Emergence of individual behaviour at the population level. Effects of density-dependent migration on population dynamics

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Abstract – The aim of this work is to study the effects of different individual behaviours on the overall growth of a spatially distributed population. The population can grow on two spatial patches, a source and a sink, that are connected by migrations. Two time scales are involved in the dynamics, a fast one corresponding to migrations and a slow one associated with the local growth on each patch. Different scenarios of density-dependent migration are proposed and their effects on the population growth are investigated. A general discussion on the use of aggregation methods for the study of integration of different ecological levels is proposed. © 2000 Académie des sciences/ Éditions scientifiques et médicales Elsevier SAS

aggregation methods / slow–fast dynamics / spatially distributed population / density dependent migrations / ecological levels of organisation

Résumé – Émergence du comportement individuel au niveau de la population. Effets des migrations densité-dépendentes sur la dynamique de la population. Le but de ce travail est l'étude des effets de différents comportements individuels sur la croissance à long terme d'une population spatialement distribuée. La population peut se développer sur deux sites, une source et un puits, connectés par des flux migratoires. Deux échelles de temps sont impliquées dans la dynamique, une échelle rapide correspondant à la migration et une échelle lente associée à la croissance de la population sur chaque site. Différents scénarios de migrations densité dépendantes sont proposés et leurs effets sur la dynamique de population sont étudiés. Une discussion générale sur l'utilité des méthodes d'agrégation des variables pour l'étude de l'intégration des différents niveaux d'organisation des systèmes écologiques conclut l'article. © 2000 Académie des sciences/Éditions scientifiques et médicales Elsevier SAS

méthodes d'agrégation / champs lents-rapides / population distribuée spatialement / migrations densité-dépendantes / niveaux d'organisation écologique

Version abrégée

Un problème majeur de l'écologie concerne l'étude de l'influence des comportements individuels sur la dynamique globale de la population et sur la stabilité des communautés. Quel est l'effet d'un changement de comportement des individus sur la dynamique globale de la population ? Le but de cet article est d'aborder ce

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problème général en l'illustrant par l'exemple d'une population pouvant se développer dans un environnement hétérogène.

Les individus peuvent se trouver sur deux sites différents, un site favorable (la source) et un site défavorable (le puits). Certaines ressources indispensables à la survie sont présentes sur la source mais en quantité limitée. De ce fait, la compétition entre les individus sur la source est importante ce qui les conduit à quitter régulièrement la source pour le puits. Un flux migratoire inverse du puits vers la source permet aux individus de revenir sur le site favorable. Les migrations entre les deux sites se produisent à l'échelle de la journée et sont donc fréquentes, en regard de la croissance des individus sur chacun des sites à laquelle est associée une échelle de temps lente.

Nous envisageons diverses hypothèses de migration dépendante de la densité et nous étudions leurs effets sur la dynamique globale de la population à long terme. Dans un premier temps, nous testons une migration du puits vers la source qui est favorisée à haute densité, c'est-à-dire que les individus quittent le puits proportionnellement à la densité d'individus sur ce site. Ce type de règle de migration provoque un effet Allee, c'est-à-dire que pour une condition initiale en dessous d'un certain seuil, la population s'éteint, alors que, au-dessus de ce seuil, elle croît exponentiellement. Un second cas est étudié correspondant à une migration du puits vers la source qui est attractive à basse densité et répulsive à haute densité. Ce modèle présente à nouveau un effet Allee, mais contrairement au cas précédent, au-dessous du seuil critique, la population ne s'éteint pas; les densités d'individus sur chaque site oscillent périodiquement. Ce phénomène correspond à l'apparition d'un cycle limite stable sous le seuil critique. Nous montrons que selon les valeurs des paramètres du modèle, il est également possible que les densités n'oscillent pas, mais tendent vers un équilibre stable.

Cet exemple simple, avec différentes règles de migration dépendante de la densité, montre clairement comment le changement de comportement des individus à l'échelle de temps journalière peut influencer la loi de croissance de la population à long terme. L'article se termine par une discussion générale concernant la pertinence des méthodes d'agrégation des variables pour l'étude de l'intégration des différents niveaux d'organisation des systèmes écologiques. Ces méthodes sont basées sur l'existence de différentes échelles de temps et permettent, à partir de la connaissance des processus se déroulant dans les niveaux inférieurs, de faire émerger la dynamique des niveaux supérieurs. Le résultat final de cette opération consiste en un système composé de niveaux d'organisation. La dynamique dans chacun des niveaux est connectée à celles des autres niveaux à travers des couplages ascendants et descendants. Les couplages ascendants prennent en compte les effets des niveaux inférieurs sur les niveaux supérieurs, c'est-à-dire l'influence des dynamiques locales sur l'évolution à long terme du système. Les couplages descendants correspondent aux effets des dynamiques globales sur les processus locaux rapides.

1. Introduction

The literature concerning population dynamics and habitat fragmentation is of increasing interest. In the early approach of Levins [1, 2], the environment is a set of patches colonised by individuals where population can grow or where extinction can occur. The variable is the proportion of occupied patches. In such metapopulation models [3, 4], the population dynamics within each patch is ignored. It is assumed that the population can rapidly reach an equilibrium density on each patch, characterised by the presence or the absence of the species. This assumption can be justified by time scale arguments. There is a fast time scale associated with the rapid transient growth dynamics of each patch sub-population. This intra-patch dynamics is not described, regarding growth or extinction of local patch sub-populations. Another slower time scale corresponds to the colonisation process as a result of migration between the different patches. The model only describes the process at the slow time scale in terms of the proportions of occupied patches.

Several authors have also considered population dynamics models in a patchy environment composed of a set of two or more separated patches, connected by migration, but they assumed that the time scales for the intra-patch dynamics and the migration were of the same order. This type of model was developed in order to study the influence of density-independent or density-dependent migration in predator–prey and host–parasitoid systems [5–8]. Moreover, numerous biological systems (see [9] for a review) have been studied for their ability to assess and behaviourally control the risk of predation: *Notonecta hoffmanni* [10]; *Notonecta undulata* [11]; the three-spined sticklebacks [12].

The present paper also deals with two time scales, but inversely to metapopulation models, the fast time scale now relates to migration between patches and the slow one to intra-patch dynamics. Few works have been devoted to this case. The fundamental reason probably lies in the fact that, by assuming strong connections between patches, one can reduce the system to a single patch. In this case, the structure of patch connections has scant qualitative influence on the global dynamics of the total population. Indeed, this is true when migration between patches is density-independent. However, the reduction

of the system to a single patch is not so trivial in the case of density-dependent migration.

Indeed, different rules for migration at the fast time scale can have important consequences on the growth of the total population at the slow time scale [13, 14]. Such models are of great interest for the study of populations living in a patchy environment and exploring it at a fast time scale. Each patch has its own characteristics and the way the animals visit and exploit different patches can have important consequences on the total population persistence or extinction.

An important aspect of ecological modelling relates to the study of the influence at the population level of the behaviours and tactics that are selected by the individuals [13, 15]. Most models in population dynamics are simple in the sense that they consider a small number of variables and parameters. For example, a system of two interacting populations is represented by a system of two ODEs, in which the variables usually are the total population densities. In such models, the internal structure of the populations is ignored; that is, any further decomposition into sub-populations, associated with ages or stages. Individual tactics related to phenotypes are not considered. From an ecological point of view, the advantage of such models is that they can usually be analytically handled, allowing one to obtain general results for the population dynamics, in terms of steady states, periodic solutions, etc. But they are very simple and many aspects are neglected that may have important effects on the global dynamics of the overall system.

In contrast, more complicated models have also been developed, that intend to take into account many details of the ecological systems [16, 17]. Such models may have many variables and parameters, and they are usually built up to take into account the detailed structure of the populations and the various interactions between the sub-populations and the environment. However, it is not clear, in the construction of such complicated models, which details should be taken into account and which of them should be ignored. Furthermore, these models are in general very difficult to analyse mathematically, and in most cases only computer simulations can be performed. Through such an approach, only the dynamics for a given set of parameters and initial conditions can be simulated, and it is often impossible to obtain general conclusions concerning the dynamics of the system. A major limitation is that some bifurcations, i.e. qualitative changes in the dynamics when parameters are varied, may take place for some untested parameter values. Hence, in such complicated systems with so many parameters, a correct complete bifurcation analysis is impossible.

Aggregation techniques constitute an alternative method between these two modelling approaches. The aggregation concept was first developed in economic modelling, and was introduced into ecological modelling by Iwasa et al. [18]. This concept deals with models where individual strategies and population dynamics are involved together. The first aspect of interest in aggrega-

tion methods is that they allow one to reduce the dimension of the mathematical model. The reduction can be performed either by an adequate change of variables (perfect aggregation, [18]) or by approximation techniques (approximate aggregation [19]). When the dynamics of the system involves at least two different time scales, we proposed approximate aggregation methods based on perturbation theory [13, 14, 20–22]. Not only is the 'aggregated' model a mathematical object that approximates the initial model, but also there is a strong relation between the complete and the aggregated models because we use the dynamic structure of the initial model in order to build the aggregated one. In most examples, a fast time scale relates to the individual level and a slow one to the population and community levels.

Indeed, the characteristic time scale at the individual level can often be supposed to equal a few days, as individuals look for resources and/or make a decision to change patches frequently. For example, Cowlishaw [23] observed a daily use of refuges by baboons as anti-predator tactics. However, the characteristic time scale at the population level may be as long as a year, or even the duration of a life cycle. This is of course not the case for all populations, but is sufficiently general to warrant investigation. From a mathematical modelling point of view, such an assumption has important consequences because it allows one to write a set of ordinary differential equations (ODEs) governing the sub-population variables with: a) fast parts corresponding to processes going on at the individual level; b) slow parts relating to processes going on at the population level. Then mathematical methods based on perturbation techniques allow one to reduce the dimension of the system of ODEs and to obtain an aggregated model governing a few global variables (for example the total populations) at the slow time scale [21]. We also refer to Poggiale [24] for continuous time models and to Bravo de la Parra and Sanchez [25] and Sanz Lorenzo [26] for discrete time models. In such a reduced global model, few parameters occur in the slow model and the method permits one to obtain relationships between global parameters and those governing the individual dynamics at the fast time scale.

An important advantage of aggregation methods is not only the dimensional reduction in order to simplify models, but also that it shows how the individual behaviour emerges at the population level [7, 13, 27–31]. It is of major importance to look for the effects of different individual tactics or strategies at the population level in the long run.

We refer to previous studies [21, 22, 24–27] for the general aspects of aggregation methods. In this paper, we focus on a particular case of a two-patch environment, in order to illustrate how aggregation techniques proceed. Population dynamics in a sink–source environment has been considered in earlier contributions [32]. Two competing species were considered in a two-patch environment, in the sense of two different types of patches. Two populations that would otherwise exclude each other

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mutually on a single patch can coexist in a two-patch system, each one occupying a patch from which the other species is excluded [32]. Many papers consider evolution time scale processes, such as the evolutionary stability of sink populations (refer to [33–35] for recent works).

The consequences for population dynamics of migrations or dispersal of a single–species population, distributed on a two-patch environment, have also been a subject of interest. For example, Pulliam [36] investigated the consequences of active dispersal on the dynamics of single-species populations. Gosselin [37] used a stochastic model to study the effects of different dispersal patterns on the extinction probabilities of a single-species population. Gyllenberg et al. [38] studied the influence of migration on the stability of population dynamics. In the same way, in this article, we apply an aggregation method in order to investigate the effects of migration behaviours at the individual level on the overall dynamics of a spatially distributed population. The population is distributed between a source and a sink, and at a fast time scale individuals migrate between the two patches. The next section is devoted to the presentation of the global model and the general form of the aggregated model. In the following section, we propose three increasingly more complex strategies for the individuals. We analyse the effects of these individual behaviours on population dynamics on the long time scale. The article ends with a general discussion about the usefulness of aggregation and approximation methods for the study of the integration of different ecological levels.

2. The model

The mathematical framework of the model is similar to the one used by Auger and Poggiale [13]. We consider a population of total density $n(t)$. This population is subdivided into two sub-populations $n_i(t)$, $i = 1,2$ (*figure 1*). The following system of two ODEs describes the growth of the sub-populations:

Figure 1. Individuals can go on two patches. k_{12} and k_{21} are the migration rates from patch 2 to 1 and from patch 1 to 2, respectively, the migration process taking place at a fast time scale.

$$\begin{cases} \varepsilon \dfrac{dn_1}{dt} = (k_{12}\, n_2 - k_{21}\, n_1) - \varepsilon r_1\, n_1 \\ \varepsilon \dfrac{dn_2}{dt} = (k_{21}\, n_1 - k_{12}\, n_2) + \varepsilon r_2\, n_2 \end{cases} \quad (1)$$

where k_{12} is the migration rate from patch 2 to patch 1 and k_{21} from patch 1 to patch 2. In general, migration rates are functions of local patch densities. In the next sections, k_{12} will remain constant and we shall study different density-dependent rules for k_{21}. ε is a small parameter ($\varepsilon \ll 1$), meaning that the migration process takes place at a fast time scale compared to the population growth evolving at a slow time scale. We assume a linear growth for sub-populations, i.e. linear growth functions on each patch, patch 1 being a sink and patch 2 a source [33]. The source is a patch on which food can be found and which has necessarily to be visited by individuals to obtain resources. In the sink, individuals cannot find enough resources to develop, and we assume that animals regularly leave the sink to go to the source, in order to obtain necessary resources for survival and reproduction. The two patches are close to each other.

As detailed in Auger and Poggiale [13], by assuming that migrations go faster than reproduction, one can approximate model (1) by an aggregated single equation governing the total population density $n = n_1 + n_2$ on the two patches. Since the micro-variables n_i, $i = 1,2$ move rapidly, we assume that they reach an attractor (equilibrium point, limit cycle, strange attractor, etc.). Roughly speaking, at the fast time scale, we can replace these micro-variables by constants depending on the attractor nature and on the macro-variable n which is almost constant at the fast time scale. In the next section, we present examples where the fast dynamics possess an equilibrium. We denote by v_i the proportion of sub-population on patch i and by $v_i^*(n)$ the proportion of population i at the fast equilibrium. These proportions depend on the migration rates k_{12} and k_{21}. It follows that the equation for the total population density:

$$\frac{dn}{d\tau} = \varepsilon(- r_1\, v_1 + r_2\, v_2)n \quad (2)$$

can be approximated by:

$$\frac{dn}{dt} = (- r_1\, v_1^*(n) + r_2\, v_2^*(n))n + O(\varepsilon) \approx r(n)n \quad (3)$$

where $t = \varepsilon\tau$ is the long time scale, τ the fast one and $r(n) = - r_1\, v_1^*(n) + r_2\, v_2^*(n)$.

Note that this model provides relationships between the population level and the individual level since the population growth rate on the long time scale $r(n)$ depends on the behavioural dynamics at the individual level. In the examples we present, we obtain explicit expressions for the equilibrium proportions $v_i^*(n)$.
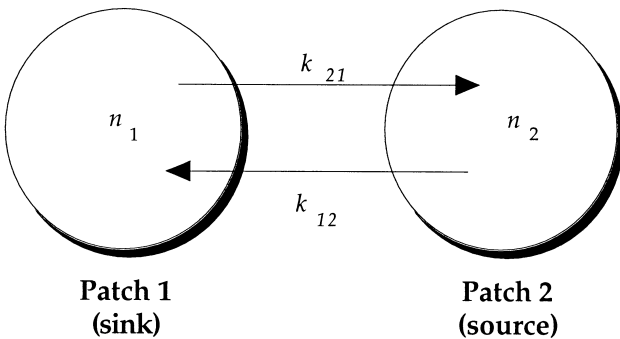
3. Effects of different migration scenarios

We shall consider three kinds of migration, increasing the complexity of the migration rates. In the first example, we assume that the migration rates are constant. This corresponds to random motion and the migration rates are those of an average individual. In the second example, migration rates are linear with respect to the local densities. This is the simplest way for modelling such behaviours as aggregative or repulsive ones. In the last example, we make the migration rates more complex by considering them as quadratic functions of the local densities. This is the simplest way to build non-monotonous functions of the local densities.

These three examples provide a sample of all possible situations. Indeed, we present the case of density-independent migration rates (random migrations), the case where there is only one global density-dependent fast equilibrium and the case where there are different possible stable fast equilibria. The last case is interesting from a general point of view since it shows how the total population density may influence the individual behaviour, with drastic consequences on the population dynamics. In this example, growth functions are monotonically growing on each patch (see model (1)). However, at the population level on the long time scale, the total population density can oscillate.

3.1. Constant migration rates

Let us assume that the individuals migrate randomly. The migration rates for an average individual k_{12} and k_{21} are constant. We give this simple example in order to illustrate briefly the method. The fast equilibrium is obtained from model (1) by neglecting the population level ($\varepsilon = 0$), and by cancelling the differential equations obtained with $\varepsilon = 0$. We obtain:

$$v_1^* = \frac{k_{12}}{k_{12} + k_{21}} = \frac{1}{1 + \dfrac{k_{21}}{k_{12}}} \quad \text{and} \quad v_2^* = \frac{k_{21}}{k_{12} + k_{21}} = \frac{1}{1 + \dfrac{k_{12}}{k_{21}}} \quad (4)$$

Note that what matters here is the ratio between the migration rates $\dfrac{k_{12}}{k_{21}}$, not the actual expression of the rates separately. By replacing the equilibrium proportions in the aggregated model (3) by their expression (4), we derived the aggregated model:

$$\frac{dn}{dt} = rn \quad (5)$$

where $r = \dfrac{-r_1 k_{12} + r_2 k_{21}}{k_{12} + k_{21}}$ is the (constant) population growth rate.

The sign of this growth rate depends on the proportions on each patch at the fast equilibrium. If there are many more individuals in the sink, the population will disap-

pear. If the major part of the population is in the source, it grows exponentially.

3.2. Linear migration rates

The simplest case of density-dependent migration is obtained when the migration rates are linear functions of the densities. As shown with equation (4), what matters is the ratio between the migration rates. Auger and Poggiale [13] considered a constant migration rate from the sink to the source and a linear migration rate from the source to the sink. This behaviour resulted in a logistic-like growth model at the population level; that is, the growth population was self-regulated. In this work, we consider the opposite case: a constant migration rate ($k_{12} = a$) from the source (patch 2) to the sink, while the migration rate from the sink (patch 1) to the source ($k_{21} = \beta n_1$) is proportional to the density of the sub-population located in the sink. This corresponds to a repulsive behaviour for the sink.

A straightforward calculation (based on (4)) gives the following fast equilibrium proportions:

$$v_1^* = \frac{-a + \sqrt{a^2 + 4a\beta n}}{2\beta n} \quad \text{and} \quad v_2^* = 1 - v_1^* \quad (6)$$

The corresponding aggregated model reads:

$$\frac{dn}{dt} = \frac{r_1 + r_2}{2\beta} \left(a - \sqrt{a^2 + 4a\beta n} \right) + r_2 n \quad (7)$$

This equation has two steady states: the origin and a positive equilibrium $n^* = \dfrac{a r_1 (r_1 + r_2)}{\beta r_2^2}$. This equilibrium is always unstable while the origin is a stable steady state. *Figure 2* illustrates the phase portrait in the plane (n_1, n_2). It is noteworthy that below a certain threshold, precisely given by n^*, the population goes extinct, while above it the population grows to infinity. This dynamical behaviour can be regarded as an Allee effect [2]. For an initial population less than n^*, the repulsive effect on the sink is weak. Thus, individuals tend to stay in this unfavourable patch, and the global population goes to extinction. Above the threshold density n^*, the repulsive effect becomes strong and individuals escape the sink to the source; consequently, the global population grows exponentially.

Levin [32] investigated competitive interactions as well as the interaction between an abundant prey and a rare predator in a two-patch environment incorporating co-operative (Allee) effects. It was shown that for a large mobility of prey, the equilibrium of the system becomes unstable. This early work showed how the speed of migration can influence the dynamics of a predator–prey system.

3.3. Quadratic migration rates

We end with an example where the fast part of model (1) can exhibit two stable equilibria. In this case, at the short
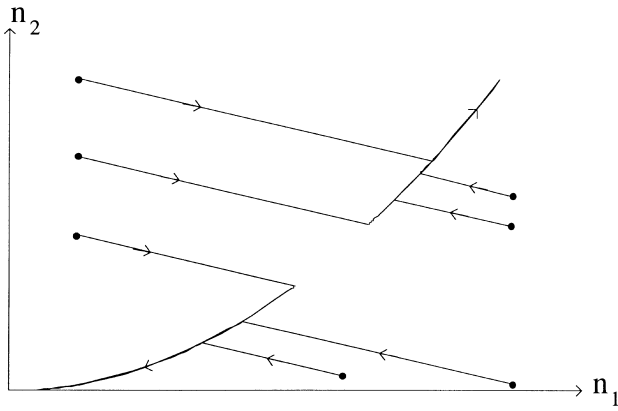
Figure 2. Computer simulation of trajectories obtained by the Runge-Kutta method using the density-dependence function $f(n_1) = 1.5n_1$. Growth rates are $r_1 = 0.2$ and $r_2 = 0.1$, and the migration rate from patch 2 to patch 1 is $k_{12} = 0.4$. The parameter ε is equal to 0.5.
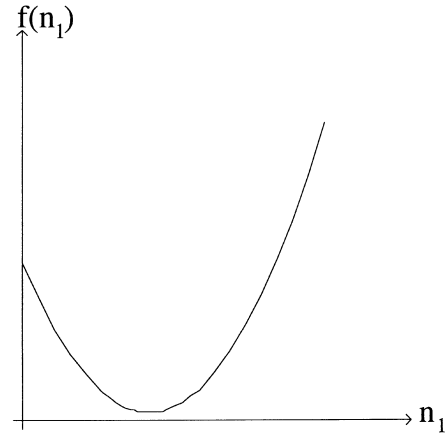

Figure 3. General shape of the density-dependent migration rate $k_{21} = f(n_1)$. Here, we chose $f(n_1) = 21(n_1)^2 - 21n_1 + 5.5$.

time scale, the proportions in each patch tend toward given values that depend on the total population density. Since this density moves slowly, we show that the fast equilibrium can become unstable and the sub-populations proportions 'jump' to another equilibrium. Thus, the aggregated model corresponding to the initial fast equilibrium is not valid any more, and another aggregated model must be calculated. As the total population density is always slowly changing, the new fast equilibrium can also become unstable and the sub-population proportions 'jump' back to the first fast equilibrium. This is a simple model in which we can analyse the effect of the individual level on the population dynamics as well as the feed-back effect of the population dynamics on the individual level. The resulting effect, in this case, is oscillation, observed on the long time scale, at the population level. We shall explain this heuristic reasoning more precisely from the following example.

Once again, we assume that $k_{12} = \delta$ is a constant and $k_{21} = an_1^2 + \beta n_1 + \gamma$ is a quadratic function of the local density in the sink. These migration rates should be interpreted as follows: at low density the individuals tend to concentrate on the sink, while at high density, they tend to aggregate on the source. Such a behaviour of changing anti-predator tactics according to density has been, for example, recently observed by Rangeley and Kramer [39] for juvenile pollocks. These fishes use two alternative anti-predator tactics (refuging or aggregation), involving fast movements between two different habitats.

There are some mathematically necessary conditions on the parameters to ensure that the migration rates remain positive: $a > 0$, $\beta < 0$ and $\beta^2 < 4a\gamma$. *Figure 3* illustrates the shape of the function k_{21}, which is denoted by $f(n_1)$. First, we look for the equilibrium of the fast part of equations (1), which satisfies the following equation:

$$\delta(n - n_1) = (an_1^2 + \beta n_1 + \gamma)n_1 \qquad (8)$$

We denote $g(n_1) = (an_1^2 + \beta n_1 + \gamma)n_1 = f(n_1)n_1$, a cubic function, which has a zero at $n_1 = 0$. The solutions

of equation (8) are obtained by the intersection between the curve of g and the straight line defined by the left-hand side. For certain parameter values, these curves can have three intersection points, leading to three steady states, as illustrated in *figure 4*.

Figure 5 shows a Runge-Kutta simulation of the phase portrait of system (1), by using a quadratic function $f(n_1) = 21n_1^2 - 21n_1 + 5.5$. This figure shows that a limit cycle emerges at the population level. It is noteworthy that the choice of an initial condition in the upper part of the phase portrait of *figure 5* leads to an unbounded growth. *Figure 6* shows the periodic variations of the patch densities $n_1(t)$ and $n_2(t)$ calculated from system (1), with the
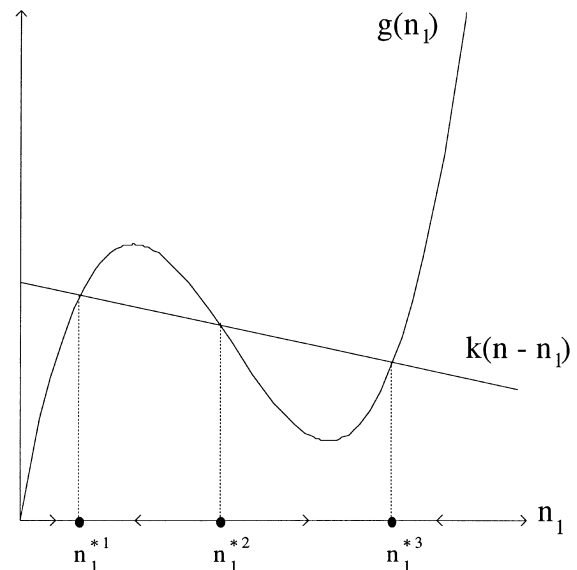
Figure 4. The fast equilibrium points are found at the intersection of $g(n_1) = n_1 f(n_1)$ and the line $k_{12}(n - n_1)$ with a negative slope $- k_{12}$. Two cases can occur: a unique stable equilibrium point (not shown); or two stable equilibrium point (n_1^{*1} and n_1^{*3}) with an unstable one (n_1^{*2}).
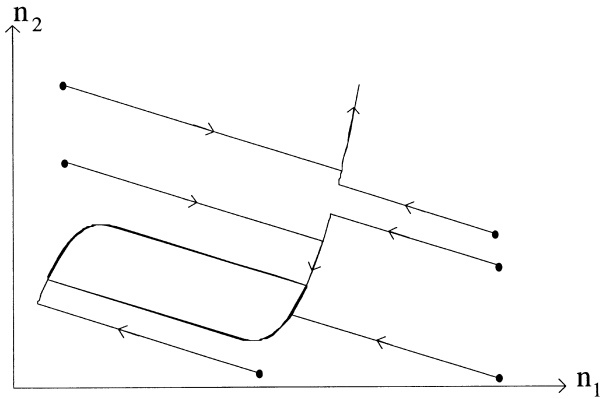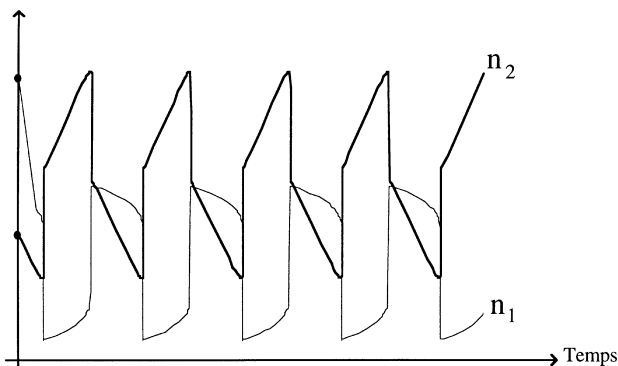
Figure 5. Computer simulation of an hysteresis cycle obtained by the Runge-Kutta method using the density-dependence function $f(n_1) = 21(n_1)^2 - 21n_1 + 5.5$. Growth rates are $r_1 = 0.2$ and $r_2 = 0.1$, and the migration rate from patch 2 to patch 1 is $k_{12} = 0.4$. The parameter ε is equal to 0.5.

Figure 7. Computer simulation of trajectories obtained by the Runge-Kutta method using the quadratic function $f(n_1) = 21(n_1)^2 - 19.4n_1 + 5.5$. In this case, the trajectories tend to a unique asymptotically stable point. Growth rates are $r_1 = 0.2$ and $r_2 = 0.1$, and the migration rate from patch 2 to patch 1 is $k_{12} = 0.4$. The parameter ε is equal to 0.5.
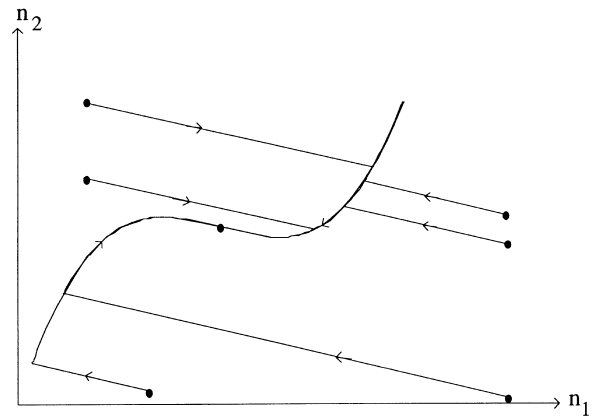
density-dependence function of *figure 3* and an initial condition leading to the limit cycle.

With such a density-dependent migration rule, we find again two kinds of global population dynamics, depending on a threshold density. Contrary to the previous case (*figure 2*) below this threshold, the population does not go extinct, but a stable limit cycle occurs (*figure 5*). Above this threshold, the strong repulsive migration from the sink causes, as previously, the exponential growth of the global population.

The hysteresis loop of *figure 5* comes from the switch between the two stable fast equilibria. The first equilibrium corresponds to many individuals on the source and few on the sink, while the second one corresponds to the reverse case. From the first fast equilibrium, the total population grows slowly. In particular, the density n_1 is low but slightly increases, involving a sudden switch in the second fast equilibrium due to the aggregative migration

Figure 6. Time variations of the patch sub-populations. Computer simulation of an hysteresis cycle obtained by the Runge-Kutta method using the density-dependence function $f(n_1) = 21(n_1)^2 - 21n_1 + 5.5$. Growth rates are $r_1 = 0.2$ and $r_2 = 0.1$, and the migration rate from patch 2 to patch 1 is $k_{12} = 0.4$. The parameter ε is equal to 0.5.

behaviour of individuals on the sink. The total population then slightly decreases, and the repulsive effect of migration pushes the individuals to run away from the sink to the source, ending the limit cycle.

Note, as shown by the Runge-Kutta simulation on *figure 7*, that another case can occur, corresponding to a unique asymptotically stable equilibrium point. Such a stable equilibrium point for the whole system corresponds to an equilibrium point for both the fast and the slow systems. In this case, there is again a threshold density, leading to either the exponential growth of the total population, or constant densities for n_1 and n_2. With an initial condition below this threshold, the total population dynamics exhibits a stable equilibrium point.

4. Conclusion

As an example of the use of aggregation methods, our model gives the possibility of describing oscillations of the total population density in a patchy environment. Such periodic oscillations have been observed for lemmings, rodents or insects [40], but are also described for host–parasitoid [41, 42] or prey–predator systems [43].

Modelling such periodic emergence of a single population usually involves delay equations [40]. Our modelling approach provides another possibility of cyclic variations of the total population as the result of the density dependence in the migration process. We showed that aggregation on the sink patch at low densities combined with aggregation on the source patch at high densities can lead to periodic oscillations.

More generally, we showed how density-dependent migrations could have, from a qualitative point of view, important consequences for the dynamics for the total population. In fact, the individual behaviour, here the

migration behaviour, can strongly determine the growth rule for the total population, either decaying to zero, growing to infinity, tending to an asymptotically stable size or exhibiting periodic oscillations.

This work shows that population dynamics have to be considered in terms of coupling between the individual and the population levels. A change of the individual fast model makes different slow growth models emerge for the total population. This can be regarded as a bottom-up coupling, that is the effect of a lower level on a more global one.

On the other hand, the fast equilibrium itself depends on values of the global variables, governing the dynamics of the system at the slow time scale. These global variables slowly change with time, and for example can provoke the loss of stability of a fast equilibrium. Such a coupling can be regarded as a top-down coupling, that is the effect of changes at the population level on the individual level.

In fact, both types of coupling (bottom-up and top-down) may occur at the same time. The overall dynamics of the system is the result of the coupled dynamics in each of its levels, the individual and the population. Integration of the different levels of organisation must then be achieved by investigating this dynamical coupling of the slow and fast processes going on at the ecological levels.

Mean field theory can also be used to describe random motion of individuals in space and to obtain general spatial patterns [44]. The moment closure method is also powerful in providing moments of different orders, for spatially distributed populations, average density, variance, etc. This method has been applied for species competing for space [45, 46].

Different time scales must be taken into account according to processes going on at the different levels of an ecological system. Slow–fast models are thus very good candidates for the study of interactions between ecological levels. Several contributions investigated slow–fast dynamics in the context of predator–prey systems [47–49]. We also refer to spatially distributed predator–prey models with density-dependent migrations [7, 14, 31, 50].

A further assumption is made regarding the choice of global variables, which are first integrals of the dynamics of the fast models [13, 20, 21]. In other words, the fast models are conservative. As a consequence, the variables that characterise the global dynamics are not defined in an arbitrary way, but they correspond to invariant quantities for the internal dynamics of the lower levels. The different levels of organisation of the system are associated with different levels of invariance.

The spatial structure of the environment can strongly influence the dynamics of the populations. For example, the Nicholson and Bailey model that describes the dynam- ics of a host–parasite system is unstable [51]. The system undergoes amplified oscillations leading to extinction of the system. However, Hassell et al. [52] have shown that when different patches are connected by migrations and when the size of the network increases, the host–parasite system does not go extinct and can maintain itself. Similar results have been obtained by Durett and Levin [53] for a hawk–dove system. These examples show that spatial connections can have important and non-trivial consequences on the overall dynamics of the system.

Slow–fast models also allow one to take into account the dynamics of spatially distributed populations such as shown in this article. However, the method can be used not only in the case of two patches, but also in the case of a complex network of interconnected patches. This method appears then very powerful, as it allows one to aggregate a large number of patch sub-populations into a single global variable (the total density summed over all patches). Such a model was performed to describe the dynamics of a trout population in an arborescent river network of 15 patches [29, 30].

An interesting perspective is to use the method for different types of large networks involving many patches and aimed at representing different types of environments: a river network, a lake, a set of interconnected meadows, etc. Aggregation methods can help in taking into account complex spatial and realistic environments, and allow one to derive a low dimension model governing the dynamics of the total system in the long run. The required condition is that the individual motion in the network is faster than the reactions occurring locally.

The aggregation method can also be used to study effects of different individual tactics described by games on the overall dynamics of the populations. Such a work was performed in the case of a domestic cat population in which the effect of individual aggressiveness on the total equilibrium density of the population was investigated [28].

Aggregation techniques present general methods for integrating biological levels of organisation. This goal can be achieved by understanding how the lower levels influence the dynamics of the global system, and inversely how the feed-back exerted by the upper levels act on local dynamics. Then, the whole system must be seen as a hierarchically organised system involving several biological levels [15]. Its evolution is the result of the coupled dynamics in each of its levels.

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