beta n^2} (r_1^1 k_{12}^1 - \alpha r_2^1 n^1 - \beta r_2^1 n^2) n^1, \\ \frac{dn^2}{dt} &= \frac{1}{k_{12}^2 + \gamma n^1 + \delta n^2} (r_1^2 k_{12}^2 - \gamma r_2^2 n^1 - \delta r_2^2 n^2) n^2. \end{aligned} \quad (29)$$

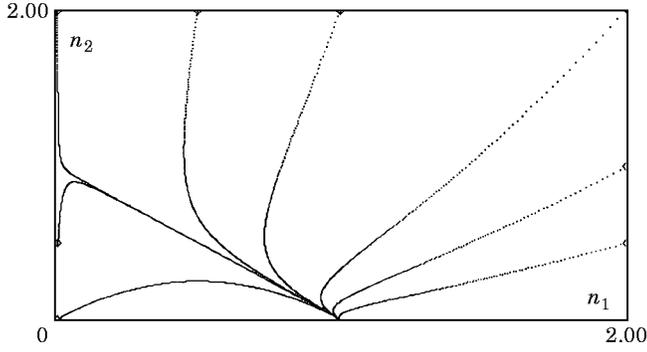


FIG. 4. Computer simulation of the competition-like model. Exclusion. All trajectories converge to  $(1, 0)$  which is stable node.  $\alpha = \beta = 1$ ,  $\gamma = \delta = 2$ ,  $\mu = \nu = 1$ ,  $\phi = \varphi = 2$ ,  $r_1^1 = r_1^2 = 1$ ,  $k_{12}^1 = k_{12}^2 = 1$ .

These equations can be rearranged in a simpler way:

$$\begin{aligned} \frac{dn^1}{dt} &= \frac{r_1^1 k_{12}^1}{k_{12}^1 + \alpha n^1 + \beta n^2} (1 - \mu n^1 - \nu n^2) n^1, \\ \frac{dn^2}{dt} &= \frac{r_1^2 k_{12}^2}{k_{12}^2 + \gamma n^1 + \delta n^2} (1 - \phi n^1 - \varphi n^2) n^2, \end{aligned} \quad (30)$$

where  $\mu$ ,  $\nu$ ,  $\phi$ ,  $\psi$  can be easily obtained. Except for the denominators, let's say  $g$ , (which are always  $> 0$ ), this model is similar to the Lotka–Volterra competition model which we have seen previously. It is easy to see that the qualitative behavior of system (30) is the same as the classical Lotka–Volterra competition model without denominators. Indeed, for local stability, one must calculate the Jacobian matrix at a steady state. The supplementary denominators  $g$  have no influence on its trace and determinant signs. It is simply a positive multiplier. When calculating the coefficients of the Jacobian matrix, we calculate derivatives of ratios  $f/g$  which are equal to  $(1/g^2)(gf' - fg')$  and simplify to  $(1/g)f'$  because  $f = 0$  at a steady state. As  $g$  is positive in the positive orthant, signs of the trace and determinant of the Jacobian matrix remain unchanged in respect to functions  $f'$ . Thus, qualitative behaviours of the aggregated model (30) and of the classical Lotka–Volterra model are the same. Figures 4 and 5 present numerical simulations of the competition-like model in two cases, a case of exclusion and a case of coexistence.

However, in case (30) competition must be interpreted as the result of a repulsive effect between individuals of the same and of the other population on the favorable patch. At large densities, individuals migrate to avoid overcrowding by both its own population and the other population. Migration causes them to leave the favorable patch to move to an unfavorable patch. As we have seen, this process

can result in coexistence or in mutual exclusion. The competition model that we have obtained could be considered as a kind of spatial competition model.

In this study, the migration rates depend on total densities. One may also consider local density dependent cases in which migration rates would depend on local densities on each particular patch. Such a case was studied for the growth of a single population on two patches for which the resulting aggregated model was of the same kind (qualitatively) as in the case of a total density dependence. In this contribution, we have limited our study mainly to total density dependence. Local density dependence will be investigated in more detail in further studies.

#### LOTKA–VOLTERRA-LIKE COMPETITION MODEL IN A MULTI-PATCH SYSTEM

The method can be extended to two populations subdivided in many patch subpopulations. Let  $n_i^1(t)$  and  $n_i^2(t)$  be population densities 1 and 2 respectively on patch  $i$  at time  $t$ ,  $i$  belongs to  $[1, N]$ .  $N$  is the total number of patches. Let us consider the following equations:

$$\begin{aligned} \varepsilon \frac{dn_i^1}{dt} &= \sum_j (k_{ij}^1 n_j^1 - k_{ji}^1 n_i^1) + \varepsilon r_i^1 n_i^1, \\ \varepsilon \frac{dn_i^2}{dt} &= \sum_j (k_{ij}^2 n_j^2 - k_{ji}^2 n_i^2) + \varepsilon r_i^2 n_i^2. \end{aligned} \quad (31)$$

$k_{ik}^\alpha$  is the migration rate from patch  $k$  to patch  $i$  for population  $\alpha$ . The growth rate of population  $\alpha$  on patch  $i$  is  $r_i^\alpha$ . Similarly to the previous case, the fast parts are conservative, i.e.:

$$n^1(t) = \sum_i n_i^1(t) \quad \text{and} \quad n^2(t) = \sum_i n_i^2(t)$$

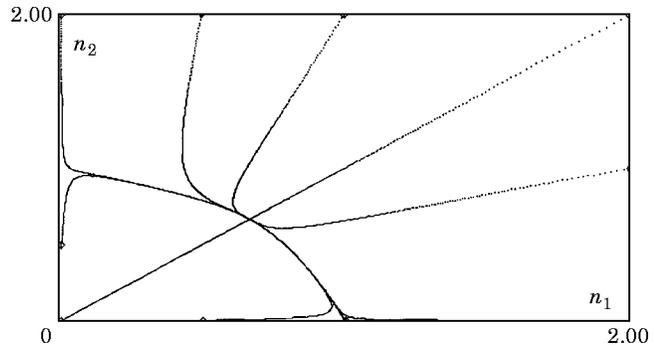


FIG. 5. Computer simulation of the competition-like model. Coexistence. All trajectories converge to a point in the positive orthant which is a stable node.  $\alpha = \delta = 2$ ,  $\beta = \gamma = 1$ ,  $\mu = \phi = 2$ ,  $\nu = \varphi = 1$ ,  $r_1^1 = r_1^2 = 1$ ,  $k_{12}^1 = k_{12}^2 = 1$ .

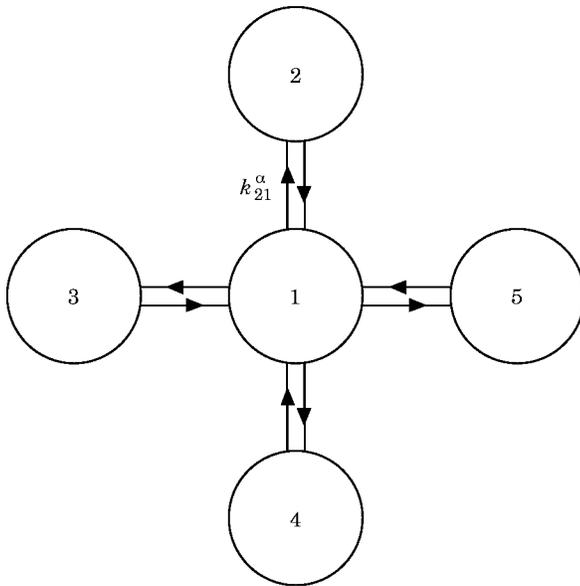


FIG. 6. Branching migration graph for population  $\alpha$ . We present an example with five patches.

are invariant for the migration process. Let us consider a particular migration graph, Fig. 6. We assume that any migration path either starts from patch 1 or reaches patch 1. This means that no connection exists between two patches  $r$  and  $s$  except for  $r = 1$  or  $s = 1$ , (Auger & Benoît, 1993, Auger & Roussarie, 1994). Equilibrium patch frequencies  $v_k^{z*}$  are:

$$r \neq 1, \quad v_r^{z*} = \frac{k_{r1}^z/k_{1r}^z}{1 + \sum_{s=2}^N k_{s1}^z/k_{1s}^z}, \quad v_1^{z*} = \frac{1}{1 + \sum_{s=2}^N k_{s1}^z/k_{1s}^z}. \tag{32}$$

The aggregated model is composed of the two following equations:

$$\frac{dn^1}{dt} = r^1 n^1, \quad \frac{dn^2}{dt} = r^2 n^2, \tag{33}$$

with

$$r^1 = \sum_i r_i^1 v_i^{1*} \quad \text{and} \quad r^2 = \sum_i r_i^2 v_i^{2*}.$$

Similar to the case of two patches, we assume that  $r_1^1$  and  $r_1^2$  are positive and that any other growth rate is negative. This means that there is a favorable patch 1 and that all other patches are unfavorable. Let us also assume that the migration rates are density dependent as follows:

$$k_{r1}^1 = \alpha_r n^1 + \beta_r n^2 \quad \text{and} \quad k_{1r}^1 = \text{constant}, \\ k_{s1}^2 = \gamma_s n^1 + \delta_s n^2 \quad \text{and} \quad k_{1r}^2 = \text{constant}, \tag{34}$$

where  $\alpha, \beta, \gamma, \delta$  parameters are positive constant. The significance of eqns (34) is similar to the two patch case. At large densities, individuals migrate from the favorable patch 1 to an unfavorable patch  $r$ . Under these assumptions, substitution of expressions (34) into the aggregated model (33) leads to a competition-like model of the general form (30).

### Conclusion

Many questions can be reconsidered in the frame of emergence. For example, how can an individual modify the stability of the population and community to which it belongs? Conversely, how global constraints influence the individual behavior at a fast timescale? This contribution provides a simple model for describing the coupled evolutions in the different levels of organization of large-scale dynamical systems. Here, we propose aggregation and emergence processes which can take place in dynamical systems involving multiple timescales. It also shows how the coupling between fast and slow dynamics going on at different levels is a real driving force for the co-evolution of the system and of its subsystems.

The method can be extended to prey-predator models and one can look for different migration processes taking into account repulsive or aggregative behaviours of the prey and predators on the different patches. According to different cases, it is possible to make different functional responses emerge. In this contribution, we have mainly focused on migration between two patches. In the case of many patches, the process of aggregation can lead to an important reduction in the dimension of the model. Our method can also be used in the case of different kinds of subpopulations, not only in a patchy environment, but to various individual states.

It is a general method for aggregation and emergence which can be applied to different cases of structured populations. It is a method devoted to the passage from a micro-level to a macro-level. This method implies that different timescales exist. Alternate approaches based on statistical mechanics of populations can also be performed (Demetrius, 1983).

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## APPENDIX

Let  $X$  be a  $C^\infty$ -vector field on  $R^{k_1} \times R^{k_2} \times R$ , such that, for each  $n \in R^{k_2}$ ,  $(0, n, 0)$  is a fixed point of  $X$ . Let  $DX(n)$  be the linear part of the vector field  $X$  at  $(0, n, 0)$ . We assume that  $DX(n)$  has  $k_1$  eigenvalues which have negative real parts, and that 0 is an eigenvalue which has multiplicity  $k_2 + 1$ . A well-known result of linear algebra claims that a splitting of the global vector space as  $E_n^s \times E_n^c$  exists, where  $E_n^s$  is the space associated to the non-zero eigenvalues, and  $E_n^c$  is the eigenspace associated to the eigenvalue 0. This vector space is called the *center space*. Using these assumptions and notations, we can express the Center Manifold Theorem (Fenichel, 1971), in the following form:

**THEOREM:** For each compact set  $\Delta \subset R^{k_2}$ , and for each positive integer  $K$ , there exists a positive real  $\varepsilon_0$  and

a  $C^K$ -map  $h: \Delta \times ]-\varepsilon_0, \varepsilon_0[ \rightarrow R^{k_1}$ , such that:

- (i)  $h(n, 0) = 0$ .
- (ii) the graph  $W$  of  $h$ , so called Center Manifold, is invariant by  $X$ .
- (iii)  $W$  is tangent to  $E_n^c$  at each  $(0, n, 0)$ .

Remark: since the unstable eigenspace is reduced to  $\{0\}$ , the center manifold is attractive. Thus, the solutions of the global vector field can be approximated by the solutions of the restriction of  $X$  to  $W$  as long as the  $n$ -component stays in the compact  $\Delta$ .

The models that we consider are written in the following form:

$$\begin{cases} \frac{dv}{d\tau} = f(v, n) + \varepsilon F(v, n) \\ \frac{dn}{d\tau} = \varepsilon g(v, n, \varepsilon) \\ \frac{d\varepsilon}{d\tau} = 0 \end{cases}$$

where  $v \in R^{k_1}$ ,  $n \in R^{k_2}$ ,  $\varepsilon \in R$ .

The fast part, obtained when putting  $\varepsilon = 0$ , has a hyperbolic stable equilibrium. This last assumption leads us to apply the previous theorem. In order to look for the fast equilibrium, we need to solve:

$$f(v, n) = 0$$

and we have assumed that this equation has a unique solution  $v^*(n)$ , for each  $n$ , we then put  $\bar{v} = v - v^*(n)$ , in order to translate the equilibrium at 0. Now, writing the system into the new variables, we obtain the following differential system:

$$\begin{cases} \frac{d\bar{v}}{d\tau} = \bar{f}(\bar{v}, n) + \varepsilon \bar{F}(\bar{v}, n, \varepsilon) \\ \frac{dn}{d\tau} = \varepsilon \bar{g}(\bar{v}, n, \varepsilon) \\ \frac{d\varepsilon}{d\tau} = 0 \end{cases}$$

$(0, n, 0)$  is an equilibrium of this system, for each  $n$ . We can calculate the linear part at such an equilibrium, and we obtain the following matrix.

$$DX(n) = \begin{pmatrix} \frac{D\bar{f}}{D\bar{v}} & * & * \\ 0 & 0 & * \\ 0 & 0 & 0 \end{pmatrix}$$

where  $D\bar{f}/D\bar{v}$  denotes the matrix obtained by derivating each component of  $\bar{f}$  with respect to each component of  $\bar{v}$ . Hence, all the eigenvalues of this matrix have negative real parts. Consequently, we can apply the Center Manifold Theorem.