



From spatially explicit ecological models to mean-field dynamics: The state of the art and perspectives

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ABSTRACT

In this paper, we provide a brief review of the well-known methods of reducing spatially structured population models to mean-field models. First, we discuss the terminology of mean-field approximation which is used in the ecological modelling literature and show that the various existing interpretations of the mean-field concept can imply different meanings. Then we classify and compare various methods of reducing spatially explicit models to mean-field models: spatial moment approximation, aggregation techniques and the mean-field limit of IBMs. We emphasize the importance of spatial scales in the reduction of spatially explicit models and briefly consider the inverse problem of scaling up local ecological interactions from microscales to macroscales. Then we discuss the current challenges and limitations for construction of mean-field population models. We emphasize the need for developing mixed methods based on a combination of various reduction techniques to cope with the spatio-temporal complexity of real ecosystems including processes taking place on multiple time and space scales. Finally, we argue that the construction of analytically tractable mean-field models is becoming a key issue to provide an insight into the major mechanisms of ecosystem functioning. We complete this review by introducing the contributions to the current special issue of Ecological Complexity.

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1. Introduction

Spatial heterogeneity is a crucial factor which shapes the dynamics of a single population and allows coexistence of a large number of species within communities and ecosystems (Kareiva, 1990; Levin, 1992; Odum and Barrett, 2004), a fact which has been recognized both in experiments/observations (Huffaker et al., 1963; Ellner et al., 2001; Molofsky and Ferdy, 2005) and theoretical models (Hutchinson, 1961; Hassell and May, 1974; Durrett and Levin, 1994a,b; Bolker and Pacala, 1997). A large number of mathematical models of heterogeneously distributed populations use an explicit spatial resolution i.e. consider the population densities as functions of space, and different modelling approaches of spatially explicit models exist in the literature – an exhaustive classification is given in the review of Bercé (2002). In particular, the reaction-diffusion framework (Cantrell and Cosner, 2003); models based on integral kernels (Kot et al., 1996); cellular automata (Ermentrout and Edelstein-Keshet, 1993; Pascual et al., 2002) coupled map lattices models based on difference equations (Hassell et al., 1991); and individual based modelling (Grimm and

Railsback, 2005; Railsback, 2006) are all quite prominent. The main goal of all these approaches is to take into account the fact that a given individual can interact only with a limited number of neighbouring individuals and the local fitness for such individual can vary across the habitat.

Considering detailed spatial structuring in ecological models can have serious drawbacks as well. The first problem comes from trying to localize animals in space in our models, since the spatial position of a single individual, a group of individuals or the entire population of non-sessile species can change across the environment significantly on rather short time scales (compared to the characteristic reproduction time). A classic example is the vertical migration of zooplankton in the water column, taking place on a timescale of several hours (the characteristic reproduction time varies from several months up to a few years) but ranging the entire habitat. As a result, the vertical distribution of animals can change hundreds of times between generations (Bollens and Frost, 1989; Ohman, 1990). There are many other ecological examples, where small-sized animals can travel several hundred meters across a lake in a day, for instance, the horizontal daily migration of certain jellyfish species (Hamner and Hauri, 1981). In such cases, a detailed description of the instantaneous location of animals provides too much information, and thus is simply not necessary. For this reason, constructing a spatial model often implies

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averaging the instantaneous distributions of individuals over certain time period and over some characteristic area.

Second, in spatially structured models the degree of freedom (the number of state variables which uniquely characterizes the system) substantially increases, in particular, the degree of freedom can be infinitely large, as in models with continuous space. Evidently, this reduces the tractability of the models, in particular, analytical treatment of spatial models becomes seriously impeded and in many cases it can be impossible. Interestingly enough, including spatial aspects such as explicit species spatial distributions or/and complex patterns movement behavior in ecological models is often required to correctly predict only some average characteristics of as the total population sizes of species as the outputs of our models (Odum and Barrett, 2004; Auger et al., 2000).

Third, implementation of complex spatial models normally implies the use of a large number of additional parameters and functions which are often unknown or poorly understood (Raick et al., 2006). This makes analysis of sensitivity of the model to variation of parameters or functions substantially more complicated compared to the non-spatial cases (Batchelder et al., 2002). This implies both a large increase of computational time and a tremendous enhancing of complexity of parameter space: even after a large number of time expensive simulations we may still poorly understand what patterns of dynamics we should expect to find in the given system and how they depend on model parameters. In the absence of solid empirical evidence, patterns of animal movement and behavioural aspects are often included in spatial models based on rough estimates or simply using common sense (e.g. Leising, 2001).

Finally, in a large number of cases we want to reveal generic mechanisms through which an ecosystem or a community functions (Petrovskii and Petrovskaya, 2012), and for this reason we only need a qualitative description of the system. The main questions include the possibility of persistence and coexistence of species as well as the eventual types of patterns of dynamics: stationary, oscillatory, chaotic, multistable, etc. From this point of view we only need to include the spatial heterogeneity in the case where the same model without space would provide qualitatively different patterns; it is also natural to do so in a way where adding spatial dimension results in a minimal increase of model complexity. This can be done by either constructing spatially implicit models, such as the famous extinction-colonization model of R. Levins (Levins, 1969, 1970) or, alternatively, by reducing complex spatially explicit models. The latter is the key topic of the current review and the current special issue of *Ecological Complexity*.

The main drawback of spatially explicit models lies in their complexity. However, sometimes it can be possible to simplify those models and describe the population dynamics in terms of some integral characteristics averaged over a large part of the habitat or even over the entire habitat (e.g. the population sizes). In theoretical ecology, such reduced models are known as mean-field models – the terminology of mean-field approximation is addressed more precisely in Section 2. In particular, this includes the replacement of IBMs (individual based models) by density-dependent Fokker–Planck-type models. The important advantage of mean-field models is that their behaviour can be better understood and thus we can have a better insight into generic mechanisms of ecosystem functioning without losing, if possible, an adequate quantitative description.

The aim of the current review is to briefly consider different approaches of reducing of spatially explicit ecological models to simpler mean-field models. The paper is organized as follows: in Section 2, we discuss different definitions of mean-field dynamics and mean-field approximation which are used in the ecological

literature; in Section 3, we consider various methods of reducing complex models to mean-field analogues which are widely used in the literature; in Section 4, we emphasize the importance of spatial scales in the construction of mean-field models; in Section 5, we consider some important future challenges in the reduction of spatially structured models, and finally, Section 6 introduces the contributions to the current special issue of *Ecological Complexity*.

2. Terminological aspects of mean-field modelling

When talking about mean-field ecological models, one needs to be precise in the definition of the description of ‘mean-field’. In fact, in the current literature there exist several ‘mean-field’ concepts, and some of them have rather different meanings. In this section, we discuss those various definitions and meanings and explain what we shall understand by ‘mean-field’ dynamics in this special issue.

In a large number of population models, the mean-field model (mean-field scenario) is defined as the one where the individuals in the habitat are well mixed and the probability of interaction of a randomly taken individual with any other individual from this population (or with an individual from another population) does not depend on the individual chosen. Also, the environment is considered to be homogeneous (e.g. no sharp gradients of resource distribution). Some classic examples are: the famous Lotka–Volterra predator–prey model (Lotka, 1925; Volterra, 1926); the seminal epidemiological model (Kermack and McKendrick, 1927) or the well-known model of cyclic competition of species (May and Leonard, 1975). The meaning of mean-field in those models is conceptually similar to that of ‘small world’ models where individuals have equal chance to interact with any other individuals regardless of the distance separating them (e.g. Durrett and Levin, 1998; Frean and Abraham, 2001).

A slightly different meaning of mean-field models is given in some theoretical works, where the authors either construct a spatially explicit model by adding dispersal terms into an initial model without space, or modify the existing terms to implicitly include the effects of heterogeneity. In this case the initial local interaction terms are often referred to as the mean-field dynamics (Pascual et al., 2001). Similarly, a mean-field approximation of an explicit spatial model is often understood as trying to predict the global model dynamics (e.g. in terms of population sizes) by neglecting the migration or dispersal terms and simply extrapolating the local interactions to the scale of the entire habitat (Bergström et al., 2006 and the references therein). Not surprisingly, such approximation often gives poor results (Bergström et al., 2006; Wallhead et al., 2008); this is often interpreted as a failure of mean-field descriptions of ecosystems.

In a number of publications, a mean-field model is understood as a simplified/reduced version of a spatially explicit model where dynamics is described in terms of integral characteristics such as the population size (or the biomass) of the species. In this case, the model equations for the population sizes can be substantially different from those which hold for local interaction: we do not assume well mixing in these system, but implicitly include the effects of heterogeneity of species distribution as well as those of the environment into models (Gubbins and Gilligan, 1997; Auger et al., 2000; Pagel et al., 2008; Pascual et al., 2011).

Often a complex spatially explicit model cannot be simplified to a system of equations in terms of only the total species biomasses or population sizes, but it is still possible to reduce the initial model to a certain closed system where some extra integral variables are also state variables, for instance including spatial moments of species densities (e.g. spatial variance, covariance, etc.). In this case, we can consider such simplified models as mean-field approximation as well (Matsusa et al., 1992; Bolker and Pacala,

1997; Dieckmann and Law, 2000; Chesson et al., 2005; Wallhead et al., 2008).

Finally, a different meaning of mean-field approximation comes from the implementation of individual based modelling (IBM). In such models each individual (or a homogeneous group of individuals or super-individual) is explicitly modelled as a discrete entity (Scheffer et al., 1995; Grimm, 1999; Railsback, 2006), and the movement of an individual is given by a set of prescribed rules. In the case, where the number of individuals is large, it becomes convenient to describe the system in terms of population densities and the master equations are, actually, the Fokker–Planck-type equations. Such replacement of a system of discrete particles with a continuous model is known as mean-field approximation (also called mean-field limit): in this case the mean-field model can be still spatially explicit (e.g. based on integro-differential equations) but its properties can be easily understood (Peruani et al., 2008; Carrillo et al., 2010; Bolley et al., 2011; Gómez-Moureló, 2005; Faugeras and Maury, 2007). This seminal idea comes from theoretical physics, where the term ‘mean-field approximation’ had been coined under a different meaning. It is well known that the complex problem of a large number interacting bodies/particles is extremely difficult to solve, but the initial many-body problem can be replaced with an equivalent problem of a single body/particle moving in the external field created by the other particles (Chaikin and Lubensky, 2007).

In this paper, we shall understand the concept of mean-field dynamics and mean-field approximation in a rather broad sense: in the case that a complex model considering spatially structured populations can be simplified to a system of closed equations for the integral characteristics, we shall refer to this model as a mean-field approximation. We shall also use mean-field approximation (mean-field limit) to refer to the reduction of IBM to density-dependent spatially explicit models.

3. Methods of reduction of spatially explicit model

There are a few major ideas behind the reduction of spatially explicit models to mean-field dynamics. Firstly, we suggest that the model trajectories, which can be considered in general to evolve in a high dimensional space (for instance, with infinite number of dimensions), are situated on a low dimensional subspace (or a manifold) S , since only in this case can we proceed to constructing a mean-field model. Usually trajectories achieve this low dimensional space/manifold from the initial conditions after some transient time period during which the model reduction is impossible: we can only use the complete model by running numerical simulations. The low dimensional set S may be the final attractor of the model or it can be an intermediate attractor in the sense that the trajectory will still be evolving on S towards its final attractor S_0 with $\dim(S_0) < \dim(S)$. The implication is that even rather complex spatial models with an infinitely large number of dimensions can be described based on simple models with a low number of dimensions (e.g. Hyman and Nicolaenko, 1986). For instance, in deterministic models the attractor of dimension m can be embedded into a Euclidian space of dimension $2m + 1$ (Takens, 1981) and thus the dynamics of the initial complex spatial system can be described based on a low dimensional model. The second major idea is that describing the evolution of trajectories on S can be done based only of some integral (macro) characteristics of the system such as the total population sizes of species, few spatial moments, etc. Finally, the total number of those integral characteristics (which can be understood as the degrees of freedom) should not largely exceed the number of species N in the system. Ideally, it should be exactly N . As such, we shall not consider as mean-field models those ones in which some species are described using their population size P , but modelling of the

others would require the spatial distributions of their density $p(x,y,z)$.

There exist a large number of different approaches/techniques for reducing of spatially explicit to mean-field models (in a various sense of ‘mean-field’ approximation, see Section 2 for details). We can roughly classify those approaches into three main families: (i) methods using moment approximation (i.e. considering first, second, etc. spatial moments); (ii) aggregation methods using the fact that the local densities can be expressed as functions of some global characteristics (e.g. population sizes); (iii) approaches of reduction of IBM to continuous (density dependent) models, i.e. considering the mean-field limit of IBMs. Below, we shall briefly characterize those families.

3.1. Spatial moments methods

Spatial moment methods are used to take into account interactions and movements of organisms in small neighborhoods compared to the total size of the habitat (Bolker and Pacala, 1997); they are widely used in stochastic population models, but can also be applied to deterministic models (Wallhead et al., 2008). In particular, the spatial moments for *continuously spatially distributed models* are defined as

$$\begin{aligned} p_i &= \frac{1}{S} \int P_i(\vec{x}) d\vec{x}, & c_{ij}(\vec{y}) &= \frac{1}{S} \int P_i(\vec{x}) P_j(\vec{x} + \vec{y}) d\vec{x}, \\ T_{ijk}(\vec{y}, \vec{z}) &= \frac{1}{S} \int P_i(\vec{x}) P_j(\vec{x} + \vec{y}) P_k(\vec{x} + \vec{z}) d\vec{x} \end{aligned} \quad (1)$$

where $P_i(\vec{x})$ is the spatial density of species i at location x (for a given moment of time), S is the area of the habitat and \vec{y} and \vec{z} are locations in the habitat. The first moments p_i are simply the average population densities. The quantities $c_{ij}(\vec{y})$ are called the pair correlations densities (the second-order spatial moments). Finally, the quantities $T_{ijk}(\vec{y}, \vec{z})$ are the correlation densities of triplets. In a similar way, one can define higher order spatial moments. Note that in stochastic models we need to average the spatial moments (1) over all possible realizations of distributions $P_i(\vec{x})$ (Keeling et al., 2002; Law and Dieckmann, 2000).

The main idea of the method is to write a system of integro-differential (or simply differential) equations for the spatial moments (Bolker and Pacala, 1997, 1999; Murrell et al., 2004). As a result, by solving the system for spatial moments one can potentially follow the dynamics of the first moments, i.e. the average population sizes of species p_i . The major difficulty in this approach is that the constructed system is actually an infinite set of equations: each equation for the spatial moment of order n contains moments of order $n + 1$, etc. Thus, we need to close the model which is typically done at the level of second order moments (pair correlations), by expressing triplets as functions of the second moments (Rand, 1999; Dieckmann and Law, 2000; Keeling et al., 2002), the rationale behind this being a fast relaxation of high order correlations compared to low-order correlations. The moments methods based on the second order correlations have become rather popular in both stochastic and deterministic ecological models (Bolker and Pacala, 1997, 1999; Keeling et al., 2002; Wallhead et al., 2008).

Pairwise approximation is the name given to a variety of moment approximation methods which are used for the reduction of stochastic cellular automata models with a discrete space (Matsuda et al., 1992; Rand, 1999). The idea is to construct a system of ODEs describing the frequency of each type of neighboring site pairs, for instance, the fraction of neighboring sites which are both occupied. In order to have the system closed, higher-order frequencies are approximated by pair frequencies starting from triplets (Matsuda et al., 1992). A drawback of this approach is that it only considers interactions between individuals

on a local spatial scale, i.e. in the interacting neighborhood. Pairwise approximation was extended in the paper by Ellner (2001) by considering multiple characteristic sizes for the local interactions depending on the type of interaction (competition, disease transmission, predation, etc.). This method has been extended in Webb et al. (2007) by considering a weighted mixture of local and global multiscale pair approximation.

Finally, another particular case of the moment approximation is the so-called *modified mean-field approach*. The reasoning behind this approach is that sometimes the second and higher spatial moments can be expressed as functions of the first moments, i.e. the mean population densities (Pascual et al., 2002, 2011) – for instance, the dynamics of a spatially heterogeneous predator–prey lattice model can be successfully described based on the classical Lotka–Volterra model where the bilinear predation terms are replaced by a product of power functions of densities of prey and predator (Pascual et al., 2011). In other words, the initial mean-field equations considering well-mixed interactions can be somehow modified to take into account spatial aggregations (clusters). The same holds true for some epidemiological models with spatial aggregation: the overall transmission rate of a disease becomes a product of power functions of the densities of susceptible and infected individuals (e.g. Gubbins and Gilligan, 1997). However, the implementation of the modified mean-field approach is restricted to a certain parameter range since, for example, in a predator–prey lattice model it requires a power law of the size distribution of connected clusters of prey (Pascual et al., 2011).

3.2. Aggregation methods

The fundamental ideas of aggregation of variables and reduction of complex models were first introduced in ecology in a general context in the seminal papers of Iwasa and colleagues (1987, 1989). Some recent works use this approach to simplify complex ecological models and suggest statistical methods of parameterization of simplified models (Raick et al., 2006 and the references therein). In spatially structured population models, the distribution of species at different locations can be approximately described as functions of certain global or macro variables (e.g. the total population sizes). For instance, in the case of a habitat consisting of a collection of patches, the relative proportion of species j in patch i can be explicitly expressed as

$$p_{ij} = F(P_1, P_2, \dots, P_m), \quad (2)$$

where P_j are the total sizes of species j . By summing up the equations for p_{ij} over the patches, we can obtain the equations in terms of total population sizes P_j , i.e. construct a mean-field model. By implementing such aggregation of variables we implicitly admit a certain pattern of species dispersal in the ecosystem. Overall, the idea that the distribution of species between patches can be expressed as a function of their total population sizes as well as that of other species was suggested in the seminal papers by Hassell and May (1973, 1974) considering host–parasitoid interaction. In those papers, the relative proportion of parasitoids was assumed to follow that of hosts. Also we can simply postulate the distribution (2) based on some empirical evidence. An important ecological example is the ideal free distribution of zooplankton grazers in the water column (Lampert, 2005; Morozov et al., 2011), and similarly, some spiders, birds and fish species can show fast migration resulting in the ideal free distribution over the environment (Godin and Keenleyside, 1984; Bernstein et al., 1988; Kacelnik et al., 1992; Milinski, 1994; Pulido and Díaz, 1997), so we can easily estimate relative proportion of species across the environment.

Interestingly, the shape of the instantaneous distribution of species (2) can be derived entirely from the initial explicit spatial model (Bernstein et al., 1999). This is the case, for example, in models where the dispersal of all species is a fast process compared to the demographic rates, i.e. the population dynamics. By formally neglecting the demographic terms on short time scales, we can derive the expressions for the relative proportion of species across the patches. Further, using the obtained distribution (2) we can analyze the population dynamics on large time scales (e.g. on demographic scales) and can follow changes in the population sizes of species. An important condition of implementation of this aggregation method is that on a short time scale the instantaneous distribution (2) should be an attractor for model trajectories (Auger et al., 2000; Poggiale et al., 2009). It can occur that the distribution of species is density-dependent: it turns out that the proportion of each species in the different locations may be a function of the total densities (El Abdillaoui et al., 2007). In this case, the description of processes at the global scale can be expressed from their local formulation and from the proportion of species in each location, providing thus different formal description of processes at large scale than local ones (see Poggiale, 1998, for instance). The discussed aggregation method is rather simple to use and it has engendered a large number of ecological applications (see Auger et al., 2012 for a review and a discussion on the more complex situations). The aggregation method can additionally be used for discrete and continuous space models such as PDE models (Sanchez et al., 2011; Auger et al., 2012).

Note that aggregation methods would also allow us to take into account several spatial scales in the case of networks of patches. Such a network can consist of groups of groups of patches, considering groups of neighboring patches with very fast intra-patches dispersal, fast intra-groups dispersal and, finally, slow demographic processes (for details see Auger et al., 2012). However, construction of efficient methods of reduction of complex ecological models with multi time and space scales ($n \geq 3$) still remains a challenge for aggregation framework.

Implementation of the aggregation technique has an advantage over the spatial moments reduction methods when we consider an environment with a pronounced heterogeneity of physical properties. Consider, for instance, the environment where the number of patches is small and the species fitness substantially varies across patches – the spatial moment approximation fails to qualitatively represent dynamics of the whole model, whereas aggregation methods give satisfactory results (Cordoleani, 2011). On the other hand, the implementation of the aggregation technique may be non-applicable in the case where dispersal rates of species are of the same order of magnitude as demographic processes.

Methods of reduction of spatially explicit systems as aggregation of variables and transition scale theory allow us to compare mathematical formulation of model equations for local processes (on microscopic level) with the resultant global model (on macroscopic level). Interestingly, the functional dependences (i.e. growth rate, predation terms, mortality, etc.) used in the equations describing the global model are usually different from those that we have in the model describing local interactions. As a result, new properties of the system emerge on a macroscopic level which is not observed on a microscopic level. Two types of emergence have been defined in the literature (Auger and Poggiale, 1998 and the references therein). The first type is the dynamical emergence corresponding to the situation, where the global dynamics is *qualitatively different* from the isolated local dynamics. The second type of emergence is called the functional emergence and refers to alteration in the mathematical formulation of functions obtained at the global level with respect to local mathematical functions, and does not require a qualitative

differences between the global and local dynamics. Note that the functional emergence (that we often observe in ecological mean-field models) does not necessarily signify the dynamical emergence since different formulations of models functions can result in a qualitatively same patterns of dynamics (Auger and Poggiale, 1998).

3.3. Mean-field limit of individual based models

Often we need to describe complex patterns of movement of individuals in space on temporal scales which are shorter than the lifespan of species, i.e. we consider kinetic equations of animal movement. An important example is modelling the collective motion of a large number of organisms: fish schools, bird flocks, swarming of social insects, etc., when the collective motion in the group emerges as result of large number of interactions on the level of individuals. On the other hand, spatial movement of an individual is largely affected by the decision making of the whole population (Okubo, 1986; Czirok and Vicsek, 2000; Couzin et al., 2005). The natural framework of modeling collective motion is the Lagrangian (IBM) framework, where the position and velocity of each individual is modeled separately. The resultant model consists of a large number of such stochastic kinetic equations so direct numeric integration of such a system is rather expensive in terms of computational time. Another major drawback is that numerical simulations do not provide us with an insight into the generic dynamical behaviour of the system. An alternative is the use of the Eulerian framework to represent the dynamics based on the densities of species: the evolution of the system for large N is described based on a density function $g(\vec{r}, \vec{v}, t)$ giving the number $dN = g(\vec{x}, \vec{v}, t) d\vec{r} d\vec{v}$ of individuals located in the spatial region $[\vec{x}, \vec{x} + d\vec{x}]$ having velocities from \vec{v} to $\vec{v} + d\vec{v}$. The species density can be computed by integrating the density function

$$\rho(\vec{r}, t) = \int g(\vec{r}, \vec{v}, t) d\vec{v} \quad (3)$$

As a result, in the mean-field limit, the initial IBM can be replaced with a kinetic Fokker–Planck equation for the macroscopic density $\rho(\vec{r}, t)$ (Neunzert, 1984; Carrillo et al., 2010), it often takes the form of a reaction–diffusion–advection equation (Petrovskii et al., 2012). The resultant density model is easier to investigate analytically (e.g. consider the stationary states) and simulate numerically. The question of the possibility of constructing of density-dependent models (i.e. the convergence to the mean-field limit) has been rigorously proven for a number of models (Braun and Hepp, 1977; Visser, 2008; Degond and Motsch, 2008; Carrillo et al., 2010; Bolley et al., 2011); however, it still remains an open problem, especially in the presence of noise. A review of methods of constructing of density-dependent models of motion is a separate issue and should be done elsewhere.

Note that the reduction of IBMs of kinetic equations of animal movement is not only important for better understanding various patterns of collective motion: it is also important for modelling patterns of non-synchronized motion of animals such as zooplankton grazers (Leising, 2001; Cottier et al., 2006; Morozov and Arashkevich, 2010) or insects (Firle et al., 1998; Petrovskii et al., 2012). Finally, complex patterns of active seed dispersal of plants, which are usually modelled based on IBMs, can be also described via simpler continuous framework using integral kernels (Powell and Zimmermann, 2004; Strigul et al., 2008).

4. Importance of spatial scales

When constructing a mean-field ecological model the characteristic size of the habitat (i.e. the spatial scale) plays an important role. In particular, the use of mean-field models can be possible

only on intermediate scales (Pascual et al., 2001) – indeed, at small spatial scales the dynamics are often stochastic, exhibiting pronounced spatial and temporal variations in the number of individuals (Keeling et al., 1997). Another important issue is the influence of neighbouring patches: the influx and outflux of organisms from the surrounding habitats can predetermine the variation in the number of individuals in the given patch. In such a situation, it is hardly possible to build a mean-field self-contained model (either stochastic or deterministic) predicting the local dynamics based only on the current number of individuals in the patch. On the other hand, averaging the population dynamics over large spatial scales can result in oversimplification. Indeed, consider a system containing a large number of patches: if the characteristic spatial scale L_1 of species interactions is much smaller than the size L of the considered environment, we can describe the system as an ensemble of a large number $m = L/L_1$ of statistically independent subsystems (note that even in the case that the system is purely deterministic, unsynchronized local oscillations can result in the emergence of such an ensemble of independent spatial clusters (Medvinsky et al., 2002)). The average over the habitat population density is given by $P = N/M$, where N is the total population size, and M is the total number of patches in the system ($M \gg 1$). On the given spatial scale the time variance of $P = N/M$ will be given by

$$\text{var}(P(t)) = \frac{1}{M^2} \text{var}(N(t)). \quad (4)$$

For the total population size we have $N = N_1 + N_2 + \dots + N_m$, where N_i are the population sizes in the independent subsystems. Let $\text{var}(N_i)$ be the variance of each subsystem (we suggest that these variances are the same), we can re-write the variation of the mean density P as

$$\text{var}(P(t)) = \frac{1}{M^2} \sum_i \text{var}(N_i) = \frac{m}{M^2} \text{var}(N_1). \quad (5)$$

Thus, for large-size ecosystems the variance (5) tends to zero and P is rather close to its mean value. This holds true even in the case of large amplitude oscillatory dynamics in local patches. Obviously, the only possible ‘mean-field’ model $P = \text{const}$ is trivial and can be rather misleading.

Interestingly, on intermediate spatial scales, patterns of mean-field dynamics can also largely depend on the size of the habitat (Rand and Wilson, 1995; Keeling et al., 1997; Donalson and Nisbet, 1999; Pascual et al., 2001). For instance, on the intermediate spatial scales an increase of the window size of averaging (i.e. the spatial resolution) can result in non-monotonic effects of spatial aggregation on the mean-field description of the system (Keeling et al., 1997). Note that the importance of scale on the simplification of spatial model also follows from a number of empirical works revealing that measurement of aggregation patterns of animals can depend on the scale of observation (Boulinier et al., 1996; Roland and Taylor, 1997; Wu and Qi, 2000; Bommarco and Banks, 2003). Another important example includes modelling active dispersal of seeds by animals. It is known that animals can bury seeds in particular sites (cache sites) and the spatial distribution of those sites on small scales can be rather complex, in particular they can be highly aggregated (Powell and Zimmermann, 2004; Lischke et al., 2007). However, on larger spatial and time scales we can describe the active dispersal of seeds based on smooth continuous dispersal kernels (Kot et al., 1996). Finally, the importance of spatial scale on model reduction can be related to the phenomenon of synchronization by external noise, which is known as the Moran effect (Royama, 1982; Ranta et al., 1997). A spatially correlated noise applied to an extended system of local oscillators of species densities may result in oscillations synchronization, i.e. the whole

population sizes will show synchronous oscillations. The Moran effect holds for both of spatially discrete (Ranta et al., 1997) and continuous systems (Petrovskii et al., 2010). Obviously, the dynamics of such metapopulations can be described based on mean-field equations, and the correlation length of the external synchronizing noise will provide a characteristic spatial scale where we can implement the mean-field approximation.

Note that reduction of explicit spatial models is intimately connected with an inverse problem, which is scaling up local ecological interactions (microscale dynamics) to macroscales. Usually, we are able to reproduce the local interactions of species both experimentally and theoretically (Luckinbill, 1974; Costantino et al., 1997; Fussmann et al., 2000 and many other examples) and to reveal and parameterize the functions that we need to use in our models. The major difficulty arises when we wish to describe population dynamics on large scales (community or ecosystem levels) based on the obtained local model. Due to the non-linear nature of local interactions we cannot implement the microscale models by replacing the local densities with population sizes: we need to incorporate effects of species aggregation into initial models operating on a microscale (Levin, 1992; Chesson, 2009). *Scale transition theory* is an efficient tool which can explain how the effects of the spatial aggregation of species would modify the behaviour of microscale models and provide the correct global dynamics operating on macroscales (Chesson, 1998; Melbourne and Chesson, 2005; Englund and Leonardsson, 2008). This technique is actually based on the spatial moment approximation (more precisely, on non-linear averaging) but differs from it in several major aspects (Chesson, 2012).

The scale transition methods use the Taylor expansion around the mean values (e.g. the mean population densities) with a further averaging. The resulting equation contains the terms with average species densities as well as expressions for statistical moments around the mean: variance, covariance, skewness, kurtosis, etc. Often we can cut the Taylor expansion at the level of second moments. For instance, averaging a non-linear function of two variables $g(X,Y)$ gives (Chesson et al., 2005; Bergström et al., 2006)

$$\langle g(X, Y) \rangle \approx g(\langle X \rangle, \langle Y \rangle) + \frac{1}{2} \frac{\partial^2}{\partial X^2} g(\langle X \rangle, \langle Y \rangle) \sigma_X^2 + \frac{\partial^2}{\partial Y \partial X} g(\langle X \rangle, \langle Y \rangle) \sigma_{X,Y} + \frac{1}{2} \frac{\partial^2}{\partial Y^2} g(\langle X \rangle, \langle Y \rangle) \sigma_Y^2, \quad (6)$$

where $\langle X \rangle$, $\langle Y \rangle$ denote the mean values; σ_X^2 and σ_Y^2 are the spatial variances of X and Y and $\sigma_{X,Y}$ is the covariance. We neglect the high order terms in approximation (6).

As an illustrative example we can apply (6) to a standard local Rosenzweig–MacArthur predator–prey model. This gives the following scaling of the local species interactions (Bergström et al., 2006)

$$\frac{d\langle P \rangle}{dt} = R(\langle P \rangle) + \frac{1}{2} \frac{d^2 R(\langle P \rangle)}{dP^2} \sigma_P^2 - \langle Z \rangle f(P) - \langle Z \rangle \frac{1}{2} \frac{d^2 f(\langle P \rangle)}{dP^2} \sigma_P^2 - \frac{df(\langle P \rangle)}{dP} \sigma_{P,Z}, \quad (7)$$

$$\frac{d\langle Z \rangle}{dt} = k\langle Z \rangle f(P) - k\langle Z \rangle \frac{1}{2} \frac{d^2 f(\langle P \rangle)}{dP^2} \sigma_P^2 - k \frac{df(\langle P \rangle)}{dP} \sigma_{P,Z} - \delta\langle Z \rangle, \quad (8)$$

where P and Z are the local densities of prey and predator, $\langle P \rangle$ and $\langle Z \rangle$ are the densities of species averaged over space; $f(P)$ is the local functional response, $R(P)$ is the local prey growth rate, and δ is the mortality of predator. By computing the derivatives of $f(P)$ and $R(P)$ one can estimate the influence of spatial heterogeneity on the predator–prey dynamics over a global scale. A particular obstacle to investigation of the properties of the scaled model (7) and (8) is that such model is not closed: we still need the values of σ_P^2 and

$\sigma_{P,Z}$. One can use some observational data to estimate the second spatial moments and use the linear autoregression methods (e.g. Jones et al., 1993; Bergström et al., 2006; Englund and Leonardsson, 2008). Another way is to construct a closed model based on moment approximations by adding the equations for σ_P^2 and $\sigma_{P,Z}$ (Wallhead et al., 2008). Finally, we can create a spatially explicit model with the given local interactions and by directly simulating this model we can estimate the effects of spatial aggregation over macroscales.

However, we should emphasize that the main aim of scale transition theory does not consist in providing a precise quantitative description of complex spatial systems (this can be done directly based on numerical solutions), rather, it is to provide a simple and efficient framework for understanding the numerical simulations of complex spatially explicit models as well as the field observations obtained on macroscale levels. In particular, the theory allows us to make important predictions regarding the coexistence and persistence of species and explain how spatial structuring can stabilize/destabilize the dynamics within a community, etc. Interestingly, understanding the key properties of ecosystem functioning can be done in a relatively simple way, by using both empirical and semiempirical methods to estimate the spatial variances and covariances (Taylor et al., 1980; Jones et al., 1993). In particular, based on empirical estimation of σ_P^2 and $\sigma_{P,Z}$ in a predator–prey model similar to (7) and (8), it has been shown that destabilization in a benthic crustacean community can be explained due to predator–prey covariance (Bergström et al., 2006). Thus, the scale transition theory provides a biological sense to the formal mathematical tools of the spatial moment approximation framework.

5. Future directions and challenges

Significant progress has been made in simplifying complex spatially explicit models and providing mean-field descriptions. There exists a tremendous amount of recent publications on the reduction of spatially structured model based on moment approximation and various aggregation methods. This is recognition of the fact that we need not only to quantitatively mimic complex patterns observed in nature, but we also need to reveal generic mechanisms of the underlying processes (Petrovskii and Petrovskaya, 2012). Very often, mean-field approximation allows us to achieve such understanding of the key ecological processes, but there still exist several important gaps in mean-field approximation which remain unaddressed or only partially addressed, and in this section we shall briefly discuss some of them.

First, an important issue is the development and implementation of techniques which would allow us to reduce individual based models (Lagrangian modelling framework) to density dependent models (Eulerian framework) in the case where organisms exhibit complex individual movement. The central question concerns the possibility of a mean-field limit of IBMs and the rate of convergence to this limit when the number of individuals $N \rightarrow \infty$. Important progress has been achieved, for instance, in modelling the collective motion of large number of individuals where the density-dependent asymptotic for $N \rightarrow \infty$ has been proven in a rigorous manner (Grünbaum, 1994; Degond and Motsch, 2008; Carrillo et al., 2010; Bolley et al., 2011). However, in reality the movement of animals is substantially more complicated than was assumed in the cited models. A notable example is the movement of zooplankton in the water column, which takes place on several time and space scales (Leising, 2001; Morozov and Arashkevich, 2010). Such motion involves a large number of individuals and combines synchronized and unsynchronized patterns of movements; there is also a large deviation in

individual characteristics (growth and consumption rates, swimming ability, preferential grazing depths, etc.) as well as the adaptive behaviour of individuals. Traditionally, the IBM framework is used to cope with such complexity and there is a widespread opinion that a density-dependent framework cannot describe the dynamics of these systems. This conclusion is partially based on some comparisons of IBMs with their density-dependent 'analogues', showing that the two approaches give different patterns of dynamics (e.g. Woods et al., 2005). Note that such a comparison is already a separate problem (Raïck et al., 2006), since it is unclear if the considered density-dependent models are the true mean-field asymptotic of the given IBMs. As such, there is an urgent need for development of the techniques of reducing spatial IBMs with complex species behaviour and a pronounced individual variation. This should include: (i) proving asymptotic convergence for $N \rightarrow \infty$ to density-dependent models and (ii) providing algorithms for constructing – density dependent – (master) equations. Advances in these directions could both facilitate the computation of equations and help understand the generic properties of the system.

Second, we often need a combination of various reduction methods to obtain a suitable mean-field approximation to model the dynamics of a given ecosystem. This is especially true for ecological models operating on multiple temporal and spatial scales, for instance, on a local spatial scale the movement of species can be often considered as a fast process compared to the demographical processes and we can apply aggregation methods to obtain the instantaneous repartition of species across patches (2). We can further follow the population dynamics in a collection of several patches based on mean-field equations, but we need to take into account the effects of the surrounding parts of the habitat where the population density can oscillate in a different phase (and the approximation (2) ceases to work for those patches). The influence of a large number of neighbourhood habitats can be included based on some moment approximation technique. Finally, on a larger spatial and time scale we often need to take into account seasonal migration of species which are often crucial for species survival and persistence (Dingle, 1996). These processes can hardly be described via a standard moment approximation scheme and again require some sort of aggregation methods, since the intensity of migration and the impact of migrating animals on the ecosystems is predetermined by the total population size. An example of such a system is the migration of large herbivorous mammals in the plains and open woodlands of Africa (Linda, 1975; Ottichilo et al., 2001). Simplification of such complex spatially structured model would definitely require a new approach, involving interplay between various reduction techniques.

Third, a pronounced heterogeneity of the environment can be a major obstacle in simplifying spatially explicit models, since approximation based on spatial moments is derived based on the assumption of statistical homogeneity of the environment (Bolker and Pacala, 1997, 1999; Dieckmann and Law, 2000; Ellner, 2001). In the case of a pronounced spatial gradient of species fitness due to some abiotic factors, we need to introduce separate spatial moments for different parts of the environment, which would make the simplified system virtually intractable, since, for instance, the average species densities may differ by several orders of magnitude along the gradient of resource distribution (Micheli, 1999; Odum and Barrett, 2004). In such a situation, implementation of aggregation methods of reduction can make sense, for instance, by considering the species to be distributed across the environment according to a certain law (2). On the other hand, aggregation methods (e.g. considering fast movement of individuals) can also fail in a large-sized ecosystem, for instance, we cannot assume that animals move fast enough to be able to travel across the whole habitat. In such situation only partial

reduction of the spatial model may be possible. Note that even in the case where a rigorous construction of a mean-field model, with trajectories close to the original spatial model, is not possible, a qualitatively similar behaviour may still be obtained using a certain mean-field model. This optimistic assumption is based on the theorem of Takens (1981) of embedding of complex system evolving on its attractor into a low dimensional space. The major problem consists in constructing the explicit model equations (master equations) in the low dimensional space. However, we can implement some time series analysis methods such as the principal component analysis (PCA) (Kendall, 1980) or other more sophisticated techniques based on various statistical approaches (Gorban et al., 2007). On the other hand, construction of the master equations can often be based on semi-empirical methods with further numerical testing against the original spatial model (Pagel et al., 2008).

Often we use mathematical modelling with the main objective of explaining the key-mechanisms underlying in the observed ecological patterns and the fact that mean-field models are particularly useful in this respect is one of the motivations for the reduction of spatially explicit models. In this case, we only require a qualitative similarity between spatially structured and mean-field models, revealing generic properties of ecosystem dynamics: stability (instability) of ecological equilibria, possibility of sustained oscillations, coexistence of species, etc. Construction of such 'minimal' models can be often done based on local interactions by modifying the growth rates, predation terms, etc. to implicitly incorporate effects of space. This is often done using a number of semi-empirical methods, (e.g. Raïck et al., 2006), and a large amount of literature exists on this topic. The difference between this approach and a more rigorous modified mean-field approach (Pascual et al., 2002, 2011) is that the former approach allows a large deviation in the quantitative predictions and is entirely focused on revealing the key ecological processes/mechanisms resulting in the observed type of patterns.

The previous idea can be illustrated based on the following ecological example. It is well known that in eutrophic environment the crucial issue for stabilization of predator–prey interactions becomes the shape of the functional response of predators (Oaten and Murdoch, 1975). In particular, a Holling type III response (which is concave downward at small and intermediate food densities) can guarantee successful top-down control in eutrophic plankton communities. Feeding experiments in laboratories, however, reveal that zooplankton grazers normally show a concave upward response (Holling type II) which is destabilizing (DeMott, 1982; Hirst and Bunker, 2003; Jeschke et al., 2004). Field observations make the things even more complicated: it was reported that often there is no local functional response of zooplankton grazers, i.e. no functional relation between the local ingestion rate and the ambient food was observed (Boyd et al., 1980; Dagg and Wyman, 1983; Morozov and Arashkevich, 2010). A typical example of the local feeding of zooplankton herbivores can be seen in Fig. 1A, where the local ingestion rates of the dominant copepod species in the Central Barents Sea (*Calanus finmarchicus*) are plotted versus the ambient concentration of Chl A in the water. The data were collected at several stations and the details on collecting the samples can be found in Morozov et al. (2008). The reason for the non-existence of any local functional response is due to the complex patterns in the individual behaviour of grazers, which involves fast active displacement in the water column (Dagg and Wyman, 1983; Ohman, 1990; Morozov and Arashkevich, 2010). A detailed description of those patterns would imply the use of complex spatially explicit models (e.g. IBMs) (Leising, 2001; Batchelder et al., 2002). However, we can easily obtain an insight to stability properties of plankton system without using complex IBMs.

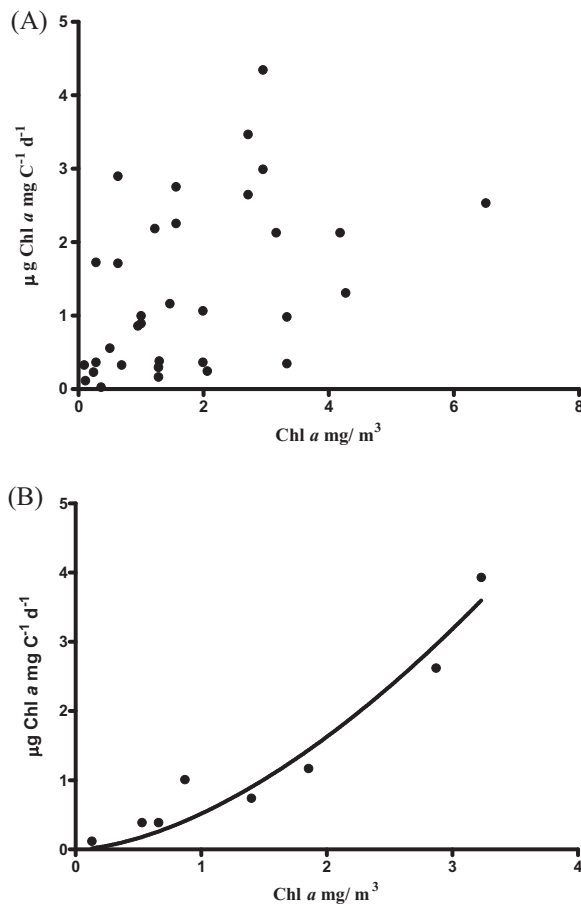


Fig. 1. Functional responses of herbivorous zooplankton (*Calanus Finmarchicus*, Central Barents Sea, 2003–2005) measured in situ. (A) Local functional response showing the ingestion rates (measured in $\mu\text{g Chl } a/(\text{mg Carbon}^{-1} \text{ day}^{-1})$) of grazers plotted against the ambient food density (measured in $\text{mg Chl } a \text{ mg/ m}^3$) at different depths in the water column. One can see the absence of clear dependence between the local food density and the ingestion rates due to the complexity of the feeding behaviour of individual grazers (see Morozov and Arashkevich, 2010 for detail). (B) Overall functional response (the mean-field response) for the whole population of zooplankton, defined as the average consumption rate per biomass of grazers in the column which is plotted against the average chlorophyll concentration $\langle P \rangle$ (the number of points corresponds to the number of observational stations). The fitted function is given by the power function $F = a(P)^\gamma$. This fitting presents the first term of expansion of the sigmoid response given by $F = a(P)^\gamma / (b(P)^\gamma + 1)$, which is well adapted in the literature (see Gentleman et al., 2003). The nonlinear regression fitting gives $a = 0.51$; $\gamma = 1.67$, $R^2 = 0.94$. The comparison of (A) and (B) shows the existence of the mean-field functional response in a clear absence of a local functional response.

In Fig. 1B, we show the overall (or mean-field) functional response of zooplankton in the water column, constructed as a function of average food density in the column, i.e. the consumption rate per-unit biomass of grazers. One can easily see that now the overall response can be approximately considered as a function of the average density of phytoplankton over the column. More interestingly, at low and intermediate densities we can fit the data with a concave downward function, thus revealing a Holling type III overall functional response. The emergence of such mean-field Holling type III response can provide an extra mechanism of stabilization (Oaten and Murdoch, 1975), thus providing a generic explanation for the efficiency of grazing control in eutrophic waters. It is well known that in a large number of cases the overall functional response of zooplankton cannot be strictly expressed as a function of the average concentration of chlorophyll alone: different vertical profiles of phytoplankton can have the same average (Ryabov et al., 2010 and the references therein). However,

we can still use a mean-field functional response similar to the one shown in Fig. 1B in generic models of plankton blooms, ignoring explicit vertical resolution (Truscott and Brindley, 1994), to explain the mechanism through which blooms are triggered. Indeed, the increase in total phytoplankton in the column takes place according to a typical scenario, where the increase of algal density occurs mostly in surface layers (Raymont, 1980; Morozov, 2010), i.e. the mean-field approach of modelling grazing is applicable.

6. Introducing the special issue ‘From spatially explicit population models to mean-field dynamics’

The current special issue of Ecological complexity brings together a series of articles considering various approaches to the reduction of complex models with explicit spatial resolution to simpler mean-field models. In particular, three important methodological frameworks are represented (see Section 3): (i) aggregation methods, (ii) scale transition theory (which is based on spatial moment approximation philosophy) and (iii) methods of reducing spatial IBM models to the mean-field limit.

The paper of Auger and colleagues is a detailed review of the *aggregation approach* in the reduction of time continuous spatial models based on using fast-slow manifolds (considering the migration and dispersal to be a fast process compared to demographic processes). The papers by Nguyen-Ngoc et al. (2012), Marvá et al. (2012) and Mose et al. (2012) present interesting illustrations of how the aggregation approach can be implemented in concrete ecological problems. In particular, V. Mose and colleagues (2012) consider the ecosystem of the Amboseli National Park in Kenya: the reduction of the initial complex model containing a large number of patches allows the authors to make an important conclusion about the need for keeping migration corridors connecting the park with the surrounding ecosystems. The paper of Nguyen-Ngoc and colleagues (2012) emphasizes the importance of density-dependent dispersal for the outcome of competition in a patchy environment. Implementation of the aggregation method allows them to analytically show the possibility of coexistence between species which locally show pre-emptive competition. Finally, the work of Marvá and co-authors (2012) shows an interesting example of application of spatial aggregation to epidemiology – considering different time scales for migration and epidemic processes makes it possible to compute the reproduction number R_0 of an infectious disease, and to show that fast migration can sometimes result in eradication of the epidemic on a network of connected patches.

In the review by Chesson (2009) the general idea of *scaling transition theory* is discussed, explaining the main aim of the method: providing a qualitative understanding of the functioning of communities based on our knowledge of local non-linear population dynamics and spatial heterogeneity. Interestingly enough, such an understanding can be obtained in a relatively simple way, without explicitly solving the underlying spatial model. The author shows that the effects of spatial variation on the community can be represented in terms of Laplace transforms and cumulant generating functions for the species fitness. As relevant ecological examples, the dynamics of insect communities is considered, and the key role of space in the coexistence of competitors is demonstrated.

The work by Romanczuk and Schimansky-Geier (2012) introduces a novel approach in reducing complex IBM models to models which use macroscopic density and velocity fields (*mean-field description or mean-field limit*). They consider the collective motion of animals in swarms with velocity alignment, and show the importance of individual behavior for the onset of collective motion. They also discuss potential difficulties in deducing the individual behavior from the mean-field measurements. Petrovskii

and colleagues (2012) use a semi-analytical approach in replacing individual based models of stochastic Brownian motion with a diffusion equation. The authors consider the motion of insects on a field with absorbing traps, and provide an efficient analytical expression to estimate the total population size of the insects, which is a vital issue for ecological monitoring. Finally, Scarsoglio and colleagues (2012) consider a stochastic differential equation for the vegetation distribution under periodical forcing, and implement a mean field analysis of the model to obtain the steady-state probability distribution (the probability density function). The use of mean field analysis on the stochastic model allows the authors to analytically demonstrate the emergence of spatial patterns due to a spatio-temporal stochastic resonance, which can potentially explain the observed spatial clusters in riparian and wetland vegetation.

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