

Population-level Consequences of Spatial Interactions

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Contents

Abstract	vii
List of papers	ix
1 Introduction	1
1.1 Spatial population dynamics	1
1.2 Individual-based stochastic processes	4
1.3 Dispersal in spatially structured populations	6
1.3.1 Stochastic dispersal in discrete space	7
1.3.2 Stochastic group-state dynamics	7
1.4 Spatio-temporal scales	8
1.5 Density-dependent dispersal	12
1.6 Dispersal behaviors and population demographics	12
1.7 Spatial functional responses	16
1.8 Empirical covariance dynamics	17
1.9 Group-structured cooperative communities	19
1.10 Acknowledgements	20
1.11 Author contributions	20
1.12 Tack	29
Appendices	31
Paper I	33
Paper II	51
Paper III	61
Paper IV	73

Abstract

How is the nature of populations governed by the movement decisions made by their members? This is the core question in this thesis. To answer this question, I first assume that individual's movement decisions are based on conditions in their local environment. Then I derive mathematical relationships that distil the character of individual movement events, and relate the sum of these events to the dynamical properties of the population. I find that the fate of populations depend delicately on the way resident individuals relocate in response to local conditions. This general conclusion is supported by results in the four papers constituting this thesis.

In the first paper we derive a deterministic approximation of a stochastic individual-based spatial predator-prey model. We show how general types of movement behaviors either stabilise or destabilise predator-prey dynamics. Based on experimental data on movement behaviors, we conclude that predator-prey dynamics are stabilised if the prey species respond stronger to predator presence than the predatory species respond to prey.

In the second paper we derive a new type of functional response that arise when there is a behavioral spatial "race" between predators and prey. Although fundamentally different from classical functional responses, the induced density-dependencies in reproduction rates are similar to those in Holling's type II and DeAngelis-Beddington's functional responses.

In the third paper we perform a novel systematic investigation of density-dependencies in population growth-rates induced by the spatial covariance in empirical predator-prey systems. We categorise three types of density dependencies: "lagged", "direct" and "independent", and find direct and especially lagged density-dependencies to be common. We find that the density-dependencies in most cases are destabilising, which is at odds with the wide-spread view that spatial heterogeneity stabilises consumer-resource dynamics. We also find dependencies of prey density to be more common than of predator density.

In the fourth paper we consider the evolution of cooperation. We formulate a stochastic individual-based group-formation process and show that profit-dependent group disengagement is evolutionarily stable and allows the emergence of stable cooperative communities.

List of papers

- I Sjödin, H., Brännström, Å., Söderquist, M., Englund, G. Population-level consequences of reactive movements in predator-prey systems. Accepted for publication in Journal of Theoretical Biology.
- II Sjödin, H., Brännström, Å., Englund, G. Space-race functional responses. Manuscript (ready to be submitted).
- III Englund, G, Sjödin, H., Bonsall, M., Cianelli, L., Frank, K., Heino, M., Janssen, A., Leonardsson, K., van der Meer, J., Nachman, G., Yu, J. Density dependence induced by the spatial covariance between predator and prey. Manuscript.
- IV Sjödin H., Brännström Å., Dieckmann U., Mazzucco, R. Contingent dispersal and the formation of cooperative groups. Manuscript.

1

Introduction

This thesis is about the interplay between the dispersal of individuals and their interactions, and how such interplay affects populations. The processes that I study span over a wide range of temporal and spatial scales - from everyday actions in the near proximity of single individuals to the evolutionary development of large-ranging populations.

Since the early history of ecology ([Malthus, 1798](#); [Lotka, 1925](#); [Volterra, 1926](#)), mathematical formulations of the changes of populations over time have typically assumed that individuals move independent of each other, and that they move very fast. These assumptions greatly reduces the possible complexity of the patterns caused by individual interactions. This kind of assumption is not at all unique to ecology and has been applied in several other fields, such as chemistry and physics. It serves as a good approximation or even as an accurate description of the processes of some system. This occurs, of course, when the actual behaviors of the granule objects in the a system aligns with the assumptions. I believe, however, that this is rarely the case in ecological systems.

The pivotal subject of this thesis is to relax the assumption of independent movements of single individuals, and also to consider processes where fast movements are appropriate, in order to understand how such individual behaviors affects the properties of populations over time.

1.1 Spatial population dynamics

Population dynamics originated from early works such as that of [Malthus \(1798\)](#). The field has thereafter branched into to an array of different applications as new questions have been asked for different types of interactions, such as, competition, mutualism, or victim-exploiter interactions. Models of such dynamics was first studied under the assumption

that spatial processes could be neglected, which typically implies that individuals of the populations are assumed to move randomly and very fast. Such conditions are, however, rarely met in nature.

The effects of spatial processes on population dynamics are in principle independent of the type of interaction we study. Therefore, and as the type of population dynamics studied in this thesis are that of two-species systems and mainly predator-prey dynamics, I will let the latter serve as the example of population dynamics in this section.

The theory of predator-prey dynamics is largely built upon the analysis of coupled differential equations where the Lotka-Volterra model is one of the first as well as one of the most simplistic predator-prey equations (Lotka, 1925; Volterra, 1926). If we denote the density of prey and predators by N and P respectively, the model may be written as

$$\begin{aligned}\frac{dN}{dt} &= rN - aNP \\ \frac{dP}{dt} &= caNP - mP,\end{aligned}\tag{1.1}$$

where r is the prey reproduction rate, a , the predator attack rate, c , the predators conversion efficiency, and m , the predator death rate. However, the Lotka-Volterra model is only one member of a family of models describing coupled predator-prey interactions, which can be generally written as

$$\begin{aligned}\frac{dN}{dt} &= b(N) - f(N, P)P \\ \frac{dP}{dt} &= cf(N, P)P - d(P),\end{aligned}\tag{1.2}$$

where then $b(N)$ is a growth function, $f(N, P)$, the functional response, and $d(P)$, a death function. Such models are typically descriptions of deterministic well-mixed populations and are relatively easy to analyse. In my perspective, however, it is desirable to attribute the systems additional complexity to reach a more adequate level of realism by including elements such as spatial structure, stochasticity, and individual-based processes.

Two common approaches are used when including this sort of elements. In one, prey and predators in systems like equation (1.2) are interpreted as concentrations at a point \mathbf{r} in a continuous space, such that $N(\mathbf{r}, t)$ and $P(\mathbf{r}, t)$. A diffusion process as an addition term then accounts for a flux of these concentrations around \mathbf{r} . Under such assumptions, equation (1.2) becomes what is called a reaction-diffusion model. This is a deterministic demographic process accounting for dispersal, that arises as an approximation of a stochastic process. The formulation involves a continuous approximation of discrete individuals, and the resulting model is a partial differential equation.

In the other approach, space is assumed to be discrete and made up of spatial compartments, usually referred to as patches, such that the variables $N(t)$ and $P(t)$ are considered as discrete random variables denoting the numbers of individuals in local patches. The probability that the number of individuals in patches changes is governed by vital processes such as those in equation (1.2) as well as of additional dispersal terms. This is an exact formulation of individual-based stochastic dynamics of demographical and spatial processes. Such a model is usually referred to as a master equation which may be analysed directly by various means. In cases where the processes exceeds certain levels of complexity, however, analytical solutions of the exact formulation can be difficult to attain. Under such circumstances we can either resort to numerical analysis, or derive deterministic approximations, one of which is the reaction-diffusion approximation. The reaction-diffusion approximation is directly related to Fokker-Planck approximations, which generally are obtained in the limit of small changes of variables, necessarily leading to an interpretation of discrete variables as continuous. If a spatial structure is included in the original formulation, also the limit of infinitesimal patch volumes becomes central, leading to a continuous space. There exists also a limit of large systems of which the stochastic behavior of a system, in a similar sense as in the Fokker-Planck limits, approaches a deterministic behavior. This type of approximation is referred to a system size expansion (van Kampen, 2007), which is more systematic compared to the Fokker-Planck approximation.

In contrast to these types of approximations, which are generally based on appropriate scaling of probabilities and the structure of the system itself, a third alternative is available where it is not the structure of the system itself that is scaled but instead the processes of the system. This is usually done by scaling rate parameters in such a way that higher order moments becomes negligible. The framework is referred to as moment closure, or moment approximation (Dieckmann et al., 2001; Keeling et al., 2002), and has been applied in the works of this thesis when deterministic approximations have been derived as analytical functions. The resulting models take the form of a system of ordinary differential equation like equation (1.2) with the exception that the system is evaluated globally such that

$$\begin{aligned}\frac{d\langle N \rangle}{dt} &= \langle b(N) \rangle - \langle f(N, P)P \rangle \\ \frac{d\langle P \rangle}{dt} &= c \langle f(N, P)P \rangle - \langle d(P) \rangle,\end{aligned}\tag{1.3}$$

where any non-linear term, such as, for instance $\langle f(N, P)P \rangle$, for an accurate description must be expanded appropriately by the central moments corresponding to the type of non-linearity of the averaged term. Averaged immigration and emigration terms cancel each other due to a conservation principle as the global system is assumed to be closed.

1.2 Individual-based stochastic processes

Ecological systems are constituted by individuals, and individuals come in whole pieces. Even though we sometimes represent population in units of biomass, which then is a continuous measure, it is inevitable that interactions between individuals, that drive the population dynamics, are best interpreted as events that involves a number of individuals in discrete units. When modelling dynamical systems that are assumed to involve discrete numbers of individuals, particles, etc., it is preferable to explicitly account for such discreteness. A common procedure is to describe the change in the number of individuals by jump processes, where a "jump" usually refers to the increase or decrease of whole numbers of individuals, usually one (van Kampen, 2007; Gardiner, 2009). It becomes necessary (and is usually desired) to describe the event of jumps by the probability that they will occur within a given time period. Such formulation entails that the system can be considered to possess a certain probability to occupy a state at any time, defined by the number of individuals in the system at that time. When the number of individuals in the system changes (when the system takes a "jump"), the system transits from its current state into a different state. It is therefore convenient to view the probabilities of such events taking place as transition probabilities. It is of course expected that any interesting dynamical system will experience a very large number of transitions over the course of time. The bookkeeping of that number of transitions over history would be a dismal assignment. However, the jump process is a Markov process which has the delightful property of being "memoryless", which means that the state of the system is completely defined by its last previous state, and any other preceding states are irrelevant. If the current state is known, the following state can be predicted.

Although one can explicitly define events, such as birth, death, and dispersal, that would cause the system state to transition into a new state, the stochastic dynamics of a general system can be regressed to fundamental positive and negative transition processes. Positive transition processes, T^+ , are those accounting for any types of events that increase the number of individuals, and negative transition probabilities, T^- , those that decrease the number of individuals.

We can take a single species system as an example, and then write the probability that the number of individuals X in the population increase by one during the time Δt due to some general positive transition process T^+ as follows

$$\Pr(X + 1, t + \Delta t | X, t) = T^+(X)\Delta t + o(\Delta t), \quad (1.4)$$

and the probability that the number of individuals X decrease by one during the time Δt due to some general negative transition process T^- as

$$\Pr(X - 1, t + \Delta t | X, t) = T^-(X)\Delta t + o(\Delta t), \quad (1.5)$$

and the probability that no transitions take place during that time is then consequently

$$\Pr(X, t + \Delta t | X, t) = 1 - (T^-(X) + T^+(X))\Delta t + o(\Delta t), \quad (1.6)$$

where $o(\Delta t)$ is a notation for the probability of having jumps larger than one, which has the property $\lim_{\Delta t \rightarrow 0} o(\Delta t)/\Delta t = 0$.

Now, I denote the probability of having exactly x individuals at time t by $p_x(t)$. The probability of having x individuals at time $t + \Delta t$ can be written as a sum of the transition probabilities in equations (1.4,1.5,1.6) at time t , which takes the form

$$p_x(t + \Delta t) = p_{x+1}(t)T^-(x+1)\Delta t + p_{x-1}(t)T^+(x-1)\Delta t + p_x(t)(1 - (T^-(x) + T^+(x))\Delta t) + o(\Delta t), \quad (1.7)$$

The differential form of equation (1.7) is usually referred to as a master equation and is defined only for very small Δt (van Kampen, 2007; Gardiner, 2009). This form is acquired after first subtracting $p_x(t)$ from both sides in equation (1.7) and then dividing by Δt , which gives

$$\frac{p_x(t + \Delta t) - p_x(t)}{\Delta t} = p_{x+1}(t)T^-(x+1) + p_{x-1}(t)T^+(x-1) + p_x(t)(T^-(x) + T^+(x)) + \frac{o(\Delta t)}{\Delta t}. \quad (1.8)$$

which, in the limit $\Delta t \rightarrow 0$, becomes

$$\frac{dp_x}{dt} = p_{x+1}(t)T^-(x+1) + p_{x-1}(t)T^+(x-1) + p_x(t)(T^-(x) + T^+(x)). \quad (1.9)$$

This single species master equation can be extended and expressed generally for s number of species, as the terms for each species' share the same general form of positive and negative transition processes. Denoting the set of state variables by $\mathbf{x} = x_1, x_2, \dots, x_s$ we can express the s -species master equation as

$$\frac{dp_{\mathbf{x}}}{dt} = \sum_{i=1}^s \left[p_{x_i+1, \hat{\mathbf{x}}} T_i^-(x_i + 1, \hat{\mathbf{x}}) + p_{x_i-1, \hat{\mathbf{x}}} T_i^+(x_i - 1, \hat{\mathbf{x}}) + p_{\mathbf{x}}(T_i^-(\mathbf{x}) + T_i^+(\mathbf{x})) \right]. \quad (1.10)$$

where $\hat{\mathbf{x}}$ denote a set of all state variables except x_i .

This form of multivariate master equation is central in this thesis. The probability $p_{\mathbf{x}}$ is here interpreted spatially such that $p_{\mathbf{x}}$ refers to the fraction of spatial sites, in the whole system, that are in the state \mathbf{x} which in a two species system ($s = 2$) translates to x_1 individuals of species 1 and x_2 individuals of species 2.

The master equation in paper I is equivalent to the form of equation (1.10) with $s = 2$ and the results in paper II is based on the same. The form of the master equation that was formulated for the system in paper IV is in principle the same, albeit, slightly more complex as the transition processes in that system differ fundamentally between states. Paper III is about understanding spatial predator-prey dynamics by linking theory and observation and is therefor not based directly on theoretical formulations of stochastic processes. Still, parts of the findings in the paper are directly linked to master equations in the same form as equation (1.10).

1.3 Dispersal in spatially structured populations

It can not be disputed that organisms disperse. Individuals deliberately propel themselves through space in search for resources or in search for shelter from predation or other dangers. Eggs or seeds are passively transported by wind, currents, or by other means relocated in space. The question is, how does dispersal of organism affect the dynamics of population on ecological and evolutionary time scales? This question has been increasingly recognised during the past couple of decades and various methods have been used to address this matter (Skellam, 1951; Huffaker, 1958; Levins, 1969; Murdoch and Stewart-Oaten, 1989; Turchin, 1989; Hanski, 1998; Dieckmann et al., 2001; Metz and Gyllenberg, 2001; Murdoch et al., 2003; Murrell et al., 2004; Brännström and Sumpter, 2005; Bergström et al., 2006; Englund and Leonerddsson, 2008; Hunsicker et al., 2011; Chesson, 2012; Cornforth et al., 2012; Parvinen et al., 2012; Barraquand and Murrell, 2013; Garcia and De Monte, 2013).

When modelling dispersal it becomes central to consider assumptions of the structure of space. Typically, two different structures are considered: (1) A continuous space, or (2) a discrete space that is made up of patches. The first case is obviously the most realistic representation. However, when considering dynamics of individuals in continuous space, it becomes necessary also to think carefully about the representation of individuals, such as the position of single individuals, the boundaries of individuals, and the appropriate scaling of probabilities of taking infinitesimal steps in space. Such representations of individuals are easily integrated in computer simulation. For the analytical modeller, however, it is indeed challenging and the presence of individuals at spatial points are typically instead

approximated by a concentration such as in diffusion models. One exception is a class of individual-based models in continuous space, including pair correlation and derivatives of that method, which allows for both discrete individuals and a continuous representation of space (Bolker and Pacala, 1997; Dieckmann et al., 2001; Murrell et al., 2004). This class of models is not covered in this thesis further than as a reference to an advanced framework of spatial modelling.

As mentioned in the previous section, the methods in this thesis are restricted to individual-based stochastic models in discrete space. Such models are very suitable when considering populations that are subdivided into groups of interacting individuals, or of populations occupying a space subdivided into patches in which individuals interact. Given that individuals are assumed to react to the presence of other individuals in their patch, the size of the patch can then be thought of as a representation of the perceptual range of individuals.

1.3.1 Stochastic dispersal in discrete space

Although space itself is continuous, the natural environment which is shaped by the organisms that inhabit it are usually heterogeneous. Some areas are visited more frequently than others due to, for instance, their suitability for various activities such as foraging or taking shelter, and on a larger spatial scale, such areas could correspond to the habitat of the species. It is reasonable to assume that the within-species as well as the between-species interactions are also most pronounced in those frequently visited areas. A model assumption of a discrete space is therefore reasonable.

Technically, the rate at which individuals leave a given area, or patch, is defined as a negative transition process. If the emigration of individuals of a given species is assumed to be linearly dependent on the number of individuals of that species in the patch, emigrations occur in linear proportion to that number and are therefore random. The process can equally well be assumed to depend non-linearly on the number of conspecific and heterospecific individuals. Emigrations then occur non-randomly and, depending on the shape of the non-linearity, individuals are either repelled by, or attracted to, the presence of other individuals.

1.3.2 Stochastic group-state dynamics

Natural communities are spatially heterogeneous. However, it is not the spatial pattern itself that directly drive the dynamics. It is rather the pattern of interactions between individuals that do so. If curious on the population dynamics emerging by these interactions,

and not on the spatial pattern per se, we could consider the heterogeneity of interactions directly.

In a spatial model of a discrete space subdivided into patches, there will exist three essential spatial states: (1) patches with interacting individuals, (2) patches with one individual, and (3) empty patches. The first spatial state is dynamically active as it potentially possesses all types of interactions. The second spatial state is partly dynamically active as we, for example, usually assume clonal reproduction. The third spatial state is dynamically passive. All states, however, could work in combination since, for instances, immigrations may occur to a single-individual patches, and the fraction of empty patches will affect the probability of migrating individuals to end up alone. In most natural situations, the choice of withdrawing from interactive situations is available to individuals, as long as they are not pursued by other individuals. In either case, the fraction of empty space may be thought of as always being in sufficient supply. As a consequence, we do not have to keep track of empty patches but only single-individual patches and all types of multi-individual patches. In fact, it is sufficient to keep track of the fractions of individuals in a community that are solitary and the fractions that are engaged in various interactive constellations. This can be reformulated as a group-dynamical process where space is implicit, and the formulation becomes invariant of assumptions of a discrete or a continuous space.

Such formulation is probably reasonable for studies of spatial dynamics in general. In some cases it is desirable to formulate a group structure rather than a spatial structure. The study on the evolution of cooperation in paper IV is such a case. Individuals cooperate (or not) within groups to make the most out of a commonly shared recourse (a public good), and individuals do not necessarily have to be in close proximity to do so.

1.4 Spatio-temporal scales

Assumptions about the spatial scale at which individuals disperse is crucial in spatial ecology, and the effects of dispersal on the systems are best studied in relation to the spatial and temporal scales of the processes in consideration (Wiens, 1989; Hastings, 1990; Levin, 1992; Bowler and Benton, 2005; Hunsicker et al., 2011). Although there exists in reality a continuum of scales which various processes act on, I find it sufficient here to discuss three conceptual spatio-temporal scales which I for convenience will term the small scale, the intermediate scale, and the meta-population scale (Figure 1.1). The relationship between these spatio-temporal scales and the processes that are pronounced on them, provides a key to unlock the class structure of spatial process and its theoretical counterparts.

The spatio-temporal scales can be envisioned conceptually in the plane of effective dispersal distances and time, as showed in Figure 1.1. This view make sense only if we embrace the fact that individuals in reality have finite travelling speeds, and that the patch size display

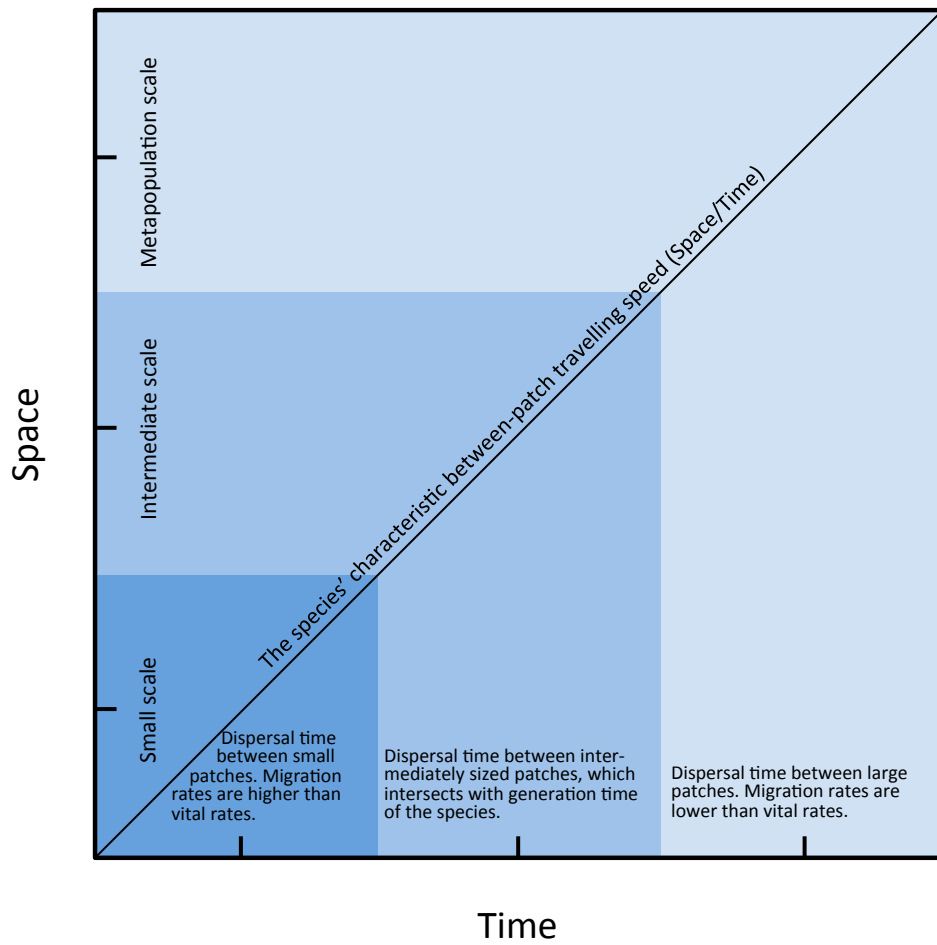


Figure 1.1: Three conceptual spatio-temporal scales.

a negative correlation with emigration rate (Englund and Hambäck, 2004). The slope of the diagonal line in Figure 1.1 represents a given species' characteristic travelling speed. Time along the horizontal axis then represent the travelling times needed to cover certain distances in space, given on the vertical axis, by travelling at the species' characteristic speed. The travelling times are relative to the reproduction rate, and the point at which birth and death rates equals emigration rates is centred on the time axis.

We usually make a distinction between spatial and non-spatial ecological models, the latter representing classical mean-field theories like that arising from studies of the Lotka-Volterra type of models. I find it more convenient, however, to not make this distinction and view these two classes of models as both being spatial, and instead consider the assumptions of spatial processes that underlie the structure of the model.

Assuming that individuals move randomly in space, independent of other individuals, and at a rate many times higher than that of vital processes (birth and death), a so called non-spatial population system is usually considered to be recovered. In theory, where the dispersal rates are assumed infinitely higher than vital rates, the dispersal processes rapidly equilibrate independently of the vital processes, and then forming a spatial random distribution on which vital interactions then are evaluated. A non-spatial system becomes then represented as a point in the lower left corner of Figure 1.1, which means that the spatial dimension is zero - the model prefix, non-spatial, is in that sense not misleading. Strictly speaking, the assumption of randomly (and fast) moving individuals is not sufficient as non-spatial models neglect any central moment. For example, the spatial variance, that would turn up for instance in logistic growth terms, would for random distributions be equal to the mean. The spatial variance, along with other central moments, quickly vanishes, however, if the population can be assumed to behave like a fluent mass and randomly disperse infinitesimal parts between patches. The resulting spatial pattern becomes homogeneous, and is then described by a probability density function sharply peaked at the mean. In the theoretical limit of a continuous population such function is then a delta function that has the property of zero variance.

However, the non-spatial models are approximations of the dynamics of a small-scale system where individuals move independently of each other. If the number of individuals in patches are very large, the variance will be small relative to quadratic interspecific interaction terms. Given such systems, non-spatial models are relatively accurate descriptions. The smaller subsample of a population's spatial distribution and the denser local populations, the more accurate the approximation becomes.

There exist also a frequently studied limit at the other end of the spectra. This theoretical limit concerns instead infinitesimal dispersal rates, in which we recover the typical metapopulation models that roots back to the classic model formulation by Levins (1969). The local demographical dynamics are thus assumed to equilibrate independent of, and between, migration events. This limit behaves better than the dispersal limit of infinite rates,

in the sense that the dynamical situation of the local population at infinite time, is typically reached already in finite time - the population demographics are either quickly stabilised or otherwise unstable. Therefore, the theoretical limit works as an efficient methodological simplification but the assumed extremely rare migration events are equivalent to the frequency of migration events expected on a large but indeed finite metapopulation scale (Figure 1.1).

In between these two opposing limits, we have systems where the vital rates are of the same order of magnitude as dispersal rates. The two limiting cases will not perform well as approximation of such systems. For a more accurate description of the dynamics here, we need to account for both the vital process and the dispersal processes at once. An equilibrium is then depending on the combination of dynamical contributions from the two types of processes. Reaction-diffusion models capture the dynamics occurring on this intermediate spatial-temporal scale, as well as appropriate formulations of master-equations and corresponding approximations.

Keeling et al. (2002) derived a moment closure approximation in order to study the effects of limited random dispersal. This approximation becomes exact in the limit of infinitely fast dispersal where the system behaves quantitatively as a non-spatial system. However, the effects arising from relaxing the assumption is traceable in the model, thus providing information on the dynamical behavior of the population at the intermediate spatio-temporal scale as dispersal becomes limited. Keeling et al. (2002) consequently showed how a non-random spatial structure emerges as the orders of dispersal rates and vital rates converge, which is discussed in more detail in paper I and in paper III. Essentially, the spatial structure emerging in Keeling's model arises from the non-linearities in the local stochastic vital processes. The differences between local populations are smoothed by dispersal as long as movement rates are large, and becomes more pronounced as movement rates decrease.

The mechanism presented by Keeling et al. (2002) is one important mechanisms that lead to spatial structures that affect non-linear processes. Another mechanism is that of contingent dispersal, where individuals migrate depending on their environment, such as the number of other conspecific or heterospecific individuals in the proximity, where the latter will be referred to as density-dependent dispersal. This mechanism forms spatial patterns independent of the magnitude of dispersal rates.

Population-level dynamical effects arising from fast density-dependent dispersal was studied in paper I for a predator-prey system. This work thus extends Keeling et al. (2002) and forms theory for the effects of spatial structures arising from density-dependent movements. As dispersal was assumed fast, the work extends also classical small-scale theory by relaxing the assumptions of mass action.

1.5 Density-dependent dispersal

Single dispersal-events are localised in space. Density-dependent dispersal have been observed frequently on relatively small scales (Hassell, 1971; Bernstein, 1984; Forrester, 1994; Kratz, 1996; Maeda et al., 1998; Zemek and Nachman, 1998; Diehl et al., 2000; French and Travis, 2001; Roll et al., 2004; Nachappa et al., 2006; Hauzy et al., 2007; Jenner and Roitberg, 2008; Hammond et al., 2012; Ohara and Takabayashi, 2012; Simonis, 2013). One may guess that density-dependent dispersal processes are dominant on this scale, while on larger scales instead random dispersal, such in Keeling et al. (2002), is more prominent.

It has been shown theoretically, however, that density-dependent dispersal is evolutionarily stable in single-species meta-populations (Kun and Scheuring, 2006; Parvinen et al., 2012). In natural predator-prey systems, studied in paper III, we find indications that signals of density-dependent dispersal is detectable on rather large scales. Population-level effects of density-dependent dispersal on intermediate scales, thus non-random limited dispersal, show additional effects to that of random limited dispersal (Fryxell and Lundberg, 1993), and affects the levels of predator and prey mean-densities, demographical dynamics, and spatial synchrony (Hauzy et al., 2010).

I find it plausible, though, that we should expect that the degree of density dependence peaks at a point of a species-characteristic scale, defined by its spatial range of activity and its perceptual range, and this scale can then be thought of as a small scale as the individuals can switch between patches frequently. This is, however, a complex matter as, for instance, the characteristic scales of the two species in a predator-prey systems are usually different, one utilises a wider spatial region than the other. The matter is complicated further when taking also the prey species' resource into account, as then the strategies of the spatial game typically depends intricately on the characteristic scales of the species involved (Hammond et al., 2012).

1.6 Dispersal behaviors and population demographics

The spatio-temporal scales at which spatial processes act, are characteristic to each specific process (Levin, 1992). The majority of the studies on the effects of spatial processes on population dynamics have been focused on intermediate- and metapopulation-scales (Skellam, 1951; Levins, 1969; Turchin, 1989; Fryxell and Lundberg, 1993; Hanski, 1998; Keeling et al., 2002). While most studies on small-scale population dynamics have assumed spatially homogeneous populations (see the vast literature on non-spatial population dynamics), some have relaxed this assumption and included heterogeneity in the systems (Murdoch and Stewart-Oaten, 1989; Krivan, 1997; Abrams, 2007; Flaxman et al., 2011). The complexity arising at this scale due to density-dependent spatial interactions, stochasticity, and

the large number of patches (to span the full region of a population), provides a range of challenging questions that are yet far from resolved.

In paper I we derive a moment-closure approximation of a stochastic individual-based predator-prey model in discrete space in order to study the emergent population-level dynamical effects of individual's dispersal behaviors on small scales, such as those of foraging and risk avoidance. This allows for an integration of the behaviors of individuals, localised in space, and the emergent global-scale population dynamics.

Our stochastic model is based on the processes of the Lotka-Volterra model which in its original form can be recovered as a limiting case. Since the only non-linear processes in the Lotka-Volterra model is that of the predators' prey-intake which is proportional to the product of the numbers of the two species, NP , the spatial covariance becomes also the only central moment that will be of significance to describe the effect of the spatial structure on demographical interaction strengths.

The spatial covariance between predators and prey, emerging from individuals' dispersal behaviors, therefore constitutes the core of the work in paper I. We find that the coefficient of co-variation,

$$C = \frac{\text{cov}(X_n, X_p)}{NP}, \quad (1.11)$$

or the per capita covariance as we call it (where X_n and X_p denote random variables, and where N and P denote spatial mean densities), is the essential component in the spatial correction of the mean-field dynamics. We show that the stability of the population dynamics is utterly dependent on the shape of $C(N, P)$ such as if the inequality

$$c \frac{\partial C}{\partial P} < \frac{\partial C}{\partial N}, \quad (1.12)$$

evaluated at a fixed point is true, the dynamics is stable, or otherwise unstable apart from when the two terms equals each other, which is a degenerate case of neutral stability.

The per capita covariance is on the small spatial-temporal scale determined mainly by dispersal process ([Hammond et al., 2012](#)). We argue that, on this spatio-temporal scale, patch emigrations are not random but should instead depend on the number of individuals within patches. Hence, we assume that emigration is density-dependent. This raises the essential question: What are the shapes of density-dependent emigration responses mediating the emigration rates?

We focus on the prey species' predator-escaping behavior $E_n(P)$, and the predator species' prey-tracking behavior $E_p(N)$. Empirical evidence, reviewed in paper I, suggest that in

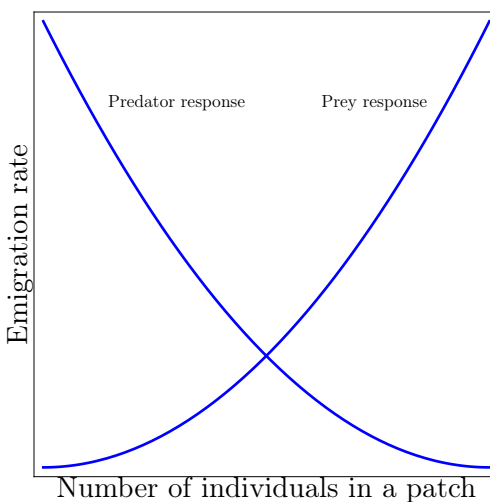


Figure 1.2: Emigration-rate responses.

natural system $E_n(P)$ is typically an increasing and accelerating function, and that $E_p(N)$ is a decreasing and decelerating function (Figure 1.2).

To generalise the results, we investigated the dynamical regimes resulting from the emerging spatial pattern, for a complete set of 16 shapes of emigration rate responses within a class of functions valid for the approximation. As shown in Figure 1.3, depending on the shapes of emigration rate responses the population-level dynamics can either be stabilised, destabilised, and in some cases both, as the dynamical regimes in these situations depend on the relation between the shapes of the two responses. As a limiting case, the neutral cycles of the original Lotka-Volterra model is recovered when emigrations occur at random (Figure 1.3 A). This is because the spatial covariance between the two species then becomes zero. Based on empirical evidence, the situation expected in nature is hence represented in Figure 1.3 H.

The analytical model derived in paper I is limited in the sense that the accuracy of the approximation relies on a parameter θ that controls the degree of density dependence in the emigration responses. The approximation becomes exact in the limit of vanishing density dependence, hence, when $\theta \rightarrow 0$. However, the approximation shows to perform well at considerable deviations from this limit (see robustness analysis in paper I). The majority of the reviewed empirical studies in paper I (Hassell, 1971; Bernstein, 1984; Kratz, 1996; Maeda et al., 1998; Zemek and Nachman, 1998; Diehl et al., 2000; French and Travis, 2001; Hauzy et al., 2007; Ohara and Takabayashi, 2012), showed a degree of density dependence for which the deterministic approximation is a good estimator of the stochastic processes. Thus, the approximation model is not restricted to conceptual theory, but can serve also as a tool in empirical approaches.

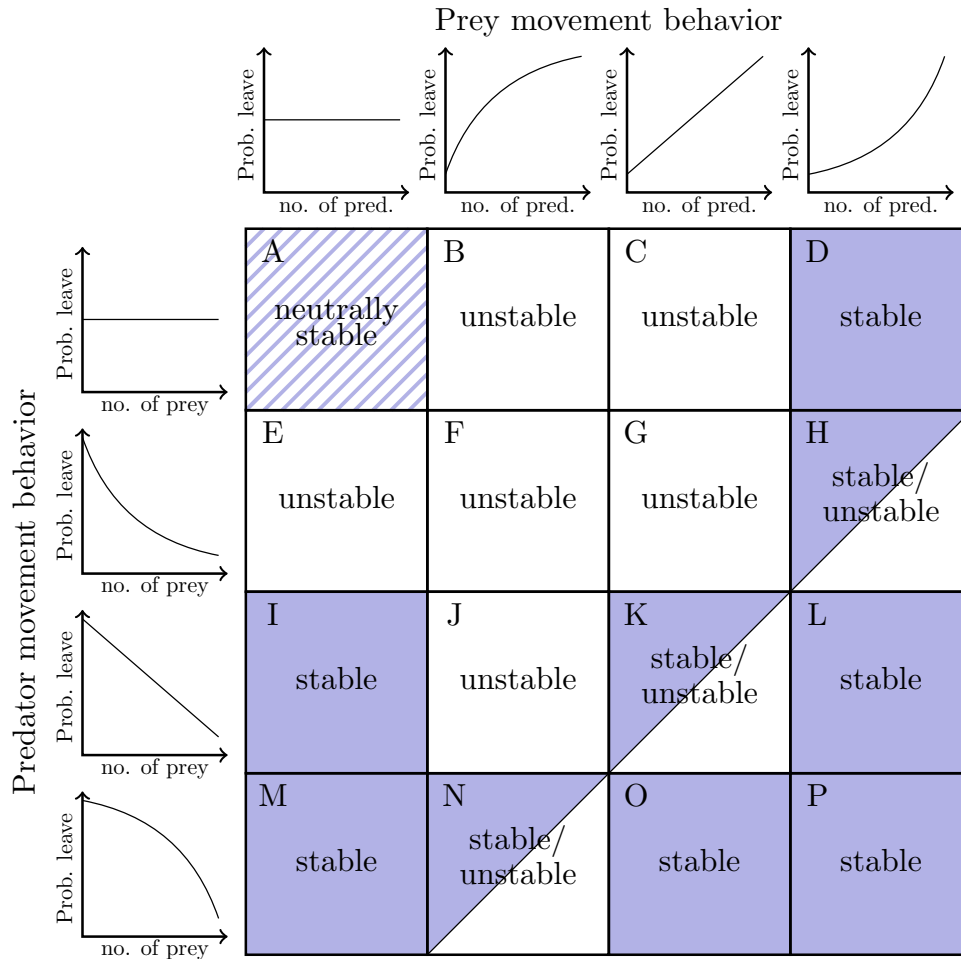


Figure 1.3: (From paper I) Effects of different emigration-rate responses on the stability of global dynamics. Stability is evaluated at the Poisson limit, i.e., when the density independent movement component is much larger than the density-dependent movement component. Plots on the edge of the matrix show the emigration-rate responses of prey (columns) and predators (rows). The vertical axis of each plot shows the probability per unit time that an individual of the reactive species will leave its current patch, while the horizontal axes show the number of individuals of the species to which it reacts.

1.7 Spatial functional responses

The functional response is an integral module in population dynamics as it describes the resource intake-rate of a species. It is a population-level descriptor of the demographical effects of individuals' behaviors. The Holling type I, type II, and type III, functional responses are probably the most frequently applied (Holling, 1959). Holling's responses along with other classical functional responses are based on the assumption that individuals forage randomly in randomly distributed resource populations (Royama, 1971; Rogers, 1972). This is well in line with non-spatial population dynamics, which are based on similar assumptions. These assumption are rarely fulfilled in natural communities and consumption-rates are consequently affected by emerging non-linearities in birth, death, and dispersal process (Englund and Leonerdsson, 2008; Hunsicker et al., 2011).

Given the assumption behind classical functional responses, the populations are independently and randomly distributed and encounters occur by chance, and the average rate at which any predator individual encounter any prey individual is then proportional to the product of their densities. This must be considered a degenerate case, and as soon as the system is perturbed from such state the average encounter-rate will either increase or decrease.

On the small spatio-temporal scale, the distribution of individuals should be described predominantly by small-scale dispersal. Empirical evidence strongly suggest that such everyday movements to a large extent are governed by predator avoidance and prey tracking (Hassell, 1971; Bernstein, 1984; Forrester, 1994; Kratz, 1996; Maeda et al., 1998; Zemek and Nachman, 1998; Diehl et al., 2000; French and Travis, 2001; Roll et al., 2004; Nachappa et al., 2006; Hauzy et al., 2007; Jenner and Roitberg, 2008; Ohara and Takabayashi, 2012; Simonis, 2013). Such processes are not random and do not give rise to random distributions, why the mechanistic underpinnings of classical functional responses are not satisfactory.

In paper II, we therefore relax the classical assumptions, by allowing individuals to relocate dependent on the number of heterospecific individuals in their local environment. We then investigate the emergent functional response and its influence on demographic stability. We restrict ourselves, however, to consider a process were handling time can be assumed negligible.

If adopting empirical estimates of individual movement-patterns, we show that the resulting functional response becomes dependent on both prey and predator densities illustrating an important interplay between the behaviors at the individual level of the two species. Although mechanistically different, this space-race functional response is related to the DeAngelis-Beddington response (Beddington, 1975; DeAngelis et al., 1975).

To understand the influence of the space-race functional response on demographic stability, one must consider the interplay between the two species behaviors. While the prey behavior,

being responsible for the predator dependence in the functional response, contributes with negative density-dependence in population-growth and therefore a stabilising influence, the predator behavior contributes in the prey dimension with a positive density-dependence and a destabilising influence. It becomes then a matter of understanding which of the two species has the strongest influence, to predict the dynamical resultant. Ultimately, it comes down to the species' *reaction efficiencies* - how well individuals distinguish between densities (and act on it by relocating themselves). The space-race functional response will induce demographical stability if the reaction efficiency of the prey increases with predator density more sharply than what the predator species' reaction efficiency do with decreasing prey density.

As the spatial distribution of individuals is scale dependent, we should expect different functional responses depending on the resolution at which we observe the community. Deriving mechanistic large-scale functional responses appropriately would be a more complicated matter as the average encounter rate would be explained by processes that are hierarchically ordered over scales. One could argue, though, that the mechanistics of functional responses should, indeed, be defined by small-scale events, as the processes necessarily are spatially localized, and that effects on the larger scales should be considered as emergents.

1.8 Empirical covariance dynamics

In paper III we look into the complex patterns in natural predator-prey systems for mechanistic links between local processes and global dynamics. We describe the spatial covariance between predators and prey that is observed in 16 empirical systems, as functions of mean densities. We assume that the local within-patch dynamics can be represented by the Lotka-Volterra model for which the covariance serves as a proxy for the spatial distribution of individuals. We then investigate whether the density dependencies in the covariance have stabilizing or destabilizing influences on the global demographical dynamics.

We suggest three categories of density dependencies in the covariance, each of which emerges from different types of local processes. (1) Direct density-dependence in the covariance is produced by local behavioral interactions such as density-dependent movements (Sjödín et al., 2013), (2) lagged density-dependence in the covariance is produced by limited movements (Keeling et al., 2002), and (3) a density-independent covariance arise when the processes underpinning the covariance are density-independent, for example, habitat choice dependent on population-external properties.

We found that 12 out of the 16 analysed systems were governed by covariances with lagged and/or direct density-dependence, of which lagged-density dependence were more prevalent.

I would like to elaborate on three aspects of this result. First, the dynamics of densities and spatial structure showed to be in large extent entangled. Therefore, and in such case, the spatial structure of, and the number of individuals in, populations should not be viewed as independent entities that can be decoupled. If one is perturbed the other is too. This phenomenon likely becomes important in the perspective of disturbances to physical environments as well as to population size directly. Second, lagged density-dependence were more prevalent than direct density-dependence. As density-dependent movements tend to be common on small scales (see section 1.5), the prevalence of lagged density-dependence could potentially be explained by the relatively large scales at which the data was sampled. Third, there is evidently an interplay between local processes and global dynamics. As the pattern we find implies that we should expect both lagged and direct density-dependencies, which can induce different global-scale effects (Keeling et al., 2002; Sjödin et al., 2013), it becomes important to understand under what conditions and at what scales respective process dominates. If both categories of density-dependence occur in one population, and pronounced at different scales, it follows that it is of significance to consider at what spatial resolution a population should be observed, as the prediction of the behavior of the population then is scale-dependent.

Furthermore, we found that the net effect of the observed density dependencies was destabilising. This result is at odds with the general view, that consumer-resource dynamics are stabilised by spatial heterogeneity, which is supported by experiments (Huffaker, 1958; Janssen et al., 1997; Holyoak, 2000; Bonsall et al., 2005; Cooper et al., 2012) and a large number of theoretical studies. The discrepancy is not easily clarified. For instance, most experimental studies have not evaluated how the stability that correlates with spatial structure relates to density dependencies induced by processes. Also, a general difficulty in empirical studies, including ours, is that all driving variables in natural systems are rarely at hand.

The question whether space stabilises population dynamics is complex. A general finding in theoretical studies is that spatial interactions either stabilise or destabilise population dynamics depending on parameter values (Reeve, 1988; Rohani and Ruxton, 1999; Keeling et al., 2002; Bergström et al., 2006; Sjödin et al., 2013; Wodarz et al., 2013). This calls for empirical answers. As we have seen, it becomes a matter of understanding the nature of a number of specific spatial processes which may act on different scales and have opposing global effects. It becomes therefor also a matter of scale, as the answer we receive by observing populations is dependent on the resolution at which the system is observed. However, this first systematic empirical study on how density dependencies in the covariance between resource and consumer affects global dynamics, provides a preliminary answer to this question.

1.9 Group-structured cooperative communities

To broaden the scope of the thesis outside the field of predator-prey dynamics, I have considered the consequences of individual behaviors to the emergence of cooperation in populations. This subject is covered in paper IV, where we ask the question: Can inter-group migration induce the emergence of stable cooperative communities? In contrast to the other studies in this thesis, I here take into account also evolutionary processes.

The Public Goods Game (PGG) is a game-theoretical concept and the multi-player counterpart to the well studied dyadic Prisoner's Dilemma. It is a formalisation of the Tragedy of the Commons ([Hardin, 1968](#)), conceptualising the problem where a common good is independently depleted by individuals acting selfishly, despite their recognition that depletion will inevitably harm the group as whole. This is, indeed, still a contemporary subject.

In the PGG, individuals in a group can choose to either cooperate or defect. Cooperators act altruistic by paying a costly investment to sustain a resource which is equally shared among all individuals in the group. Defectors act only in self-interest by exploiting the resource that has been made available by cooperating individuals ([Sigmund, 2010](#)).

Cooperation can be observed at most levels of biological and social organisation. A common observation is that not all individuals in a population cooperate, there is instead a mix of cooperation and defection. However, basic theoretical single-group PGG models predict that all group members inevitably choose to defect. Despite the fact that the group as a whole would benefit from the synergy arising if all individuals cooperate, the most profitable instantaneous choice for the individual is always to free ride.

The ubiquity of cooperation among non-relatives is puzzling as it seems to contradict the principles of Darwinian evolution. It is therefore of great interest to understand which mechanisms are at work to actually allow the emergence of cooperation. Regulating mechanisms such as reciprocity ([Axelrod and Hamilton, 1981](#)), punishment ([Gintis, 2000](#)) and reward ([Milinski et al., 2002](#)), work to maintain cooperation on populations. These kinds of mechanisms, however, are effective only in when individuals have a memory of previous interactions and can identify defectors and cooperators. Under more neutral and anonymous circumstances, a passive mechanism of voluntary participation facilitate cooperation ([Hauert et al., 2002](#)). In such Voluntary Public Goods Game, individuals in a population are allowed, after each round of a game, to choose whether to join the next public goods game as cooperators or a defectors, or to stand by as loners - receiving a small and fixed payoff. The coexistence of the three strategies is not stable but display a "Red Queen type of evolution" - the fractions of cooperators, defectors, and loners, oscillate indefinitely as the individuals constantly needs to adjust their strategies. In the long run, ironically, individuals payoffs average out to equal the loner's payoff.

While the majority of the theoretical games studied assume dyadic interactions, the Public

Goods Game assume that n individuals in a group interact ($n = 2$ gives the Prisoner's Dilemma). A group, in contrast to a pair, can vary infinitely in size and composition, and the properties of groups (Sasaki et al., 2007; Cornforth et al., 2012), and the group structure in populations (Tarnita et al., 2009; van Veelen et al., 2010; Garcia and De Monte, 2013), have significant effects on the degree of cooperation in the system. The underlying group-formation processes governed by the behaviors of individuals, and the interplay between the evolution of these behaviors and the group-structure is not yet understood.

In paper IV, we derive an individual-based stochastic group formation process, where the behaviors of individuals, their evolution, and hence the feedbacks between behavior and group structure, can be studied explicitly in order to learn how cooperation develops in such system. We show that, when individuals evolve an ability to sense their profits in groups, and use this information to decide whether to remain in the current group, or to disengage in order to either join a different group or to become solitary (receiving a small fixed solitary payoff), profitable cooperative communities of coexisting cooperators and defectors spontaneously (without regulating mechanisms) emerge from initial non-cooperative populations. The community is stable and the average payoff of individuals becomes several times higher than the solitary payoff, suggesting that the simplistic mechanism of disengagement allows an evolutionary trajectory that does not obey a Red Queen mechanism.

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1.11 Author contributions

Paper I: The study was initiated by Göran Englund and Åke Brännström. The modelling framework was developed by Henrik Sjödin and Åke Brännström. Henrik Sjödin performed all analysis and wrote the majority of the text. Göran Englund wrote the introduction and reviewed all text. Åke Brännström reviewed all text and mathematical derivations, and counselled in mathematical derivation. Mårten Söderquist and Henrik Sjödin developed and compiled the C++ program used for numerical analysis of master equations.

Paper II: Henrik Sjödin och Göran Englund conceived the study. Henrik Sjödin performed all analysis and wrote the majority of the text. Göran Englund and Åke Brännström wrote part of the text and reviewed all text. Åke Brännström reviewed mathematical derivations.

Paper III: Göran Englund and Henrik Sjödin conceived the study. Göran Englund och Henrik Sjödin performed statistical analysis with advice from Jun Yu. Michael Bonsall, Lorenzo Cianelli, Kenneth Frank, Mikko Heino, Arne Janssen, Kjell Leonardsson, Jaap van der Meer and Gösta Nachman contributed with experimental and empirical data.

Paper IV: Henrik Sjödin, Åke Brännström, Rupert Mazzucco and Ulf Dieckmann conceived the study and developed the modelling framework. Henrik Sjödin performed all analysis and wrote the text. Åke Brännström, Ulf Dieckmann and Rupert Mazzucco reviewed the text and mathematical derivations.

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