Scaling up predator–prey dynamics using spatial moment equations

Frédéric Barraquand¹,²,³* and David J. Murrell⁴,⁵

¹Centre d’Etudes Biologiques de Chizé, CNRS, Beauvoir-sur-Niort, France; ²Université Pierre et Marie Curie - Paris 6, Paris, France; ³Department of Arctic and Marine Biology, University of Tromsø, Tromsø, Norway; ⁴Department of Genetics, Environment and Evolution, University College London, Darwin Building, London, UK; and ⁵CoMPLEX, University College London, Physics Building, London, UK

Summary

1. Classical models of predator–prey dynamics, commonly used in community and evolutionary ecology to explain population cycles, species coexistence, the effects of enrichment, or predict the evolution of behavioural traits, are often based on the mass-action assumption. This means encounter rates between predators and prey are expressed as a product of predator and prey landscape densities; as if the system was well-mixed.

2. While mass-action may occur at small spatial scales, spatial variances and covariances in prey and predator densities affect encounter rates at large spatial scales. In the context of host–parasitoid interactions, this has been incorporated into theory for some time, but for predators, well-mixed or other ad hoc models are often used despite empirical evidence for intricate spatial variation in predator and prey numbers.

3. We review the classical models and concepts, their strengths and weaknesses, and we present two recent spatial moment approaches that scale up predator–prey population dynamics from the individual or patch level to large spatial scales. Both methods include descriptors of spatial structure as corrections to encounter rates, but differ in whether or not these descriptors have dynamics that are explicit functions of movements, births and deaths.

4. We describe how these spatial moment techniques work, what new results they have so far produced, and provide some suggestions to improve the connection of predator–prey theoretical models to empirical studies.

Key-words: functional response, mass-action, moment closure, point process, predator–prey models, spatial heterogeneity

Introduction

Since the pioneering work of Lotka and Volterra, predator–prey models have helped ecologists understand a great number of ecological phenomena. Predator–prey models show when trophic interactions can lead to population cycles (e.g. May 1972; Maynard Smith & Slatkin 1973; Tanner 1975; Andersson & Erlinge 1977; Hanski et al. 2001; King & Schaffer 2001; Turchin & Batzli 2001), and they are the basic building blocks of larger, food-web models that address the links between the stability and diversity of ecosystems (e.g. May 1973; Gross et al. 2009; McCann 2011). They have a long history of addressing how changes in primary productivity (enrichment) can affect ecosystems (Rosenzweig 1971; Oksanen et al. 1981; Arditi, Ginzberg & Akcakaya 1991; Lundberg & Fryxell 1995; Oksanen & Oksanen 2000; Gross, Ebenhoh & Feudel 2004; Fussmann & Blasius 2005; Murrell 2005), and are even used to study the evolution of behavioural traits, thanks to the development of adaptive dynamics theory (review in Abrams 2000). For all these reasons and more, predator–prey models play a central role in ecological theory, and now span the whole spectrum of ecological models, from theoretical to applied models (e.g. small mammal population dynamics, Hanski et al. 2001; King & Schaffer 2001; or marine food webs, Yodzis 1994, 1998).

Predator–prey demographic models have developed largely around the concepts of functional and numerical responses of predators (see eqns 1-2 below). Classically, these models are written as systems of ordinary differential equations

\[
\frac{dV}{dt} = \Phi(V) - g(V,P) \times P \quad \text{eqn 1}
\]

(prey rate of change) prey growth functional response predator density

\[
\frac{dP}{dt} = f(V,P) \times P - \mu P \quad \text{eqn 2}
\]

(predator rate of change) numerical response predator density predator mortality

The very simple Lotka-Volterra assumes \( \phi(V) = rV \), \( g(V,P) = aV \) and \( f(V,P) = eV(V,P) \) while the more popular Rosenzweig-MacArthur model assumes logistic growth, \( \phi(V) = rV(1-\frac{V}{K}) \) where \( K \) is a carrying capacity, and a saturating functional response, \( g(V,P) = \frac{aV}{1+P/h} \) where \( h \) is a handling time (as described by Holling 1959). Other choices are possible for the functional response (see Appendix S1), notably models that make the functional responses depend on the density of...
predators (Skalski & Gilliam 2001), the prey-to-predator ratio (Abrams & Ginzburg 2000; Arditi & Ginzburg 2012) or densities of other prey species, which is important in food webs (McCann 2011). The numerical response is often used in a more general sense in empirical studies, including emigration/immigration processes of mobile predators (Andersson & Erlinge 1977). In Lotka-Volterra models and their derivatives, the numerical response \( f(V,P) = SV(P) \) is stunningly simple (linear) and obeys the ‘biomass conversion rule’ (Ginzburg 1998), as it assumes that offspring production is a function of resource consumption. Not all models obey that rule (see Appendix S1). Note also that an alternative route to specify precise functional forms is to analyze the behaviour of these models for arbitrary functions (May 1972; Gross et al. 2009; Yeakel et al. 2011). Both these models and the associated concepts of functional and numerical responses have been quite useful to explain the effect of predators on their prey, for example why and when population oscillations can occur because of predator–prey interactions (e.g. in rodents, Andersson & Erlinge 1977). Saturating functional responses are thought very likely to generate limit cycles when predators possess a clear numerical response (Rosenzweig & MacArthur 1963), although the cycling might occur for other reasons as well, e.g. fixed maturation delays in the numerical response (Maynard Smith 1974; Wang et al. 2009).

There is, however, an often unquestioned assumption at the core of the classic predator–prey theory (e.g. Berryman 1992): that populations of prey and predators are well-mixed, i.e. spatial averages of densities are a sufficient description of the system. This owes much to the Lotka-Volterra tradition where the basic encounter rate is expressed in a mass-action fashion, as a product of prey and predator densities. This approach is often called ‘mean-field’ modelling, in connection to the physical origin of these models (Dieckmann, Law & Metz 2000). Many explicitly spatial models are also mean-field models in a sense, but at the subpopulation or patch level – a scale at which mass-action is indeed more likely to happen. More information on mass-action and its limits is given in Appendix S2.

Spatial and/or stochastic extensions to the basic models have fueled the growth of predator–prey theory (e.g. Gurney & Nisbet 1978; de Roos, McCauley & Wilson 1991, 1998; Wilson, McCauley & de Roos 1993; Keitt & Johnson 1995; McCauley, Wilson & de Roos 1996; Cuddington & Yodzis 2000). They show, among other things, why some predator–prey systems might persist at the landscape scale despite local extinction (Gurney & Nisbet 1978; Hassell 2000); produce travelling waves (see Sherratt & Smith 2008, for a review), or when spatial variation above the population level should stabilize populations (review in Briggs & Hoopes 2004). Many authors have used explicitly spatial individual-based models, with clear assumptions on local space-use and movements, to relax the mass-action assumption (e.g. de Roos, McCauley & Wilson 1991; Wilson, McCauley & de Roos 1993; Keitt & Johnson 1995; McCauley, Wilson & de Roos 1996; Cuddington & Yodzis 2000). Despite their important contributions to predator–prey theory, these individual-based models have an arguably limited scope, because they are specified mostly as computer simulations. Their algorithmic nature is appealing as they are relatively easy to implement, and they have few restrictions on the amount of biological detail that can be included; but they are hard to analyse fully and like all theory, care must be taken not to overparameterise the model.

Here we review the predator–prey modelling literature using mathematical tools called spatial moments. Spatial moments, such as spatial covariances, express the degree to which populations of predators and prey are spatially correlated (i.e. clustered/associated, randomly distributed, or segregated). These tools are of intermediate complexity between classical mean-field models and spatially explicit models, and it is often possible to calculate these correlations on real populations to correct predator–prey encounter rates. The most theoretical spatial moment models can be formally derived from individual-level models, and bridge the gap between simple, fully analytical mean-field models and complex individual-based simulations. We believe that starting from the individual and scaling up whilst maintaining a degree of mathematical tractability makes this approach most relevant to ecological theory.

The manuscript is organised around the central concept of moment closure. While the term may be new to some, most ecologists have already encountered the basic idea of moment closure, and much ecological data is summarised by some notion of central tendency (first moment) and variance (second moment) whilst ignoring higher order moments (i.e. skew, kurtosis, etc.). In dynamic spatial models, moment closure aims to capture the main features of the spatial structure using lower order spatial moments (the space-averaged, or mean densities, and their covariance across space). The moment closure arises because the dynamics of the mean density depends on the dynamics of spatial covariances, which in turn depends on the dynamics on higher-order moments, in an infinite regress. A mathematical illustration of this linkage is presented in Appendix S3 for interested readers, but the important point to remember is that we need to cut off this infinite chain at some point. Fortunately, it is often possible for the higher-order moments to be well approximated by functions of lower-order moments such as spatial means and spatial covariances, and methods of varying complexity can be used to do so, depending on the modeller’s objectives.

In the following, we discuss models according to the closure method they use, starting from the simplest well-mixed models to models including fixed descriptors of spatial structure (first-order closure) to models including dynamic descriptors of spatial structure (second-order closure). First-order closure models, with a rather low degree of complexity, should appeal mostly to empiricists trying to integrate spatial structure into populations models, especially when it comes to the study of cyclic predator–prey systems. Second-order models are currently more theoretical tools, mostly linking deterministic equations to mathematically rigorous individual-based models (IBM). This combination of mathematically well-defined IBMs and new approximation techniques provide new insights into the role of spatial correlations in modeling ecological and evolutionary dynamics. The components of some IBMs bear a promising resemblance to current space-use data (home range
estimates, dispersal kernels), which suggest they could be parametrized, and potentially simplified thanks to second-order methods in the future.

In their overview of consumer-resource dynamics, Murdoch, Briggs & Nisbet (2003) concluded that these methods were ‘still in their infancy’. However, progress has subsequently been made for both first and second-order closures, and we hope reviewing this body of work will help researchers to get a grip of the new methods, and increase the frequency of their use within the ecological community. Similar endeavours to popularize spatial moment equations have been undertaken before, notably by Dieckmann, Law & Metz (2000), where the focus is mostly on plant population dynamics, or Lion & Baulen (2008), in the context of the evolution of altruism (see also Bolker 2004). Both Bolker (2004) and Lion & Baulen (2008) provide good categorisations of the various kinds of models, especially with respect to the treatment of space.

Whilst it is reasonable to assume in most cases that plant communities cannot obey mass-action mixing, this is less clear for animal communities, because animals are able to move widely. However, although most animals can move in ways that would render the community well-mixed, most of them rarely do so. Many consumers are anchored to some spatial location (e.g. a nest or refuge), and deplete their resources locally (as in seabirds, e.g. Elliott et al. 2009); other animals avoiding conspecifics can produce similar space-use patterns, especially in vertebrates (Brown & Orians 1970; Moorcroft & Lewis 2006). Following Murdoch, Briggs & Nisbet (2003), such social organisation leads to within-population spatial structure. A population is here understood to be a demographic unit within which most changes in numbers occur because of birth and death processes, rather than movements (Berryman 2002). Within-population spatial structure has been rather well investigated in insect parasitoids (Hassell 2000; Murdoch, Briggs & Nisbet 2003), and we know for instance that host-independent parasitoid aggregation is stabilizing while host-dependent aggregation is often destabilizing (Murdoch, Briggs & Nisbet 2003). We know comparatively less in vertebrate predator–prey systems, on which most of the biological examples in this review will focus. We provide an illustration of how within-population spatial structure can affect predator–prey encounter rates in Fig. 1.

Historically, however, among-population spatial structure (at the metapopulation, or regional level) has been investigated first in ecological theory, as unstable well-mixed models predicted the collapse of host–parasitoid systems that persisted in the wild. It has then been suggested that asynchronous fluctuations of locally unstable populations may produce regional persistence (Nicholson 1933), and this has strongly influenced both ecological theory and the modelling habits of theoreticians. In Appendix S4, we review shortly the literature on spatial predator–prey interactions to better connect spatial moment equations to earlier work, and why the neglected within-population spatial structure can matter.

Before heading to the next section and spatial moment methods, we should mention that in comparison to the great number of models parametrised (except in parasitoids and maybe other insects), there is little evidence for or against mass-action in natural systems. A recent exception is Mols et al. (2004), where the authors demonstrated that great tits encounter moth caterpillars at a rate less than proportional to prey density; this empirical study inspired several articles on the potential reasons for the absence of linear relationship between predator encounter rate and prey density (Ruxton 2005; Travis & Palmer 2005; Ioannou, Ruxton & Krause 2008). Clearly ecologists have an interest in these matters, but the mass-action assumption is rarely verified and we believe the lack of tests of the mass-action assumption is probably due to the success of the functional response as a concept. Functional responses computed at a large spatial scale (e.g. Redpath & Thirgood 1999) are large-scale phenomenological descriptors, and do not reflect directly individual diet choice and physiological constraints. The encounter rate in absence of handling/satiation can saturate as well in heterogeneous landscapes or with restricted movements (e.g. Keitt & Johnson 1995; Pascual, Roy & Laneri 2011), which means large-scale functional response $g(F)$ encompasses both kinds of nonlinearities, those due to spatial structure and those due to handling/satiation. To obtain a more mechanistic understanding of the functional response, one needs to derive encounter rates, which requires the separation of searching from handling time (as in Mols et al. 2004). This is not often done, though it is the only way to test the assumption of mass-action, and understand better the relationship between encounter rate and prey density (see Appendix S5 for more on estimating functional responses from data, and issues related to the spatial scale of measurement).

First-order closure: beyond simple mass-action

In this section, we describe relatively simple methods to incorporate spatial structure into predator–prey interactions, that relate the spatial (or sometimes social) structure of the populations to the densities. We begin by modifications of mass-action using scaling laws, accounting for animal grouping behaviour or limited movements in the formulation of encounter rates. These can be considered as very simple first-order closures because only the first spatial moments (the landscape densities) are considered, though they are not sensu stricto moment methods.

Scaling laws for animal groups

Imagine that individuals are distributed in space as tightly clustered groups. These groups may occur for instance because prey exhibit strong anti-predatory behaviour (such as many large herbivores) and because predators’ mating systems or hunting tactics constrain them to stay in groups (Taylor 1984; Cosner et al. 1999; Fryxell et al. 2007). In that case, if both predator groups and prey groups are tightly packed and randomly roaming over space, then it makes sense to think of mass action at a higher organisational level - that of the group. In the following, we highlight Fryxell et al.’s (2007) approach to this scenario.
The relationship between the density of prey groups \( V_g \) and prey density \( V \) may be empirically determined from field data as a regression on a log scale to produce the power-law relationship, \( V_g = cV^h \). This prey group density can then be incorporated in the functional response. The model is applied to lions, in which two time-limiting processes are capturing (capture time \( h_1 \)) and digesting the prey (digestion time \( h_2 \)). The predator group size, \( G \), is assumed to be constant with respect to lion numbers. The functional response for a singly foraging predator is then:

\[
\frac{xV_g}{xV_g + \frac{(1-xV_g)h_2}{h_2}}
\]

where the area of discovery \( x \) can be expressed as speed \( \times \) perceptual radius \( \times \) capture probability on encounter. When predators forage in groups, the functional response (i.e. the kill rate per lion per unit area per unit time) is equal to:

\[
\sum \frac{xV_g}{xV_g + \frac{(1-xV_g)h_2}{h_2}}
\]

This expression takes into account the fact that the time to capture the prey is not dependent on the group size (in other predator–prey systems, this might be debatable), while the time needed to eat a prey item decreases with group size. The division by group size is needed to give an intake rate per capita, and the final expression can be written \( \frac{xV_g}{G} \).

Fryxell et al. (2007) show that, when considering empirically measured parameters, a functional response including group size stabilises predator–prey population dynamics which corresponds well to the situation being modelled.

Such methods are expected to be adequate when groups are strongly clustered, and when one can define a relationship between average prey population density and prey group size; while they are expected to fail when groups are somehow more diluted in space, or when there are no groups but only spatial variation between sites (similar methods for such cases are presented below).

**Mass Action and Power Functions**

Using power functions to modify predator–prey encounter rates, as done above, is well-rooted in the chemical origins of predator–prey theory (Heesterbeek 2000). Chemists modify the well-mixed encounter rates between chemical components.
by inserting exponents in the reaction rate \( a V^p \). These exponents, in the context of chemical reactions, express the complexity of the reaction occurring (the reaction order), while in the context of predator–prey dynamics, these exponents are purely phenomenological. Keitt & Johnson (1995) showed using IBMs that these exponents were below unity when interactions and movements were restricted in space, indicating some saturation of the kill rate is related to movements, and not just satiation or handling. Their analyses showed the exponents were decreasing when increasing the fractal dimension of the landscape or decreasing the movement ranges. In other words, when movements are restricted or the landscape is heterogeneous, an increase in large-scale prey density increases the predator intake less than proportionally to the landscape densities, and hence mass-action models overestimate encounter rates.

Similar methods have been used by Pascual & Levin (1999), Pascual, Mazzea & Levin (2001) and Pascual, Roy & Franc (2002) to simplify strategic IBMs. The equations are slightly different, but again exponents modulating encounter rates are introduced. Pascual, Roy & Laneri (2011) argue that these exponents act as a first-order closure method introduced. Pascual, Roy & Laneri (2011) argue that these exponents are different, but again exponents modulating encounter rates are introduced. Pascual, Roy & Laneri (2011) argue that these exponents are different, but again exponents modulating encounter rates are introduced. Pascual, Roy & Laneri (2011) argue that these exponents are different, but again exponents modulating encounter rates are introduced. Pascual, Roy & Laneri (2011) argue that these exponents are different, but again exponents modulating encounter rates are introduced. Pascual, Roy & Laneri (2011) argue that these exponents are different, but again exponents modulating encounter rates are introduced. Pascual, Roy & Laneri (2011) argue that these exponents are different, but again exponents modulating encounter rates are introduced. Pascual, Roy & Laneri (2011) argue that these exponents are different, but again exponents modulating encounter rates are introduced. Pascual, Roy & Laneri (2011) argue that these exponents are different, but again exponents modulating encounter rates are introduced. Pascual, Roy & Laneri (2011) argue that these exponents are different, but again exponents modulating encounter rates are introduced. Pascual, Roy & Laneri (2011) argue that these exponents are different, but again exponents modulating encounter rates are introduced. Pascual, Roy & Laneri (2011) argue that these exponents are different, but again exponents modulating encounter rates are introduced. Pascual, Roy & Laneri (2011) argue that these exponents are different, but again exponents modulating encounter rates are introduced. Pascual, Roy & Laneri (2011) argue that these exponents are different, but again exponents modulating encounter rates are introduced. Pascual, Roy & Laneri (2011) argue that these exponents are different, but again exponents modulating encounter rates are introduced. Pascual, Roy & Laneri (2011) argue that these exponents are different, but again exponents modulating encounter rates are introduced. Pascual, Roy & Laneri (2011) argue that these exponents are different, but again exponents modulating encounter rates are introduced. Pascual, Roy & Laneri (2011) argue that these exponents are different, but again exponents modulating encounter rates are introduced. Pascual, Roy & Laneri (2011) argue that these exponents are different, but again exponents modulating encounter rates are introduced. Pascual, Roy & Laneri (2011) argue that these exponents are different, but again exponents modulating encounter rates are introduced. Pascual, Roy & Laneri (2011) argue that these exponents are different, but again exponents modulating encounter rates are introduced. Pascual, Roy & Laneri (2011) argue that these exponents are different, but again exponents modulating encounter rates are introduced. Pascual, Roy & Laneri (2011) argue that these exponents are different, but again exponents modulating encounter rates are introduced. Pascual, Roy & Laneri (2011) argue that these exponents are different, but again exponents modulating encounter rates are introduced.

\[ I_L = g(V) + \frac{1}{2} \sum_{i=1}^{n} (V_i - \bar{V})^2 g''(V) \]  
\text{eqn 3}

because first order terms cancel each other out. One can recognise the expression of the spatial variance in the latter expression, and simplifying again we obtain the final expression

\[ I_L = g(\bar{V}) + \frac{1}{2} \sigma^2 g''(\bar{V}) \]  
\text{eqn 4}

In many cases, \( g \) should be saturating (\( g'' \) is negative), and due to Jensen’s inequality, spatial variance in prey density reduces the intake rate. We implicitly assume patches are randomly sampled; the predator does not actively respond to spatial variability. The variance correction can be interpreted as a limitation in the predator’s ability to exploit very rich prey patches because its intake rate saturates, and similar methods have been used in the study of risk sensitive foraging, when variance is temporal rather than spatial (see e.g. Real & Caraco 1986). If at the local (patch) spatial scale predators have a type III (sigmoid) response, for instance because predators do not perceive prey well below a given threshold, then the spatial correction will have a positive effect at low prey average densities and a negative effect at high prey average densities.

**NON-LINEAR SPATIAL AVERAGING: EXTENSION TO A POPULATION OF PREDATORS**

When considering several predators, the total kill rate depends not only on the spatial variance but also on the spatial covariance between predators and prey. In this case, although this is common practice, it is inadequate to think only of a per capita measure of intake, such as a local functional response \( g(V) \), because predators might be very unevenly distributed so that \( \frac{g(V)}{P} \neq g(V) \bar{P} \); the total prey kill rate per patch \( N_e \) is then a more useful quantity, as shown by Bergström, Englund & Leonardsson (2006) and previously by Murdoch & Stewart-Oaten (1989).

Writing \( N_e \) the number of prey eaten per unit space per unit time in a given patch, and Taylor-expanding with respect to prey and predator densities, one arrives at the general expression

\[ N_e = N_e(\bar{V}, \bar{P}) + \frac{\partial^2 N_e}{\partial V^2} \sigma^2 + \frac{\partial^2 N_e}{\partial V \partial P} C + \frac{\partial^2 N_e}{\partial P^2} \sigma_p^2 + \text{h.o.t.} \]  
\text{eqn 5}

where \( C = \text{Cov}(V, P) \) and h.o.t. means ‘higher order terms’. In the simplest case, where we consider neither prey handling nor predator interference, so that \( N_e = \frac{z}{P \text{(mass-action within a patch is more likely if the spatial scale considered is small enough)}} \), the expected kill rate becomes

\[ N_e \approx z \bar{V} \bar{P} + zC = z V_{\text{perceived}} \bar{P} \]  
\text{eqn 6}

where \( V_{\text{perceived}} \) is the density felt by a randomly chosen predator \( (V_{\text{perceived}} = \frac{\bar{V}}{C/P}) \) (see Appendix S3 for more mathematical details). The immediate lesson for the ecological reader is that when implemented in moment equations models, kill rates depend on the predator–prey spatial covariance, and therefore on predator and prey movement behaviour between.
patches. In other words, kill rates depend on who is winning the predator–prey race (Sih 1984), i.e. are the predators more efficient at locating prey or prey at avoiding them? If \( C < 0 \) the prey is winning, and conversely if \( C > 0 \) the predator is winning the behavioural race. As we shall see later (section ‘Second-order closure: introducing covariance dynamics’), a similar expression arises in the context of more complex moment models considering individual discreetness, and central place foraging alone can easily lead to a negative spatial correlation between predators and prey.

We will detail below some key assumptions and results of Bergström, Englund & Leonardsson (2006). Together with Melbourne & Chesson (2006), it is – to date – the most elaborate study on predator–prey dynamics merging spatial moment models with empirical studies (see also Englund and Leonardsson 2008 to follow the story).

AN EMPIRICALLY BASED PREDATOR–PREY MOMENT MODEL


2. Large-scale statistical measures obtained from field data.

3. A scaling-up procedure such as the one highlighted above.

4. An empirical moment closure method, that is a key ingredient of the model.

Here, moment closure means obtaining a dynamical system for the densities that does not depend on other variables (higher-order moments, see Appendix S3). In mathematical terms, it means finding functions \( f_1, f_2, f_3 \) relating the covariances to average densities, i.e. such that \( \sigma^2_N = f_1(\bar{x}, \bar{p}), \sigma^2_P = f_2(\bar{x}, \bar{p}), C = f_3(\bar{x}, \bar{p}) \). The closure method of Bergström, Englund & Leonardsson (2006) is an empirical regression of the spatial covariances and spatial variances with respect to predator and prey densities, that allows one to close the dynamical system, i.e. remove the dependency on higher moments. Consequently, the relationships of variances and covariances to the average densities are empirically determined, and do not arise directly from individual movement behaviours that are inserted into the model. This is both a weakness and a strength, since in general movement parameters are less well-known than demographic ones; in the next section we consider cases where these covariances have a dynamics of their own, and therefore movement parameters can be varied.

One of the main findings of Bergström, Englund & Leonardsson (2006) is that, given the empirically measured type III functional response at the patch scale, as well as the relationship between spatial covariance and average densities, the spatial model predicts cycles where the non-spatial model (ignoring spatial variability) predicts stability. The authors find the cycles predicted by the spatial (i.e. moment equations) model congruent with the cycles observed in the field. Interestingly, the conclusion drawn here is opposite to common theoretical findings about the role of spatial structure in stabilising predator–prey interactions (Briggs & Hoopes, 2004). The reason for these cycles lies in the empirically grounded relationship between the spatial covariance at time \( t \) and prey density at time \( t - 1 \), i.e. \( C(t) = f_3(N_t, N_{t-1}, P) \). Hence, an implicit delay generated by movement processes is causing the cycles, and such delays in movement responses of predators have been shown to happen in other invertebrate systems (e.g. Winder et al. 2001). The other point we draw attention to is that the functional response does not have the same shape during the various phases of the cycle (Englund & Leonardsson, 2008), and this again shows the importance of deriving the large-scale functional responses, rather than assuming a fixed shape on the basis of small-scale measurements.

Overall this method could be called empirical moment closure, because higher-order moments are empirically related to first moments, the landscape-scale densities. However, in Appendix S6 we show how similar moment equations can be applied to theoretical questions as well, by redemonstrating in a concise way Murdoch & Stewart-Oaten’s (1989) classic result that predators aggregating to prey density is not sufficient to promote community stability/prey regulation when time is continuous.

CONCLUSION: FIRST ORDER-CLOSURE

We conclude this section with a few words of caution. Firstly, the spatial covariances have no dynamics of their own and scaling relationships between covariances and densities are empirically derived, which means that approximations are valid within the range of parameter values and densities encountered in the specific community only. One cannot just modify these relationships to consider what would happen if predators were to move twice as much, and models derived from individual movements are required for this (see below). The simplicity of the first-order closure is also a strength, however, in that movement parameters are notoriously difficult to measure in the field. Hence these methods might appeal to those working with observational data, especially on predator–prey population cycles. Secondly, the models presented above are deterministic and neglect all sorts of stochasticity (i.e. demographic or environmental). Fluctuation corrections for demographic stochasticity could however be derived assuming Poisson variation around averages (see Cantrell & Cosner, 2004, in a PDE context). Finally, we note that although these methods are presented in a continuous-time framework, nothing prevents their application in a discrete-time setting (which might even be more practical in applied cases).

Second-order closure: introducing covariance dynamics

The essential ingredient of the models presented in this section is the same as before, i.e. if in a patch there are densities \( V \) and \( P \) of prey and predators, and the local rate of encounters can be described by mass-action, then the expected rate of encounters between predators and prey is \( \bar{z} = z V P \)
$+\alpha \text{Cov}(V, P) = \nu F P + \alpha C$, by a simple application of the definition of the spatial covariance, $C = TP - FP$. In itself the decomposition is not new, it was already present in Murdoch & Stewart-Oaten (1989); the difference here is that instead of being a constant factor or a function of densities, the covariance possess a dynamics $\frac{dC}{dt}$ of its own (as already highlighted in Appendix S3). Keeling, Wilson & Pacala (2000, 2002) develop the basic theory for stochastic predator–prey systems with a large number of equally accessible patches. We summarize their results in section ‘Adding a covariance equation: spatial structure as a time delay’. The assumption of an infinite number of equally accessible patches removes the stochasticity when considering spatial averages, since averaging over space or over samples is then identical. However, the overwhelming evidence suggests that in most cases all patches are not equally accessible to an individual, and this is especially likely if there are a large number of patches. For most animals, the probability of moving to some patch for foraging or dispersal purposes is likely to decay smoothly with distance; and we therefore need methods able to simplify the spatially explicit dynamics of collections of individuals with spatially restricted movements and interactions. In the following section, we show how this can be done by approximating individual-based models (IBMs). In Fig. 1 and Appendix S4, we highlight the importance of within-population spatial structure. IBMs are excellent tools to take into account such very local spatial structure in predator–prey interactions.

**SCALING UP IBMS BY THINKING IN TERMS OF PAIRS OF INDIVIDUALS**

A considerable number of papers have considered spatially explicit predator–prey IBMs on lattices in the last two decades, studied by simulations and compared to mean-field deterministic models (de Roos, McCauley & Wilson 1991; McCauley, Wilson & de Roos 1993, 1996; Wilson, McCauley & de Roos 1993, 1995; Keitt & Johnson, 1995; Wilson, 1996, 1998; Cuddington & Yodzis 2000, 2002; Hosseini, 2003, 2006). They have shown (among other things) in what way individual discreteness alone can lead to spatial patterning, how limited movements can stabilise predator–prey dynamics (i.e. reduce cycles) or show the effect of spatial dimensionality on predator–prey dynamics. Here, we will focus on recent approximations of these IBMs, that are mathematically derived and do not assume mass-action mixing.

The basic method, as described above, consists of deriving equations for the spatial variance and covariances of prey and predator densities. In a landmark paper, Matsuda et al. (1992) also showed how mathematical techniques of statistical physics, used to simplify stochastic and spatial interacting systems on lattices, could be applied to biological problems. The basic idea is to think not only in terms of individuals, but in terms of pairs of individuals, and interactions between them. Hence, in the context of predator–prey interactions, one would focus on describing the dynamics of the density of pairs of neighboring predator and prey cells on a lattice – instead of just describing densities of prey and predator cells. These methods have been very helpful in the related field of parasite-host dynamics (classic example in Boots, 1999, and recent review in Messinger & Ostling 2009). Notably, they have helped to decipher the influence of spatial structure (i.e. limited mixing) on the relationship between transmission rate and virulence. These techniques are usually grouped under the banner of pair/covariance/moment equations or approximations, the term ‘pair approximation’ being generally used for lattices whose cells contain either 0 or 1 individual, i.e. probabilistic cellular automata (discrete time) or interacting particle systems (continuous time). We will focus on methods in continuous space because we know them better, although the principles are essentially the same. On biological grounds, the usefulness of both representations of space can be argued, depending on the particular species one has in mind. Continuous-space moment equations are more general, and lend themselves very well to the comparison with spatial statistics for point patterns that are currently applied in ecology (e.g. in plants, Law et al. 2009 or to birds of prey nest spacing, Cornulier & Bretagnolle, 2006). On the other hand, pair approximations on lattices usually generate simpler equations, IBMs on lattices are also easy to implement, and in some systems data may be naturally available on a lattice (e.g. a grid of territories occupied or empty).

**DYNAMIC SPATIAL POINT PROCESSES AND MOMENT APPROXIMATIONS IN CONTINUOUS SPACE**

**Dynamic spatial point processes: ecological rationale**

The dynamic point process approach (Bolker & Pacala, 1997; Dieckmann & Law, 2000), initially developed with plants in mind, represents individuals as points in space to which discrete events (giving birth, death, or movement) happen in continuous time, as a function of the composition of the neighborhoods of the individuals. The point location, in the context of predator–prey dynamics, could represent either the location of a nest or den around which predator activity is distributed, or more generally the center of the home range. Alternatively, if movement behaviours are specified it may also describe the actual location of the individual. Thinking of birds and mammals, these models imply that prey individuals located closer to the predator nest or den are more likely to be killed than those far away (see Fig. 2 for examples of predation intensity maps, generated by different predator spacing patterns and predator home range size, in two-dimensional space).

Moment approaches show very clearly that a negative spatial correlation is to be expected between predators and prey because of prey depletion alone. Interestingly, this is commonly observed in avian central-place foragers roughly corresponding the assumptions of these models (i.e. predators have a nest so that their probability of attack decays with distance from the nest). Good examples can be found in colonial birds of prey (Bonal & Aparicio, 2008), and in seabirds (Elliott et al. 2009), although in the latter their clustering is rather extreme due to the scarcity of breeding habitat. Similar space-use patterns are observed in ungulate-carnivore systems, but in that...
case they owe much to the territorial behaviour of predators (Mech, 1977; Moorcroft & Lewis, 2006).

The models assume that each individual can give birth, move, or be killed as a result of competition or predation. For example, in these models, the probabilistic death rate of a prey individual located at point \( x \) can be written

\[
d + d' \sum_{j=1, j \neq x}^n w(x_j - x) + \alpha \sum_{j=1}^n a(x_j - x)
\]

**eqn 7**

The first term describes the density-independent death rate of a prey individual, in absence of competitors or predators. Longevity is exponentially distributed, and in these ideal circumstances, its average is \( 1/d \). If such a prey individual has a production of \( b \) offspring per unit time, its expected maximum lifetime reproductive success will be \( b/d \).

In the presence of competitors (second term), the death rate is increased on average by a factor \( d' \) per competitor, but not all competitors are equal: their effect is weighted by their spatial distance \( \xi \) to the focal individual through the kernel \( w(\xi) \). We note in passing that similar approaches would be possible with respect to distance in age or size, but this possibility has yet to be explored. A similar computation is performed to find the predator-induced mortality (third term in eqn 7): the effect of each predator is weighted by its distance to the prey \( \xi \) through the kernel \( a(\xi) \). One might think of \( \xi \) as the distance to the center of the predator’s home range, where the prey is more likely to get eaten. In that case, \( a(\xi) \) can be interpreted as the utilisation distribution of the predator, and estimated with usual home range methods (Worton, 1987). New methods for spatially explicit capture-recapture also produce similar point pattern/space use data (e.g. Royle et al. 2009).

Expressions similar to eqn 7 can be derived to make birth and movement rates dependent on local densities. Although the mathematics of these models can sometimes be difficult, notably because of the use of Dirac delta functions to represent individuals in more mathematical treatments (Dieckmann &

---

**Fig. 2.** Predation intensity maps of nesting predators. The first column presents three types of point patterns. If these points are thought of as predators’ nests, and predators have a Gaussian-shaped home range of width \( \sigma \), the second and third column represent the predation pressures at any location in space, for small (second column) and large (third column) home range size. Predation intensity is obtained by summing all predators utilisation distributions \( a \) for all locations in space. Readers familiar with kernel density estimation might want to think of predation intensity as a kernel estimation of local predator density with bandwidth parameter \( \sigma \). Space-use by territorial predators corresponds to a nest spacing identical to the regular point pattern with small home ranges (\( \sigma = 0.025 \)), while colonial predators are more likely to have nest spaced as in the clumped point pattern, with large overlapping home ranges (\( \sigma = 0.15 \)).
Scaling-up predator–prey dynamics

IBM
\[
\frac{dN_i}{dt} = (b - d)N_i - d \int w(\xi)C_{iv}(\xi)d\xi - \alpha \int a(\xi)C_{ip}(\xi)d\xi
\]
competition between prey
predation
eqn 8

\[
\frac{dN_p}{dt} = \epsilon \times \alpha \int a(\xi)C_{ip}(\xi)d\xi - \mu N_p - \mu' \int w_{pp}(\xi)C_{pp}(\xi)d\xi
\]
conversion
predation
competition between predators
eqn 9

Here, as remarked above, the pair densities \(C_{ij}(\xi)\) have dynamics of their own (see Bolker, 2004; Murrell, 2005, for details). The pair densities dynamics \(C_{ij}(n)\) for \(i \neq v, p\) depend in turn of triplet densities \(T_{ik}(\xi, \xi', \xi'')\), and the hierarchy of moments is closed by expressing the densities of triplets as a function of the densities of pairs (for more on that topic, see Murrell, Dieckmann & Law 2004).

This model shows that because of depletion, there is – on average – a spatial segregation between predators and prey \((C_{vp}(0)/N_vN_p < 1, \text{see Murrell} 2005)\). Such spatial segregation arises in the model because the foraging of predators is distance-dependent, as in many central-place or territorial foragers, and this lowers the encounter/kill rate when compared to the mass-action prediction. Note that even when the dynamics of the second moments are hard to obtain, models simulations are nicely summarized by empirical computations of these quantities (e.g. Bjørnstad & Bascompte 2001).

WHAT HAVE WE LEARNED SO FAR WITH SECOND-ORDER CLOSURE MODELS?

Adding a covariance equation: spatial structure as a time delay

Using moment approximations to stochastic models (with individual birth, death, and movement events), and based on a large number of equally accessible patches, Keeling, Wilson & Pacala (2000, 2002) show with a suite of models that the existence of an additional state variable to prey and predator densities, the average covariance between predator and prey densities in each patch, introduces time delays. This is a classic result on dynamical systems; an increase in dimension can be equated to the incorporation of a delay. However, the authors show the covariance dynamics are relatively rapid, especially if movement rates are high, and they depend mainly on the prey and predator average densities (rather than variances).

Assuming random movements, the depletion of prey items generates a negative spatial covariance between predators and prey. Such spatial ‘segregation’ (on average), depending on the closure assumption, leads to either smaller predation rates when compared to the equivalent mean-field model, or a qualitative shift consisting in the stabilisation of unstable interactions. As said above, Keeling, Wilson & Pacala show the spatial covariance dimension can be assimilated to an additional
time delay in the model, and that here – this would not the case for every model – the time delay is stabilising. Or in other words, limited movements induce some kind of ‘spatial memory’ that stabilises the model.

Density-dependent movements and grazing processes

While their model is aimed at modelling grazing processes, Marion, Swain & Hutchings (2005) propose a quite general IBM simplified to pseudo-spatial and discrete-space (patches) moment equations. An important feature of their model is that forager movements are directed towards richer patches. Individual foragers eat discrete bites in swards, which makes the model applicable as well to discrete prey individuals rather than bites, and foragers move to taller swards (richer patches) when possible (no predator demography). In the one-patch model (thereby well-mixed), the covariance between foragers and plants is zero, and the model is stable; however this changes when the environment consists of many patches. In a first step, Marion, Swain & Hutchings (2005) assume individuals have large-scale perception and movement abilities. Analysis of the model shows that at first, the spatial covariance is negative, as foragers deplete their resources locally, but the covariance soon becomes positive as the spatial heterogeneity created by depletion makes foragers move to richer patches. This positive covariance destabilises the system and prey abundance crashes, since even at low average prey densities the predators are experiencing high resource levels. In contrast, when perception and movements are restricted to neighbouring patches, the system can persist, and this shows how limited movement or perception are crucial to avoiding too high intake rates that induce resource suppression.

Prey fecundity, prey dispersal and predator home range size

Murrell (2005) showed the spatial segregation between predators and prey typically leads to a higher prey density than in the mass-action limit, and increasing prey movement (dispersal) rates or prey fecundity can lower the prey density in the model highlighted above. This is caused by prey movement decreasing the segregation of predators and prey, and therefore leading to higher encounter rates. Further simulations indicated that the finding holds if predator direct competition is weak, but not if predator density is constant or strongly regulated by competition with other predators: a strong predator numerical response to prey density is needed for increased prey movement to lower prey landscape density. Dispersal is not directed in the basic model and this means that prey movement, which may happen either at birth or as an adult leads to a decrease in the average spatial segregation between predators and prey, since prey may move into the home range of a predator. This in turn leads to increased predation rates, higher predator fecundities, and finally lower prey densities. Invasion analyses on the prey and predator components of these models (i.e. consideration of adaptive dynamics; Barraquand & Murrell 2012a,b) show that unless a trade-off reflecting travelling costs is implemented in the model, predators should always have the largest possible home ranges, and prey individuals can be selected not to disperse even when kin competition is present. This is because the spatial correlation between predators and prey is negative, so that many prey individuals are located in zones of reduced predation pressure. When prey kin competition is very high, prey might be selected to disperse, but when the predator numerical response is strong, prey dispersal will eventually depress prey population size (Barraquand & Murrell, 2012b).

Ratio-dependent predation

Using a verbal/conceptual model, proponents of ratio-dependent functional responses (Ginzburg & Jensen 2008; Arditi & Ginzburg 2012) suggest that a ratio-dependent functional response might correspond to indirect interference between localised predators having overlapping home ranges. The point process models presented above are ideal to verify such intuitions, and suggest it might not always be so. As the spatial scale parameter (home range size) of the attack kernel, or predator utilization distribution $a(\xi)$ increases, the system becomes more and more well-mixed, and in the limit of infinite home ranges the kill rate is $\alpha N_v/N_p$ (Murrell 2005; Barraquand & Murrell 2012a); completely overlapping home ranges lead instead to pure mass action. We believe this is largely because in the model we use, prey depletion occurs concurrently with prey and predator reproduction, while Arditi & Ginzburg (2012) assume prey depletion has to be integrated over longer time intervals corresponding to the generation time of predators.

In fact, to obtain landscape-scale ratio-dependence in the point process model, the average predator has to eat $\alpha N_v/N_p$ prey per unit time, which corresponds to $\pi \int a(\xi) C_{vp}(\xi) d\xi = \alpha N_v$. A sufficient condition for a total kill rate $\alpha N_v$ is that $C_{vp}(\xi)/N_v$, the density of predators at distance $\xi$ from a randomly chosen prey, is independent of the expected landscape density of predators $N_p$. This can happen, for instance, if predators are aggressive and exhibit spacing / territorial behaviour, in which case the density of predators is dependent upon predator-predator competition and cannot affect the density a prey individual ‘sees’. More work is needed to understand in what conditions simple encounter rate formulations such as mass-action or ratio-dependence can be obtained as limit cases of more complex models.

Reduction of cycles and spatial synchrony

Using a similar approach to Murrell (2005), Ovaskainen & Cornell (2006) consider a point process host–parasitoid model whose mean-field equivalent is the Lotka-Volterra predator–prey model (see also Bolker 2004). As with previous theoretical results (Pascual, Mazzega & Levin 2001) they show that cycling of densities is reduced by localised predation. However, further analysis of the pair correlation functions shows the cycling to continue locally, and that the spatial scale of prey population synchrony may extend well beyond that of individual dispersal. The result has been found in a single-species context by Lande, Engen & Saether (1999), who
showed that it is the signature of weak local density-dependence; here, the situation is similar, as Ovaskainen & Cornell (2006) consider a pure LV model without prey density-dependence. Their approach is based on a perturbation expansion which is another, mathematically more elegant way of closing an infinite hierarchy of moments.

**CONCLUSION: SECOND-ORDER CLOSURE**

This section has shown that by deriving moment equations from individual-based movement processes, one can answer a number of current ecological questions. These range from classical concerns in population dynamics about the influence of localised foraging on cycling and spatial synchrony, to more behavioural questions about prey dispersal and predator home ranges.

A great number of difficulties remain with the kind of models presented above – which should be related to their young age. Firstly, all moment equations are approximations of individual-based models once a closure method has been implemented, and therefore these approximations may fail in some regions of parameter space. However, the benefit of the direct connection to the IBM allows for a better understanding of mechanisms. Secondly, it has so far been difficult to include event rates that have non-linear relationships to local densities, although Taylor expansions of non-linear functions around expected densities seem to yield promising results (Barraquand 2010). Given the ubiquity of these non-linearities in ecological systems (e.g. the local type II functional response, reproductive allee effects) it seems a major impediment to the application of the models to real-world systems, and the reason why first-order closure might in some cases be preferable. Finally, a core assumption of these models is that interactions occur on a pairwise basis, so the consumption of prey is dependent on the local density of predator individuals. This might seem reasonable in many cases, but foraging activity may well be affected by the presence of individuals of other species, and this would lead to higher order interactions being required (Barraquand 2010). It is currently very difficult to approximate stochastic IBMs that include such indirect interactions.

**General conclusion and perspectives**

Most population dynamics models describing interacting populations of predators and prey are not fully derived from interactions between individuals. They either assume that these populations are well-mixed, neglecting local spatial structure, or assume phenomenological functional responses, whose functional forms reflect a mixture of physiological and movement processes. Two recent books on population/community dynamics illustrate that trend (Murdoch, Briggs & Nisbet 2003; Turchin 2003), although they both acknowledge the importance of limited movements and spatial variation in life-history traits in structuring natural communities (especially Murdoch, Briggs & Nisbet 2003, Chapter 10). We present three types of moment approximations to include spatial structure with predator–prey demography, having different strengths and weaknesses. Among first-order closure techniques, scaling encounter rates with power laws is relatively easy, but require groups to be very well defined, and is unlikely to be of use for species that do not exhibit strong social structure, at least in semi-empirical contexts. Non-linear spatial averaging, in contrast, seems a highly promising technique and is relatively easy to implement. It is probably more appropriate when large numbers of individuals are considered, when local functional forms are likely to be strongly non-linear (notably in cyclic systems), and also when little information about movements is available. Because of its simplicity, non-linear spatial averaging can be incorporated into models that already deviate from the classic Lotka-Volterra framework to incorporate other realistic features of predator–prey systems (e.g. stage-specific predation rates, multiple prey and predators, weak predator numerical responses). It is therefore likely that in many empirical examples, this would be the only type of approximation feasible. In constrast, second-order moment approximations are more desirable when one wants to test hypotheses about movements, because movements change the dynamics of second-order moments only; or when we have detailed space-use data (e.g. home range and dispersal movement kernels); or in purely theoretical settings. In our opinion, a challenge for empiricists is to collect enough information to go beyond mass-action modelling (i.e. to know when it fails), and parametrize models with first-order closure as in Bergström, Englund & Leonardsson (2006). The main challenge for theoreticians is to incorporate more foraging behaviour, i.e. travel time constraints and fitness-maximising behaviour such as included in Anderson (2010), into the moment equation framework. Other challenges (see Appendix S7 for details) pertain to better incorporating territorial behaviour into functional and numerical responses (Moorcroft & Lewis 2006; Arditi & Ginzburg 2012), integrating the frequent spatial variability in prey accessibility (Sutherland 1996), and coupling different spatial scales (Inchausti & Ballesteros 2008). As was recently highlighted in another review (Morales et al. 2010), it is quite desirable to integrate what we know of animal space use into population and community dynamics. Empirical studies report match–mismatch of spatial distributions across trophic levels (Rose & Leggett 1990; Chase 1998; Gremillet et al. 2008; Hagen et al. 2010), and highlight distance effects to the nests/dens of top predators in trophic cascades (Kharitonov et al. 2008; Miller et al. 2012). Moment equations, as well as other scaling-up techniques, can be useful to integrate such spatial variability into population models.

**Acknowledgements**

Thanks to John Fryxell and Stephen Cornell for constructive comments on a previous version. We are grateful to the associate editor, an anonymous reviewer, and Lev Ginzburg, for suggestions that improved the manuscript. FB also thanks Steve Redpath, Jason Matthiopoulos, and Leslie New for discussions on functional responses. This work originated as part of FB’s PhD at University Paris 6, funded by the French ministry of Research. FB is currently funded by the EU Biodiversity project Ecocycle. The research was partly supported by the Natural Environment Research Council (UK) Blue Skies Fellowship NE/D009367/1 to DJM.

References


Appendix S3. Derivation of spatial moment equations and illustration of the need for moment closure.

Appendix S4. Historical account of spatial structure and its role in predator–prey dynamics.

Appendix S5. Choices of measurement scales when estimating functional responses from data.
