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DEPARTMENT OF MATHEMATICS

Ph.D.THESIS

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of
nonlinear dynamical systems

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Approximate aggregation of nonlinear dynamical systems

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CERTIFICA

Que el Consejo de Departamento del Departamento de Matemáticas, en su sesión del 23 de Mayo de 2011, consideró que el presente Trabajo de Investigación, titulado "**Aproximate aggregation of nonlinear dynamical systems**", presentado por **D. Marcos Marvá Ruiz**, reúne los méritos suficientes para que su autor pueda optar al grado de Doctor, y pueda ser defendido ante el tribunal correspondiente que ha de juzgarlo.

Y para que así conste se firma el presente certificado en Alcalá de Henares a 26 de Mayo de 2011.

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D. Rafael Bravo de la Parra, Catedrático de Universidad del Departamento de Matemáticas de la Universidad de Alcalá, como Director de la Tesis realizada por el Doctorando D. Marcos Marvá Ruiz,

CERTIFICA

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Director de la Tesis

Fdo.- Rafael Bravo de la Parra

UNIVERSIDAD DE ALCALÁ, PATRIMONIO DE LA HUMANIDAD

A Eva, por supuesto

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Resumen

Esta tesis se enmarca dentro del campo de la biología matemática. Los resultados matemáticos obtenidos extienden resultados previos en relación a la agregación aproximada de sistemas con dos escalas de tiempo.

En la Naturaleza, muchos fenómenos son el resultado de la concurrencia de distintos procesos que pueden desarrollarse, o no, en escalas de tiempo similares. En esta tesis consideramos sistemas que combinan dos procesos que evolucionan en escalas de tiempo diferentes, a los que llamaremos proceso rápido y proceso lento. Estos sistemas proporcionan modelos de la realidad muy detallados pero, en general, mucho más complicados de estudiar que aquellos modelos que incluyen un único proceso. Bajo ciertas condiciones es posible aprovechar la diferencia de escalas de tiempo para construir un sistema (llamado agregado) de menor dimensión que el sistema original. Las técnicas de agregación aproximada establecen bajo qué condiciones tiene sentido construir el sistema agregado y, en ese caso, qué información asintótica de la dinámica del sistema original es posible obtener a través del estudio del sistema agregado.

El objetivo de esta tesis es extender las técnicas de agregación aproximada disponibles para sistemas no lineales con dos escalas de tiempo, tanto discretos como de ecuaciones diferenciales ordinarias no autónomas. Además, aplicamos estos resultados al estudio de modelos poblacionales con dos escales de tiempo. Supondremos, sin pérdida de generalidad, que el vector de variables de estado X representa los individuos de una población estructurada.

El capítulo 1 trata los sistemas discretos no lineales con dos escalas de tiempo. Los resultados más generales disponibles para la agregación aproximada de este tipo de sistemas se verifican bajo condiciones que, *en la práctica*, son difíciles de comprobar, lo que limita su aplicabilidad. Hasta donde sabemos, en el estudio de modelos concretos, el proceso lento puede ser representado por una función general de clase $\mathcal{C}^1$, mientras que el proceso rápido es descrito por una matriz (constante) estocástica regular. En nuestros resultados presentamos clases de funciones, más generales que las representadas por matrices estocásticas regulares, adecuadas para describir el proceso rápido y que, en particular, pueden incluir términos no lineales.

En la sección 1.2 suponemos que el proceso rápido preserva el número total de individuos $y = \|X\|_1$ y que está representado por una matriz estocástica regular tal que sus entradas son función de clase $\mathcal{C}^1$ de la variable y que, tal y como está definida, es función de las variables de estado. Se demuestra entonces que

el correspondiente sistema con dos escalas de tiempo es susceptible de ser estudiado con las técnicas de agregación antes mencionadas. Esta hipótesis significa que la evolución de la población bajo la acción del proceso rápido depende del tamaño total de la población en ese momento. Utilizamos estos resultados para estudiar distintos modelos poblacionales que combinan un proceso demográfico y otro migratorio que discurren conforme a escalas de tiempo diferentes. Dichos modelos son analizados intercambiando el papel del proceso rápido y del lento. De entre los resultados obtenidos a partir del estudio del sistema agregado, cabe destacar nuevas interpretaciones de modelos poblacionales clásicos o situaciones en las que se produce el efecto Allé.

En la sección 1.3 consideramos sistemas en los que las variables de estado están parcialmente acopladas bajo la acción de la dinámica rápida. Dicho de otro modo; bajo la acción del proceso rápido, la evolución de una parte de la población depende del estado de la otra parte de la población. Esta idea es plasmada como sigue. Supongamos que la población está dividida en dos grupos. La evolución de los individuos de cada grupo está descrita por una matriz estocástica regular positiva, de modo que las entradas de la matriz que controla el segundo grupo de variables son función (de clase $\mathcal{C}^2$) del primer grupo de varibles. Se demuestra que el correspondiente sistema con dos escalas de tiempo verifica las hipótesis necesarias para poder ser analizado con las técnicas de agregación aproximada. Aplicamos estos resultados a una comunidad con hospedadores y parasitoides en un hábitat fragmentado. Consideramos que los desplazamientos de individuos entre las distintas regiones suceden con mayor frecuencia que las interacciones entre hospedadores y parasitoides a nivel local. Suponemos, además, que los hospedadores se mueven de forma aleatoria, mientras que los parasitoides tienen preferencia por aquellas zonas con mayor densidad de hospedadores. Usando las técnicas de agregación aproximada se demuestra que el sistema completo puede exhibir equilibrios asintóticamente estables. Por el contrario, *en ausencia de desplazamientos*, tales equilibrios no existen.

En el capítulo 2 se estudia la agregación aproximada de sistemas no autónomos de ecuaciones diferenciales ordinarias con dos escalas de tiempo. La herramienta fundamental es un teorema debido a F.C. Hoppensteadt y relativo a perturbaciones singulares de sistemas con dos escalas de tiempo en intervalos no acotados. Este teorema establece condiciones que permiten estudiar ciertas propiedades dinámicas de sistemas no autónomos con dos escalas de tiempo a partir de dos problemas auxiliares más sencillos que el original. Este teorema es muy general pero, como contrapartida, requiere de una serie de hipótesis restrictivas y complicadas de verificar. Las hipótesis se refieren a la regularidad de las funciones involucradas en el sistema y a la estabilidad de las soluciones de los sistemas auxiliares.

A grandes rasgos, probamos que las condiciones de regularidad se cumplen tanto para sistemas periódicos (sección 2.2) como para sistemas asintóticamente autónomos (sección 2.3). Y, lo que es más importante, demostramos que en esos casos las condiciones sobre la estabilidad de las soluciones de los sistemas auxiliares pueden ser enunciadas en términos de ciertos sistemas variacionales. Esto simplifica enormemente el estudio del sistema completo a través de dichos sistemas auxiliares. Estos resultados son aplicados a distintos modelos poblacionales.

Consideremos sistemas periódicos que describen poblaciones espacialmente distribuidas en un hábitat heterogéneo. Supongamos que los desplazamientos de individuos entre las distintas zonas que componen el hábitat son más rápidos que las interacciones entre individuos en cada una de esas zonas. En una primera aplicación estudiamos un sistema depredador-presa de tipo Lotka-Volterra con refugio para las presas e interferencia entre los predadores. Rasgo este último que resulta especialmente relevante para adecuar modelos a conjuntos de datos reales. Obtenemos condiciones que garantizan la coexistencia o la exclusión de los depredadores en térmios de ciertos parámetros "vitales" derivados del estudio del modelo agregado. En una segunda aplicación consideramos una población afectada por una epidemia con múltiples cepas. A partir del sistema agregado obtenemos números reproductivos y números reproductivos de invasión para el sistema no autónomo espacialmente distribuido. Dichas cantidades son coherentes con la definición habitual para modelos no espaciales. Al comparar esos números reproductivos con los obtenidos en el caso no espacialmente distribuido, se pone de manifiesto que determinadas tasas de desplazamiento en la escala rápida implican que la epidemia es erradicada (resp. persistente) en situaciones en las que, *en ausencia de desplazamientos*, el modelo predice lo contrario.

Finalmente, estudiamos un modelo eco-epidemiológico asintóticamente autónomo. El proceso lento corresponde a un modelo depredador presa de tipo Lotka-Volterra. Los depredadores están afectados por una epidemia que sigue la ley de transmisión dependiente de la frecuencia. Aunque la epidemia no es mortal de necesidad, a largo plazo aumenta la mortalidad de los depredadores que la han padecido. Se demuestra que el tamaño de la población de depredadores (resp. presas) es mayor (resp. menor) cuando la epidemia es erradicada que cuando se vuelve endémica. En este último caso, los tamaños poblacionales dependen de los valores de los parámetros que describen el proceso epidemiológico. Por tanto, la introducción de una epidemia en este tipo de comunidades se postula como un mecanismo para controlar los tamaños poblacionales.

Abstract

This thesis must be placed somewhere in mathematical biology. We deal with two time scale systems and mathematical results achieved herein concern extending previous results in approximate aggregation methods.

In Nature, many phenomenon are the result of the concurrence of several processes which may evolve, or not, within similar time scales. Considering systems coupling two processes evolving at different time scales yields more detailed but also more complicated models than those models including a single process. Under certain conditions, taking advantage of the difference between these time scales allow us to derive an aggregated (less dimensional) system. Approximate aggregation techniques not only describe how to perform such a reduction, but also which dynamical information about the original system can be retrieved from the study of the aggregated system.

The main objective of this thesis is extend previous results in the approximate aggregation of nonlinear discrete dynamical systems and nonautonomous ordinary differential equation systems. These results are applied to de study of different two time scales population models. We assume, without lost of generality, that the state variables vector represents an structured population.

In chapter 1 we deal with two time scale nonlinear discrete systems. The most general results in approximate aggregation for this kind of systems hold under general hypothesis which are, *in practice*, difficult to be checked. To the best of our knowledge, applications consider general $\mathcal{C}^1$ functions representing the slow process while regular (constant) stochastic matrices are used to describe the fast process. Our results enhance the class of suitable functions for describing the fast process, in particular, allowing nonlinear terms.

In section 1.2 we assume that fast dynamics is conservative of the total population size $y = \|X\|_1$. We consider a regular stochastic matrix whose entries are $\mathcal{C}^1$ function of y (which depends on the state variables) standing for the fast process. Then, we show that the corresponding two time scales system is susceptible of being approximately aggregated. This assumption means that the behavior of the population at the fast time scale depends on the current total population size. We apply this result to the study of different population models coupling demographic and migratory processes which take place at different time scales. An analysis of these models, exchanging the role of slow and fast dynamics, completes the section. The reduction process gives rise to new interpretations of well known discrete models, including some Allee effect scenarios.

In section 1.3 we let the state variables to be partially coupled at the fast time scale. Namely, the evolution within the fast time scale of a group of state variables depends on the current state of the rest of the state variables. The idea is conveyed as follows. Let us group the state variables in two groups. The evolution of each group at the fast time scale is driven by a regular stochastic matrix, such that the entries of the matrix governing the evolution of the second group of variables are $\mathcal{C}^2$ function of the variables of the first block. We show that the corresponding two time scales system is also susceptible of being approximately aggregated. We apply this settings to a host-parasitoid community inhabiting a chain of patches. Movements between patches are considered to be faster than host-parasitoid interactions. Parasitoid movements depend on host densities at each patch in such a way that parasitoids avoid those patches with low host densities. We found that the complete model can exhibit asymptotically stable equilibrium points while *in absence of migrations* the contrary was expected.

In chapter 2 we deal with two time scales nonautonomous ordinary differential equation systems. Our results are based on a theorem due to F.C. Hoppensteadt concerning singular perturbations of two time scales systems on the infinite interval. This theorem states conditions allowing the study of certain dynamical properties of nonautonomous two time scale systems analyzing auxiliary systems which are simpler that the original system. This theorem is a general one. As a counterpart, it holds under restrictive and difficult to check hypotheses. These requirements are regularity conditions concerning those functions involved in the system and stability conditions for the solutions of the auxiliary systems.

Our results show, roughly, that these regularity conditions hold when considering periodic systems (section 2.2) or asymptotically autonomous systems (section 2.3). Most important, we show that in these cases, the stability conditions can be restated in terms of adequate variational problems, which simplifies drastically the study of the complete system through the auxiliary ones. We apply these results to different population models.

We consider periodic spatially distributed populations in a patchy heterogeneous environment and displacements between patches are assumed to be faster than local interactions. In a first application we analyze a periodic Lotka-Volterra predator-prey type model with refuge for prey and predator interference. The last feature has been proven to be relevant when fitting models to real data. We obtain conditions for coexistence and predator exclusion in terms of certain "vital" parameters derived from the study of the aggregated model. In a second application we consider a spatially distributed periodic multi strain epidemic model.

We are able to define reproduction numbers and invasion reproduction numbers of the spatially distributed nonautonomous model through the aggregated system which are coherent with those defined for non spatially distributed models. Comparing these reproduction numbers with their non spatially distributed counterparts, we showed that adequate fast migration rates entail persistence or eradication of epidemic strains in regions where *in absence of migrations* the contrary was expected.

Finally, we study an asymptotically autonomous eco-epidemiologic model. We consider a Lotka-Volterra predator-prey model as a slow process. This community system is coupled with a SIR epidemic model following the frequency-dependent transmission law affecting predators. We show that predator (prey) population size is larger (smaller) in the free disease state than in the endemic disease scenario. In this case, population sizes depends on epidemic parameter values. Then, epidemics are a suitable mechanism for controlling predator and prey community population size.

Contents

Notation.

$\mathbb{N}$	The set of natural numbers.
$\mathbb{R}$	The set of real numbers.
$\mathbb{R}^n$	The set of real vectors with n entries.
$\mathbb{R}_+^N$	The non-negative cone $\left\{(x_1, \cdots, x_N) \in \mathbb{R}^N;\, x_i \geq 0,\, \forall i\right\}$.
$\mathbf{I}$	Identity matrix of appropriate dimension.
$\mathbf{I}_n$	Identity matrix of dimension n.
$\sigma(A)$	spectrum of matrix A.
$\rho(A)$	spectral radius of matrix A.
$\mathcal{C}^k(\mathcal{X}_1;\, \mathcal{X}_2)$	Set of functions mapping $\mathcal{X}_1$ in $\mathcal{X}_2$ with continuous k-fold partial derivatives.
$\Vert \cdot \Vert$	Norm of the object between bars.
$\mathcal{M}_{n\times k}(A)$	Set of matrices with n rows and k columns and entries belonging to A.
$\mathcal{M}_n(A)$	Set of square matrices of dimension n and entries belonging to A.
diag$(\mathcal{B}_1, ..., \mathcal{B}_q)$	block diagonal matrix being $\mathcal{B}_1, \cdots, \mathcal{B}_q$ the blocks.

Introduction.

This thesis must be placed somewhere in mathematical biology. We deal with two time scale systems and mathematical results achieved herein concern extending previous results in approximate aggregation methods.

In applied disciplines there is a continuous feedback between theoretical and applied results. As it happens with problems coming from Physics, many times the study of concrete biological problems motivates developing general mathematical results. Conversely, abstract mathematical theories specialize in easy-to-use tools accessible for non mathematician applied scientists remaining, nevertheless, valid for very general classes of systems. In applied mathematics applications can be as important as the mathematical tools supporting them.

We deal with systems of difference equation and systems of nonautonomous ordinary differential equation. In both cases we consider two time scales systems. Even if these systems are of different nature, considering time scales confers them common characteristics. In the sequel, we provide with a biological framework for the thesis and its translation to mathematical language. A summary of approximate aggregation philosophy and an schema of the organization of the thesis complete this introduction.

Hierarchy, time scales and approximate aggregation in ecology.

In ecology, it is usual to consider different organization levels: from cells up to ecosystems, passing through tissues, organs, individuals, populations or communities. This consideration provides scientists with a hierarchy to classify natural processes according with. Entities belonging to each organization level interact among them. In addition, there are vertical interactions as well, meaning that these organization levels are not sealed. Whatever happen in one of them has an effect on other levels.

Hierarchy theory provides a conceptual framework of how processes and components of an ecological system interrelate and how they can be ordered [59] and [91]. Once we have got knowledge on each single process, scientists focus on how these processes interact. Each organization level consists of interacting entities with their own dynamics evolving within its own characteristic time scale. Those entities of a given level with strong or fast interactions can be grouped giving rise to the entities at next level. Mathematically, the process of up-scaling consists in deriving global variables and their dynamics from the lower level based on the existence of different time scales. In other words, from a mathematical point of view, a model including processes belonging to different organization levels can be seen as a system with different time scales.

In addition, getting knowledge of each single process related with each level is, without doubt, of great interest. Usually, a first attempt for doing it consist in considering non structured models, which are the simplest ones. These models consider homogeneous populations and are constricted to studying the evolution of the total population size. In many cases non structured models do not describe accurately the dynamics of the population because do not consider heterogeneity. Namely, individuals are assumed to be identical, which is far from realistic [23]. Thus, improving the model requires structuring the population into different classes according to the characteristics of the study.

Summing up, the aim of being as realistic as possible makes considering structured populations and time scales which yields more detailed but complicated models. However, sometimes we can take advantage of the existence of two different time scales to reduce the dimension of the corresponding system. Under certain hypothesis, assuming that the dynamics of the fast process attains certain asymptotically stable state, an aggregated (less dimensional) system can be built. The reduction process is included in the so-called *approximate aggregation of variables* methods [6] which consist of describing the dynamics of a complex system involving many coupled variables through the dynamics of a reduced system, the *aggregated system*, formulated in terms of a few *global variables*. Aggregation methods study the relationship between a large class of two-time scales complex systems and their corresponding aggregated or reduced counterparts. The aim of aggregation methods is twofold. On the one hand they construct the reduced systems that summarize the dynamics of the complex ones, thus simplifying their analytical study. On the other hand, these techniques look at the relationship in the opposite sense, the complex system serves as explanation of the simple form of the aggregated one.

A natural question arises then: how coherent both the initial and the reduced system are? When the behavior of the original and the aggregated dynamics is the same, it is said that the system is *perfectly aggregated* [54]. Perfect aggregation holds under very restrictive conditions. Weaker hypotheses yield different (but approximated) dynamics on the reduced system [55], [5]. Then, approximate aggregation techniques study which dynamical information of the general system can be recovered from the study of the reduced system. In other words, aggregation techniques state conditions assuring that certain asymptotic behaviors of the aggregated system entail that of the original system.

Approximate aggregation is a label collecting different type of techniques sharing the ideas previously stated. In fact, aggregation techniques deal with both discrete and continuous dynamical systems. Moreover, regarding continuous systems, aggregation techniques specializes for autonomous ordinary differential equations, delayed differential equations, partial differential equations [6] and, as we will see, for nonautonomous ordinary differential equations.

Time scales and its applications.

Far from being a trick, considering models with time scales cames across from simple observation of Nature. This idea is related with classifying processes in different organization levels and, of course, it is not exclusive of Biology. For instance, there are recently published results in business [106], automatic control [97], [63], manufacturing flow control models [33], hydrology [4], marine geology [26], agronomic engineering [105], signal processing [37], [14], electrical engineering [57], crystallography [80], ferromagnetism [47], astronomy [94], physics of plasma [53] and small-world network physics [75].

In population dynamics non-structured models are the simplest ones. These models consider homogeneous populations and are constricted to studying the evolution of the total population size. In particular, individuals are considered to be identical. In many cases this assumption leads to so simple models which do not describe accurately the dynamics of the population.

For instance, survival or reproductive skills are individual characteristics, and may depend on age, size, sex,... [23]. Thus, populations can be structured into different classes depending on the characteristic of study so that individuals belong to a given class. However, even individuals belonging to the same class may evolve in a different way depending on the environmental conditions of the habitat they are living in. Therefore, spatial distribution is another feature to be taken into account when describing a population.

The underlying idea is that of considering structured populations in order to retain its heterogeneity; we may arrange the corresponding classes attending to individual features or spatial distribution. Structured populations within the context of hierarchy theory and its organization levels constitutes a natural framework for considering two time scale models. According with Auger *et.al.* [6] a cornerstone concept in approximate aggregation is that of *emergence*. That is, approximate aggregation is not merely a reduction of the dimension of the initial model, but it also provides information about the influence of fast processes at the global level in the long term, which is called emergence (see [11] and [6] for further details on functional emergence and dynamical emergence).

The following paragraphs are aimed to gain an insight on different situations where approximate aggregation has proven to work, rather than providing with an exhaustive list of items. Some of these applications have motivated parts of this thesis:

- **Populations structured by space**. It is reasonable assuming that individuals may evolve different under different environmental conditions. A population can be structured according to its spatial distribution by considering fragmented (patchy) habitats such that those parameters describing the environmental conditions in each patch take different values. For instance, those parameters describing demographic processes (see [73] or, as well, [72] in section 1.3), competition between species (see [71]), predator-prey interactions (see [78], see also [67] in section 2.2), epidemic processes (see [66] in section 2.2) have different values in each patch, which yields heterogeneity. Considering individual displacements between these patches to be faster than local interactions gives rise to two time scales systems.

- **Populations structured by an individual features**. A typical example is that of demographic processes on age structured populations. Individuals are classified according to reproductive skills (non reproductive and reproductive). Considering demography to be faster than migrations yields two time scale systems, as those presented in [86] or [68] in section 1.2. On the other hand, in eco-epidemic models, as those presented in [9] and [35], an epidemic process affecting predators evolves faster than predator-prey interactions. In this case predator population has been structured according to being susceptible, infected or recovered individual in the epidemic process; in section 2.3 we present an eco-epidemic model too.

From another point of view, it is of great interest studying the effect of individual behavior on the whole population. Sometimes it is reasonable assuming that individual actions evolve much faster than collective ones, as the later are, somehow, the sum of the formers. This considerations allow one to build up two time scales systems. As a matter of fact, several works study the effect of individual behavioral plasticity on the whole population by considering hawk-dove tactic (or hawk-dove-bully tactics) as fast dynamics in front of slow demographic processes [83], [8], [24] or [79].

Organization of the thesis.

This thesis deals with the approximate aggregation of some nonlinear two time scales systems and its application in the study of different population models.

The systems treated can be classified into two large categories that are included respectively in chapters 1 and 2. Chapter 1 deals with discrete dynamical systems and chapter 2 is devoted to nonautonomous systems of ordinary differential equations. The methods presented in each of these chapters require quite different approaches, so we are providing specific detailed introductions at the beginning of each of them in contrast with the short and general one done so far.

Both chapters share a common structure. They include in a first section, named introduction, a detailed review of the approximated aggregation methods previously developed for the corresponding type of system, either discrete or ordinary differential equations. This introduction motivates and presents the study undertaken in subsequent sections where we first develop new theoretical results that are further through various applications in relevant population dynamics models encompassing host-parasitoid, predator-prey, epidemiology and eco-epidemiology models with different population structures.

The bibliography and the list of publications complete the thesis.

Chapter 1

Contributions to the approximate aggregation of two time scales discrete dynamical systems.

1.1 Introduction.

Discrete systems are prescribed when the state variables change according to a fixed step in the independent variable (typically, time) instead of varying continuously. Perhaps the most known example is that of bank interest. It is easy to find examples in Nature. For instance, many species reproduce once or twice per year. Other species perform seasonal migrations, and so on.

We consider systems coupling two processes, each of them evolving at a different time scale. A first decision consist in choosing the time unit of the system. As usual, each of the processes is modeled by means of a map applied on the state variables. It is a problem to approximate the effect of one of the maps over a projection interval which is different from its own. As we will see, this consideration yields two different families of systems, both of them susceptible of being approximately aggregated under the appropriate hypotheses.

Concerning discrete systems, perfect aggregation of variables was initially suggested by Leontief in the 50's to John Ching-Han Fei [31] in the framework of input-output problems, in Economy. Later on, Simon and Ando [95] carried on with perfect aggregation, applying those ideas in automatic control theory and economy. In these works, the authors considered models with only one process and thus, it did not make sense distinguishing time scales.

First attempts to approximate aggregating a discrete system dealt with linear models and were done by Sánchez, Bravo de la Parra and Auger. In [19], the authors considered the fast time unit for the time unit of the system, while in [84] the slow time unit was considered. They built up the classes of systems corresponding to each case. Subsequently, they stated the first properties and results concerning the approximate aggregation of two time scales discrete dynamical systems. The following subsections are devoted to a brief oversight of these two modalities.

Before proceeding, let us state a general notation which will be kept all along this chapter. According with the biological framework stated in the introduction we consider, without lost of generality, that state variables stand for a population. Hierarchic organization levels and heterogeneity lead to populations structured into groups and subgroups. In other words, we study the evolution of this population considering two processes directly related to this structure. Thus, population vector state at time n is given by

$$X_n = (\mathbf{x}_n^1, \cdots, \mathbf{x}_n^q), \tag{1.1}$$

where $\mathbf{x}_i = (x_n^{i1} \cdots, x_n^{iN_i})$ defines the population in group $i = 1, \cdots, q$ and x_n^{ij} is the size of subgroup j in group i at time n. Let $N = N_1 + \cdots + N_q$ be the total number of subgroups, so that $X_n \in \Omega_N \subset \mathbb{R}_+^N$ for each $n \geq 0$, where Ω_N is an open, bounded, connected and non-empty subset of $\mathbb{R}_+^N$.

Regarding the two processes involved in two time scales models, general functions $F, S \in \mathcal{C}^1(\Omega_N; \Omega_N)$ stand for the fast and the slow dynamics. We will use capital calligraphic letters instead of regular ones whenever the corresponding functions specialize in a dot-matrix form, that is, $F(X) := \mathcal{F}X$.

Systems built upon the fast time unit.

The construction and approximate aggregation of two time scales linear discrete systems based on the fast time scale was carried on in [19], [21] and [84] while a particular nonlinear case was studied in [20].

In the sequel, we describe the construction of such kind of systems and summarize the main results achieved.

Linear case. We follow, essentially, [84], where fast and slow dynamics were assumed to be linear.

Namely, the slow dynamics, for a certain fixed projection interval, was represented by a nonnegative projection matrix $\mathcal{S}$. Matrix $\mathcal{S}$ was divided into blocks $\mathcal{S}_{ij} \in \mathcal{M}_{N_i \times N_j}(\mathbb{R})$, with $i, j = 1, \cdots, q$, so that there is a correspondence between matrix blocks and population subgroups

$$\mathcal{S} = \begin{pmatrix} \mathcal{S}_{11} & \cdots & \mathcal{S}_{1q} \\ \cdots & \cdots & \cdots \\ \mathcal{S}_{q1} & \cdots & \mathcal{S}_{qq} \end{pmatrix} \tag{1.2}$$

namely matrix $\mathcal{S}_{ij}$ stands for the transference of individuals of the different subgroups of group j to the different subgroups of group i. The kind of matrices used is known in the population dynamics literature as Leftkovich matrices. The fast dynamics is internal, conservative of the total number of individuals and with an asymptotically stable distribution among the subgroups for every group $i = 1, \cdots, q$. For each group $i = 1, \cdots, q$, the fast dynamics is represented by a nonegative projection matrix $\mathcal{F}_i$ of dimensions $N_i \times N_i$. Thus, matrix

$$\mathcal{F} = \mathsf{diag}(\mathcal{F}_1, \cdots, \mathcal{F}_q) \tag{1.3}$$

stands for the fast dynamics of the whole population.

It is considered as projection interval of the system that associated to matrix $\mathcal{F}$. Therefore, it is needed to approximate the effect of matrix $\mathcal{S}$ over a projection interval much shorter than its own. For that purpose, matrix

$$\mathcal{S}_\varepsilon = \varepsilon \mathcal{S} + (1 - \varepsilon) I_N,$$

it is defined, where ε is a positive number close to zero reflecting the ratio of slow to fast time scale and I_N is the identity matrix. One may see matrix $\mathcal{S}_\varepsilon$ as a matrix which makes $\mathcal{S}$ act in a proportion ε, with ε as small as wanted, and letting variables unchanged in proportion $1 - \varepsilon$. Namely, matrices $\mathcal{S}$ and $\mathcal{S}_\varepsilon$ are related by the following property:

Proposition 1.1.1 *If $\mathcal{S}$ has a dominant eigenvalue λ with an associated eigenvector $\mathbf{v}$, then $\varepsilon\lambda + (1 - \varepsilon)$ is the strictly dominant eigenvalue of $\mathcal{S}_\varepsilon$ and $\mathbf{v}$ is also its associated eigenvector.*

From a mathematical point of view, proposition 1.1.1 reflects the fact that the asymptotic dynamics of $\mathcal{S}$ has been approximately translated to the characteristic time scale of $\mathcal{F}$. In fact, proposition 1.1.1 implies that the dynamics associated to S and S_ε have the same asymptotically stable stage distribution. Besides, S_ε has a much greater growth rate than S because $\varepsilon\lambda + (1-\varepsilon) = 1 + \varepsilon(\lambda - 1)$ is closer to 1 than λ. With this idea in mind, the fast and the slow processes are combined to build up the *complete system* as follows

$$X^{\varepsilon}_{n+1} = \mathcal{S}_\varepsilon \mathcal{F} X^{\varepsilon}_n = \mathcal{F} X^{\varepsilon}_n + \varepsilon\left(\mathcal{S} - I_N\right)\mathcal{F} X^{\varepsilon}_n \tag{1.4}$$

which is an ε-perturbation of system

$$X_{n+1} = \mathcal{F} X_n. \tag{1.5}$$

In order to reduce the system some assumptions on the fast dynamics must be maken. When considering two time scales systems, in order to perform the approximate aggregation, it is assumed that the fast dynamics acts instantaneously in front of the slower process attaining certain stable equilibrium state. This idea is conveyed assuming that the fast dynamics is conservative of certain variables called *global* or *aggregated variables* for the state variables and with an asymptotically stable distribution. In former works, global variables were known as *macro-variables* (this terminology comes from Economics).

In the linear case presented here, these assumptions on the fast dynamics are met if block matrices $\mathcal{F}_i$, $i = 1, \cdots, q$ are primitive with dominant eigenvector $\lambda = 1$ and left and right eigenvectors $\mathbf{u}_i$ and $\mathbf{v}_i$, respectively, are chosen so that $\mathbf{u}_i > 0$, $\mathbf{v}_i > 0$ and $\mathbf{u}_i^T \mathbf{v}_i = 1$. Then, we have that

$$\lim_{k\to\infty} \mathcal{F}_i^k = \mathbf{v}_i \mathbf{u}_i^T = \bar{\mathcal{F}}_i. \tag{1.6}$$

In particular, this is met if $\mathcal{F}_i$ is a regular stochastic matrix for every $i = 1, \cdots, q$. In this case $\mathbf{u}_i$ can be taken to be a vector with all its entries equal to 1 and then $\mathbf{v}_i$ is the stationary probability distribution associated to $\mathcal{F}_i$. Assuming that fast dynamics has already attained its asymptotic state allows one to approximate $\mathcal{F}$ in system (1.4) by

$$\bar{\mathcal{F}} := \mathsf{diag}(\bar{\mathcal{F}}_1, \cdots, \bar{\mathcal{F}}_q).$$

This yields the *auxiliary system*

$$X^{\varepsilon}_{n+1} = \mathcal{S}_\varepsilon \bar{\mathcal{F}} X^{\varepsilon}_n, \tag{1.7}$$

which is a sort of bridge between the general and the aggregated system. From equation (1.6) it is straightforward that

$$\bar{\mathcal{F}} = \mathcal{E}\mathcal{G} \tag{1.8}$$

where $\mathcal{G} = \mathrm{diag}(\mathbf{u}_1^T, \cdots, \mathbf{u}_q^T)$ and $\mathcal{E} = \mathrm{diag}(\mathbf{v}_1, \cdots, \mathbf{v}_q)$. Defining the *global variables*

$$Y_n^\varepsilon = \mathcal{G} X_n^\varepsilon$$

we get the *aggregated system* for these global variables, which reads as follows

$$Y_{n+1}^\varepsilon = \mathcal{G}\, \mathcal{S}_\varepsilon\, \mathcal{E} Y_n^\varepsilon = \bar{\mathcal{S}}_\varepsilon\, Y_n^\varepsilon \tag{1.9}$$

where $\bar{\mathcal{S}}_\varepsilon = \varepsilon\, \mathcal{G}\mathcal{S}\mathcal{E} + (1-\varepsilon)I = \varepsilon\, \bar{\mathcal{S}} + (1-\varepsilon)I$. Note that this procedure yields an approximation that allows one to reduce a system with N variables to a new system with q variables. In most practical applications, q will be much smaller than N.

Relationship between systems (1.4), (1.7) and (1.9) are proved in [19] assuming that $\bar{\mathcal{S}}$ is primitive.

Proposition 1.1.2 *Under the previous conditions, let $\lambda > 0$ be the strictly dominant eigenvalue of $\bar{\mathcal{S}}$, and $\mathbf{w}$ and $\mathbf{v}$ its associated left and right eigenvectors. Then, it follows that*

1. *the strictly dominant eigenvalue of matrix $\bar{\mathcal{S}}_\varepsilon$ is $\varepsilon\lambda + (1-\varepsilon)$ and $\mathbf{w}$ and $\mathbf{v}$ are its associated left and right eigenvectors.*
2. *the strictly dominant eigenvalue of matrix $\mathcal{S}_\varepsilon \bar{\mathcal{F}}$ is also $\varepsilon\lambda + (1-\varepsilon)$, and $\mathcal{G}^T\mathbf{w}$ and $\mathcal{E}\mathbf{v}$ are its associated left and right eigenvectors.*
3. *the strictly dominant eigenvalue of matrix $\mathcal{S}_\varepsilon \mathcal{F}$ is of the form*

   $$\varepsilon\lambda + (1-\varepsilon) + \mathcal{O}(\varepsilon^2)$$

   and the corresponding left and right eigenvectors are of the form

   $$\mathcal{G}^T\mathbf{w} + \mathcal{O}(\varepsilon^2) \qquad \text{and} \qquad \mathcal{E}\mathbf{v} + \mathcal{O}(\varepsilon^2),$$

   respectively.

So, the elements describing the asymptotic behavior of the complete system (1.4) can be approximated by the corresponding elements if the aggregated system (1.9)

In [20] and [21] a system with linear fast dynamics and a general nonlinear slow dynamics is reduced by means of a center manifold theorem.

1.1.1 Systems build upon the slow time unit.

It is not always possible to choose as time unit the fast one. It may happen that during a fast time unit, the action of the slow process is not describable. Nevertheless, the converse holds. Whenever the system is expressed in the slow time unit the existence of a faster process can be represented by letting it act a number k of times between times n and $n+1$. The larger is k, the more different are the time scales. Let us note $X_{k,n+1}$ the vector of state variables at time $n+1$ considering that the fast process has acted k times between times n and $n+1$.

In the sequel, we will examine results found in the literature concerning the approximate aggregation of linear and nonlinear two time scales systems based upon the slow time unit.

Linear autonomous systems.

The construction of a two time scales linear system performed in [84] and [86] yields system:

$$X_{k,n+1} = \mathcal{S}\,\mathcal{F}^k X_{k,n}; \qquad X_{k,0} = X_0, \tag{1.10}$$

where matrices $\mathcal{S}$ and $\mathcal{F}$ are those in (1.2) and (1.3) respectively, the super-index k stands for the k-fold power of $\mathcal{F}$ and reflects the ratio between time scales. Assuming that fast dynamics has already attained its asymptotic state allows us to approximate $\mathcal{F}^k$ in (1.10) by

$$\bar{\mathcal{F}} := \lim_{k\to\infty} \mathcal{F}^k$$

where $\bar{\mathcal{F}} :=$ diag$(\bar{\mathcal{F}}_1, \cdots, \bar{\mathcal{F}}_q)$ and each $\bar{\mathcal{F}}_i$ is given by (1.6). This yields the corresponding *auxiliary system*

$$X_{n+1} = \mathcal{S}\bar{\mathcal{F}} X_n, \tag{1.11}$$

which plays an equivalent role to system (1.7), being the link between the general system (1.10) and the corresponding aggregated one (to be derived). Moreover, matrix $\bar{\mathcal{F}}$ decomposes as $\bar{\mathcal{F}} = \mathcal{E}\mathcal{G}$, where matrices $\mathcal{E}$ and $\mathcal{G}$ are those in (1.8). Defining the *global variable* as $Y_n = \mathcal{G}X_n$ yields the *aggregated system* for these global variables, which reads as follows

$$Y_{n+1} = \mathcal{G}\,\mathcal{S}\,\mathcal{E} Y_n = \bar{\mathcal{S}} Y_n. \tag{1.12}$$

The following proposition collects the main results achieved in [20]

Proposition 1.1.3 *Let matrices $\mathcal{S}$ and $\mathcal{F} := diag(\mathcal{F}_1, \cdots, \mathcal{F}_q)$ be, respectively, a Leftkovich matrix and a block diagonal matrix with each block being a regular stochastic matrix. Assume that matrix $\bar{\mathcal{S}}$ defined in (1.12) is primitive. Let λ be the strictly dominant eigenvector of $\bar{\mathcal{S}}$ and let $\mathbf{w}$ and $\mathbf{v}$ be left and right eigenvectors associated with λ.*

1. *Consider the auxiliary system (1.11) along with any initial value X_0 and X_n the corresponding solution. It follows that*

$$\lim_{n\to\infty} \frac{X_n}{\lambda^n} = \frac{\langle \mathbf{w}, \mathcal{G}X_0\rangle}{\langle \mathbf{w}, \mathbf{v}\rangle} \frac{1}{\lambda} \mathcal{S}\mathcal{E}\mathbf{v}$$

2. *Matrix $\mathcal{S}\mathcal{F}^k$ has a strictly dominant eigenvalue*

$$\mu_k = \lambda + \frac{\langle \mathcal{G}^T\mathbf{w}, \mathcal{S}(\mathcal{F} - \bar{\mathcal{F}})^k \mathcal{S}\mathcal{E}\mathbf{v}\rangle}{\langle \mathcal{G}^T\mathbf{w}, \mathcal{S}\mathcal{E}\mathbf{v}\rangle} + o(\alpha^{2k}) = \lambda + O(\alpha^k)$$

and associated to μ_k there exist left and right eigenvectors that can be written as follows

$$\mathcal{G}^T\mathbf{w} + O(\alpha^k) \qquad \textit{(positive)}$$

$$\mathcal{S}\mathcal{E}\mathbf{v} + O(\alpha^k) \qquad \textit{(non negative)}$$

3. *Consider the general system (1.10) along with any initial value X_0 and X_n the corresponding solution. It follows that*

$$\lim_{n\to\infty} \frac{X_n}{(\lambda_k)^n} = \frac{\langle \mathbf{w}, \mathcal{G}X_0\rangle}{\langle \mathbf{w}, \mathbf{v}\rangle} \frac{1}{\lambda} \mathcal{S}\mathcal{E}\mathbf{v} + O(\alpha^k)$$

where $\alpha \in (0, 1)$.

With system (1.10) as a departure point, approximate aggregation methods for time discrete autonomous linear systems have been extended to nonautonomous and stochastic linear systems and to nonlinear autonomous systems. The complete system in all these extensions is written using the slow time unit.

Linear nonautonomous systems.

Nonautonomous systems are appropriate to describe populations living in an environment that changes with time. Therefore, both the slow and the fast process are functions of time. We follow [7] in order to describe the corresponding results. Basing the model on the slow time scale, it is possible to extend system (1.10) to the nonautonomous case

$$X_{k,n+1} = \mathcal{S}(n)\,\mathcal{F}^k(n)X_{k,n}; \qquad X_{k,0} = X_0. \tag{1.13}$$

as done in [88]. Authors let matrices $\mathcal{S}(n)$ and $\mathcal{F}(n) = \mathsf{diag}(\mathcal{F}_1(n), \cdots, \mathcal{F}_q(n))$, which stand for the slow and the fast dynamics, respectively, to be function of time n. Moreover, for each n and $i = 1, \cdots, q$ matrix $\mathcal{F}_i^k(n)$ is primitive and 1 is its strictly dominant eigenvalue. This property implies that there exists

$$\bar{\mathcal{F}}_i(n) := \lim_{k\to\infty} \mathcal{F}_i^k(n) = \mathbf{v}_i(n)\mathbf{u}_i(n),$$

where $\mathbf{v}_i(n) > 0$ and $\mathbf{u}_i(n) > 0$ are the right and left eigenvectors associated to 1 verifying that $\mathbf{v}_i^T(n)\mathbf{u}_i(n) = 1$. Defining $\mathcal{G}(n) := \mathsf{diag}(\mathbf{u}_1^T(n), \cdots, \mathbf{u}_q^T(n))$ and $\mathcal{E}(n) := \mathsf{diag}(\mathbf{v}_1(n), \cdots, \mathbf{v}_q(n))$ we get the corresponding auxiliary system

$$X_{n+1} = \mathcal{S}(n)\,\bar{\mathcal{F}}(n)X_n; \qquad X_0 = X^0, \tag{1.14}$$

where $\bar{\mathcal{F}}(n) := \mathcal{E}(n)\mathcal{G}(n)$. Finally, aided by the global variables $Y_n := \mathcal{G}(n)X_n$ the aggregated system is defined through

$$Y_{n+1} = \mathcal{G}(n+1)\mathcal{S}(n)\mathcal{E}(n)Y_n = \bar{\mathcal{S}}(n)Y_n; \qquad Y_0 = Y^0. \tag{1.15}$$

As before, dimension of system (1.15) is q while dimension of system (1.13) is N, with $q < N$. In [88] it was shown that for any finite value of n, the population vector of the original system can be approximated through the population vector of the reduced system by means of

$$X_n = \mathcal{S}(n)\mathcal{E}(n)Y_n + o(\alpha^k), \tag{1.16}$$

where $\alpha \in (0, 1)$

Relationship between the original system (1.13) and the aggregated system (1.15) depends on the pattern of the temporal variations of the fast dynamics matrix. Three different patterns were investigated.

Periodic environments were addressed in [85] by assuming that $\mathcal{S}(n + m) = \mathcal{S}(n)$ and $\mathcal{F}(n+m) = \mathcal{F}(n)$ for certain positive integer m. Letting matrix $\bar{A} := \bar{\mathcal{S}}(m-1)\cdots\bar{\mathcal{S}}(1)\bar{\mathcal{S}}(0)$ to be primitive, the authors achieved similar results to those in the autonomous one. This means that the dominant eigenvalue and the corresponding eigenvector of the complete system can be derived as a perturbation of an expression depending on the dominant eigenvalue of the aggregated system and its associated eigenvector, respectively.

In [85] it was discussed time varying **environments that asymptotically stabilize**, that is, such that

$$\lim_{n\to\infty} \mathcal{S}(n) = \mathcal{S}_*$$

and

$$\lim_{n\to\infty} \mathcal{F}(n) = \mathcal{F}_* = \mathsf{diag}(\mathcal{F}_{1*}, \cdots, \mathcal{F}_{q*}).$$

It was assumed that for all $n \geq 0$ matrices $\bar{\mathcal{S}}(n)$ have no zero columns and that matrix $\bar{\mathcal{S}}_*$ is primitive. The results achieved were similar to those in the autonomous and the periodic cases.

Finally, the case of **environments changing with time in a general fashion** was discussed in [18] and [88]. Obviously, in that case it is not possible to expect that population grows exponentially or that population structure converges to a certain vector. However, given a general system

$$Z(n+1) = A(n)Z(n),$$

under quite general conditions the population structure $Z(n)/\|Z(n)\|$ "forgets its past". This means that under the same sequence of environmental variations, different initial values $Z(0) \neq Z'(0)$ lead to population structures getting more and more similar (even though they do not necessarily converge). That is, it may happen that

$$\lim_{n\to\infty} \left\| \frac{\prod_{j=0}^{n} A(n)Z(0)}{\| \prod_{j=0}^{n} A(n)Z(0)\|} - \frac{\prod_{j=0}^{n} A(n)Z'(0)}{\| \prod_{j=0}^{n} A(n)Z'(0)\|} \right\| = 0$$

but

$$\lim_{n\to\infty} \left\| \prod_{j=0}^{n} A(n)Z(0) - \prod_{j=0}^{n} A(n)Z'(0) \right\| \neq 0$$

This property is known as weak ergodicity. The study of the property of weak ergodicity for the original and for the aggregated system was carried out in [88]. It was shown that under quite general settings, if k is large enough in system (1.13), then very general sufficient conditions for weak ergodicity are satisfied simultaneously for both systems. Such a conditions are related with the positivity of the product of a consecutive number of matrices in the system.

Up to now, we have considered nonautonomous systems where fast dynamics changes at the slow times scale, that is, environmental conditions related with the fast dynamics do not change with the fast time unit, which seems unrealistic. Therefore, in [18] it was treated a model such that fast process varies within each slow time step $[n, n+1)$, by means of

$$X_{k,n+1} = \mathcal{S}(n)\mathcal{F}(k,n)\mathcal{F}(k-1,n)\cdots\mathcal{F}(1,n)\mathcal{F}(0,n)X_{k,n}.$$

Thus, the product $\mathcal{F}(k,n)\mathcal{F}(k-1,n)\cdots\mathcal{F}(1,n)\mathcal{F}(0,n)$ replaces $\mathcal{F}^k(n)$ and describes, for each $n \geq 0$, the evolution of the environmental conditions of the fast dynamics within $[n, n+1)$. The approximate aggregation and the relationship between the general and the aggregated system was performed in [18]. In order to aggregate this system, it is needed that matrices $\mathcal{F}(k,n)$ tend to appropriate matrices when $k \to \infty$ for all $n \geq 0$.

Linear stochastic systems.

The aggregation results obtained for nonautonomous systems were further extended to some linear stochastic systems in [87]. In order to build such a system, it is considered a population living in an habitat that can exhibit l different environmental states, $\{1, \cdots, l\}$. Let X_n be the population vector state and let τ_n be a random variable defining the environmental conditions in the time step $[n-1, n)$. Stochasticity can be introduced in system (1.10) letting the matrix coefficients depend on τ_n, that is

$$X_{k,n+1} = \mathcal{S}(\tau_{n+1})\,\mathcal{F}^k(\tau_{n+1})X_{k,n}; \qquad X_{k,0} = X_0. \tag{1.17}$$

The reduction process can be performed assuming conditions implying that each matrix $\mathcal{F}_i(\sigma)$, for any value of $\sigma \in \{1, \cdots, l\}$, is primitive with strictly dominant eigenvalue equal to 1. As in the nonautonomous case, in [87], it was shown that for any finite value of n, the population vector of the original system can be approximated through the population vector for the reduced system by means of

$$X_{k,n} = \mathcal{S}(\tau_{n+1})\mathcal{E}(\tau_{n+1})Y_{n-1} + o(\delta^k),$$

where $o(\delta^k)$ depends of n and $\delta \in (0,1)$. The previous expression is the counterpart of (1.16). Matrix $\mathcal{E}(\tau_n)$, whose entries depend on the random variable τ_n, is related with the decomposition of $\lim_{k\to\infty} \mathcal{F}^k(\tau_n)$.

In particular, in [89] it was considered the case of a Markovian environmental process. The cornerstone concept in this case is the stochastic growth rate (in the sequel, s.g.r.) which is the equivalent of the dominant eigenvalue in the linear case. Assuming that a) τ_n is an homogeneous Markov chain with a primitive matrix of transition probabilities, b) the set of matrices $\{\bar{\mathcal{S}}(1), \ldots, \bar{\mathcal{S}}(l)\}$ is an ergodic set (see [93]) it can be proven (see [101]) that there exists the aforementioned s.g.r.:

$$a := \lim_{n\to\infty} \frac{\log \|Y_n\|}{n},$$

where the limit holds with probability 1. In [87] it was shown that if matrices $\{\mathcal{S}(1), \cdots, \mathcal{S}(l)\}$ have no zero rows, then for large enough k the set $\{\mathcal{S}(1)\mathcal{F}^k(1), \cdots, \mathcal{S}(l)\mathcal{F}^k(l)\}$ is ergodic. Therefore, the original system (1.17) verifies that there exists an s.g.r.:

$$a_k := \lim_{n\to\infty} \frac{\log \|X_{k,n}\|}{n}.$$

In addition, it is proved that

$$\lim_{k\to\infty} a_k = a.$$

Thus, if k is large enough, the s.g.r. a_k of the original system can be approximated through that of the reduced system.

Nonlinear autonomous systems.

A first attempt to generalize the formulation stated in system (1.10) was done in [20], where the fast dynamics was kept linear while the slow dynamics was nonlinear. Further developments have been done considering nonlinear fast and slow processes. Namely, in [90] was addressed the problem of the approximate aggregation of system

$$X_{k,n+1} = S \circ F^{(k)}(X_{k,n}) \tag{1.18}$$

considering general functions $F,\, S \in \mathcal{C}^1(\Omega_N;\, \Omega_N)$ instead of linear maps. As usual, F and S stand for the fast and the slow dynamics and must fulfill certain hypothesis. Results in [90] are our departure point. Therefore, in what follows, we detail the results achieved there for the approximate aggregation of system (1.18). Two hypothesis are needed. The first one keeps the spirit of condition (1.6) and reads as follows:

Hypothesis 1.1.4 *Let $\Omega_N \subset \mathbb{R}^N$ be a nonempty, bounded, open set. For each initial value $X \in \Omega_N$ the fast dynamics tends to and equilibrium. That is, there exists a mapping $\bar{F} \in \mathcal{C}^1(\Omega_N; \Omega_N)$, such that*

$$\forall X \in \Omega_N \quad , \quad \lim_{k\to\infty} F^{(k)}(X) = \bar{F}(X), \tag{1.19}$$

where the super-index (k) *stands for the k-fold composition of* F*. Moreover, there exist a nonempty, bounded, open set* $\Omega_q \subset \mathbb{R}^q$ *with* $q < N$*, and two mappings*

$$G : \Omega_N \to \Omega_q,\ G \in \mathcal{C}^1(\Omega_N) \qquad E : \Omega_q \to \Omega_N,\ E \in \mathcal{C}^1(\Omega_q)$$

such that $\bar{F}$ *can be expressed as*

$$\bar{F} = E \circ G. \tag{1.20}$$

Limit (1.19) in hypothesis 1.1.4 allows to approximate system (1.18) by means of the *auxiliary system*

$$X_{n+1} = S \circ \bar{F}\left(X_n\right), \tag{1.21}$$

meaning that the fast dynamics has already attained its equilibrium. That is why the sub-index k in the state variables vector has been dropped. Moreover, thanks to decomposition (1.20), the *global variables* can be defined by

$$Y_n := G(X_n). \tag{1.22}$$

The *reduced* or *aggregated* system which approximates system (1.18) is given by

$$Y_{n+1} = G \circ S \circ E\left(Y_n\right). \tag{1.23}$$

We recall that through this procedure we have constructed an approximation allowing study a system with N variables through a system with q variables. The following proposition, whose proof can be found in [90], shows that the dynamics of the auxiliary system (1.21) and the dynamics of the reduced system (1.23) determine each other. Actually, this is an example of perfect aggregation [54].

Proposition 1.1.5 *Let* $X_0 \in \Omega_N$ *and* $Y_0 := G(X_0) \in \Omega_q$*. Then, the solution* X_n *of the auxiliary system* (1.21) *corresponding with the initial condition* X_0 *and the solution* Y_n *of the aggregated system* (1.23) *corresponding to the initial condition* Y_0 *are related by the following expressions*

$$Y_n = G(X_n), \qquad X_n = E(Y_{n-1})\ ,\ n = 1, 2, ...$$

In addition, given an extra assumption, for each n fixed it is possible to approximate the solution of the original system (1.18) by means of the solution of the aggregated model (1.23).

Proposition 1.1.6 *Let $X_0 \in \Omega_N$ and let $Y_0 := G(X_0) \in \Omega_q$. Let n be a fixed positive integer and assume that there exists a non-empty bounded and open set Ω such that $\bar{\Omega} \subset \Omega_N$, Ω contains the points*

$$\{X_0, X_{i+1} := E(Y_i), \quad i = 0, \cdots, n-1\},$$

and $\lim_{k\to\infty} F^{(k)} = \bar{F}$ is uniform in Ω. Then, the solution $X_{k,n}$ of the original system (1.18) *corresponding with the initial condition X_0 and the solution Y_n of the reduced system* (1.23) *corresponding with the initial condition Y_0 are related by the following expressions*

$$Y_n = \lim_{k\to\infty} G(X_{k,n}), \quad \lim_{k\to\infty} X_{k,n} = E(Y_{n-1}).$$

The following theorem, whose details can be found in [90], guarantees that the existence of an equilibrium point Y^* for the aggregated system implies, for k large enough, the existence of an equilibrium X_k^* for the original system, which can be approximated in terms of Y^*. Moreover, in the hyperbolic case, the stability of Y^* is equivalent to the stability of X_k^* and in the asymptotically stable (A.S.) case, the basin of attraction of X_k^* can be approximated in terms of the basin of attraction of Y^*.

Theorem 1.1.7 *Consider system* (1.18) *and assume that hypothesis 1.1.4 holds. Let $Y^* \in \mathbb{R}^q$ be an equilibrium point of system (1.23) so that, according with proposition 1.1.5 it follows that $X^* = E(Y^*)$ is a fixed point of the auxiliary system* (1.21). *In addition, assume the following*

Hypothesis 1.1.8 *There exists a non-empty, open, bounded set $\Omega \subset \Omega_N$ such that $X^* \in \Omega$, $\bar{\Omega} \subset \Omega_N$ and the limits*

$$\lim_{k\to\infty} F^{(k)} = \bar{F} \tag{1.24}$$

and

$$\lim_{k\to\infty} DF^{(k)} = D\bar{F} \tag{1.25}$$

are uniform in Ω. As usual, DF represents the differential of function F.

In addition to hypothesis $(1.1.8)$, *let us assume that 1 is not an eigenvalue of $D[E \circ S\,(G(Y^*))]$. Then, there exist $r > 0$ and an integer $k_0 \geq 0$ such that*

1. *$X* := G(Y^*)$ is an equilibrium point of the auxiliary system (1.21). Moreover, for each $k \geq k_0$ the general system (1.18) has an unique equilibrium point $X_k^* \in \bar{B}\left(X^*; r\right)$ and*

   $$\lim_{k\to\infty} X_k^* = X^*,$$

   where $\bar{B}\left(X^*; r\right)$ stands for the set $\left\{Z \in \mathbb{R}^N;\ \|X^* - Z\| \leq r\right\}$.

2. *Let Y^* be hyperbolic. Then, X^* is also hyperbolic. Besides, there exists $k^* \geq 0$ such that for all $k \geq k^*$ the equilibrium point X_k^* is also hyperbolic. Moreover, X^* and X_k^* are A.S. (resp. unstable) if and only if Y^* is A.S. (resp. unstable).*

3. *Let Y^* be hyperbolic and A.S. Let $X_0 \in \Omega_N$ be such that $Y_0 := G(X_0)$ satisfies that*

   $$\lim_{n\to\infty} (S \circ \bar{F})^{(n-1)}(Y_0) = Y^*.$$

   Assume the following hypothesis

   Hypothesis 1.1.9 *There exists an open set $Q \in \Omega_N$ containing the set $\{X_0,\, X_{n+1} := E(Y_n),\, i = 0, 1, \cdots\}$ and such that $\lim_{k\to\infty} F^{(k)} = \bar{F}$ is uniform in Q*

   Then, there exists a positive integer k^{**} such that $k \geq k^{**}$,

   $$\lim_{n\to\infty} (S \circ F^{(k)})^{(n)}(X_0) = X_k^*.$$

Remark 1.1.10 *Although it is not stated in theorem 1.1.7, these results are also valid for m-periodic points (see [90] for further details).*

Remark 1.1.11 *hypotheses 1.1.8 and 1.1.9 can be synthesized into a more restrictive one, assuming that limits (1.24) and (1.25) are uniform in Ω_N.*

1.1.2 Contents of this chapter.

The departure point in this chapter is theorem 1.1.7 and concerns two time scale systems based on the slow unit time. Namely, we deal with systems of the form of (1.18), that is

$$X_{n+1,k} = S \circ F^{(k)}(X_{n,k}).$$

According with [90], *in practice*, it is difficult to decide whether function F decomposes as hypothesis 1.1.4 prescribes. Moreover, even if one is able to get such a decomposition, conditions stated in hypothesis 1.1.8 are hard to be checked.

In this chapter we provide with some general classes of systems for which function $F(\cdot)$ defining the fast dynamics fulfills hypotheses 1.1.4, 1.1.8 and 1.1.9. Up to now only linear maps have been considered for the fast dynamics. Namely, $F(X) = \mathcal{F}X$ being $\mathcal{F}$ an appropriate matrix with constant coefficients or, in the nonautonomous case, $F(n, X) = \mathcal{F}(n)X$ where the entries of matrix $\mathcal{F}(n)$ depend on time. It makes sense also consider that how the state variables evolve within the fast time scale from time n to time $n+1$ depend on the current state of such a state variables. This idea is conveyed, for instance, considering

$$F(X) = \mathcal{F}(X)X$$

instead of $F(X) = \mathcal{F}X$. We adopt this approach in this chapter considering different classes of functions of the form $F(X) = \mathcal{F}(X)X$, which we describe summarily in the sequel.

In the context of populations structured in groups and subgroups, when the fast dynamics of each group is driven by a regular stochastic matrix we get that the total number of individuals of each group is a global variable. We note Y the vector containing these global variables, which is function of the state variables. In section 1.2 (see also [68]) we study the approximate aggregation of system (1.18) with a nonlinear fast dynamics of the form

$$F(X) = \text{diag}(\mathcal{F}_1(Y), \cdots, \mathcal{F}_q(Y))X,$$

where $\text{diag}(\mathcal{F}_1(Y), \cdots, \mathcal{F}_q(Y))$ is a block diagonal matrix and, for each Y, $\mathcal{F}_j(Y)$ is a regular stochastic matrix for each $j = 1, \cdots, q$. These settings are applied to several population models driven by demographic and migratory processes evolving at different time scales. We analyze these models exchanging the role of the slow and fast dynamics. As a result of this analysis, we slightly extend the settings presented in this paragraph.

In section 1.3 we deal with the approximate aggregation of systems of the form of (1.18) where the fast dynamics is given by

$$F(X) = \text{diag}(\mathcal{F}_1, \mathcal{F}_2(\mathbf{x}_1))X,$$

$X = (\mathbf{x}_1, \mathbf{x}_2)$ stands for the state variables vector, $\text{diag}(\mathcal{F}_1, \mathcal{F}_2(\mathbf{x}_1))$ is a block diagonal matrix and, without lost of generality, matrices $\mathcal{F}_1$ and $\mathcal{F}_2(\mathbf{x}_1)$ are regular stochastic matrices. Of course, matrices $\mathcal{F}_1$ and $\mathcal{F}_2(\mathbf{x}_1)$ can be replaced by adequate block diagonal matrices. We apply these results to the study of a host parasitoid populations spread through a net of patches where individuals can move between adjacent patches and parasitoids move toward regions with high host density. Considering In that displacements between patches are faster than local host parasitoid interactions yields a two time scales model matching with the aforementioned assumptions. These results are collected in [72].

1.2 Fast dynamics depending on global variables.

The main goal of this section is to apply the aggregation of variables method to the reduction of a general class of nonlinear discrete models with two time scales which fits in the framework of the original formulation made in [90] through system (1.18)

$$X_{k,n+1} = S \circ F^{(k)}(X_{k,n}).$$

Functions $S, F \in \mathcal{C}^1(\Omega_N; \Omega_N)$ stand for the fast and the slow dynamics, $X \in \Omega_N$ and $\Omega_N \subset \mathbb{R}^N$ is an open bounded nonempty set. As we mentioned in the introduction, for a particular two time scales discrete model it is difficult to prove that hypotheses 1.1.4, 1.1.8 and 1.1.9 are met. We present a class of models for which these hypotheses are meet and so, theorem 1.1.7 applies. Applications to population dynamics complete the section.

1.2.1 General settings and main results.

We start describing the model and its mathematical features. Without lost of generality, let us assume that at time n the state variable vector represent an structured population given by

$$X_n = (\mathbf{x}_n^1, \cdots, \mathbf{x}_n^q),$$

where $\mathbf{x}_i = (x_n^{i1} \cdots, x_n^{iN_i})$ defines the population in group $i = 1, \cdots, q$ and x_n^{ij} is the size of subgroup j in group i at time n. Let $N = N_1 + \cdots + N_q$ be the total number of subgroups.

Many applications consider that fast dynamics is internal, conservative of the total number of individuals and with an asymptotically stable distribution among groups for every group $i = 1, \cdots, q$. This idea is conveyed, for instance, representing the fast dynamics of each group by a projection matrix $\mathcal{F}_i$ which is a regular stochastic matrix of dimensions $N_i \times N_i$ for $i = 1, \cdots, q$. Thus,

$$F(X) = \mathcal{F}X = \mathsf{diag}(\mathcal{F}_1, \cdots, \mathcal{F}_q)X$$

stands for the fast dynamics of the whole population. In this case, hypotheses 1.1.4 and 1.1.8 are trivially satisfied if these projection matrices are constant. For instance, we may think on an age-structured population with q age classes and individuals spread among m different patches. Demography stands for the slow dynamics while migrations between patches is the fast dynamics. In this context $\mathbf{x}^i$ stands for the spatial distribution of individuals belonging tho the i-fold age class, for $i = 1, \cdots, q$. The aforementioned consideration entails that individuals of each age class reach an stable spatial distribution.

Our aim in what follows is to extend this configuration to the nonlinear case in which such a projection matrices depend on the total number of individuals of each group, as we did in [68]. To be precise, the total number of individuals of the i-fold group is given, obviously, by $x^{i1} + \cdots + x^{iN_i} = \mathbf{1}_i^T \mathbf{x}^i$, where $\mathbf{1}_i := (1, \ldots, 1)^T \in \mathbb{R}^{N^i}$. Thus, we get the vector whose entries are the total number of individuals of each group by means of

$$\mathcal{U}X := \mathsf{diag}\,(\mathbf{1}_1^T, \cdots, \mathbf{1}_q^T)X, \tag{1.26}$$

where $\mathcal{U}X \in \mathbb{R}^q$. Next we set up appropriate functions describing the internal dynamics of each group. Let us note $\Omega_q := \mathcal{U}\Omega_N$. For each $i = 1, \cdots, q$, let $\mathcal{F}_i(\cdot) \in C^1(\Omega_q)$ be a matrix function such that for all $Y \in \Omega_q$, $\mathcal{F}_i(Y)$ is a regular stochastic matrix of dimensions $N^i \times N^i$. As a consequence, 1 is an eigenvalue simple and strictly dominant in modulus for $\mathcal{F}_i(\mathcal{U}X)$, with associated right and left eigenvectors $\mathbf{v}_i(\mathcal{U}X)$ and $\mathbf{1}_i$, respectively. The eigenvector $\mathbf{v}_i(\mathcal{U}X)$ is the asymptotically stable probability distribution, i.e., $\mathbf{v}_i(\mathcal{U}X) > 0$ and $\mathbf{1}_i^T \mathbf{v}_i(\mathcal{U}X) = 1$. The fast dynamics for the whole population is represented by the block diagonal matrix:

$$\begin{gathered} F(X) := \mathsf{diag}\,(\mathcal{F}_1(\mathcal{U}X), \ldots, \mathcal{F}_q(\mathcal{U}X))\,X = \mathcal{F}(\mathcal{U}X)X, \\ F^{(k)}(X) = \mathcal{F}^k(\mathcal{U}X)X. \end{gathered} \tag{1.27}$$

The Perron-Frobenius theorem applies to each matrix $\mathcal{F}_i(Y)$ and we have

$$\overline{\mathcal{F}}_i(\mathcal{U}X) := \lim_{k\to\infty} \mathcal{F}_i^k(\mathcal{U}X) = (\mathbf{v}_i(\mathcal{U}X)| \ldots |\mathbf{v}_i(\mathcal{U}X)) = \mathbf{v}_i(\mathcal{U}X)\mathbf{1}_i^T$$

and

$$\overline{\mathcal{F}}(\mathcal{U}X) := \lim_{k\to\infty} \mathcal{F}^k(\mathcal{U}X) = \mathsf{diag}(\mathcal{F}_1(\mathcal{U}X), \cdots, \mathcal{F}_q(\mathcal{U}X)). \tag{1.28}$$

If we note

$$\bar{F}(X) := \mathsf{diag}\,(\bar{\mathcal{F}}_1(\mathcal{U}X), \ldots, \bar{\mathcal{F}}_q(\mathcal{U}X))X = \bar{\mathcal{F}}(\mathcal{U}X)X$$

and, $\forall Y \in \Omega_q$,

$$\begin{aligned} G(X) &:= \mathcal{U}X, \\ E(Y) &:= \mathsf{diag}\,(\mathbf{v}_1(Y), \ldots, \mathbf{v}_q(Y))Y, = \mathcal{V}(Y)Y, \end{aligned} \tag{1.29}$$

we also have

$$\bar{F}(X) = \lim_{k\to\infty} F^{(k)}(X) = E \circ G(X) = \mathcal{V}(Y)\mathcal{U}X.$$

We have the shown that $F(X)$ verifies hypothesis 1.1.4 with

$$Y = \mathcal{U}X \tag{1.30}$$

being the global variables. Using $F(X)$ as fast dynamics we can write the following nonlinear two time scales model of the form (1.18).

$$X_{k,n+1} = S\left(\mathcal{F}^k(\mathcal{U}X_{k,n})X_{k,n}\right). \tag{1.31}$$

whose corresponding *auxiliary system* is $X_{n+1} = S\left(\bar{\mathcal{F}}(\mathcal{U}X_n)X_n\right)$ and its *aggregated system* reads as follows

$$Y_{n+1} = \mathcal{U}S\left(\mathcal{V}(Y_n)Y_n\right). \tag{1.32}$$

The following step in order to apply theorem 1.1.7 to system (1.31) is proving that the map F defined by (1.27) also verifies hypothesis 1.1.8. For doing this, we first need the following lemma.

Lemma 1.2.1 *Let $\mathcal{F}(\cdot)$ be a $\mathcal{C}^1$ matrix function defined on Ω_q, such that for each $Y \in \Omega_q$, $\mathcal{F}(Y)$ is a $n \times n$ regular stochastic matrix. Let us consider the function $\mathbf{v} : \Omega_q \to \mathbb{R}^n$ where $\mathbf{v}(Y)$ is the unique eigenvector associated to eigenvalue 1, normalized by the condition $\mathbf{1}_n^T\mathbf{v}(Y) = 1$. Then, $\mathbf{v} \in C^1(\Omega_q)$.*

Proof.– For each $Y \in \Omega_q$, the normalized eigenvector $\mathbf{v}(Y)$ associated to the eigenvalue 1 is the unique solution to the system:

$$\left\{ \begin{array}{rcl} (\mathcal{F}(Y) - I_n)\mathbf{v} & = & \mathbf{0} \\ \mathbf{1}_n^T \mathbf{v} & = & 1 \end{array} \right. \tag{1.33}$$

Set $Y_0 \in \Omega_q$ and let $\mathbf{v}(Y_0)$ be the corresponding solution to (1.33). Since $\mathbf{1}_n^T(\mathcal{F}(Y) - I_n) = \mathbf{0}_n^T$, an elementary application of the Rank theorem (see, for instance, [107])allows to solve the system (1.33) in a neighborhood of $(Y_0, \mathbf{v}(Y_0))$, $N(Y_0) \subset \Omega_q \times \mathbb{R}^n$, by eliminating the last row of the matrix $P(Y) - I_n$. As an immediate consequence, this theorem assures that the function $\mathbf{v}(\cdot)$ defined implicitly by system (1.33) is C^1 in a neighborhood of Y_0, as we wanted to prove.

■

Let us observe that the application of the Rank theorem to system (1.33) is based on the following elementary result: for each $n \times n$ regular stochastic matrix $\mathcal{F}_0$, we have:

$$\text{Rank} \begin{pmatrix} \mathcal{F}_0 - I_n \\ \mathbf{1}_n^T \end{pmatrix} = n.$$

Regarding hypothesis 1.1.8, let us notice that for each $Y \in \Omega_q$, matrix $\mathcal{F}(Y)$ can be written as:

$$\mathcal{F}(Y) = (\mathbf{v}(Y)|\mathcal{R}(Y)) \begin{pmatrix} I_q & O \\ O & \mathcal{H}(Y) \end{pmatrix} \begin{pmatrix} \mathbf{1}^T \\ \mathcal{W}(Y) \end{pmatrix} = \mathcal{V}(Y)\mathcal{U} + \mathcal{Q}(Y)$$

with $\mathcal{Q}(Y) := \mathcal{R}(Y)\mathcal{H}(Y)\mathcal{W}(Y)$, $\mathcal{R}(Y)$, $\mathcal{W}(Y)$ are suitable matrices and $\mathcal{H}(Y)$ corresponds to the Jordan blocks of $\mathcal{F}(Y)$ associated to eigenvalues of modulus strictly less than 1. Therefore

$$\rho(\mathcal{Q}(Y)) < 1, \forall Y \in \Omega_q \tag{1.34}$$

where ρ denotes the spectral radius.

Moreover, straightforward calculations lead to

$$\mathcal{F}^k(Y) = \mathbf{v}(Y)\mathbf{1}^T + \mathcal{Q}^k(Y) \quad , \quad k = 1, 2, \ldots \tag{1.35}$$

Bearing in mind lemma 1.2.1, and since $\mathcal{F} \in C^1(\Omega_q)$, let us observe that we also have $\mathcal{Q} \in C^1(\Omega_q)$.

We are now able to prove the following:

Proposition 1.2.2 *The maps* F *and* $\bar{F}$ *defined in* (1.27) *and* (1.28) *satisfy that:*

1. $\lim_{k\to\infty} F^{(k)} = \bar{F}$

2. $\lim_{k\to\infty} DF^{(k)} = D\bar{F}$

uniformly on each compact set $K_N \subset \Omega_N$*.*

Proof.– We already know that limit 1 holds pointwise. Moreover, from (1.35) we have, for each $X \in \Omega_N$:

$$\|F^k(X) - \bar{F}(X)\| = \|\mathcal{F}^k(\mathcal{U}X)X - \mathcal{E}(\mathcal{U}X)\mathcal{U}X\| \leq \|\mathcal{Q}^k(\mathcal{U}X)\|\|X\|.$$

Therefore, as $\mathcal{U}$ is a constant matrix, to prove (i) it is enough to prove that, for each compact set $K_q \subset \Omega_q$ we have

$$\sup_{Y\in K_q} \|\mathcal{Q}^k(Y)\| \longrightarrow 0 \ (k \to \infty)$$

which, in turn, will be a consequence of the existence of two constants $C > 0$ and $\beta \in (0,1)$ such that

$$\forall Y \in K_q \quad , \quad \|\mathcal{Q}^k(Y)\| \leq C\beta^k \ , \ k = 1, 2, \dots \tag{1.36}$$

Since $\mathcal{Q}(\cdot)$ is continuous, the spectral radius $\rho(\mathcal{Q}(\cdot))$ is also continuous on Ω_q and then, bearing in mind (1.34), we can assure the existence of a constant α with $0 < \alpha < 1$ such that $\sup_{Y\in W} \rho(\mathcal{Q}(Y)) \leq \alpha$, where W is some bounded open set with $K_q \subset W$ and $\bar{W} \subset \Omega_q$.

Let β be fixed with $\alpha < \beta < 1$ and set $Y \in W$. It is a well known fact that there exists a matrix norm $\|\cdot\|_Y$ (depending on Y) for which $\|\mathcal{Q}(Y)\|_Y < \beta$. The continuity of matrix $\mathcal{Q}(\cdot)$ and of the norm allow us to assure the existence of an open neighborhood of Y, $B(Y) \subset W$, such that $\sup_{Z\in B(Y)} \|\mathcal{Q}(Z)\|_Y \leq \beta$.

Obviously, the family $\mathcal{B} := \{B(Y) \ ; \ Y \in W\}$ is an open covering of K_q and since K_q is a compact set, there exist a finite collection of points $Y_j \in W$, $j = 1, \dots, r$ such that $K_q \subset \cup_{j=1}^r B(Y_j)$. Then, for each $Y \in K_q$ there exists $j \in \{1, \dots, r\}$ such that $\|\mathcal{Q}(Y)\|_{Y_j} \leq \beta$, and therefore $\|\mathcal{Q}^k(Y)\|_{Y_j} \leq \beta^k$, $k = 1, 2, \dots$. As a consequence, bearing in mind that all the matrix norms are equivalent, we have that $\|\mathcal{Q}^k(Y)\| \leq C_j\beta^k$, for some constant $C_j > 0$. Choosing $C := \max(C_1, \dots C_r)$, the estimation (1.36) holds.

To prove the assertion (ii) let us notice that (1.35) implies that

$$\forall X \in \Omega_N \quad , \quad DF^k(X) = D\bar{F}(X) + D[\mathcal{Q}^k(\mathcal{U}X)X].$$

Therefore, we have to prove that, for each compact set $K_N \subset \Omega_N$ we have

$$\sup_{X \in K_N} \|D[\mathcal{Q}^k(\mathcal{U}X)X]\| \longrightarrow 0 \ (k \to \infty).$$

Let us start with some straightforward calculations. Let $A(\cdot) := (a_{ij}(\cdot))_{i,j=1}^N$ be a C^1 matrix function defined on Ω_N and set R the scalar function defined on Ω_N by $R(X) := A(X)X$, $X := (x_1, \dots, x_N)^T \in \Omega_N$. A direct calculation of the partial derivatives leads to the following expression:

$$DR(X) = A(X) + \begin{pmatrix} \displaystyle\sum_{j=1}^N x_j \textsf{grad}\, a_{1j}(X) \\ \vdots \\ \displaystyle\sum_{j=1}^N x_j \textsf{grad}\, a_{Nj}(X) \end{pmatrix}.$$

Choosing $A(X) := \mathcal{Q}^k(\mathcal{U}X)$ in the above expression, with the help of the chain rule we have:

$$D[\mathcal{Q}^k(\mathcal{U}X)X] = \mathcal{Q}^k(\mathcal{U}X) + \begin{pmatrix} \displaystyle\sum_{j=1}^N x_j \textsf{grad}\, q_{1j}^{(k)}(\mathcal{U}X) \\ \vdots \\ \displaystyle\sum_{j=1}^N x_j \textsf{grad}\, q_{Nj}^{(k)}(\mathcal{U}X) \end{pmatrix} \mathcal{U}$$

where we have denoted by $q_{ij}^{(k)}(Y)$ the entries of matrix $\mathcal{Q}^k(Y)$.

Let $K_N \subset \Omega_N$ be a compact set and set $K_q := \mathcal{U}K_N \subset \Omega_q$, which is also a compact set. Bearing in mind (1.36), the above expression leads to the following estimation:

$$\begin{aligned} \|D[\mathcal{Q}^k(\mathcal{U}X)X]\| \ &\le C_1\beta^k \\ &\quad + C_2\|\mathcal{G}\|\|X\| \max_{i,j=1,\dots,N} \left(\sup_{Y \in K_q} \left| \frac{\partial q_{ij}^{(k)}}{\partial y_s}(Y) \right| \ , \ s = 1, \dots, q \right) \end{aligned}$$

where $C_1 > 0$, $C_2 > 0$ are two constants whose specific values are not relevant.

For each $Y := (y_1, \dots, y_q)^T \in \Omega_q$ and $k = 1, 2, \dots$ we have

$$\begin{aligned} \frac{\partial \mathcal{Q}^k}{\partial y_s}(Y) \ &= \frac{\partial \mathcal{Q}}{\partial y_s}(Y)\mathcal{Q}(Y)\overset{(k-1)}{\cdots}\mathcal{Q}(y) \\ &\quad + \mathcal{Q}(Y)\frac{\partial \mathcal{Q}}{\partial y_s}(Y)\mathcal{Q}(Y)\overset{(k-2)}{\cdots}\mathcal{Q}(Y) + \cdots + \mathcal{Q}(Y)\overset{(k-1)}{\cdots}\mathcal{Q}(Y)\frac{\partial \mathcal{Q}}{\partial y_s}(Y) \end{aligned}$$

and since $\mathcal{Q}(\cdot)$ has continuous partial derivatives, then bounded on each compact set, we can conclude that

$$\sup_{X\in K_N} \|D[\mathcal{Q}^k(\mathcal{U}X)X]\| \leq C_1\beta^k + C_3k\beta^{k-1} \longrightarrow 0 \ (k\to\infty)$$

as we wanted to prove.

■

Once we have proved that function F defined in (1.27) verifies hypotheses 1.1.4 and 1.1.8, theorem 1.1.7 yields the following result that allows us to study some asymptotic behaviors of system (1.31) in terms of the aggregated system (1.32).

Theorem 1.2.3 *Consider the general two time scales system* (1.31) *given by*

$$X_{k,n+1} = S(\mathcal{F}^k(\mathcal{U}X_{k,n})X_{k,n})$$

where $X \in \Omega_N$, $\Omega_N \subset \mathbb{R}^N$ *is an open bounded nonempty set,* $S \in \mathcal{C}^1(\Omega_N)$, $\mathcal{U}$ *and* $\mathcal{F}(\cdot) \in \mathcal{C}^1(\Omega_q)$ *are those defined by* (1.26) *and* (1.27) *and* $\Omega_q = \mathcal{U}\Omega_N$. *Consider as well the corresponding auxiliary system* $X_{n+1} = S(\bar{\mathcal{F}}(\mathcal{U}X_n)X_n)$ *and the aggregated system* (1.32) *that we have derived in the previous paragraphs*

$$Y_{n+1} = \mathcal{U}S\left(\mathcal{V}(Y_n)Y_n\right)$$

where $\mathcal{V}(\cdot)$ *is that defined in* (1.29) *and* Y *stands for the global variables defined through* (1.30). *Let* $Y^* \in \Omega_q$ *be a hyperbolic equilibrium point of system* (1.32). *Then, there exist* $r \in \mathbb{R}$ *with* $r > 0$ *and an integer* $k_0 \geq 0$ *such that for all* $k \geq k_0$ *the following holds:*

1. $X^* := \mathcal{V}(Y^*)Y^*$ *is an hyperbolic fixed point of the auxiliary system. Moreover, system* (1.31) *has an unique equilibrium point* X_k^* *in* $\bar{B}(X^*;r)$ *which is hyperbolic and satisfies*

$$\lim_{k\to\infty} X_k^* = X^*,$$

   where $\bar{B}(X^*;r) = \left\{Z \in \mathbb{R}^N;\ \|Z - X^*\| \leq r\right\}$.

2. X^* *and* X_k^* *are asymptotically stable (resp. unstable) if and only if* Y^* *is asymptotically stable (resp. unstable).*

3. *Let* Y^* *be asymptotically stable and let* $X_0 \in \Omega_N$ *be such that the solution* $\{Y_n\}_{n=0,1,\ldots}$ *of the aggregated system* (1.32) *corresponding with the initial data* $Y_0 := \mathcal{U}X_0$ *satisfies that* $\lim_{n\to\infty} Y_n = Y^*$*. Then, there exists* $k_1 \geq 0$ *such that for each* $k \geq k_1$*, the solution of system* (1.31) *with initial value* $X_{k,0} = X_0$ *satisfies that*

$$\lim_{n\to\infty} X_{k,n} = X_k^*.$$

Proof.– From the previous analysis in follows that hypothesis 1.1.8 holds any compact set of Ω_N. As a consequence, hypothesis 1.1.9 holds too. The regularity conditions imposed in hypothesis 1.1.4 hold immediately from the $\mathcal{C}^1$ regularity of eigenvectors $\mathbf{v}_i(\cdot)$, $i = 1, \cdots, q$, as established in lemma 1.2.1. Then, the theorem holds.

■

In the sequel, this reduction procedure is applied to several models of population dynamics driven by demographic and migratory processes which take place at two different time scales. An analysis of these models exchanging the role of the slow and fast dynamics is provided: when a Leslie type demography is faster than migrations, a multi-attractor scenario appears for the reduced dynamics. Most important, in this example we extend slightly the framework presented in theorem 1.2.3. On the other hand, when the migratory process is faster than demography, the reduction process gives rise to new interpretations of well known discrete models, including some Allee effect scenarios.

In some applications, particularly in ecology, it would be more realistic to have the fast dynamics dependent on the state variables and not just on the global variables as in theorem 1.2.3. Nevertheless, it does not seem easy to find a proof for the most general case and specific proofs should be provided for each particular case of fast dynamics depending on state variables as we do in section 1.3. On the other hand, as we will see in the next section, it is possible to develop interesting applications keeping within the framework of theorem 1.2.3.

1.2.2 Multi-patch models with fast migrations.

We begin treating the case of a population inhabiting a multi-patch environment but with no further structure, that is, a population constituted by just one group which is subdivided into N subgroups representing the local populations at the N patches making up its habitat.

As a consequence, the population vector at time n is $X_n = (x_n^1, \dots, x_n^N)^T$, the fast dynamics (associated in our models to the migration process) is represented by a regular (one block) stochastic matrix $\mathcal{F}(y)$, whose entries depend on the total population $y := x^1 + \cdots + x^N \in \mathbb{R}$, and the slow dynamics is represented by a function $S \in \mathcal{C}^1(\Omega)$ which gives the local demography in each patch. By the sake of simplicity and without lost of generality, in what follows we consider a two patches environment, i.e. $N = 2$. Thus, the slow dynamics is described by

$$S(X_n) := (s_1(x_n^1), s_2(x_n^2)), \qquad X_n := (x_n^1, x_n^2)$$

where s_i, $i = 1, 2$, are two non-negative $\mathcal{C}^1$ functions defined on $\mathbb{R}_+$. The migration matrix $\mathcal{F}(y)$ is written in terms of $\mathcal{C}^1$ real functions $a, b : \mathbb{R}_+ \to (0, 1)$:

$$\mathcal{F}(y) := \begin{pmatrix} 1 - a(y) & b(y) \\ a(y) & 1 - b(y) \end{pmatrix}.$$

Since $\mathcal{F}(y)$ is a regular stochastic matrix, we have

$$\bar{\mathcal{F}}(y) := \lim_{k\to\infty} \mathcal{F}^k(y) = (\mathbf{v}(y)|\mathbf{v}(y))$$

where

$$\mathbf{v}(y) := \begin{pmatrix} v_1(y) \\ v_2(y) \end{pmatrix} = \begin{pmatrix} \dfrac{b(y)}{a(y) + b(y)} \\ \dfrac{a(y)}{a(y) + b(y)} \end{pmatrix}.$$

A straightforward application of the results established in section 1.2 leads to the aggregated system:

$$y_{n+1} = s_1\left(v_1(y_n) y_n\right) + s_2\left(v_2(y_n) y_n\right). \tag{1.37}$$

We study equation (1.37) by setting concrete (and well known) local dynamics.

Source-sink Malthusian local demography.

We will carry out a detailed analysis of the above model assuming that a malthusian dynamics acts at each patch, that is:

$$S(X_n) := (d_1 x_n^1, d_2 x_n^2). \tag{1.38}$$

Moreover we will assume that $0 < d_1 < 1 < d_2$, which means that patch 1 behaves as a sink and patch 2 as a source.

We provide a complete analysis of (1.38) by considering a and b as monotone functions of the global variable y. Far from plain, we find out a rich behavior. In particular, we provide an explanation of two classical mono-species discrete models (due to Beverton-Holt and Ricker, respectively) in terms of a sink-source environment with fast density dependent migrations coupled to simple local malthusian dynamics. On the other hand, we notice in advance that when both $a(y)$ and $b(y)$ are simultaneously increasing or decreasing functions yield more complicated dynamics and Allee effect scenarios may arise.

When the slow dynamics is given by (1.38), the aggregated model (1.37) reads as:

$$y_{n+1} = \left(\frac{d_1 b(y_n) + d_2 a(y_n)}{a(y_n) + b(y_n)}\right) y_n := h(y_n) y_n. \tag{1.39}$$

It is evident that $y_0 = 0$ is a fixed point of the above model, but we are mainly interested in the existence and stability properties of the positive fixed points y_*, which are the solutions to equation $h(y) = 1$.

To study the behaviour of function h, we should take into account its derivative:

$$h'(y) = (d_2 - d_1)\frac{a'(y)b(y) - a(y)b'(y)}{[a(y) + b(y)]^2}.$$

For the sake of simplicity we restrict our analysis to the case in which functions $a(y)$, $b(y)$ are monotone. When one of them is increasing and the other is decreasing, it is evident that $h(y)$ is strictly monotone. Therefore, whether function $h(y)$ crosses or not the line $y = 1$ is completely determined by the values $h(0)$ and $h(\infty) := \lim_{y\to+\infty} h(y)$. Moreover, in the case in which y_* exists, it is unique and its stability is determined by the value $h'(y_*)y_*$. On the other hand, the stability of the fixed point $y_0 = 0$ depends on the value of $h(0)$.

These results are summarized as follows:

$a(y)$	$b(y)$	$h(0)$	$h(\infty)$	$y_0 = 0$	y_*
$\searrow$	$\nearrow$	> 1	$\in (0,1)$	U.	$\exists$, U. or A.S.
$\searrow$	$\nearrow$	> 1	> 1	U.	$\nexists$
$\searrow$	$\nearrow$	$\in (0,1)$	$\in (0,1)$	G.A.S.	$\nexists$
$\nearrow$	$\searrow$	$\in (0,1)$	> 1	A.S.	$\exists$, U.
$\nearrow$	$\searrow$	$\in (0,1)$	$\in (0,1)$	G.A.S.	$\nexists$
$\nearrow$	$\searrow$	> 1	> 1	U.	$\nexists$

where the arrows $\searrow$ and $\nearrow$ stand for a decreasing and an increasing function respectively , and U., A.S. and G.A.S. stand for unstable, asymptotically stable and globally asymptotically stable, respectively.

The fact that local dynamics are of malthusian type allows extinction and unbounded growing to be expected at a global level. Nevertheless, as we see in the first row of the previous table, appropriate density dependent migration rates can lead the corresponding model to posses a positive asymptotically stable equilibrium. Two examples are described below.

If we choose

$$a(y) := \frac{\alpha - d_1(1+\beta y)}{d_2 - d_1} \quad \text{and} \quad b(y) := \frac{d_2(1+\beta y) - \alpha}{d_2 - d_1} \tag{1.40}$$

for positive parameters α and β, direct calculations yield the corresponding aggregated system (1.39)

$$y_{n+1} = \frac{\alpha y_n}{1+\beta y_n},$$

that is, the classical Beverton-Holt equation [17] which, for $\alpha > 1$, possesses a positive equilibrium $y^* = (\alpha - 1)/\beta$ globally asymptotically stable. Condition $a(y), b(y) \in (0,1)$ is needed, which is true if

$$\frac{\alpha - d_2}{\beta d_1} < y < \frac{\alpha - d_1}{\beta d_2}.$$

We expect to explain the Beverton-Holt model through the two time scales spatially distributed source sink malthusian model for initial values close to the corresponding equilibrium $y^* = (\alpha - 1)/\beta$, which happens when the following holds

$$1 < \alpha < \min\left\{\frac{d_2 - d_1}{1 - d_1}, \frac{d_2 - d_1}{d_2 - 1}\right\}.$$

If we choose

$$a(y) := \frac{e^{r(1-y/K)} - d_1}{d_2 - d_1} \quad \text{and} \quad b(y) := \frac{d_2 - e^{r(1-y/K)}}{d_2 - d_1}.$$

where r and K are positive parameters, the aggregated system obtained is the Ricker equation [81]

$$y_{n+1} = \exp(r(1 - y_n/K))y_n.$$

Condition $a(y), b(y) \in (0,1)$ must hold which, in this case, is true if

$$\max\left\{K\left(1 - \frac{\ln(1+d_1)}{r}\right),\ K\left(1 - \frac{\ln d_2}{r}\right)\right\} < y < K\left(1 - \frac{\ln d_1}{r}\right).$$

The positive equilibrium of the Ricker equation is $y_* = K$. Then, our interpretation of the Ricker equation through a two time scales spatially distributed models holds whenever the corresponding initial values of the aggregated system are chosen close enough to $y_* = K$.

Similar approaches using aggregation methods for ordinary differential equations were presented in [10] and [12]. Besides, some others interpretations of this type have been recently presented by Geritz and Kisdi [36]. There, starting from a continuous-time resource-consumer model for the dynamics within a year, a discrete-time model for the between-year dynamics is derived. This model is analyzed assuming that the within-year resource dynamics in absence of consumers takes different functional forms. Considering particular constant rates for the influx and efflux of the resource, the Beverton-Holt model, the Ricker model and many other models are recovered. Further models derived by systematically varying the within year patterns of reproduction and aggression between individuals can be found in [29].

We have noticed that Allee effect may arise when both $a(y)$ and $b(y)$ are simultaneously increasing or decreasing functions. We illustrate this fact with the next example. Let us assume that $a(y)$ and $b(y)$ are increasing functions given by

$$a(y) := \frac{y^2}{y^2+\beta} \text{ and } b(y) := \frac{y^2+\beta}{y^2+\delta} \quad , \quad 0<\beta<\delta.$$

Function $h(y)$ in (1.39) becomes

$$h(y) = \frac{d_1\left(y^2+\beta\right)^2 + d_2\left(y^2+\delta\right)y^2}{\left(y^2+\beta\right)^2 + \left(y^2+\delta\right)y^2}.$$

The qualitative analysis of equation (1.39) is straightforward having in mind that positive solutions are decreasing if $h(y) < 1$, increasing if $h(y) > 1$ and the positive fixed points are the roots of equation $h(y) = 1$. Since $h(0) = d_1 < 1$, the fixed point $y_0^* = 0$ is always asymptotically stable.

To find when $h(y) < 1$ and when $h(y) > 1$ we know that $h(0) = d_1 < 1$ and $\lim_{y\to\infty} h(y) = (d_1 + d_2)/2$. Moreover, if we look at the sign of $h'(y)$,

$$h'(y) = \frac{2(d_2-d_1)y\left((2\beta-\delta)y^4 + 2\beta^2y^2 + \beta^2\delta\right)}{\left(2y^4 + (2\beta+\delta)y^2 + \beta^2\right)^2},$$

we see that if $\delta \le 2\beta$ then $h(y)$ is increasing in $[0,\infty)$ while if $\delta > 2\beta$ then $h(y)$ is increasing in $[0, y_M)$ and decreasing in (y_M, ∞), where $y_M = \sqrt{\beta\delta/(\delta-2\beta)}$ is the only positive root of equation $h'(y) = 0$. Thus, we have:

- If $\delta \le 2\beta$ and $(d_1+d_2)/2 \le 1$, there is no positive fixed point.
- If $\delta \le 2\beta$ and $(d_1+d_2)/2 > 1$, there is a positive fixed point which is unstable.
- If $\delta > 2\beta$ and $h(y_M) < 1$, there is no positive fixed point.
- If $\delta > 2\beta$ and $h(y_M) = 1$, y_M is the only positive fixed point and it is unstable.
- If $\delta > 2\beta$, $h(y_M) > 1$ and $(d_1+d_2)/2 \ge 1$, there is a positive fixed point, $y_1^* < y_M$, which is unstable.
- If $\delta > 2\beta$, $h(y_M) > 1$ and $(d_1+d_2)/2 < 1$, there are two positive fixed points, $y_1^* < y_M < y_2^*$. In this case the positive solutions of equation (1.39), which are all monotone, verify the following:

  If the initial condition $y_0 < y_1^*$ *then* $\lim_{n\to\infty} y_n = 0$ *and if* $y_0 > y_1^*$ *then* $\lim_{n\to\infty} y_n = y_2^*$,

  i.e., at low population densities population gets extinct, while the evolution of population densities above y_1^* leads to y_2^*.

As we see in the last case, an Allee effect scenario appears out of local malthusian dynamics in a sink-source environment with fast density dependent migrations.

We consider now source-sink local demography of Beverton-Holt type together with monotone nonlinear fast migrations depending on global variables. That is, in lieu of (1.38), we assume that the slow dynamics is given by:

$$S(X_n) := \left(\frac{d_1 x_n^1}{1+c_1 x_n^1}, \frac{d_2 x_n^2}{1+c_2 x_n^2}\right) \quad , \quad 0 < d_1 < 1 < d_2 \ , \ c_i > 0 \ , \ i = 1,2$$

and that functions $a(y)$, $b(y)$ defining the fast dynamics $\mathcal{F}(y)$ are given by

$$a(y) := \frac{y}{1+y} \quad ; \quad b(y) := \frac{1}{1+y}.$$

In this situation, the aggregated system (1.37) reads:

$$y_{n+1} = h(y_n) y_n \quad ; \quad h(y_n) := \frac{d_1}{1+(1+c_1)y_n} + \frac{d_2 y_n}{1+y_n+c_2 y_n^2}.$$

Arguing in a similar way to the previous section, we obtain that $y_0 = 0$ is an equilibrium point which is always A.S. since $h(0) = d_1 < 1$.

The positive equilibria, if they exist, are the positive solutions to $h(y) = 1$. Notice that

$$h'(y) = -\frac{d_1(1+c_1)}{[1+(1+c_1)y]^2} + \frac{d_2(1-c_2y^2)}{(1+y+c_2y^2)^2}.$$

If $d_2 > d_1(1+c_1)$, then there exists a unique value $y_M \in (0, 1/\sqrt{c_2})$ such that $h'(y_M) = 0$ and moreover h takes its maximum value at this point. Therefore, bearing in mind that $h(0) = d_1 < 1$ and $h(+\infty) = 0$, the equation $h(y) = 1$ will have either two positive solutions or none according to $h(y_M) > 1$ or $h(y_M) < 1$ respectively. One sufficient condition for $h(y_M) > 1$ is that $h(1/\sqrt{c_2}) > 1$ which yields a relationship between the parameters of the model. In turn, a simple sufficient condition for this is $d_2 > 1 + 2\sqrt{c_2}$. Summing up, we can assure that for large enough values of d_2 the aggregated model has two positive equilibria $0 < y_* < y_{**}$ such that y_* is unstable and y_{**} can be asymptotically stable or unstable.

1.2.3 An age-structured population model with fast demography.

In this application we switch the role of migrations and demography as fast and slow process. This section can be considered as an extension of some results in [86], where a linear case is discussed. The theory developed in section 1.2.1 does not exactly match with the setting here, but it can be easily adapted: everything works if the fast dynamics is given by a non-negative $\mathcal{C}^1$ matrix function whose dominant eigenvalue is 1 and the corresponding associated normalized left eigenvector is constant. We note in advance that this adaptation slightly modifies the meaning of the corresponding global variables, which we will clarify in the following paragraphs.

Let us consider an age-structured population distributed between two spatial patches. We distinguish two age classes: juvenile (class 1, non reproductive) and adult (class 2, reproductive) so that the state of the population at time n is represented by a vector:

$$X_n := (x_n^1, x_n^2)^T \in \mathbb{R}_+^4, \quad x_n^i := (x_n^{i1}, x_n^{i2})^T,\ i = 1, 2$$

where x_n^{ij} stands for the individuals of class j inhabitant patch i.

Let us set demography as a local process driven by a Leslie $\mathcal{C}^1$ matrix function:

$$\mathcal{L}_i(y) := \begin{pmatrix} 0 & f^i(y) \\ s_1^i(y) & s_2^i(y) \end{pmatrix},\ i = 1, 2; \qquad \forall y \in \mathbb{R}_+$$

where, as usual, $f^i(\cdot)$ stands for the fertility rate of the adults and $s^i_{2j}(\cdot)$, $j = 1, 2$, stand for the survival rate of each age class. In order to fit in the framework of section 1.2.1, let us impose that 1 is the strictly dominant in modulus eigenvalue of matrix $L_i(\cdot)$, which yields

$$s^i_2(y) + f^i(y)s^i_1(y) = 1,\ i = 1, 2, \quad \forall y \in \mathbb{R}_+. \tag{1.41}$$

As a consequence, we can find associate positive right and left eigenvectors $\mathbf{v}_i(y)$, $\mathbf{u}_i(y)$, which can be chosen normalized by the condition $\mathbf{u}^T_i(y)\mathbf{v}_i(y) = 1$. In fact, these vectors are given by

$$\mathbf{u}_i(y) = \begin{pmatrix} 1 \\ \dfrac{1}{s^i_1(y)} \end{pmatrix} := \begin{pmatrix} u^i_1(y) \\ u^i_2(y) \end{pmatrix};$$

$$\mathbf{v}_i(y) = \begin{pmatrix} \dfrac{f^i(y)s^i_1(y)}{1 + f^i(y)s^i_1(y)} \\ \\ \dfrac{s^i_1(y)}{1 + f^i(y)s^i_1(y)} \end{pmatrix} := \begin{pmatrix} v^i_1(y) \\ v^i_2(y) \end{pmatrix}.$$

The general theory of non-negative matrices applies, so that there exists the limit

$$\bar{\mathcal{L}}_i(y) := \lim_{k\to\infty} L^k_i(y) = \mathbf{v}_i(y)\mathbf{u}^T_i(y),\ i = 1, 2, \quad \forall y \in \mathbb{R}_+.$$

The fast dynamics for the whole population will be represented by the block diagonal matrix

$$\mathcal{L}(Y) := \begin{pmatrix} \mathcal{L}_1(y_1) & 0 \\ 0 & \mathcal{L}_2(y_2) \end{pmatrix}, \quad \forall Y := \begin{pmatrix} y_1 \\ y_2 \end{pmatrix} \in \mathbb{R}_+.$$

Bearing in mind the above considerations, it is evident that the following limit exists

$$\bar{\mathcal{L}}(Y) := \lim_{k\to\infty} \mathcal{L}^k(Y) = \begin{pmatrix} \bar{\mathcal{L}}_1(y_1) & 0 \\ 0 & \bar{\mathcal{L}}_2(y_2) \end{pmatrix} = \mathcal{V}(Y)\mathcal{U}(Y)$$

where, as in section 1.2.1, we have introduced the notations

$$\mathcal{V}(Y) := \mathsf{diag}\,(\mathbf{v}_1(y_1), \mathbf{v}_2(y_2)); \quad \mathcal{U}(Y) := \mathsf{diag}\,(\mathbf{u}^T_1(y_1), \mathbf{u}^T_2(y_2)).$$

In addition, we consider migrations between patches. To simplify, we will consider a linear process represented by a constant stochastic matrix

$$\mathcal{M} := \left(\begin{array}{cccc} 1-a_1 & 0 & a_2 & 0 \\ 0 & 1-b_1 & 0 & b_2 \\ a_1 & 0 & 1-a_2 & 0 \\ 0 & b_1 & 0 & 1-b_2 \\ \end{array} \right) , \quad a_i, b_i \in (0,1)\ ,\ i=1,2$$

where a_i and b_i stand for the fraction of juvenile and adult individuals which move from patch i respectively.

In this section we are assuming that demography is much faster than migrations and spatially internal, that is, demography is local and only dependent on the population on each patch. In order to be able to retain the smoothness results established in section 1.2.1, we assume that matrix $\mathcal{U}(\cdot)$ is constant. To met this assumption we only need to suppose that $s_1^i(\cdot)$, the survival rate of juveniles at patch $i=1,2$, is constant. Then, global variables are defined by

$$Y_n := \mathcal{U}X_n = \left(\begin{array}{c} x_n^{11} + (1/s_1^1)x_n^{12} \\ x_n^{21} + (1/s_1^2)x_n^{22} \end{array} \right) := \left(\begin{array}{c} y_n^1 \\ y_n^2 \end{array} \right)$$

which have a biological meaningful interpretation as they are the population at each patch weighted by its reproductive values. This quantity is interpreted as a sort of vital projection of the population at each region: the average number of individuals which will rise from the actual population. Summing up, we can interpret the dependence (independence) of the coefficients of matrix $\mathcal{L}(y)$ on global variables as follows. Letting f^i and $s_2^i(\cdot)$, for $i=1,2$ depend on global variables means that fertility and survival rates of the reproductive class is related with its capability for perpetuate the population. This allows to simulate self-regulation assuming, for instance, that f^i decreases as global variables increase. Besides, assuming $s_1^i(\cdot)$ to be constant means that juvenile survival rate does not depend on such an ability.

Finally, the slow-fast model that we are considering is:

$$X_{k,n+1} = \mathcal{M}\mathcal{L}^k(\mathcal{U}X_{k,n})X_{k,n}$$

which, arguing as in section 1.2.1, can be reduced to the following system expressed in terms of the global variables:

$$Y_n = \mathcal{U}\mathcal{M}\mathcal{V}(Y_n)Y_n.$$

Direct substitutions lead to the following nonlinear aggregated system:

$$\begin{cases} y^1_{n+1} & = \left[u^1_1(1-a_1)v^1_1(y^1_n) + u^1_2(1-b_1)v^1_2(y^1_n)\right] y^1_n \\ & + \left[u^1_1 a_2 v^2_1(y^2_n) + u^1_2 b_2 v^2_2(y^2_n)\right] y^2_n, \\ y^2_{n+1} & = \left[u^2_1 a_1 v^1_1(y^1_n) + u^2_2 b_1 v^1_2(y^1_n)\right] y^1_n \\ & + \left[u^2_1(1-a_2)v^2_1(y^2_n) + u^2_2(1-b_2)v^2_2(y^2_n)\right] y^2_n, \end{cases}$$

to which the general results on stability of equilibria established in section 1.2.1 apply.

To perform an numerical analysis of this system, set

$$f^i(y^i) := \frac{\alpha_i}{1+y^i}, \quad \alpha_i \geq 0\ ,\ i = 1, 2$$

which provides the aggregated system:

$$\begin{cases} y^1_{n+1} & = \left[\dfrac{(1-a_1)\alpha_1 s^1_1 + (1-b_1)(1+y^1_n))}{1+\alpha_1 s^1_1 + y^1_n}\right] y^1_n \\ & + \left[\dfrac{s^2_1(a_2\alpha_2 + b_2(1+y^2_n)/s^1_1)}{1+\alpha_2 s^2_1 + y^2_n}\right] y^2_n \\ y^2_{n+1} & = \left[\dfrac{s^1_1(a_1\alpha_1 + b_1(1+y^1_n)/s^2_1)}{1+\alpha_1 s^1_1 + y^1_n}\right] y^1_n \\ & + \left[\dfrac{(1-a_2)\alpha_1 s^2_1 + (1-b_2)(1+y^2_n)}{1+\alpha_2 s^2_1 + y^2_n}\right] y^2_n \end{cases}$$

whose fixed points are the solutions to

$$(1.42) \quad \begin{cases} 0 & = & -\dfrac{a_1\alpha_1 s^1_1 + b_1(1+y^1)}{1+\alpha_1 s^1_1 + y^1}\ y^1 + \dfrac{s^2_1(a_2\alpha_2 + b_2(1+y^2)/s^1_1)}{1+\alpha_2 s^2_1 + y^2}\ y^2 \\ 0 & = & \dfrac{s^1_1(a_1\alpha_1 + b_1(1+y^1)/s^2_1)}{1+\alpha_1 s^1_1 + y^1}\ y^1 - \dfrac{a_2\alpha_1 s^2_1 + b_2(1+y^2)}{1+\alpha_2 s^2_1 + y^2}\ y^2. \end{cases}$$

Obviously, $(y^1_0, y^2_0) := (0, 0)$ is a fixed point to equation (1.42). Moreover, there are no fixed points of the form $(y^1, 0)$ or $(0, y^2)$ with $y^1 > 0$ or $y^2 > 0$. Further

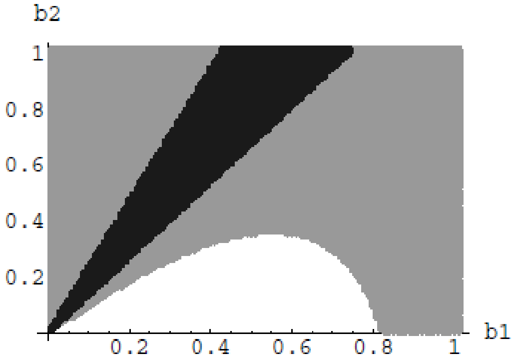

Figure 1.1: Basins of attraction of the asymptotically stable fixed points (0, 0), (3.44, 1.57) (too small to be plotted in this picture) and (5.36, 2.68). Parameter values: $a_1 = 0.1$, $a_2 = 0.3$, $b_1 = 0.3$, $b_2 = 0.7$, $\alpha_1 = 100$, $\alpha_2 = 45$, $s_1^1 = 0.3$, $s_1^2 = 0.1$.

calculations give rise to

$$y^2 = \frac{a_2 b_1 \alpha_2 (y^1 + 1)}{a_1 b_2 \alpha_1} - 1$$

where y^1 is any solution to equation

$$\frac{a_1 \alpha_1 s_1^1 + b_1(1 + y^1)}{1 + \alpha_1 s_1^1 + y^1}\, y^1 = \frac{s_1^2 \left(a_2 \alpha_2 + \frac{a_2 b_1 \alpha_2 (1+y^2)}{a_1 \alpha_1 s_1^1} \right)}{\alpha_2 s_1^2 + \frac{a_2 b_1 \alpha_2 (1+y^1)}{a_1 b_2 \alpha_1}} \left[\frac{a_2 b_1 \alpha_2 (y^1 + 1)}{a_1 b_2 \alpha_1} - 1 \right].$$

Numerical experiments carried out using a large range for the parameters show that there are several scenarios for which there exists a positive asymptotically stable fixed point, as well as several scenarios for which there exist two positive asymptotically stable fixed points. This is shown for particular values of the parameters in figure 1.1 and figure 1.2.

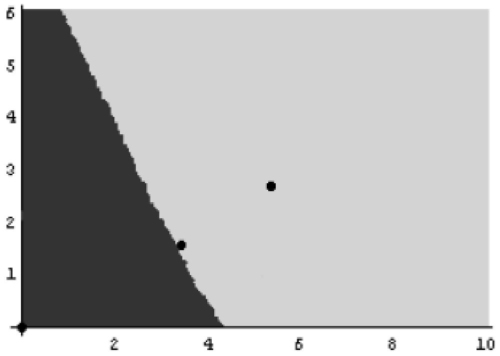

Figure 1.2: From white to black, zones with none, one or two positive asymptotically stable fixed points. Parameter values: $a_1 = 0.1$, $a_2 = 0.3$, $b_1 = 0.3$, $b_2 = 0.7$, $\alpha_1 = 100$, $\alpha_2 = 45$, $s_1^1 = 0.3$, $s_1^2 = 0.1$. b_1 and b_2 range from 0.01 up to 1.0, step 0.005.

Conclusions.

In this section we have presented a general class of nonlinear two-time scales discrete dynamical systems susceptible of being reduced by means of the so-called aggregation of variables method. These systems can be used as models for population dynamics that combine both migratory and demographic processes taking place at different time scales. In the applications proposed herein we have considered situations in which demography can be considered fast with respect to migration and, conversely, models in which displacement are faster than demography.

In both cases, we have let the fast dynamics depend on global variables. Even if its not a general assumption, when incorporated to simple two time scale models it turned out to promote richer behavior. Namely, Alleé effect, multi attractor scenarios or even reinterpretation of classical population models. These results point out the importance of considering two time scale models including a sort of self-regulation at the fast time scale. That is, models where within the fast time scale how individuals evolve depend on the current state of these individuals, rather that on the total population size or other global variable.

The following section goes in this direction.

1.3 Fast dynamics depending on some state variables.

The approach of this section is motivated by the study of a host-parasitoid model [72]. In this work, we consider hosts and parasitoids spread in a chain of patches. Assuming individual movements between patches to be faster than host-parasitoid interactions at each patch yields a two time scales system. On the one hand, hosts migration rates were constant. On the other hand, parasitoids seek for those regions were host density is high avoiding those with low host density. Thus, parasitoid migration rates from each patch depend on hosts density in that patch. We are still dealing with a population structured into two groups (hosts and parasitoids) and subgroups (host and parasitoid densities in each region).

Next, we generalize this schema to an arbitrary amount of groups and subgroups.

1.3.1 General settings and main results.

We proceed with the theoretical settings. Without lost of generality, we refer to a population divided in q groups, and each group for $i = 1, \cdots, q$ divided into N_i subgroups. Let x_n^{ij} stand for the number of individuals of subgroup j, $(j = 1, \cdots, N_i)$ of group i at time n. The state variables in group j are collected in vector $\mathbf{x}_n^i$ at time n which in turn are assembled in vector

$$X_n = (\mathbf{x}_n^1, \cdots, \mathbf{x}_n^q).$$

The novelty relies in the fact that, at the fast time scale, the evolution of some groups depends on the state of other group at the fast time scale. We classify groups in two different classes. On the one hand those evolving independently at the fast time scale, whose fast dynamics is represented by a constant matrix. Without lost of generality, these groups are assumed to be the first h and are labeled by $I_1 := \{1, \cdots, h\}$. On the other hand, the rest of the groups, the $q - h$ groups, labeled with $I_2 := \{h + 1, \cdots, q\}$, whose dynamics depend on the state variables of those groups in I_1. We note the population corresponding to both subsets by $X^1 = (\mathbf{x}^1, \cdots, \mathbf{x}^h) \in \mathbb{R}^{d_1}$, with $d_1 = N_1 + \cdots + N_h$, and $X^2 = (\mathbf{x}^{h+1}, \cdots, \mathbf{x}^q) \in \mathbb{R}^{d_2}$, with $d_2 = N_{h+1} + \cdots + N_q$, respectively. Thus, we have $X = (X^1, X^2)$ and $d_1 + d_2 = N$. We assume that $X \in \Omega_N \subset \mathbb{R}^N$, where Ω_N is an open bounded nonempty set. We also note

$$\Omega_{d_1} := \left\{X^1 \in \mathbb{R}^{d_1};\ \exists X^2 \in \mathbb{R}^{d_2};\ (X^1, X^2) \in \Omega_N\right\}$$

and

$$\Omega_{d_2} := \left\{X^2 \in \mathbb{R}^{d_2};\ \exists X^1 \in \mathbb{R}^{d_1};\ (X^1, X^2) \in \Omega_N\right\}$$

the restrictions of Ω_N to $\mathbb{R}^{d_1}$ and $\mathbb{R}^{d_2}$, respectively.

We assume that fast dynamics is conservative of the total number of individuals and internal to each group. We represent it by means of a block diagonal matrix $\mathcal{F}$ with q blocks (one for each group). Let $\mathcal{F}_1$ be the submatrix of $\mathcal{F}$ describing the evolution of groups belonging to I_1, that is,

$$\mathcal{F}_1 = \mathsf{diag}(\mathcal{F}_{1,1}, \cdots, \mathcal{F}_{1,h}) \tag{1.43}$$

where each block $\mathcal{F}_{1,i}$ is a regular stochastic matrix for $i = 1, \cdots, h$. Let $\mathcal{F}_2$ be the submatrix of $\mathcal{F}$ describing the evolution of groups belonging to I_2 depends on $X^1 \in \Omega_{d_1}$ through

$$\mathcal{F}_2(X^1) = \mathsf{diag}(\mathcal{F}_{2,h+1}(X^1), \cdots, \mathcal{F}_{2,q}(X^1)) \tag{1.44}$$

where $\mathcal{F}_2(\cdot) \in \mathcal{C}^2(\Omega_{d_1})$ and for each $X^1 \in \Omega_{d_1}$ each block $\mathcal{F}_{2,j}(X^1)$ is also a regular stochastic matrix, for $j = h+1, \cdots, q$. Thus, fast dynamics is given by

$$F(X) = \begin{pmatrix} \mathcal{F}_1 & 0 \\ 0 & \mathcal{F}_2(X^1) \end{pmatrix} \begin{pmatrix} X^1 \\ X^2 \end{pmatrix}. \tag{1.45}$$

Finally, combining fast dynamics with a general slow process represented by $S \in \mathcal{C}^1(\Omega_N)$ yields the general system

$$X_{k,n+1} = S \circ F^{(k)}(X_{k,n}) \tag{1.46}$$

where k represents the ratio of the fast to the slow time scale. From (1.45), straightforward calculations yield

$$F^{(k)}(X) = \begin{pmatrix} \mathcal{F}_1^k & 0 \\ & \\ 0 & \mathcal{F}_2\left(\mathcal{F}_1^{k-1}X^1\right) \ldots \mathcal{F}_2\left(\mathcal{F}_1^1 X^1\right) \mathcal{F}_2\left(X^1\right) \end{pmatrix} \begin{pmatrix} X^1 \\ X^2 \end{pmatrix} \tag{1.47}$$

thus, first block evolves according to the powers of $\mathcal{F}_1$ while the dynamics of the second block is governed by means of an inhomogeneous matrix product.

The goal of this section consists in proving that system (1.46) is susceptible of being aggregated according to [90]. So we start by showing that hypotheses 1.1.4 holds; i.e., there exists $\bar{F}(X)$, the pointwise limit of $F^{(k)}(X)$ as $k \to \infty$, that can be appropriately decomposed allowing the definition of global variables and the reduction of the system.

We have assumed that $\mathcal{F}_{1,i}$ is a regular stochastic matrix for any $i \in I_1$. In this case, it is well known that

$$\lim_{k\to\infty} \mathcal{F}_{1,i}^k = \bar{\mathcal{F}}_{1,i} = \mathbf{v}_{1,i}\mathbf{1}^T$$

where $\mathbf{1}^T = (1, \cdots, 1)$ (of appropriate dimension) and $\mathbf{v}_{1,i}$ are, respectively, the left and right eigenvectors associated to the eigenvalue 1 such that $\mathbf{1}^T\mathbf{v}_{1,i} = 1$. We define

$$\begin{aligned} \bar{\mathcal{F}}_1 &:= \mathsf{diag}(\bar{\mathcal{F}}_{1,1}, \cdots, \bar{\mathcal{F}}_{1,h}) \\ &= \mathsf{diag}(\mathbf{v}_{1,1}, \cdots, \mathbf{v}_{1,h})\mathsf{diag}(\mathbf{1}_{1,1}^T, \cdots, \mathbf{1}_{1,h}^T) \\ &=: \mathcal{V}_1\mathcal{U}_1 \end{aligned} \tag{1.48}$$

In the same way, we have assumed that $\mathcal{F}_{2,i}(X^1)$ is a regular stochastic matrix for any $i \in I_2$ and any $X^1 \in \Omega_{d_1}$. Thus,

$$\lim_{k\to\infty} \mathcal{F}_{2,i}^k(X^1) = \bar{\mathcal{F}}_{2,i}(X^1) = \mathbf{v}_{2,i}(X^1)\mathbf{1}^T, \qquad \forall X^1 \in \Omega_{d_1},$$

where $\mathbf{1}^T$ and $\mathbf{v}_{2,i}(X^1)$ are, respectively, the left and right eigenvectors associated to the eigenvalue 1 such that $\mathbf{1}^T\mathbf{v}_{2,i}(X^1) = 1$. We define

$$\begin{aligned} \bar{\mathcal{F}}_2(X^1) &:= \mathsf{diag}(\bar{\mathcal{F}}_{2,h+1}(X^1), \cdots, \bar{\mathcal{F}}_{2,q}(X^1)) \\ &= \mathsf{diag}(\mathbf{v}_{2,h+1}(X^1), \cdots, \mathbf{v}_{2,q}(X^1))\mathsf{diag}(\mathbf{1}_{1,1}^T, \cdots, \mathbf{1}_{1,h}^T) \\ &=: \mathcal{V}_2(X^1)\mathcal{U}_2 \end{aligned} \tag{1.49}$$

Proposition 1.3.1 *Assume that the entries of matrix $\mathcal{F}_2(\cdot) \in \mathcal{C}^1(\Omega_{d_1})$ are continuous functions of $X^1 \in \Omega_{d_1}$. Then, the entries of matrix $\bar{\mathcal{F}}_2(\cdot)$ are continuous functions of $X^1 \in \Omega_{d_1}$ too. Assuming previous settings for every $X = (X^1, X^2) \in \Omega_N$ the pointwise limit of the sequence $\{F^{(k)}(X)\}$ exists:*

$$\bar{F}(X) := \lim_{k\to\infty} F^{(k)}(X) = \begin{pmatrix} \bar{\mathcal{F}}_1 & 0 \\ 0 & \bar{\mathcal{F}}_2\left(\bar{\mathcal{F}}_1 X^1\right) \end{pmatrix} \begin{pmatrix} X^1 \\ X^2 \end{pmatrix}$$

Proof.– From the expression of $F^{(k)}(X)$ and the definitions of $\bar{\mathcal{F}}_1$ and $\bar{\mathcal{F}}_2$ the only fact remaining to be proved is that

$$\lim_{k\to\infty} \mathcal{F}_2\left(\mathcal{F}_1^{k-1}X^1\right)\cdot\mathcal{F}_2\left(\mathcal{F}_1^{k-2}X^1\right)\cdot\ldots\cdot\mathcal{F}_2\left(\mathcal{F}_1X^1\right)\cdot\mathcal{F}_2\left(X^1\right)=\bar{\mathcal{F}}_2\left(\bar{\mathcal{F}}_1X^1\right) \tag{1.50}$$

Unless otherwise stated the matrix norm that we use is the 1-norm, i.e., for any matrix $A=(a_{ij})_{i,j=1}^n$, $\|A\|=\sup\limits_{j=1,\ldots,n}\sum\limits_{i=1}^n|a_{ij}|$. If A is stochastic then $\|A\|=1$ and if A and B are both stochastic they verify $\|A-B\|\leq 2$. From theorem 1.2 in [93] we get that

$$\|\mathcal{F}_1^k-\bar{\mathcal{F}}_1\|=o(\gamma^k) \tag{1.51}$$

for any γ such that $|\lambda_2|<\gamma<1$, being λ_2 the subdominant eigenvalue of matrix $\mathcal{F}_1$. The fact that $\mathcal{F}_2(\cdot)\in\mathcal{C}^1(\Omega_{d_1})$ implies that there exist a constant $M>0$ such that

$$\|\mathcal{F}_2\left(\mathcal{F}_1^kX^1\right)-\mathcal{F}_2\left(\bar{\mathcal{F}}_1X^1\right)\|\leq M\|\mathcal{F}_1^k-\bar{\mathcal{F}}_1\| \tag{1.52}$$

And, thus, from (1.51) and (1.52) we obtain that for any $\varepsilon'>0$ there exist k_0' such that for every $k\geq k_0'$ we have

$$\|\mathcal{F}_2\left(\mathcal{F}_1^kX^1\right)-\mathcal{F}_2\left(\bar{\mathcal{F}}_1X^1\right)\|\leq\varepsilon'\gamma^k \tag{1.53}$$

We also have that

$$\lim_{k\to\infty}\|\mathcal{F}_2^k\left(\bar{\mathcal{F}}_1X^1\right)-\bar{\mathcal{F}}_2\left(\bar{\mathcal{F}}_1X^1\right)\|=0 \tag{1.54}$$

and, thus, for any $\varepsilon''>0$ we can choose k_0'' such that for every $k\geq k_0''$ it holds that

$$\|\mathcal{F}_2^k\left(\bar{\mathcal{F}}_1X^1\right)-\bar{\mathcal{F}}_2\left(\bar{\mathcal{F}}_1X^1\right)\|<\varepsilon'' \tag{1.55}$$

Now, with the help of (1.53) and (1.55), let us prove (1.50): For any $\varepsilon>0$, let k_0' and k_0'' be the positive integers for which taking, respectively, $\varepsilon'=(1-\gamma)\varepsilon/2$ and $\varepsilon''=\varepsilon/6$ we have that (1.53) and (1.55) hold, and choose $k_0=k_0'+k_0''$. The proof will be finished as soon a we show that for any $k\geq k_0$ we have that

$$\|\mathcal{F}_2\left(\mathcal{F}_1^{k-1}X^1\right)\mathcal{F}_2\left(\mathcal{F}_1^{k-2}X^1\right)\cdots\mathcal{F}_2\left(\mathcal{F}_1X^1\right)\mathcal{F}_2\left(X^1\right)-\bar{\mathcal{F}}_2\left(\bar{\mathcal{F}}_1X^1\right)\|<\varepsilon \tag{1.56}$$

To simplify notations let us call $\mathcal{F}_k = \mathcal{F}_2\left(\mathcal{F}_1^{k-1}X^1\right)$, $\mathcal{F} = \mathcal{F}_2\left(\bar{\mathcal{F}}_1 X^1\right)$ and $\bar{\mathcal{F}} = \bar{\mathcal{F}}_2\left(\bar{\mathcal{F}}_1 X^1\right)$. With this notation the first term in (1.56) become:

$$\begin{aligned}
&\left\|\mathcal{F}_k \cdot \mathcal{F}_{k-1} \cdot \ldots \cdot \mathcal{F}_1 - \bar{\mathcal{F}}\right\| \\
&\leq \left\|\mathcal{F}_k \cdot \mathcal{F}_{k-1} \cdot \ldots \cdot \mathcal{F}_1 - \mathcal{F}^k\right\| + \left\|\mathcal{F}^k - \bar{\mathcal{F}}\right\| \\
&\leq \left\|\mathcal{F}_k \cdot \mathcal{F}_{k-1} \cdot \ldots \cdot \mathcal{F}_1 - \mathcal{F} \cdot \mathcal{F}_{k-1} \cdot \ldots \cdot \mathcal{F}_1\right\| \\
&+ \left\|\mathcal{F} \cdot \mathcal{F}_{k-1} \cdot \ldots \cdot \mathcal{F}_2 \cdot \mathcal{F}_1 - \mathcal{F}^k\right\| + \left\|\mathcal{F}^k - \bar{\mathcal{F}}\right\| \\
&\leq \left\|\mathcal{F}_k - \mathcal{F}\right\| + \left\|\mathcal{F} \cdot \left(\mathcal{F}_{k-1} \cdot \ldots \cdot \mathcal{F}_2 \cdot \mathcal{F}_1 - \mathcal{F}^{k-1}\right)\right\| + \left\|\mathcal{F}^k - \bar{\mathcal{F}}\right\| \\
&\leq \cdots \leq \\
&\leq \sum_{s=k-k_0''+1}^{k} \left\|\mathcal{F}_s - \mathcal{F}\right\| + \left\|\mathcal{F}^{k_0''} \cdot \left(\mathcal{F}_{k-k_0''} \cdot \ldots \cdot \mathcal{F}_2 \cdot \mathcal{F}_1 - \mathcal{F}^{k-k_0''}\right)\right\| \\
&+ \left\|\mathcal{F}^k - \bar{\mathcal{F}}\right\| \\
&\leq \sum_{s=k-k_0''+1}^{k} \varepsilon'\gamma^s + \left\|(\mathcal{F}^{k_0''} - \bar{\mathcal{F}}) \cdot \left(\mathcal{F}_{k-k_0''} \cdot \ldots \cdot \mathcal{F}_2 \cdot \mathcal{F}_1 - \mathcal{F}^{k-k_0''}\right)\right\| \\
&+ \left\|\bar{\mathcal{F}} \cdot \left(\mathcal{F}_{k-k_0''} \cdot \ldots \cdot \mathcal{F}_2 \cdot \mathcal{F}_1 - \mathcal{F}^{k-k_0''}\right)\right\| + \varepsilon'' \\
&\leq \frac{\varepsilon'}{1-\gamma} + 2\varepsilon'' + 0 + \varepsilon'' = \varepsilon.
\end{aligned}$$

■

As a direct consequence of proposition 1.3.1, we get the corresponding *auxiliary system*

$$X_{n+1} = S \circ \bar{F}\left(X_n\right) X_n = S\left(\bar{\mathcal{F}}_1 X_n^1,\, \bar{\mathcal{F}}_1(\bar{\mathcal{F}}_1 X_n^1) X_n^2\right)$$

Next, we build up an aggregated system for system (1.46) decomposing $\bar{F}(X)$ as hypothesis 1 prescribes. Namely, thanks to (1.48) and (1.49), we define functions

$$G(X) := \left(\mathcal{U}_1 X^1, \mathcal{U}_2 X^2\right) \in \mathbb{R}^h \times \mathbb{R}^{q-h}$$

and

$$E(Y) := \left(\mathcal{V}_1 Y^1, \mathcal{V}_2(Y^1) Y^2\right) \in \mathbb{R}^{d_1} \times \mathbb{R}^{d_2}$$

From (1.48) and (1.49) we obtain that

$$\bar{F}(X) = \left(\mathcal{V}_1\mathcal{U}_1X^1, \mathcal{V}_2(X^1)\mathcal{U}_2X^2\right).$$

We Define global variables as

$$Y = (Y^1, Y^2) = G(X) = \left(\mathcal{U}_1X^1, \mathcal{U}_2X^2\right), \tag{1.57}$$

we note $\Omega_q := (\mathcal{U}_1\,\mathcal{U}_2)\Omega_N$ and, finally, we get the *aggregated system*

$$Y_{n+1} = \left(\mathcal{U}_1 \quad \mathcal{U}_2 \right) S\left(\mathcal{V}_1Y_n^1, \mathcal{V}_2(Y_n^1)Y_n^2\right) \tag{1.58}$$

We recall that the aggregated system is a q-dimensional one, while the complete system is of dimension N, with $N > q$. In order to apply theorem 1.1.7 to system (1.46) we focus now in proving that $F(X)$ verifies hypothesis 1.1.8. We need to prove that limits

$$\lim_{k\to\infty} F^{(k)}(X) = \bar{F}(X) \tag{1.59}$$

and

$$\lim_{k\to\infty} DF^{(k)}(X) = D\bar{F}(X) \tag{1.60}$$

are uniform on compact sets of Ω_N.

Proposition 1.3.2 *Under the previous conditions, limit* (1.59) *is uniform on compact sets of* Ω_N.

Proof.– It is a consequence of proposition 1.3.1. Getting back to the proof (and notation) of that proposition, we just need to prove that k_0' and k_0'' can be chosen independently of $X' \in \mathcal{K}^1$ where $\mathcal{K}^1$ is the projection on $\mathbb{R}^{d_1}$ of the compact set $\mathcal{K} \in \Omega_N$.

The fact that $\displaystyle\bigcup_{k=0}^{\infty}\{\mathcal{F}_1^kX^1 : X^1 \in \mathcal{K}^1\}$ is bounded, due to the convergence of $\{\mathcal{F}_1^kX^1\}$, implies that we can choose a unique M in (1.52) valid for any $X^1 \in \mathcal{K}^1$ and thus the same holds for k_0' in (1.53). Concerning k_0'', we notice that

$$\begin{aligned}
&\|\mathcal{F}_2^{k+1}\left(\bar{\mathcal{F}}_1X^1\right) - \bar{\mathcal{F}}_2\left(\bar{\mathcal{F}}_1X^1\right)\| \\
&= \|\mathcal{F}_2^{k+1}\left(\bar{\mathcal{F}}_1X^1\right) - \bar{\mathcal{F}}_2\left(\bar{\mathcal{F}}_1X^1\right)\cdot\mathcal{F}_2\left(\bar{\mathcal{F}}_1X^1\right)\| \\
&\leq \|\mathcal{F}_2^{k}\left(\bar{\mathcal{F}}_1X^1\right) - \bar{\mathcal{F}}_2\left(\bar{\mathcal{F}}_1X^1\right)\|\cdot\|\mathcal{F}_2\left(\bar{\mathcal{F}}_1X^1\right)\| \\
&= \|\mathcal{F}_2^{k}\left(\bar{\mathcal{F}}_1X^1\right) - \bar{\mathcal{F}}_2\left(\bar{\mathcal{F}}_1X^1\right)\|
\end{aligned}$$

and so $\{\|\mathcal{F}_2^k\left(\bar{\mathcal{F}}_1X^1\right) - \bar{\mathcal{F}}_2\left(\bar{\mathcal{F}}_1X^1\right)\|\}_{k\in\mathbb{N}}$ is a non increasing sequence of continuous functions defined on a compact set $\mathcal{K}^1$ and converging pointwise to the continuous function 0, what implies its uniform convergence.

■

In order to prove that limit (1.60) is uniform on compact sets we first calculate the Jacobian matrices of functions $\bar{F}(X)$ and $F^{(k)}(X)$; that is

$$J\bar{F}(X) = \begin{pmatrix} \bar{F}_1 & 0 \\ J_{X^1}\left(\bar{\mathcal{F}}_2(\bar{\mathcal{F}}_1X^1)X^2\right) & \bar{F}_2(\bar{F}_1X^1) \end{pmatrix}$$

$$JF^{(k)}(X) = \begin{pmatrix} F_1^k & 0 \\ J_{X^1}\left(\prod_{j=0}^{k-1}\mathcal{F}_2(\mathcal{F}_1^{k-j-1}X^1)X^2\right) & \prod_{j=0}^{k-1}\mathcal{F}_2(\mathcal{F}_1^{k-j-1}X^1) \end{pmatrix}$$

Comparing those expressions and thanks to proposition 1.3.2, the only thing we need to prove is that

$$\lim_{k\to\infty} J_{X^1}\left(\prod_{j=0}^{k-1}\mathcal{F}_2(\mathcal{F}_1^{k-j-1}X^1)X^2\right) = J_{X^1}\left(\bar{\mathcal{F}}_2(\bar{\mathcal{F}}_1X^1)X^2\right) \tag{1.61}$$

is uniform on compact sets. There is some previous work to be done before proceeding;

Lemma 1.3.3 *Given a matrix function $A(X^1)$, it follows that*

$$J_{X^1}\left(A(X^1)X^2\right)$$

is a matrix of dimension $d_2 \times d_1$ such that each column $j = 1, \cdots, d_1$ is of the form

$$\tfrac{\partial}{\partial x_j^1}\left(A(X^1)\right)X^2$$

where we use the notation $X^1 = (x_1^1, \cdots, x_{d_1}^1)$.

Proof.– Straightforward calculations yield the result.

■

Lemma 1.3.4 *Let $\Omega_{d_1} \subset \mathbb{R}^{d_1}$ be an open bounded nonempty set and $\mathcal{M}(\cdot) \in \mathcal{C}^2(\Omega_{d_1})$ be a matrix function such that for each $X^1 \in \Omega_{d_1}$, $\mathcal{M}(X^1)$ is a regular stochastic matrix, $\mathbf{v}(X^1) > 0$ be the unique eigenvector of matrix $\mathcal{M}(X^1)$ associated to eigenvalue 1 that verifies $\mathbf{1}^T\mathbf{v}(X^1) = 1$ and $\mathbf{v}(X^1)\mathbf{1}^T = \bar{\mathcal{M}}(X^1)$. Then,*

1. *Vector* $\mathbf{v}(X^1)$ *and matrix* $\bar{\mathcal{M}}(X^1)$ *are functions of class* $\mathcal{C}^2(\Omega_{d_1})$*.*
2. *Limit*
$$\lim_{k\to\infty} (\mathcal{M}(X^1))^k = \bar{\mathcal{M}}(X^1)$$
is uniform on compact sets of Ω_{d_1}*, where the super index* k *stands for the powers of* $\mathcal{M}(X^1)$*.*
3. *Limit*
$$\lim_{k\to\infty} \tfrac{\partial}{\partial x_j^1} \left(\mathcal{M}(X^1)\right)^k = \tfrac{\partial}{\partial x_j^1}\bar{\mathcal{M}}(X^1)$$
is uniform on compact sets of Ω_{d_1} *for* $j = 1, \cdots, s$*.*

Proof.– It follows easily from those of lemma 1.2.1 and proposition 1.2.2.

■

In order to keep the exposition as clear as possible, an without loss of generality, we assume from now on that matrix $\mathcal{F}_2$ consists on a single block. We recall that function matrix $\mathcal{F}_2(\cdot) \in \mathcal{C}^2(\Omega_{d_1})$. Using lemma 1.3.4 we already know that function matrix $\bar{\mathcal{F}}_2(\cdot) \in \mathcal{C}^2(\Omega_{d_1})$. Consider the Jordan form to matrix $\mathcal{F}_2(X^1)$, it follows that

$$(1.62)\qquad \begin{aligned} \mathcal{F}_2(X^1) &= (\mathbf{v}(X^1)|\mathcal{R}_2(X^1)) \begin{pmatrix} 1 & O \\ O & \mathcal{H}_2(X^1) \end{pmatrix} \begin{pmatrix} \mathbf{1}^T \\ \mathcal{S}_2(X^1) \end{pmatrix} \\ &= \bar{\mathcal{F}}_2(X^1) + \mathcal{Q}(X^1), \end{aligned}$$

where

$$(1.63)\qquad \mathcal{Q}(X^1) := \mathcal{R}_2(X^1)\mathcal{H}_2(X^1)\mathcal{S}_2(X^1) = \mathcal{F}_2(X^1) - \bar{\mathcal{F}}_2(X^1),$$

$\mathcal{R}_2(X^1)$ and $\mathcal{S}_2(X^1)$ are suitable matrices and $\mathcal{H}_2(X^1)$ corresponds with the Jordan blocks of $\mathcal{F}_2(X^1)$ associated to eigenvalues of modulus strictly smaller than 1. We recall that

$$\rho(\mathcal{Q}(X^1)) < 1,$$

where ρ stands for the spectral radius. Besides, from its definition, matrix function $\mathcal{Q}_2(\cdot) \in \mathcal{C}^2(\Omega_q)$. It is clear that columns of $\mathcal{F}_2(X^1)$ and $\bar{\mathcal{F}}_2(X^1)$ sum 1 and therefore, from equation (1.62) any column of $\mathcal{Q}(X^1)$ sums up to 0. Then, it is straightforward that

$$\bar{\mathcal{F}}_2(X^1)\bar{\mathcal{F}}_2(X^1) = \bar{\mathcal{F}}_2(X^1), \qquad \bar{\mathcal{F}}_2(X^1)\mathcal{Q}(X^1) = 0,$$

in particular matrix $\bar{\mathcal{F}}_{2j}$ is idempotent.

Lemma 1.3.5 *Let* $\mathcal{Q}(\cdot) \in \mathcal{C}^2(\Omega_{d_1})$ *be a matrix function defined in* (1.63)*. Let* $\mathcal{K}^1 \subset \mathbb{R}^{d_1}$ *be a compact set such that* $\mathcal{F}_1^k \mathcal{K}^1$ *is in the domain of* $\mathcal{Q}$ *for* $k = 0, 1, 2, \cdots$*. Then, there exist a positive constants* $C > 0$*,* $\beta \in (0,1)$ *and positive integer* $m_0 > 0$ *such that for all* $X^1 \in \mathcal{K}^1$ *and for all* $k \geq p \geq m_0$ *it follows that*

$$\|\mathcal{Q}(\mathcal{F}_1^k X^1)\mathcal{Q}(\mathcal{F}_1^{k-1} X^1)\cdots \mathcal{Q}(\mathcal{F}_1^p X^1)\| \leq C\beta^{k-p+1}$$

Proof.– Let us define

$$\bar{\mathcal{K}}^1 := \mathsf{Cl}\left\{\mathcal{F}_1^j X^1;\ X^1 \in \mathcal{K}^1,\ j = 0,1,2,\cdots\right\},$$

where $\mathsf{Cl}(\mathcal{X})$ stands for the clausure of $\mathcal{X}$. The spectral radius of a matrrix depends contiunuosly on the coefficients of this matrix. Thus, there exists

$$\max_{X^1 \in \bar{\mathcal{K}}^1} \rho\left(\mathcal{Q}(X^1)\right) = \hat{\beta}$$

and we can choose $\beta \in (\hat{\beta}, 1)$. On the other hand, for each $X^1 \in \bar{\mathcal{K}}^1$ a norm $\|\cdot\|_{X^1}$ exists such that

$$\|\mathcal{Q}(X^1)\|_{X^1} < \beta$$

and, because of the continuity of the norm, there exists $\delta_{X^1} > 0$ such that

$$\|X^1 - Y^1\| < 2\delta_{X^1} \Rightarrow \|\mathcal{Q}(Y^1)\|_{X^1} < \beta.$$

Let us note

$$V_{X^1} := \left\{Y^1 \in \bar{\mathcal{K}}^1;\ \|X^1 - Y^1\| < \delta_{X^1}\right\}.$$

Then, $= \{V_{X^1}\}_{Y^1 \in \bar{\mathcal{K}}^1}$ is a open covering of the compact set $\bar{\mathcal{K}}^1$ so that we can choose a finite subcovering, that is

$$\bar{\mathcal{K}}^1 \subset V_{X_1^1} \cup \cdots \cup V_{X_k^1}.$$

We define

$$\delta := \min\left\{\delta_{X_1^1}, \cdots, \delta_{X_k^1}\right\}$$

and we chose an integer $m_0 > 0$ such that for all $m \geq m_0$

$$\max_{X^1 \in \bar{\mathcal{K}}^1} \|\bar{\mathcal{F}}_1 X^1 - \mathcal{F}_1^m X^1\| < \delta.$$

Given $X^1 \in \mathcal{K}^1$ there exists $j \in \{1, \cdots, k\}$ such that $\bar{\mathcal{F}}_1 X^1 \in V_{X_j^1}$; therefore, for each $m \geq m_0$ it follows that

$$\|\mathcal{F}_1^m X^1 - X_j^1\| \leq \|\mathcal{F}_1^m X^1 - \bar{\mathcal{F}}_1 X^1\| + \|\bar{\mathcal{F}}_1 X^1 - X_j^1\| < \delta + \delta_{X_j^1} \leq 2\delta_{X_j^1}$$

and

$$\|\mathcal{Q}(\mathcal{F}_1^m X^1)\|_{X_j^1} < \beta.$$

From the last inequality, we get that

$$\|\mathcal{Q}(\mathcal{F}_1^k X^1)\mathcal{Q}(\mathcal{F}_1^{k-1} X^1)\cdots\mathcal{Q}(\mathcal{F}_1^m X^1)\|_{X_j^1} \leq \beta^{k-p+1}$$

for all $k \geq p \geq m_0$, $X^1 \in \mathcal{K}^1$ such that $\bar{\mathcal{F}}_1 X^1 \in V_{X_j^1}$. Finally, because of the equivalence of norms, there exists $C > 0$ such that

$$\|\cdot\|_1 \leq C\|\cdot\|_{X_j^1} \qquad \forall\, j = 1, \cdots, k$$

which finishes the proof.

■

Lemma 1.3.6 *There exist constants* $\pi_j > 0$, *for* $j \in \{1, \cdots, x_{d_1}\}$ *such that*

$$\sup_{\substack{k\,\in\,\mathbb{N}\\ X^1\,\in\,\mathcal{K}^1}} \left\| \frac{\partial}{\partial x_j^1} \prod_{j=0}^{k-1} \mathcal{F}_2(\mathcal{F}_1^{k-j-1} X^1) \right\|_1 = \pi_j$$

Proof.– Let us introduce some notation which will be kept up to the end of these chapter:

$$\mathcal{F}_j \equiv \mathcal{F}_2(\mathcal{F}_1^{j-1} X^1), \qquad \bar{\mathcal{F}}_j \equiv \bar{\mathcal{F}}_2(\mathcal{F}_1^{j-1} X^1), \qquad \mathcal{Q}_j \equiv \mathcal{F}_j - \bar{\mathcal{F}}_j,$$

$$\mathcal{P}_k(X^1) \equiv \prod_{j=0}^{k-1} \mathcal{F}_2(\mathcal{F}_1^{k-j-1} X^1) = \mathcal{F}_k \cdots \mathcal{F}_1 \qquad \text{and} \qquad \mathcal{P}_{j,k} := \mathcal{F}_k \cdots \mathcal{F}_j$$

We ward that with this notation, when $j = 2$, $\mathcal{F}_2(\mathcal{F}_1^{j-1} X^1)$ is noted by $\mathcal{F}_2$, which should be not confussed with $\mathcal{F}_2(\cdot)$ defined in (1.44). For a fixed integer $m_0 \geq 0$ it is straightforward that

$$\mathcal{P}_k = \mathcal{P}_{m_0+1,k}\mathcal{P}_{m_0},$$

which yields

$$\tfrac{\partial}{\partial x_j^1}\mathcal{P}_k = \tfrac{\partial}{\partial x_j^1}\left(\mathcal{P}_{m_0+1,k}\right)\mathcal{P}_{m_0} + \mathcal{P}_{m_0+1,k}\ \tfrac{\partial}{\partial x_j^1}\mathcal{P}_{m_0}$$

so that

$$\left\|\tfrac{\partial}{\partial x_j^1}\mathcal{P}_k\right\|_1 \leq \left\|\tfrac{\partial}{\partial x_j^1}\mathcal{P}_{m_0+1,k}\right\|_1 + \left\|\tfrac{\partial}{\partial x_j^1}\mathcal{P}_{m_0}\right\|_1$$

We also have,

$$\mathcal{P}_k \equiv \mathcal{F}_2(\mathcal{F}_1^{k-1}X^1)\mathcal{F}_2(\mathcal{F}_1^{k-2}X^1)\cdots\mathcal{F}_2(X^1) \in \mathcal{C}^1(\mathcal{K}^1),$$

therefore, there exists

$$\sup_{X^1\in\mathcal{K}^1}\left\|\tfrac{\partial}{\partial x_j^1}\mathcal{P}_{m_0}(X^1)\right\|_1 := \mathcal{D}_{m_0}.$$

Moreover, keeping in mind that $\bar{\mathcal{F}}_j\bar{\mathcal{F}}_i = \bar{\mathcal{F}}_j$ and $\bar{\mathcal{F}}_j\mathcal{Q}_i = 0$ for any $i,j = 0,1,2,\cdots$, it follows that

$$\begin{aligned}\mathcal{P}_{m_0+1,k} &= \mathcal{P}_k\cdots\mathcal{P}_{m_0+1} = (\bar{\mathcal{P}}_k+\mathcal{Q}_k)\cdots(\bar{\mathcal{P}}_{m_0}+\mathcal{Q}_{m_0})\\ &= \bar{\mathcal{F}}_k + \mathcal{Q}_k\bar{\mathcal{F}}_{k-1} + \mathcal{Q}_k\mathcal{Q}_{k-1}\bar{\mathcal{F}}_{k-2} + \cdots\\ &\quad +\mathcal{Q}_k\mathcal{Q}_{k-1}\cdots\mathcal{Q}_{m_0+2}\bar{\mathcal{F}}_{m_0+1} + \mathcal{Q}_k\mathcal{Q}_{k-1}\cdots\mathcal{Q}_{m_0+1}.\end{aligned}$$

As functions $\bar{\mathcal{F}}_2(\cdot)$ and $\mathcal{Q}(\cdot)$ are of class $\mathcal{C}^2$, there exist constants $\mathcal{D}_{\bar{\mathcal{F}}}$ and $\mathcal{D}_{\mathcal{Q}}$ such that

$$\sup_{X^1\in\mathcal{K}^1}\left\|\tfrac{\partial}{\partial x_j^1}\bar{\mathcal{F}}_2(X^1)\right\|_1 := \mathcal{D}_{\bar{\mathcal{F}}} \qquad \text{and} \qquad \sup_{X^1\in\mathcal{K}^1}\left\|\tfrac{\partial}{\partial x_j^1}\mathcal{Q}(X^1)\right\|_1 := \mathcal{D}_{\mathcal{Q}}.$$

Then, it follows that

$$\begin{aligned}\left\|\tfrac{\partial}{\partial x_j^1}\mathcal{P}_{m_0+1,k}\right\|_1 &\le \left\|\tfrac{\partial}{\partial x_j^1}\bar{\mathcal{F}}_k\right\|_1 + \left\|\tfrac{\partial}{\partial x_j^1}\mathcal{Q}_k\right\|_1 + \|\mathcal{Q}_k\|_1\left\|\tfrac{\partial}{\partial x_j^1}\bar{\mathcal{F}}_{k-1}\right\|_1\\ &+\left\|\tfrac{\partial}{\partial x_j^1}\left(\mathcal{Q}_k\mathcal{Q}_{k-1}\right)\right\|_1 + \|\mathcal{Q}_k\mathcal{Q}_{k-1}\|_1\left\|\tfrac{\partial}{\partial x_j^1}\bar{\mathcal{F}}_{k-2}\right\|_1\\ &\cdots\\ &+\left\|\tfrac{\partial}{\partial x_j^1}\left(\mathcal{Q}_k\ldots\mathcal{Q}_{m_0+2}\right)\right\|_1 + \|\mathcal{Q}_k\ldots\mathcal{Q}_{m_0+2}\|_1\left\|\tfrac{\partial}{\partial x_j^1}\bar{\mathcal{F}}_{m_0+1}\right\|_1\\ &+\left\|\tfrac{\partial}{\partial x_j^1}\left(\mathcal{Q}_k\mathcal{Q}_{k-1}\ldots\mathcal{Q}_{m_0+1}\right)\right\|_1\\ &\le \mathcal{D}_{\bar{\mathcal{F}}_2}\left(1+\|\mathcal{Q}_k\|_1+\|\mathcal{Q}_k\mathcal{Q}_{k-1}\|_1+\cdots+\|\mathcal{Q}_k\ldots\mathcal{Q}_{m_0+2}\|_1\right)\\ &+\left\|\tfrac{\partial}{\partial x_j^1}\mathcal{Q}_k\right\|_1+\cdots+\left\|\tfrac{\partial}{\partial x_j^1}\left(\mathcal{Q}_k\mathcal{Q}_{k-1}\ldots\mathcal{Q}_{m_0+1}\right)\right\|_1\end{aligned}$$

Let us point out that

$$\begin{aligned}\left\|\frac{\partial}{\partial x_j^1}\left(\mathcal{Q}_k\mathcal{Q}_{k-1}...\mathcal{Q}_j\right)\right\|_1 &= \textstyle\sum_{i=j}^k \left\|\mathcal{Q}_k...\mathcal{Q}_{1-1}\frac{\partial}{\partial x_j^1}\left(\mathcal{Q}_i\right)\mathcal{Q}_{i+1}...\mathcal{Q}_j\right\|_1 \\ &\leq \textstyle\sum_{i=j}^k \|\mathcal{Q}_k...\mathcal{Q}_{1-1}\|_1 \left\|\frac{\partial}{\partial x_j^1}\mathcal{Q}_i\right\|_1 \|\mathcal{Q}_{i+1}...\mathcal{Q}_j\|_1.\end{aligned}$$

Therefore, thanks to lemma 1.3.5 we get that

$$\left\|\frac{\partial}{\partial x_j^1}\left(\mathcal{Q}_k\mathcal{Q}_{k-1}...\mathcal{Q}_j\right)\right\|_1 \leq (k-j+1)C\beta^{k-i}\mathcal{D}_{\mathcal{Q}}C\beta^{i-j} = (k-j+1)C^2\mathcal{D}_{\mathcal{Q}}\beta^{k-j}.$$

Thus, lemma 1.3.5 implies that

$$\begin{aligned}\left\|\frac{\partial}{\partial x_j^1}\mathcal{P}_{m_0+1,k}\right\|_1 &\leq \mathcal{D}_{\bar{\mathcal{F}}_2}(1+C\beta+b\beta^2+\cdots+C\beta^{k-m_0-1}) \\ &+(k-j+1)C^2\mathcal{D}_{\mathcal{Q}}\beta^{k-j}\end{aligned}$$

which is bounded from above for all $k \geq m_0$ and for all $X^1 \in \mathcal{K}^1$. So there exists

$$\mathcal{D}_{m_0+1,k} := \sup_{\substack{k\,\in\,\mathbb{N} \\ X^1\,\in\,\mathcal{K}^1}} \left\|\frac{\partial}{\partial x_j^1}\mathcal{P}_{m_0+1,k}\right\|_1$$

and $\pi_j \leq \mathcal{D}_{m_0} + \mathcal{D}_{m_0+1,k}$.

■

Proposition 1.3.7 *Under the previous conditions along with* $\mathcal{F}_2(\cdot) \in \mathcal{C}^2(\Omega_q)$*, limit* (1.60) *is uniform on compact sets of* Ω_N*.*

Proof.– Let us fix $\varepsilon > 0$ and let $\mathcal{K}$ be a compact subset of Ω_N. Using the notation introduced in lemma 1.3.6, we have that

$$\bar{\mathcal{F}}X^2 - \mathcal{P}_kX^2 = \left(\bar{\mathcal{F}}X^2 - \mathcal{F}^kX^2\right) + \left(\mathcal{F}^kX^2 - \mathcal{P}_kX^2\right)$$

So, having in mind (1.61), lemma 1.3.3 and the fact that X^2 varies on a compact set we just need to prove that

$$\lim_{k\to\infty}\frac{\partial}{\partial x_j^1}\left(\bar{\mathcal{F}} - \mathcal{F}^k\right) = 0 \tag{1.64}$$

and

$$\lim_{k\to\infty}\frac{\partial}{\partial x_j^1}\left(\mathcal{F}^k - \mathcal{P}_k\right) = 0 \tag{1.65}$$

uniformly on $\mathcal{K}^1 := \left\{X^1 \in \mathbb{R}^{d_1};\, \exists X^2 \in \mathbb{R}^{d_2} \text{ such that } (X^1, X^2) \in \mathcal{K}\right\}$.

Limit (1.64) follows immediately from lemma 1.3.4. Therefore, there exists $\hat{k} \geq 0$ such that for all $k \geq \hat{k}$

$$\sup_{X^1 \in \mathcal{K}^1} \left\| \tfrac{\partial}{\partial x_j^1} \bar{\mathcal{F}} - \tfrac{\partial}{\partial x_j^1} \mathcal{F}^k \right\| < \frac{\varepsilon}{2}, \qquad \forall\, X^1 \in \mathcal{K}^1$$

On the other hand, regarding limit (1.65), we note that

$$\begin{aligned}
\mathcal{F}^k - \mathcal{P}_k \; &= \mathcal{F}\mathcal{F}^{k-1} - \mathcal{F}\mathcal{P}_{k-1} + \mathcal{F}\mathcal{P}_{k-1} - \mathcal{F}_k \mathcal{P}_{k-1} \\
&= \mathcal{F}\left(\mathcal{F}^{k-1} - \mathcal{P}_{k-1}\right) + \left(\mathcal{F} - \mathcal{F}_k\right)\mathcal{P}_{k-1} \\
&= \mathcal{F}\left(\mathcal{F}\left(\mathcal{F}^{k-2} - \mathcal{P}_{k-2}\right) + \left(\mathcal{F} - \mathcal{F}_{k-1}\right)\mathcal{P}_{k-2}\right) + \left(\mathcal{F} - \mathcal{F}_k\right)\mathcal{P}_{k-1} \\
&= \mathcal{F}^2\left(\mathcal{F}^{k-2} - \mathcal{P}_{k-2}\right) + \mathcal{F}\left(\mathcal{F} - \mathcal{F}_{k-1}\right)\mathcal{P}_{k-2} + \left(\mathcal{F} - \mathcal{F}_k\right)\mathcal{P}_{k-1} \\
&= \mathcal{F}^3\left(\mathcal{F}^{k-3} - \mathcal{P}_{k-3}\right) + \mathcal{F}^2\left(\mathcal{F} - \mathcal{P}_{k-2}\right)\mathcal{P}_{k-3} \\
&\quad + \mathcal{F}\left(\mathcal{F} - \mathcal{F}_{k-1}\right)\mathcal{P}_{k-2} + \left(\mathcal{F} - \mathcal{F}_k\right)\mathcal{P}_{k-1} \\
&= \mathcal{F}^\alpha\left(\mathcal{F}^{k-\alpha} - \mathcal{P}_{k-\alpha}\right) + \textstyle\sum_{j=1}^{\alpha} \mathcal{F}^{j-1}\left(\mathcal{F} - \mathcal{P}_{k-j+1}\right)\mathcal{P}_{k-j} \\
&= \left(\mathcal{F}^\alpha - \bar{\mathcal{F}}\right)\left(\mathcal{F}^{k-\alpha} - \mathcal{P}_{k-\alpha}\right) + \textstyle\sum_{j=1}^{\alpha} \mathcal{F}^{j-1}\left(\mathcal{F} - \mathcal{P}_{k-j+1}\right)\mathcal{P}_{k-j}
\end{aligned}$$

Thus;

$$\tfrac{\partial}{\partial x_j^1}\left(\mathcal{F}^k - \mathcal{P}_k\right)$$

$$= \tfrac{\partial}{\partial x_j^1}\left(\mathcal{F}^\alpha - \bar{\mathcal{F}}\right)\left(\mathcal{F}^{k-\alpha} - \mathcal{P}_{k-\alpha}\right) \tag{1.66}$$

$$+ \left(\mathcal{F}^\alpha - \bar{\mathcal{F}}\right)\tfrac{\partial}{\partial x_j^1}\left(\mathcal{F}^{k-\alpha} - \mathcal{P}_{k-\alpha}\right) \tag{1.67}$$

$$+ \sum_{j=1}^{\alpha} \tfrac{\partial}{\partial x_j^1}\left(\mathcal{F}^{j-1}\right)\left(\mathcal{F} - \mathcal{F}_{k-j+1}\right)\mathcal{P}_{k-j} \tag{1.68}$$

$$+ \sum_{j=1}^{\alpha} \mathcal{F}^{j-1}\tfrac{\partial}{\partial x_j^1}\left(\mathcal{F} - \mathcal{F}_{k-j+1}\right)\mathcal{P}_{k-j} \tag{1.69}$$

$$+ \sum_{j=1}^{\alpha} \mathcal{F}^{j-1}\left(\mathcal{F} - \mathcal{F}_{k-j+1}\right)\tfrac{\partial}{\partial x_j^1}\mathcal{P}_{k-j} \tag{1.70}$$

In the sequel we will show that there exists $\tilde{k} \geq 0$ such that for all $k \geq \tilde{k}$ each of the expression (1.66) up to (1.70) is bounded from above by $\varepsilon/10$:

1. It is straightforward that
$$\left\| \tfrac{\partial}{\partial x_j^1} \left(\mathcal{F}^\alpha - \bar{\mathcal{F}}\right) \left(\mathcal{F}^{k-\alpha} - \mathcal{P}_{k-\alpha}\right) \right\| \leq 2 \left\| \tfrac{\partial}{\partial x_j^1} \left(\mathcal{F}^\alpha - \bar{\mathcal{F}}\right) \right\|$$
and lemma 1.3.3 yields the existence of $k_1 \geq 0$ such that for all $k \geq k_1$
$$\left\| \tfrac{\partial}{\partial x_j^1} \left(\mathcal{F}^\alpha - \bar{\mathcal{F}}\right) \right\| < \frac{\varepsilon}{20}, \qquad \forall\, X^1 \in \mathcal{K}^1.$$

2. Regarding addend (1.67), reasoning as in lemma 1.3.6 it follows the existence of
$$\phi_j := \sup_{\substack{k \,\in\, \mathbb{N} \\ X^1 \,\in\, \mathcal{K}^1}} \left\| \tfrac{\partial}{\partial x_j^1} \mathcal{F}^{k-\alpha} \right\|_1$$
Then,
$$\left\| \left(\mathcal{F}^\alpha - \bar{\mathcal{F}}\right) \tfrac{\partial}{\partial x_j^1} \left(\mathcal{F}^{k-\alpha} - \mathcal{P}_{k-\alpha}\right) \right\| \leq \left(\phi_j + \pi_j\right) \left(\mathcal{F}^{k-\alpha} - \mathcal{P}_{k-\alpha}\right)$$
and it is straightforward that there exists $k_2 \geq 0$ such that for all $k \geq k_2$
$$\left\| \left(\mathcal{F}^\alpha - \bar{\mathcal{F}}\right) \tfrac{\partial}{\partial x_j^1} \left(\mathcal{F}^{k-\alpha} - \mathcal{P}_{k-\alpha}\right) \right\| < \frac{\varepsilon}{10}, \qquad \forall\, X^1 \in \mathcal{K}^1.$$

3. We deal now with (1.68); it is straightforward that
$$\left\| \sum_{j=1}^{\alpha} \tfrac{\partial}{\partial x_j^1} \left(\mathcal{F}^{j-1}\right) \left(\mathcal{F} - \mathcal{F}_{k-j+1}\right) \mathcal{P}_{k-j} \right\| \leq \phi_j \sum_{j=1}^{\alpha} \left\| \mathcal{F} - \mathcal{F}_{k-j+1} \right\|.$$
From the fact that $\mathcal{F}_1^k \to \bar{\mathcal{F}}_1$ uniformly on compact sets we get the existence of $k_3 \geq 0$ such that for all $k \geq k_3$
$$\left\| \sum_{j=1}^{\alpha} \tfrac{\partial}{\partial x_j^1} \left(\mathcal{F}^{j-1}\right) \left(\mathcal{F} - \mathcal{F}_{k-j+1}\right) \mathcal{P}_{k-j} \right\| < \frac{\varepsilon}{10}, \qquad \forall\, X^1 \in \mathcal{K}^1.$$

4. For dealing with (1.69) we recall that $\mathcal{F}_2(\cdot) \in \mathcal{C}^2(\Omega_q)$ and that $\mathcal{K}^1$ is compact; therefore, there exists Lipschitz constants L_j for the partial derivatives of $\mathcal{F}_2(\cdot)$; namely
$$\left\| \tfrac{\partial}{\partial x_j^1} \mathcal{F}_2(X_1^1) - \tfrac{\partial}{\partial x_j^1} \mathcal{F}_2(X_2^1) \right\| \leq L_j \|X_1^1 - X_2^1\|.$$

As a consequence:

$$\begin{aligned}\left\|\sum_{j=1}^{\alpha}\mathcal{F}^{j-1}\tfrac{\partial}{\partial x_j^1}\left(\mathcal{F}^k-\mathcal{F}_{k-j+1}\right)\mathcal{P}_{k-j}\right\| &\leq \sum_{j=1}^{\alpha}\left\|\tfrac{\partial}{\partial x_j^1}\mathcal{F}-\tfrac{\partial}{\partial x_j^1}\mathcal{F}_{k-j+1}\right\| \\ &\leq L\sum_{j=1}^{\alpha}\|\bar{\mathcal{F}}_1-\mathcal{F}_1^{k-j+1}\|.\end{aligned}$$

where $L:=\max\{L_1,\cdots,L_{d_1}\}$. Reasoning as we did when dealing with (1.68), we get the existence of $k_4\geq 0$ such that for all $k\geq k_4$

$$\left\|\sum_{j=1}^{\alpha}\mathcal{F}^{j-1}\tfrac{\partial}{\partial x_j^1}\left(\mathcal{F}^k-\mathcal{F}_{k-j+1}\right)\mathcal{P}_{k-j}\right\|<\frac{\varepsilon}{10}.$$

5. The fact the norm of (1.70) is bounded from above by $\varepsilon/10$, which follows arguing in a similar way as we did for (1.68) which yields the corresponding integer k_5.

Therefore, choosing $k\geq\tilde{k}=\max\{k_1,\cdots,k_5\}$ it follows that

$$\sup_{X^1\in\mathcal{K}^1}\left\|\tfrac{\partial}{\partial x_j^1}\mathcal{F}^k-\tfrac{\partial}{\partial x_j^1}\mathcal{P}_k\right\|<\frac{\varepsilon}{2}$$

Then, for each $\varepsilon>0$ there exists $k_*\geq\max\left\{\hat{k},\tilde{k}\right\}$ such that

$$\sup_{\mathcal{K}}\left\|\tfrac{\partial}{\partial x_j^1}\bar{\mathcal{F}}X^2-\tfrac{\partial}{\partial x_j^1}\mathcal{P}_kX^2\right\|<\frac{\varepsilon}{2}+\frac{\varepsilon}{2}=\varepsilon$$

for every $k\geq k_*$, which finishes the proof.

■

After proving that function F defined in (1.2) verifies hypotheses 1.1.4 and 1.1.8, theorem 1.1.7 yields the following result that allows to study some asymptotic behaviors of system (1.46) in terms of the aggregated system (1.58).

Theorem 1.3.8 *Consider the general two time scales system* (1.46) *given by*

$$X_{k,n+1}=S\left(\mathcal{F}_1^kX_{k,n}^1,\mathcal{F}_2\left(\mathcal{F}_1^{k-1}X_{k,n}^1\right)\ldots\mathcal{F}_2\left(\mathcal{F}_1^1X_{k,n}^1\right)\mathcal{F}_2\left(X_{k,n}^1\right)X_{k,n}^2\right)$$

where $X=(X^1,X^2)\in\Omega_N$, $\Omega_N\subset\mathbb{R}^N$ *is an open bounded nonempty set,* $X^i\in\Omega_{d_i}\subset\mathbb{R}^{d_i}$, Ω_{d_i} *is the restriction of* Ω_N *to* $\mathbb{R}^{d_i}$ *for* $i=1,2$, $S\in\mathcal{C}^1(\Omega_N)$

and matrices $\mathcal{F}_1$ *and* $\mathcal{F}_2(\cdot) \in \mathcal{C}^2(\Omega_{d_1})$ *are those defined by* (1.43) *and* (1.44). *Consider as well the corresponding aggregated system* (1.58) *that we have derived in the previous paragraphs*

$$Y_{n+1} = \begin{pmatrix} \mathcal{U}_1 & \mathcal{U}_2 \end{pmatrix} S\left(\mathcal{V}_1 Y_n^1, \mathcal{V}_2(Y_n^1) Y_n^2\right)$$

where $\mathcal{U}_1$ *and* $\mathcal{V}_1$ *were defined in* (1.48) *and* $\mathcal{U}_2$, $\mathcal{V}_2(\cdot)$ *were defined in* (1.49) *and* Y *stands for the global variables defined in* (1.57). *Let* $Y_* \in \Omega_q$ *be a hyperbolic equilibrium point of system* (1.58) *with* $Y^* = (Y_*^1, Y_*^2) \in \mathbb{R}^h \times \mathbb{R}^{q-h}$. *Then, there exist a positive constant* $r > 0$ *and an integer* $k_0 \geq 0$ *such that for all* $k \geq k_0$ *it follows that*

1. $X^* := (\mathcal{V}_1 Y_*^1, \mathcal{V}_2(Y_*^1) Y_*^2)$ *is an hyperbolic equilibrium of the corresponding auxiliary system. Moreover, system* (1.46) *has an unique equilibrium point* $X_k^* \in \bar{B}(X^*; r)$ *which is hyperbolic and satisfies*

   $$\lim_{k\to\infty} X_k^* = X^*,$$

   where $\bar{B}(X^*; r)0 \left\{Z \in \mathbb{R}^N;\ \|X^* - Z\| \leq r\right\}$.

2. X^* *and* X_k^* *are asymptotically stable (resp. unstable) if and only if* Y^* *is asymptotically stable (resp. unstable).*

3. *Let* Y^* *be asymptotically stable and let* $(X_0^1, X_0^2) \in \Omega_N$ *be such that the solution* $\{Y_n\}_{n=0,1,\ldots}$ *of system* (1.58) *corresponding with the initial data* $Y_0 := (\mathcal{U}_1 X_0^1, \mathcal{U}_2 X_0^2)$ *satisfies that* $\lim_{n\to\infty} Y_n = Y^*$. *Then, there exists* $k_1 \geq 0$ *such that for each* $k \geq k_1$, *the solution of system* (1.46) *with initial value* $X_{k,0} = X_0$ *satisfies that*

   $$\lim_{n\to\infty} X_{k,n} = X_k^*.$$

1.3.2 A host-parasitoid model with density-dependent dispersal in a chain of patches.

In this section we present a time discrete spatial host-parasitoid model. The environment is a chain of patches connected by migration events. Local host-parasitoid interactions are described by the classical Nicholson-Bailey model. The patches are assumed to be close enough to support the assumption of frequent patch to patch migration with respect to local interactions.

Since the pioneers works of Comins [27] and Hassell [42], the study of spatial dynamics of host-parasitoid associations has received a lot of attention (see [22] for a review). At the landscape level, hosts and parasitoids can frequently move from a favorable patch to another one. French and Travis [100] suggested that parasitoids are able to disperse more than once during the dispersal period, and can therefore "compare" host densities of several patches. Most parasitoids and hosts are sensitive to chemical products (pheromones) whose detectability depends on the density of organisms that are locally present (see [100] and [104]). When the density of host is high on a given patch, parasitoids should rather remain on that patch than move to another one. It is thus important to incorporate density dependent dispersal of organisms into models. We assume the following; when host density is small (resp. high) at a given patch, the proportion of parasitoids leaving this patch is close to unity (resp. to zero).

Sebsequently we combine these processes evolving in different time scales to build up a two time scales discrete model matching with system (1.46). Thus, we apply the aggregation result stated in this section to obtain a reduced model that governs the total host and parasitoid densities. Then, we analyze the aggregated system in order to obtain information about the original model.

Building up the model.

We consider a host-parasitoid system in a spatial environment which is a chain of q patches. Let $h_{i,n}$ and $p_{i,n}$ be, respectively, the host and parasitoid density on patch i, $i \in \{1, \cdots, q\}$ at each generation n. We define the population vector as follows

$$X_n = (h_{1,n}, h_{2,n}, ..., h_{q,n}, p_{1,n}, p_{2,n}, ..., p_{q,n})^T = (H_n, P_n)^T$$

where the upper index T denotes, as usual, transposition. The complete model couples migrations between patches as well as local host-parasitoid interactions. In the sequel, we will write down equations describing both processes.

Host-parasitoid dispersal submodel.

We assume that individuals can move over a distance of k patches at each generation, in a diffusion-like dispersal process. In order to compute the distribution obtained for hosts and parasitoids, we discretize this process in time and decompose it into k elementary dispersal events consisting in movements from one patch to one of its nearest neighbors.

In case of pure random walk, insects starting on a patch would be distributed according to a Gaussian distribution centered on this particular patch after dispersal. In the present model, hosts move according to an asymmetrical dispersal process, a biased random walk, while parasitoids dispersal is host density-dependent.

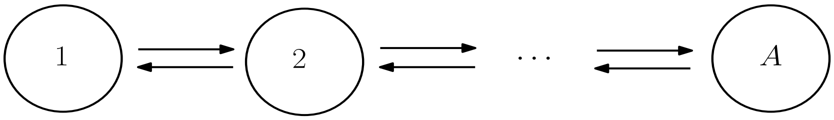

Figure 1.3: Chain of patches.

Host movements correspond to an asymmetric (biased) random walk: probabilities to go to the left or to the right patch are not the same. Let f be the proportion of hosts moving from any patch to the neighboring patch situated on its left between two time steps of migration. We define parameter $\alpha > 0$ and assume that the proportion of migrants from any patch to the neighboring patch on its right is αf at each elementary dispersal event. When $\alpha > 1$, the proportion of hosts moving to the right is larger than in the opposite direction. Thus, after several elementary migration events, one expects to end up with a spatial host distribution shifted towards the right hand side of the chain. On the contrary, when $\alpha < 1$, the proportion of hosts moving to the left is larger than in the opposite direction and one expects a spatial host distribution shifted towards the left. The proportion of hosts leaving a patch to go to left and right ones must be smaller than 1, and thus we assume that $(1 + \alpha)f < 1$.

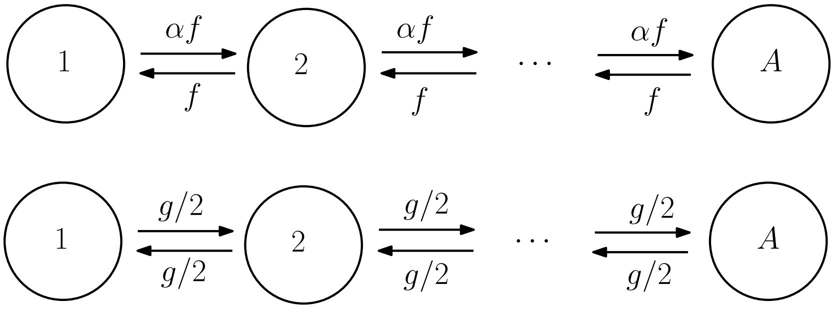

Figure 1.4: Chain of patches and migration scheme.

For parasitoids we assume a host density-dependent dispersal process. Dispersal corresponds to a random walk, but the probability of leaving the patch (and thus the proportion of migrants) depends on the density of hosts on that patch. Parasitoids may use chemical stimuli from their hosts (Vinson 1976). Host stimuli are highly reliable but not very detectable (Vet and Dicke 1992). In this model, if the parasitoid is unable to detect the presence of hosts thanks to the pheromones left by hosts, it will leave the patch. In our model, if the parasitoid is unable to detect the presence of hosts, it will leave the patch. Thus the density of hosts on a patch directly affects the proportion of migrants that will stay on that patch, as this proportion is related to the probability to find hosts pheromones which increases with density of hosts. Let $g(h_{i,n})$ be the proportion of parasitoids leaving any patch i to go to the two neighboring patches at each elementary dispersal event, which only depends on the density of hosts on patch i at time step n. In this study, $g(h_{i,n})$ is given by a general classical type of function of the following form:

$$g(h_{i,n}) = \frac{1}{1+\tau h_{i,n}^{\beta}} \tag{1.71}$$

where τ and β are positive parameters. A similar host density dependent dispersal process for parasitoids was used in the case of two spatial patches in Lett et al. (2003). Here, we extend the model to a chain of any number of patches.

Curves obtained for different values of β intersect at $\left(h = (1/\tau)^{\frac{1}{\beta}}, g = 0.5\right)$ figure 1.5 shows function $g(h_{i,n})$ for $\tau = 1$ and different values of β. As modifying parameter corresponds to changing scale for hosts, we will assume that $\tau = 1$ in all this study. The main idea in equation (1.71) is that when many

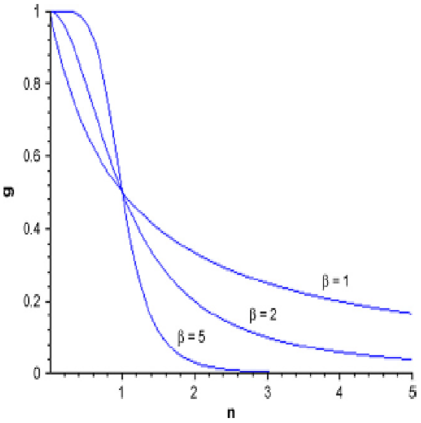

Figure 1.5: The proportion g of migrant parasitoids as a function of host density h, for $\tau = 1$ and different values of parameter β.

hosts are available on patch i, parasitoids remain on this patch. On the contrary, when few hosts are present there, parasitoids leave the patch. This shift in the parasitoid behavior (stay or leave) is all the more "brutal" than β is large. We will later study the influence of β on the model.

We assume that parasitoids leaving patch i go in equal proportions to the two neighbouring patches. Then for any patch $1 < i < q$, the elementary dispersal process reads as follows:

$$(1.72) \qquad \begin{cases} h_{i,n+1} = [1-(1+\alpha)f]h_{i,n} + \alpha f h_{i-1,n} + f h_{i+1,n} \\ p_{i,n+1} = [1-g(h_{i,n})]p_{i,n} + \frac{1}{2}g(h_{i-1,n})p_{i-1,n} + \frac{1}{2}g(h_{i+1,n})p_{i+1,n} \end{cases}$$

and for patches at both ends of the chain

$$(1.73) \qquad \begin{cases} h_{1,n+1} = [1-\alpha f]h_{1,n} + f h_{2,n} \\ p_{1,n+1} = [1-\frac{1}{2}g(h_{1,n})]p_{1,n} + \frac{1}{2}g(h_{2,n})p_{2,n} \\ h_{q,n+1} = [1-f]h_{q,n} + \alpha f h_{q-1,n} \\ p_{q,n+1} = [1-\frac{1}{2}g(h_{q,n})]p_{q,n} + \frac{1}{2}g(h_{q-1,n})p_{q-1,n} \end{cases}$$

The elementary dispersal process can be therefore described by the following system:

$$X_{n+1} = F(X_n).$$

We recall that, right here, the time unit $n \mapsto n+1$ corresponds to the fast dynamics. Function F is a block diagonal matrix noted by:

$$(1.74) \qquad F(X_n) := \mathcal{F}(X_n)X_n = \begin{pmatrix} \mathcal{F}_h & 0 \\ 0 & \mathcal{F}_p(H_n) \end{pmatrix} \begin{pmatrix} H_n \\ P_n \end{pmatrix}$$

Summing up equations (1.72) and (1.73), we get matrix $\mathcal{F}_h \in \mathcal{M}_{q\times q}(\mathbb{R})$, which stands for host migrations and is given by

$$(1.75) \quad \mathcal{F}_h = \begin{pmatrix} 1-\alpha f & f & 0 & \cdots & \cdots & 0 \\ \alpha f & 1-(1+\alpha)f & f & \ddots & \cdots & 0 \\ 0 & \ddots & \ddots & \ddots & \ddots & \vdots \\ \vdots & \ddots & \ddots & \ddots & 0 & 0 \\ \vdots & \ddots & \ddots & \alpha f & 1-(1+\alpha)f & f \\ 0 & \cdots & \cdots & 0 & \alpha f & 1-f \end{pmatrix}$$

On the other hand, matrix $\mathcal{F}_p(H_n) \in \mathcal{M}_{q\times q}(\mathcal{C}^1(\mathbb{R}))$ defines parasitoid migrations according to equations (1.72) and (1.73) as well, namely,

$$\mathcal{F}_p(H_n) = \begin{pmatrix} 1-\frac{g(h_{1,n})}{2} & \frac{g(h_{2,n})}{2} & 0 & \cdots & \cdots & 0 \\ \frac{g(h_{1,n})}{2} & 1-g(h_{2,n}) & \frac{g(h_{3,n})}{2} & \ddots & \cdots & 0 \\ 0 & \ddots & \ddots & \ddots & \ddots & \vdots \\ \vdots & \ddots & \ddots & \ddots & 0 & 0 \\ \vdots & \ddots & \ddots & \frac{g(h_{q-2,n})}{2} & 1-g(h_{q-1,n}) & \frac{g(h_{q,n})}{2} \\ 0 & \cdots & \cdots & 0 & \frac{g(h_{q-1,n})}{2} & 1-\frac{g(h_{q,n})}{2} \end{pmatrix} \tag{1.76}$$

As dispersal is the fast process, we will allow k migrations within each single slow time unit. It follows from equation (1.75) that host migrations matrix does not change during migration process. Parasitoids migration matrix changes with each hosts migration, as shown in equation (1.76). Let us note the migration matrix after k elementary dispersal process as follows:

$$X_{n+1} = F^{(k)}(X_n) \tag{1.77}$$

where $F^{(k)}(X_n)$ is recursively defined by:

$$F^{(k)}(X_n) := \begin{cases} \mathcal{F}(X_n)X_n & \text{for } k = 1 \\ \mathcal{F}(F^{(k-1)}(X_n))F^{(k-1)}(X_n) & \text{for } k > 1 \end{cases}$$

This model is a discrete version of a reaction-diffusion model with a parasitoid diffusion coefficient depending on the host population density. Such a model has been developed in the continuous case (see 9.3 in Mathematical Biology by J.D. Murray [70]). In our model, the parameter k corresponds to the speed of the diffusion process and thus the diffusion coefficient. The parameter k is also the radius of the distribution after dispersal. This allows the model to be more flexible than models considering only migration on the nearest neighbors: patch sized can be chosen arbitrary small compared to the distance insects can travel in one generation, thus it would not be relevant to prevent individuals for moving farther. Furthermore, multiple host density-dependent elementary dispersal events allow parasitoid to leave the patch if no hosts are present, preventing the unrealistic case where parasitoids would stay on an empty patch. In addition, this migration model is less extreme than Ideal Free Distribution, which does not describe the intrinsic process of dispersal, allowing individuals to reach any patch in the environment, regardless of their mobility. In our model, the dispersal process is explicit with respect to several contributions in which the dispersal process is not described, and where hosts and parasitoids are distributed among spatial patches according to some given distributions (Hassell and May, [43], [44]; Hassell et al. [45]). In our model, the parameter k allows to make the diffusion process more or less fast, which would correspond in the continuous case to increase or decrease of the diffusion coefficient.

Local interactions: host-parasitoid dynamics.

On each patch $i \in 1, \cdots, q$ of the chain, we assume that hosts and parasitoids interact according to the Nicholson Bailey model

$$\begin{cases} h_{i,n+1} = \lambda_i h_{i,n} e^{-a_i p_{i,n}} = z_i \left(h_{i,n}, p_{i,n}\right) \\ p_{i,n+1} = c_i h_{i,n} \left(1 - e^{-a_i p_{i,n}}\right) = k_i \left(h_{i,n}, p_{i,n}\right) \end{cases} \tag{1.78}$$

where λ_i is the host growth rate on patch i, a_i the searching efficiency of parasitoids and c_i the average number of viable parasitoids that emerge from an host parasitized at the previous generation. Let us define a map $S : \mathbb{R}^{2q} \to \mathbb{R}^{2q}$ through $S = (z_1, \cdots, z_q, k_1, \cdots, k_q)$, where where functions z_i and k_i, for $i \in \{1, \cdots, q\}$, are defined by equation (1.78) and describe the local host-parasitoid interactions.

The complete model.

The complete model combines the two previous submodels as follows:

$$X_{n+1} = S \circ F^{(k)}(X_n) \tag{1.79}$$

We consider the slow time scale for this model: one time step corresponds to a single event of reproduction, and thus one generation. Therefore, it is assumed that between time n and $n+1$ hosts and parasitoids first explore the environment by performing k elementary dispersal events before settling down, then they enter a phase where they have local demographic and parasitism interactions. Local interactions occur at the same time on every patch. Thus, all patches are synchronized. This model matches with (1.46), so that we can apply the aggregation results stated early.

The reduced model.

It is straightforward that theorem 1.3.8 applies to system (1.79). Thus, we can study the complete system (1.79) by means of a reduced one. Direct calculations show that global variables are given by the total number of host and parasitoids

$$h = h_1 + \cdots + h_q \qquad p = p_1 + \cdots + p_q.$$

In order to build up the reduced system, we identify the stable asymptotic distributions for host and parasitoid migrations, respectively. On the one hand,

$$\lim_{k\to\infty} \mathcal{F}_h^{(k)} = (\nu^*|\cdots|\nu^*)$$

where

$$\nu^* = \left(\frac{1-\alpha}{1-\alpha^q}, \cdots, \frac{1-\alpha}{1-\alpha^q}\,\alpha^{i-1}, \cdots, \frac{1-\alpha}{1-\alpha^q}\,\alpha^{q-1}\right)^T .$$

On the other hand, after some algebra,

$$\lim_{k\to\infty} \mathcal{F}_p^{(k)}(X^1) = (\mu^*(\nu^* h)|\cdots|\mu^*(\nu^* h))$$

where

$$\mu^*(h) := \mu^*(\nu^* h) = \left(\frac{1+h_1^{*\beta}}{1+\sum_{j=1}^q h_j^{*\beta}}, \cdots, \frac{1+h_q^{*\beta}}{1+\sum_{j=1}^q h_j^{*\beta}}\right)^T .$$

provided $h_i^* = \dfrac{1-\alpha}{1-\alpha^q}\,\alpha^{i-1}\,h$. Then,

$$\lim_{k\to\infty} \mathcal{F}^{(k)}(X_n) = \left(\bar{\mathcal{F}}_p H,\, \bar{\mathcal{F}}_h(\nu^* H)P\right) = (\nu^* h,\, \mu^*(h)p) = E\circ G(X_n),$$

where function G is defined as follows

$$\begin{array}{rcl} G:\Omega_{2q} & \longrightarrow & \Omega_2 \\ X & \longrightarrow & G(X) = G(H,P) = (h,p) \end{array}$$

while function E is defined by means of

$$\begin{array}{rcl} E:\Omega_2 & \longrightarrow & \Omega_{2q} \\ (h,p) & \longrightarrow & E(h,p) = (\nu^* h, \mu^*(h)p) \end{array}$$

which gives the equilibrium of fast dynamics for the particular values n and p of the global variables. And finally the corresponding aggregated system reads as follows

$$(h_{n+1}, p_{n+1}) = Y_{n+1} = G\circ S\circ E(Y_n) = G\circ S\circ E(h_n, p_n),$$

that is, the corresponding aggregated system reads as

$$\left\{\begin{array}{l} h_{n+1} = h_n \displaystyle\sum_{i=1}^q \lambda_i \nu_i^* e^{-a_i \mu_i^*(h_n)p_n}, \\ p_{n+1} = h_n \displaystyle\sum_{i=1}^q c_i \nu_i^* \left(1-e^{-a_i \mu_i^*(h_n)p_n}\right), \end{array}\right. \tag{1.80}$$

Let us consider its associated fixed point equations

$$
\begin{cases} h = h \displaystyle\sum_{i=1}^{q} \lambda_i \nu_i^* e^{-a_i \mu_i^*(h) p}, \\ p = h \displaystyle\sum_{i=1}^{q} c_i \nu_i^* \left(1 - e^{-a_i \mu_i^*(h) p}\right). \end{cases} \tag{1.81}
$$

Proposition 1.3.9 *(Trivial and semi-trivial fixed points.) Consider the fixed point equation* (1.81). *If follows that*

- $(h, p) = (0, 0) =: E_0$ *is a fixed point for* (1.81).
- $(h, p) = (h_*, 0) =: E_1(h_*)$ *for all* $h_* > 0$ *are fixed points for* (1.81) *whenever* $\sum_{i=1}^{q} \lambda_i \nu_i^* = 1$.

We seek for non trivial fixed points. For this purpose, we will show the existence of an invariant convex compact region for (1.80). The existence of an invariant region for the aggregated system entails that to the auxiliary system, but not to the general system. Nevertheless, using the Brouwer's fixed point theorem we get the existence of at least one fixed point for the aggregated system.

Proposition 1.3.10 *(Non-trivial fixed points.) Consider system* (1.80) *and assume that*

$$
\sum_{i=1}^{q} \frac{\lambda_i \nu_i^*}{\Lambda^{a_i/(a\delta)}} > 1. \tag{1.82}
$$

for certain constants $a \le \min\{a_i\}$ *and* $\delta \le \min\{\mu_i\}$. *Then, there exists a region* $\mathcal{R} = [h_m, h_M] \times [p_m, p_M] \subset \mathbb{R}_+^2$ *such that* $(h_0, p_0) \in \mathcal{R}$ *implies* $(h_n, p_n) \in \mathcal{R}$ *for all* $n \ge 0$.

Proof.– Given (h, p), let us note (h_+, p_+) its successor according to equations (1.80), that is,

$$
\begin{cases} h_+ := h \displaystyle\sum_{i=1}^{q} \lambda_i \nu_i^* e^{-a_i \mu_i^*(h) p}, \\ p_+ := h \displaystyle\sum_{i=1}^{q} c_i \nu_i^* \left(1 - e^{-a_i \mu_i^*(h) p}\right). \end{cases} \tag{1.83}
$$

Let us consider $\check{c} > 0$ (to be determined later) and δ, $\hat{\delta}$ such that

$$0 < \delta < \hat{\delta} < \min\{\mu_i^*(h),\, i \in 1, \cdots, q,\, n \in [0, \infty)\} < 1$$

along with

$$\begin{array}{ll} a := \min\{a_i;\ i = 1, \cdots, q\}, & \hat{a} := \max\{a_i;\ i = 1, \cdots, q\}, \\ \lambda := \min\{\lambda_i;\ i = 1, \cdots, q\}, & \Lambda := \max\{\lambda_i;\ i = 1, \cdots, q\}, \\ c := \min\{c_i;\ i = 1, \cdots, q\}, & \hat{c} := \max\{c_i;\ i = 1, \cdots, q\}, \end{array}$$

all of them positive constants. We will use these constants to build up several auxiliary "bounding " discrete difference equation systems and such that h_m, h_M, p_m, p_M are among their fixed points. Namely, the systems and the corresponding fixed points are the following ones:

$$\text{(1.84)} \qquad \begin{cases} h_{n+1} = \Lambda h_n e^{-a\delta p_n}, \\ p_{h+1} = \hat{c} h_n (1 - e^{-\hat{a} p_n}), \end{cases} \qquad \begin{aligned} p_M &= \frac{\ln \Lambda}{a\delta}, \\ h_M &= \frac{p_M}{\hat{c}\,(1 - e^{-\hat{a} p_M})}. \end{aligned}$$

$$\text{(1.85)} \qquad \begin{cases} h_{n+1} = \Lambda h_n e^{-a\hat{\delta} p_n}, \\ p_{n+1} = \check{c} h_n (1 - e_n^{-\hat{a} p}), \end{cases} \qquad \begin{aligned} p_m &= \frac{\ln \Lambda}{a\hat{\delta}}, \\ h_* &= \frac{p_m}{\check{c}\,(1 - e^{-\hat{a} p_m})}. \end{aligned}$$

$$\text{(1.86)} \qquad \begin{cases} h_{t+1} = \Lambda h_n e^{-a\hat{\delta} p_n}, \\ p_{t+1} = c h_n (1 - e^{-a\hat{\delta} p_n}), \end{cases} \qquad \begin{aligned} p_m &= \frac{\ln \Lambda}{a\hat{\delta}}, \\ h_m &= \frac{p_m}{c(1 - e^{-a\hat{\delta} p_m})}. \end{aligned}$$

Let us check several facts. It is straightforward that $0 < p_m < p_M$. On the one hand, by direct calculations, we get that

$$\text{(1.87)} \qquad h_m = \frac{\ln \Lambda}{a\hat{\delta} c \left(1 - \frac{1}{\Lambda}\right)}, \qquad h_M = \frac{\ln \Lambda}{a\delta \hat{c} \left(1 - \frac{1}{\Lambda^{\hat{a}/(a\delta)}}\right)}.$$

Moreover, it is clear that

$$\lim_{\delta \to 0} \frac{\ln \Lambda}{\delta a \hat{c} \left(1 - \frac{1}{\Lambda^{\hat{a}/(a\delta)}}\right)} = +\infty,$$

thus, we can choose δ small enough such that $h_m < h_M$.

Moreover, we claim that $\breve{c}$ can be chosen so that $0 < \breve{c} < c$ and $h_M = h_*$. It is straightforward that $\Psi(p) = \frac{p}{\hat{c}(1-e^{\hat{a}p})}$ is strictly increasing for $p > 0$. Thus, $p_m < p_M$ implies $\Psi(p_m) < \Psi(p_M)$ can diminish $\breve{c}$ so that $h_* = h_M$. It must be pointed out that the smaller is δ, the greater are p_M and h_M.

Suppose that $h \in [h_m, h_M]$ and $p \in [p_m, p_M]$. We recall the fact that the fact that $\sum_{i=1}^{q} \nu_i^* = 1$. Then, thanks to equation (1.85), we have

$$\begin{aligned} h_+ &= h \sum_{i=1}^{q} \lambda_i \nu_i^* e^{-a_i \mu_i^*(h) p} \\ &\leq h_M \Lambda \sum_{i=1}^{q} \nu_i^* e^{-a_i \mu_i^*(h) p} \\ &\leq h_M \Lambda e^{-a\hat{\delta} p_m} = h_M, \end{aligned} \tag{1.88}$$

moreover, keeping in mind condition (1.82), it follows that

$$\begin{aligned} h_+ &= h \sum_{i=1}^{q} \lambda_i \nu_i^* e^{-a_i \mu_i^*(h) p} \\ &\geq h_m \sum_{i=1}^{q} \lambda_i \nu_i^* e^{-a_i p_M} \\ &= h_m \sum_{i=1}^{q} \lambda_i \nu_i^* \Lambda^{\frac{-a_i}{a\delta}} > h_m, \end{aligned} \tag{1.89}$$

From equation (1.85), it follows that

$$\begin{aligned} p_+ &= h \sum_{i=1}^{q} c_i \nu_i^* \left(1 - e^{-a_i \mu_i^*(h) p}\right) \\ &\leq h_M \hat{c} \sum_{i=1}^{q} \nu_i^* \left(1 - e^{-a_i \mu_i^*(h) p}\right) \\ &\leq h_M \hat{c} \left(1 - e^{-\hat{a} p_M}\right) = p_M, \end{aligned} \tag{1.90}$$

and finally, using (1.86)

$$\begin{aligned} p_+ &= h\sum_{i=1}^{q} c_i\nu_i^*\left(1-e^{-a_i\mu_i^*(h)p}\right) \\ &\geq h_m c\sum_{i=1}^{q}\nu_i^*\left(1-e^{-a_i\mu_i^*(h)p}\right) \qquad (1.91) \\ &\geq h_m c\left(1-e^{-a\hat{\delta}p_m}\right) = p_m. \end{aligned}$$

From (1.88), (1.90) and (1.91) we have that

$$(h,p)\in[h_m,h_M]\times[p_m,p_M]\Rightarrow(h_+,p_+)\in(h_m,h_M]\times[p_m,p_M].$$

■

Corollary 1.3.11 *(Non trivial fixed points.) Under the hypothesis of the previous proposition, there exists at least one non-trivial fixed point for system* (1.80) *in* $\mathcal{R}$.

Proof.– The region $\mathcal{R}$ is an invariant, compact, convex region for the map induced by (1.80). The the conclusion follows from an straightforward application of the Brouwer's fixed point theorem.

■

Previous results can be deepened under the assumptions of $\lambda_i \equiv \lambda$ and $c_i \equiv c$ for $i = 1, \cdots, q$. In such a case equation (1.81) reads as follows

$$(1.92) \qquad \begin{cases} h = h\lambda\displaystyle\sum_{i=1}^{q}\nu_i^* e^{-a_i\mu_i^*(h)p}, \\ p = hc\displaystyle\sum_{i=1}^{q}\nu_i^*\left(1-e^{-a_i\mu_i^*(h)p}\right). \end{cases}$$

Supposing that $h \neq 0$ (1.92) simplifies in

$$(1.93) \qquad \begin{cases} 1 = \lambda\displaystyle\sum_{i=1}^{q}\nu_i^* e^{-a_i\mu_i^*(h)p}, \\ p = hc\displaystyle\sum_{i=1}^{q}\nu_i^*\left(1-e^{-a_i\mu_i^*(h)p}\right). \end{cases}$$

Observe that from the first equation in (1.93)

$$\sum_{i=1}^{q} \nu_i^* e^{-a_i \mu_i^*(h) p} = \frac{1}{\lambda}.$$

Thus, rearranging terms in (1.93) yields

$$p = hc\left(1 - \frac{1}{\lambda}\right). \tag{1.94}$$

Therefore, system (1.81) possesses a non trivial equilibrium if, and only if, the equation

$$\phi(h) := \sum_{i=1}^{q} \nu_i^* e^{-a_i \mu_i^*(h) hc\left(1-\frac{1}{\lambda}\right)} = \frac{1}{\lambda} \tag{1.95}$$

has a solution. Actually, as

$$\phi(0) = 1 \qquad \text{and} \qquad \lim_{n\to\infty} \phi(h) = 0,$$

equation (1.95) has a solution whenever $\lambda > 1$. We will denote the non trivial equilibrium of equation (1.81) $E_2 := (h_*, p_*)$, where h_* stands for a solution of equation (1.95) and $p_* := h_* c\left(1 - \dfrac{1}{\lambda}\right)$.

Remark 1.3.12 *The number of fixed points for equation* (1.92) *equals the number of solutions of equation* (1.95)*.*

We now turn our attention to the stability of the fixed points of system (1.80). Let us define the function

$$W(h,p) := \left(h \sum_{i=1}^{q} \lambda_i \nu_i^* e^{-a_i \mu_i^*(h) p}, h \sum_{i=1}^{q} c_i \nu_i^* \left(1 - e^{-a_i \mu_i^*(h) p}\right)\right), \tag{1.96}$$

which jacobian matrix is

$$JW(h,p) := \begin{pmatrix} W_{11}(h,p) & W_{12}(h,p) \\ W_{21}(h,p) & W_{22}(h,p) \end{pmatrix} \tag{1.97}$$

and, noting by $(\cdot)'$ the derivative with respect of h, the corresponding entries are given by

$$W_{11}(h,p) = \sum_{i=1}^{q} \lambda_i \nu_i^* e^{-a_i \mu_i^*(h) p} - h \sum_{i=1}^{q} \lambda_i \nu_i^* a_i (\mu_i^*(h))' p \; e^{-a_i \mu_i^*(h) p},$$

$$W_{12}(h,p) = -h\sum_{i=1}^{q}\lambda_i\nu_i^* a_i\mu_i^*(h)e^{-a_i\mu_i^*(h)p},$$

$$W_{21}(h,p) = \sum_{i=1}^{q} c_i\nu_i^*\left(1-e^{-a_i\mu_i^*(h)p}\right) + h\sum_{i=1}^{q} c_i\nu_i^* a_i(\mu_i^*(h))'p\; e^{-a_i\mu_i^*(h)p},$$

and

$$W_{22}(h,p) = h\sum_{i=1}^{q} c_i\nu_i^* a_i\mu_i^*(h)e^{-a_i\mu_i^*(h)p}.$$

Proposition 1.3.13 *The trivial fixed point* E_0 *of* (1.83) *is asymptotically stable if, and only if,* $\sum_{i=1}^{q}\lambda_i\nu_i^* < 1$.

Proof.– It follows immediately from the fact that

$$JW(0,0) = \begin{pmatrix} \sum_{i=1}^{q}\lambda_i\nu_i^* & 0 \\ 0 & 0 \end{pmatrix},$$

■

Remark 1.3.14 *We already know that* $E_1(h_*)$ *is a fixed point if, and only if,* $\sum_{i=1}^{q}\lambda_i\nu_i^* = 1$*. On the other hand, direct calculations yield*

$$JW(h_*,0) = \begin{pmatrix} \sum_{i=1}^{q}\lambda_i\nu_i^* & -h_*\sum_{i=1}^{q}\lambda_i\nu_i^* a_i\mu_i^*(h_*) \\ 0 & h_*\sum_{i=1}^{q} c_i\nu_i^* a_i\mu_i^*(h_*) \end{pmatrix}.$$

That is, when linearizing around a semi-trivial fixed point 1 *is in the spectrum of* $JW(h^*,0)$*. Thus, it is not a hyperbolic fixed point and our results do not apply to.*

Regarding the stability of possible positive non-trivial fixed points, we were unable to achieve a simple condition based tr$(JW(h,p))$ and $\det(JW(h,p))$ (see bellow) even in the particular case in which $\lambda_i = \lambda$, $c_i = c$ and $a_i = a$ for $i = 1,\ldots,q$. Therefore, in the general case the stability conditions must be numerically checked using the following criterion. Let (h_*,p_*) be a fixed point to equation

$$(x_{n+1},y_{n+1}) = W(x_n,y_n).$$

Then, (h_*,p_*) is asymptotically stable if, and only if,

$$|tr(JW(h_*,p_*)| < 1 + \det(JW(h_*,p_*)) < 2. \tag{1.98}$$

Summary of results.

In the following paragraphs we summarize the analytical results obtained regarding existence and stability of fixed points. We illustrate with numerical simulations the case in which the aggregated model dynamics tends to an equilibrium. In addition, numerical results show the existence of an attracting closed invariant curve; unfortunately, we have no analytic results allowing to translate this behavior to the complete system.

The origin is trivially fixed point of model (1.80) and it is asymptotically stable if, and only if $\sum_{i=1}^{q} \lambda_i c_i < 1$.

Under condition $\sum_{i=1}^{q} \lambda_i \nu_i^* = 1$ the points of $\{(h, 0);\ h > 0\}$ are fixed points of the aggregated model (1.80) known as semi-trivial fixed points and corresponding with the parasitoid free equilibrium. These equilibrium points of the aggregated system are not hyperbolic, so that do not provide any information about the complete system.

We show the existence of at least a positive fixed point (h^*, p^*) which verifies equation (1.80) when $\lambda_i = \lambda$, $c_i = c$ and $a_i = a$ for $i = 1, \cdots, q$. In more general cases, existence and uniqueness of a non-trivial positive equilibrium has to be found numerically solving :

$$\begin{cases} 1 = \displaystyle\sum_{i=1}^{q} \lambda_i \nu_i^* e^{-a_i \mu_i^*(h) p}, \\ p = h \displaystyle\sum_{i=1}^{q} c_i \nu_i^* \left(1 - e^{-a_i \mu_i^*(h) p}\right). \end{cases}$$

Thanks to the results in previous section, the existence of a hyperbolic fixed point (h_*, p_*) to the aggregated system (1.80) implies the existence of a sequence of fixed points (H_k^*, P_k^*) for the general system (1.79) for large enough values of k (that is, if the time scales are different enough) such that

$$\lim_{k \to \infty} (H_k^*, P_k^*) = (\nu^* h_*, \mu^*(\nu^* h_*) p_*) .$$

The local stability of (H_k^*, P_k^*) is determined by the local stability of (h^*, p^*), which must be determined numerically (for instance, by calculating the trace and the determinant of its Jacobian matrix); if (h^*, p^*) is an asymptotically stable (resp. unstable) equilibrium of the aggregated system (1.80), then so is (H_k^*, P_k^*) for the complete model (1.79) for k large enough. In addition, thanks to theorem 1.3.8, in the asymptotically stable case, the basin of attraction of (H_k^*, P_k^*) can be approached by means of that of (h^*, p^*), as shown in figure 1.7.

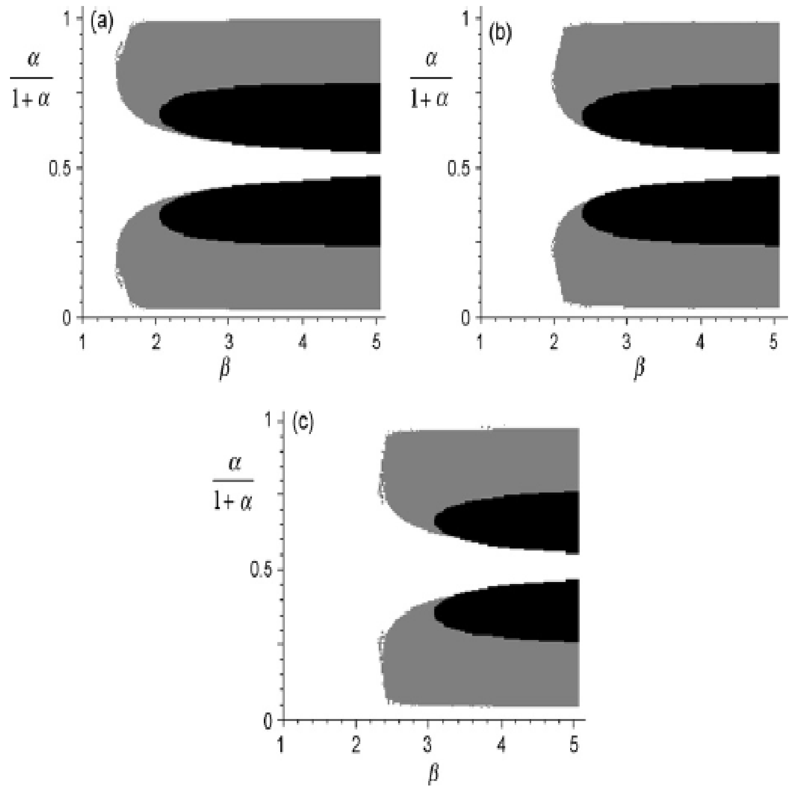

Figure 1.6: Domain of stability (in black) and of persistence (in grey) of the positive fixed point of the aggregated model for different values of parasitoid aggregation parameter b and host migration asymmetry parameter a for a chain with $q = 5$ patches, $\lambda_2 =$ and (a) $a_i c_i = 0.05$, (b) $a_i c_i = 0.5$ and (c) $a_i c_i = 1$, for $i \in 1, \cdots, q$.

Conclusions.

In the model presented herein, we have limited our study to a chain of patches and can be seen as a discrete version of a reaction-diffusion model with parasitoid diffusion coefficients depending on the host population density (see section 9.3 in [70]). An increase of the time scale factor k of the diffusion process in our model would have the same effect than an increase of the diffusion coefficient in a continuous time model. In our model, the parameter k can also be associated to the radius of the distribution after dispersal: k is the maximum number of patches an individual can go through during one generation. Multiple host density-dependent elementary dispersal events allow parasitoid to leave the patch if no hosts are present, preventing the unrealistic situation where parasitoids would stay on an empty patch. In addition, this dispersal model is less extreme than the ideal free distribution, which does not describe the intrinsic process of dispersal, allowing individuals to reach any patch in the environment, regardless of their mobility.

The expression of the aggregated model (1.80) differs from the Nicholson-Bailey model given in the local scale (1.78). While the local Nicholson-Bailey submodel always provides instability, thanks to theorem 1.3.8, the complete model may exhibit locally asymptotically stable (resp., unstable) hyperbolic equilibrium points. We point out that this asymptotically stable equilibrium imply local stability. Thus, there is different behavior at local scale and at global scale, which is known as functional emergence. This means that the outcomes are *qualitatively* different of those expected for each of the simple processes considered in the two time scales model. Hence, density-dependent dispersal promotes emergence, which makes the aggregated model a useful tool to analyze the global dynamics of the system.

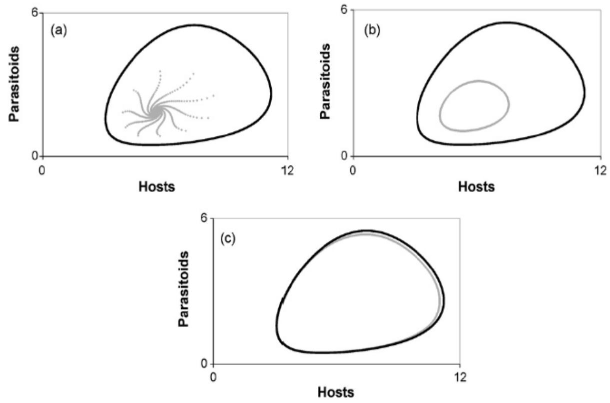

Figure 1.7: Trajectories of the complete (grey) and aggregated (black) models with the set of parameters $\alpha = 2.3$, $\beta = 3$, $\lambda = 1.5$, $a_i = 0.5$, $c_i = 1$ $i = 1, \cdots, 5$ and different values of k. Part of transient dynamics has not been represented. (a) For $k = 15$ the attractor of the complete model is an equilibrium point. (b) For $k = 20$ 20, the attractor of both the complete and the aggregated model is of the same type. (c) For $k = 50$ the attractor of the complete model almost matches the one of the aggregated model.

On the other hand, numerical simulations show the existence of invariant attracting curves for the aggregated system. Even if such numerical simulations show agreement between both the aggregated and the complete models, there are no theoretical results supporting such an agreement.

1.4 Conclusions and perspectives.

In this chapter we have dealt with discrete two time scale systems built upon the slow time unit. The prototype of such kind of systems is

$$X_{k,n+1} = S \circ F^{(k)}(X_{k,n}), \tag{1.99}$$

where functions F and S describe the fast and the slow dynamics, respectively. The super-index (k) stands for the k-fold composition of F and reflects the ratio between time scales (that is, F acts k times for each action of S). To the best of our knowledge, the most general results in approximate aggregation of this kind of systems are collected in theorem 1.1.7 from [90]. Apart from describing conditions allowing the reduction procedure, theorems in [90] allow to translate the existence of asymptotically stable (respectively, unstable) hyperbolic fixed points and periodic solutions found for the aggregated system to the complete system. These results hold upon general but restrictive hypothesis. In practice, the main difficulties for ascertaining whether a system like (1.99) fulfils those conditions fall into the function describing the fast dynamics. As a matter of fact, up to now, applications consider fast dynamics of the form

$$F(X) = \mathcal{F}X, \tag{1.100}$$

where $\mathcal{F}$ is a regular stochastic matrix.

Our results in this chapter, contained in sections 1.2 and 1.3, provide with general classes of two time scale systems susceptible of being approximately aggregated according with [90] and extending the assumption (1.100). Besides, these classes of functions have proven to be of interest in applications.

Results achieved in section 1.2 are collected in [68] and address systems whose fast dynamics depends on global variables. Without lost of generality, let us consider that state variables vector X represents a population and that the fast dynamics is conservative of the total population $y = \|X\|_1$. Then, we have considered

$$F(X) = \mathcal{F}(y)X,$$

where $\mathcal{F}(y)$ is a regular stochastic matrix and its entries are $\mathcal{C}^1$ function of y. This assumption means that the behavior of the population at the fast time scale depends on the current total population size. From a different point of view, we can say that fast dynamics depend on the state variables through the global variable y. We have shown in theorem 1.2.3 that the reduction process described in [90] applies to this setting and we applied it to different models of population dynamics coupling demographic and migratory processes which take place at different time scales. An analysis of these models, exchanging the role of the slow and fast dynamics, completes the section.

In a first application, we also consider individual displacements to be faster than demography. In this case migratory parameters depend on the total population size. As in the previous example, we have simulated spatial heterogeneity decomposing the habitat in two patches linked by migrations (displacements) and letting demographic parameters to be different at each patch. Namely, one of the patches was a sink and the other one was a source. In this case, the two dimensional system reduced to an scalar equation, which is much simpler to analyze. In particular, we have shown that appropriate migration rates give rise to new interpretations of well known discrete models (Beverton-Holt and Ricker equations) and may induce Allee effect. The details of all these results can be found in [68].

In a second application, we consider an age structured population in a patchy environment evolving under a Leslie type demographic process, which is faster than displacements between patches. Assuming that fecundity and mortality parameters of each age class depend on the corresponding age class size (the number of individuals belonging to each age class) we found a multi-attractor scenario from the study of the aggregated model. The reduction process allows us to analyze a four dimensional system through a two dimensional one.

Section 1.3 is based on the results achieved in [72]. There, we let the state variables to be partially coupled at the fast time scale. We mean that the evolution within the fast time scale of a group of state variables depend on the current state of other group of state variables. The idea is conveyed as follows: let the vector of state variables $X = (X_1, X_2)$ represent two structured populations. Define

$$F(X) = (\mathcal{F}_1 X_1,\, \mathcal{F}_2(X_1) X_2),$$

where $\mathcal{F}_1$ and $\mathcal{F}_2(X_1)$ are regular stochastic matrices for each X_1 and the entries of $\mathcal{F}_2$ are $\mathcal{C}^2$ function of X_1. The main result of this section, collected in theorem 1.3.8, proves that the corresponding complete system is susceptible of being approximately aggregated, as it fulfills those hypothesis in [90]. These settings came across from an interesting application on host-parasitoid community inhabiting a chain of patches with an arbitrary number of patches A. Movements between patches are considered to be faster than host-parasitoid interactions. Parasitoid movements depend on host densities at each patch; meaning that parasitoids avoid those patches with low host densities. The complete system consists on a set of $2A$ equations. It is not possible to handle it analytically, even for low values of A. Nevertheless, aggregation techniques allow the study of such a system through a two dimensional one (see [72] for the details). As a result, we found the existence of asymptotically stable equilibrium points while, *in absence of migrations*, only unstable outcomes are possible.

Regarding perspectives, it would be of interest to extend the work done in sections 1.2 and 1.3 to deal with fully coupled fast dynamics of the form

$$F(X) = \mathcal{F}(X)X,$$

where $\mathcal{F}(X)$ is a regular stochastic matrix for each X.

Besides, results in [90] provide no information about non hyperbolic fixed points (or non hyperbolic periodic orbits) nor about invariant or attracting objects different from hyperbolic equilibria or periodic orbits. Thus, it is of interest results contributing to translate information about invariant or attracting objects as well as the stability of non hyperbolic fixed points for the complete system through the aggregated system.

Chapter 2

Contributions to the approximate aggregation of nonautonomous ordinary differential equations.

2.1 Introduction.

In Nature, many physical parameters describing environmental conditions, as light, temperature, relative humidity,. . . , change with time. These environmental changes have strong influence on individuals and induce different responses in the behavior of populations living in. Vital processes as feeding or reproductive tasks, migrations or activity level vary with time. Thus, nonautonomous systems are realistic models for describing a population living and interacting in changing environments.

If we consider that these changes evolve continuously (smoothly), then systems of differential equations provide a more accurate description of reality than systems of difference equations.

The above comments along with the considerations on Hierarchy Theory made in section 1.2 provide us with the basic ingredients describing the kind of systems we will deal with: two time scales nonautonomous ordinary differential equation (ODE) systems. The idea of considering time dependence comes across as a natural extension of the available techniques for the approximate aggregation of two time scales autonomous ordinary differential equation systems.

Time dependence may occur in many different ways. Nonautonomous systems specialize according to specific features, namely, depending on how the coefficients of the system vary with time. Among them, we find periodic systems and asymptotically autonomous systems, which are in the scope of our study.

Let us recall the difficulties and aims related with two time scales approximate aggregation problems. Considering a detailed model containing two different processes evolving at different time scales yields detailed but complicated models. Sometimes, under certain conditions, we can take advantage of the existence of two different time scales to reduce the dimension of the corresponding system getting an *aggregated system* (less dimensional) to study the complete system. We face the problem of determining which dynamical properties of the aggregated system remain valid for the complete system. Approximate aggregation techniques for autonomous ordinary differential equations were introduced in [54], where perfect aggregation problems were addressed. Perfect aggregation arises when the behavior of the original and the aggregated dynamics are equivalent and only holds under very restrictive conditions. Soon, these results were extended to approximate aggregation through [5] and [55]. From a mathematical point of view, this results on approximate aggregation, which we will described later on, are based upon appropriate center manifold theorems due to Fenichel [32]. Many different and interesting applications have been developed using these techniques; see, for instance [6], [7] and references therein.

As a matter of fact we briefly introduce several applications on autonomous ordinary differential equations which somehow motivate or precede those developed herein. There is a range of applications on population dynamics spatially distributed in patchy environments (see, for instance, [77] and [78]). These models let population displacements between heterogeneous patches to be faster than local community interactions. On the other hand, in [9] it was addressed the study of autonomous two time scales eco-epidemic models. Namely, a classical predator-prey system such that an epidemic process affected predators at the fast time scale.

From the best of our knowledge, the only result of approximate aggregation of a two time scales nonautonomous system is found in [76]. In this work only the fast dynamics was considered to be nonautonomous and assumed to tend to an stationary periodic solution depending on global variables. Averaging techniques and the Fenichel center manifold theorems [32] allow to proceed to the reduction of the system. In our work, we introduce periodic time dependence on both the slow and the fast dynamics and we use the Hoppensteadt theorems on singular perturbations [52] to justify the suggested reduction procedure.

In the following, we summarize the main results and the underlying ideas in the approximate aggregation of two time scales autonomous ordinary differential equation systems. Next, we introduce a theorem due to Hoppensteadt [52], which is the cornerstone of the reduction procedure described herein. The introduction finishes describing the contents of this chapter.

2.1.1 Two time scales autonomous ordinary differential equation systems.

Let us recall the notation introduced in the previous chapter: let $\Omega_N \subset \mathbb{R}^N$ be an open, bounded, connected and non-empty set. State variables are represented by $\mathbf{n} \in \Omega_N$. The prototype of two time scales autonomous ordinary differential equations system is that of the form

$$\begin{cases} \dfrac{d\mathbf{n}}{d\tau} = \mathbf{f}(\mathbf{n}) + \varepsilon\, \mathbf{s}(\mathbf{n}), \\ \mathbf{n}(\tau_0) = \mathbf{n}^0 \end{cases} \tag{2.1}$$

where functions $\mathbf{f} = (f_1, \cdots, f_N)\,, \mathbf{s} = (s_1, \cdots, s_N) \in \mathcal{C}^1(\Omega_N)$ stand for the fast and the slow dynamics, respectively. The parameter ε is a small positive real number and means that the speed of the process described by $\mathbf{s}$ is slow when compared to $\mathbf{f}$, that is, the smaller is ε, the smaller is the contribution of function s to the derivative $d\mathbf{n}/d\tau$. In other words, the smaller is ε, the bigger is the difference between the characteristic time scales of the two processes involved in system (2.1).

When dealing with structured populations, that is, with populations divided in groups and subgroups, the state variables vector can be written as

$$\mathbf{n} = (\mathbf{n}^1, \cdots, \mathbf{n}^q) \qquad \text{with} \qquad \mathbf{n}_k = (n^{i1}, \cdots, n^{iN_i}),$$

where q is the number of groups, each of them consisting of N_i subgroups, for $i = 1, \cdots q$. Thus, n_{ij} is the number of individuals of the j-fold subgroup, $j \in \{1, \cdots, N_i\}$ of group i, with $i \in \{1, \cdots, q\}$.

System (2.1) provides a natural way of introducing the construction of a general two time scales model. Nevertheless, the reduction process begins properly with system (2.1) written in its equivalent slow-fast form. Namely, it is needed a suitable change of variables $(\mathbf{x}, \mathbf{y}) \to \mathbf{n}(\mathbf{x}, \mathbf{y})$, with $(\mathbf{x}, \mathbf{y}) \in \mathbb{R}^{N-k} \times \mathbb{R}^k$, such that (2.1) becomes

$$\left\{\begin{aligned} \frac{d\mathbf{x}}{d\tau} &= \mathbf{F}(\mathbf{x},\mathbf{y}) + \varepsilon\,\mathbf{S}(\mathbf{x},\mathbf{y}), & \mathbf{x}(\tau_0) &= \mathbf{x}, \\ \frac{d\mathbf{y}}{d\tau} &= \varepsilon\,\mathbf{G}(\mathbf{x},\mathbf{y}), & \mathbf{y}(\tau_0) &= \mathbf{y}, \end{aligned}\right. \tag{2.2}$$

where variables $\mathbf{x}$ and $\mathbf{y}$ are known as *fast variables* and *slow variables*, respectively, and functions $\mathbf{F}$, $\mathbf{S}$, $\mathbf{G} \in \mathcal{C}^1(\Omega_N)$. Finding the transformation $(\mathbf{x},\mathbf{y}) \to \mathbf{n}(\mathbf{x},\mathbf{y})$ which yields the slow-fast form (2.2) of system (2.1) could be a difficult task. The construction of general algorithms solving this problem is presently an active research line. On the other hand, in some applications, as we will see later, the context provides a natural way to define the so called *slow variables* $\mathbf{y}$ and, thus, to express system (2.1) in the slow-fast form. The definition of the slow variables in the autonomous case can be found in [6].

The underlying idea is the following. The transformation of variables $(\mathbf{x},\mathbf{y}) \to \mathbf{n}(\mathbf{x},\mathbf{y})$ leads system (2.1) into system (2.2) allowing, under certain conditions, a sort of variables decoupling. Assume that the fast dynamics posses an asymptotically stable equilibrium $\mathbf{x}^*(\mathbf{y})$ (at $\varepsilon = 0$). Therefore, such an equilibrium persists under small perturbations ($\varepsilon \sim 0$). The reduction techniques provide conditions to allow the study of the long term behavior of system (2.2) by means of the less-dimensional or *aggregated system*

$$\left\{\begin{array}{l} \dfrac{d\mathbf{y}}{dt} = \mathbf{G}(\mathbf{x}^*(\mathbf{y}),\mathbf{y}), \\ \mathbf{y}(t_0) = \mathbf{y}_0, \end{array}\right. \tag{2.3}$$

where $t = \varepsilon\tau$. The Geometrical Singular Perturbation theory, in the sequel GSP, provides with results to deal with such kind of systems. The most important ones have to do with the persistence of invariant manifolds to small enough perturbations. These manifolds are center manifolds containing the nontrivial part of the whole dynamics of the complete system (2.2).

Reduction theorem in the autonomous case.

In order to deal with system (2.2) we introduce an equation for ε;

$$(2.4) \qquad \begin{cases} \dfrac{d\mathbf{x}}{d\tau} = \mathbf{F}(\mathbf{x},\mathbf{y}) + \varepsilon\,\mathbf{S}(\mathbf{x},\mathbf{y}), \\[2ex] \dfrac{d\mathbf{y}}{d\tau} = \varepsilon\,\mathbf{G}(\mathbf{x},\mathbf{y}), \\[2ex] \dfrac{d\varepsilon}{d\tau} = 0. \end{cases}$$

System (2.4) can be seen as an ε-perturbation of the system obtained with $\varepsilon = 0$. The conditions for the reduction are the following ones:

(C1) We recall that slow variables $\mathbf{y}$ are constant when $\varepsilon = 0$. Assume that, for each $\mathbf{y} \in \mathbb{R}^k$, there exists at least one equilibrium $(\mathbf{x} = \mathbf{x}^*(\mathbf{y})\,, \mathbf{y}\,, 0)$, defined by

$$\mathbf{F}(\mathbf{x},\, \mathbf{x}^*(\mathbf{y})) = 0.$$

Consider the set:

$$\mathcal{M}_0 := \left\{(\mathbf{x},\, \mathbf{y},\, \varepsilon);\, \mathbf{x} = \mathbf{x}^*(\mathbf{y})\,, \mathbf{y} \in \mathbb{R}^k,\, \varepsilon = 0\right\}.$$

This invariant set for the unperturbed system shall play the role of the invariant normally hyperbolic manifold in the GSP theory.

(C2) Consider $J(\mathbf{y})$ the linear part of system (2.4) around the equilibrium point $(\mathbf{x}^*(\mathbf{y})\,, \mathbf{y}\,, 0)$. Assume that the Jacobian matrix $J(\mathbf{y})$ has $N-k$ eigenvalues with negative real parts and $k+1$ null eigenvalues. With this condition, the set $\mathcal{M}_0$ is *n*ormally hyperbolic since, at each point in $\mathcal{M}_0$, the restriction of the linear part to the $\mathcal{M}_0$ normal space has negative eigenvalues.

Under these conditions, the main result in approximate aggregation of autonomous ODE systems is the following [6].

Theorem 2.1.1 *Under the conditions (C1) and (C2), for each compact subset* $\mathcal{K} \in \mathbb{R}^N$ *and for each integer* $r > 1$*, there exists a real number* ε *and a* $\mathcal{C}^r$ *function* Ψ*,*

$$\begin{array}{rcl} \Psi : \mathcal{K} \times [0,\varepsilon] & \to & \mathbb{R}^{N-k} \\ (\mathbf{y},\varepsilon) & \mapsto & \mathbf{x} = \Psi(\mathbf{y},\varepsilon) \end{array}$$

such that:

1. *$\Psi(\mathbf{y},0)=\mathbf{x}^*(\mathbf{y})$*
2. *The graph $\mathcal{W}$ of Ψ is invariant under the flow defined by the vector field (2.4).*
3. *At each point $(\mathbf{x}^*(\mathbf{y}),\, \mathbf{y},\, 0)) \in \mathcal{M}_0$, $\mathcal{W}$ is tangent to the central eigenspace E^c associated with the eigenvalues of $J(\mathbf{y})$ with null real parts.*

This means that considering the restriction of the vector field to the invariant manifold entails reducing the dimension of the system. The reduced system, called aggregated system, is:

$$\frac{d\mathbf{y}}{dt}=G(\Psi(\mathbf{y},\varepsilon),\mathbf{y}),$$

with $t=\varepsilon\tau$. Typically $\varepsilon\sim 0$, and it is usual to approximate the aggregated system by means of

$$\frac{d\mathbf{y}}{dt}=G(\Psi(\mathbf{y},0),\mathbf{y}). \tag{2.5}$$

Just recall that function Ψ is of class $\mathcal{C}^r$ and $\Psi(\mathbf{y},0)$ in (2.5) is the zero order term of the Taylor expansion corresponding to Ψ in ε around $\varepsilon=0$. Thus, calculating higher order terms we can get a more accurate approximation of the aggregated system.

In the following, we deal with the approximate reduction of the nonautonomous counterpart of system (2.2). Our results do not relay on the GSP theory. Instead of this, our work is based upon a theorem due to Hoppensteadt [52], which we will present in the next section.

2.1.2 The Hoppensteadt theorem.

In this section we recall the settings used by Hoppensteadt in [52] to achieve the aforementioned results. In [52], Hoppensteadt deals with an initial value problem of the form

$$\begin{cases} \varepsilon\dfrac{d\mathbf{x}}{dt}=\varpi(t,\mathbf{x},\mathbf{y},\varepsilon), & \mathbf{x}(t_0)=\mathbf{x}_0,\\ \dfrac{d\mathbf{y}}{dt}=\varphi(t,\mathbf{x},\mathbf{y},\varepsilon), & \mathbf{y}(t_0)=\mathbf{y}_0. \end{cases} \tag{2.6}$$

Functions $\varpi = (\varpi_1, \cdots, \varpi_{N-q})$ and $\varphi = (\varphi_1, \cdots, \varphi_q)$ are of class $\mathcal{C}^2([t_0, \infty) \times \mathbb{R}^{N-q} \times \mathbb{R}^q \times [0, \varepsilon_0])$. System (2.2) is a particular case of system in (2.6). Just writing system (2.2) in terms of $t = \varepsilon\tau$ yields

$$\begin{cases} \varepsilon \dfrac{d\mathbf{x}}{dt} = \mathbf{F}(\mathbf{x}, \mathbf{y}) + \varepsilon\, \mathbf{S}(\mathbf{x}, \mathbf{y}), \\ \\ \dfrac{d\mathbf{y}}{dt} = \mathbf{G}(\mathbf{x}, \mathbf{y}). \end{cases}$$

Together with problem (2.6), Hoppensteadt considers two other related problems. Letting $\varepsilon = 0$ leads to the *degenerated system*

$$\begin{cases} 0 = \varpi(t, \mathbf{x}, \mathbf{y}, 0), \\ \dfrac{d\mathbf{y}}{dt} = \varphi(t, \mathbf{x}, \mathbf{y}, 0), \\ \mathbf{y}(t_0) = \mathbf{y}_0, \end{cases} \tag{2.7}$$

The other associated system is obtained by means of the *stretching* change of independent variable $s = (t - \alpha)/\varepsilon$ in (2.6) that yields, at $\varepsilon = 0$,

$$\begin{cases} \dfrac{d\mathbf{x}}{ds} = \varpi(\alpha, \mathbf{x}, \mathbf{y}, 0), \\ \dfrac{d\mathbf{y}}{ds} = 0, \end{cases}$$

where $\mathbf{y}$ is constant and so the previous system can be written in terms of parameters $\alpha \in \mathbb{R}$ and $\boldsymbol{\beta} \in \mathbb{R}^k$ as

$$\begin{cases} \dfrac{d\mathbf{x}}{ds} = \varpi(\alpha, \mathbf{x}, \boldsymbol{\beta}, 0), \\ \mathbf{x}(0) = \mathbf{x}_0, \end{cases} \tag{2.8}$$

which is known as the *boundary layer problem*: In addition, the following conditions are required:

(I) Problem (2.6) has a solution $(\mathbf{x}(t), \mathbf{y}(t))$ defined for $t \in I := [t_0, \infty)$. If this condition holds, we can apply an obvious transformation so that this solution is $(\mathbf{0}, \mathbf{0})$ for $t \in I$. Moreover, given, $0 < R \in \mathbb{R}$, let us define

$$S_R := \{(\mathbf{x}, \mathbf{y}) \in \mathbb{R}^{N-k} \times \mathbb{R}^k;\ \|(\mathbf{x}, \mathbf{y})\| \leq R\}$$

(II) It holds that $\varpi, \varphi, \varpi_t, \varpi_{\mathbf{x}}, \varpi_{\mathbf{y}}, \varphi_t, \varphi_{\mathbf{x}}, \varphi_{\mathbf{y}} \in \mathcal{C}\left(I \times S_R \times [0, \varepsilon_0]\right)$.

(III) There exists a bounded $\mathcal{C}^2$ function $\mathbf{x} = \mathbf{x}(t, \mathbf{y})$ such that

$$\varpi(t, \mathbf{x}(t, \mathbf{y}), \mathbf{y}, 0) = 0, \qquad \forall (t, \mathbf{y}) \in I \times S_R$$

and $\mathbf{x}(t, \mathbf{y})$ is isolated, meaning that $\mathbf{z} \neq \mathbf{x}(t, \mathbf{y})$ and $\varpi(\mathbf{z}, \mathbf{y}) = 0$ implies $|\mathbf{z} - \mathbf{x}(t, \mathbf{y})| > R$.

Assuming this condition, there is no loss of generality in considering that $\mathbf{x}(t, \mathbf{y}) = 0$ for all $(t, \mathbf{y}) \in I \times S_R$. If this were not the case, the transformation

$$\mathbf{x} = \mathbf{z} + \mathbf{x}(t, \mathbf{y}) \tag{2.9}$$

allows us to write (2.7) in the more convenient form

$$\begin{cases} \dfrac{d\mathbf{y}}{dt} = \varphi(t, \mathbf{0}, \mathbf{y}, 0), \\ \\ \mathbf{y}(t_0) = \mathbf{y}_0 \end{cases} \tag{2.10}$$

for further purposes.

(IV) Function φ is continuous at $\mathbf{x} = 0$ and $\varepsilon = 0$ uniformly in $(t, \mathbf{y}) \in I \times S_{R_\mathbf{y}}$, where

$$S_{R_\mathbf{y}} := \{\mathbf{y} \in \mathbb{R}^k;\ \exists\, \mathbf{x} \in \mathbb{R}^{N-k} \text{ such that } (\mathbf{x}, \mathbf{y}) \in S_R\}$$

and $\varphi(t, \mathbf{0}, \mathbf{y}, 0), \varphi_\mathbf{y}(t, \mathbf{0}, \mathbf{y}, 0)$ are bounded on $(t, \mathbf{y}) \in I \times S_{R_\mathbf{y}}$. Notice that

$$\varphi_\mathbf{y}(t, \mathbf{0}, \mathbf{y}, 0) = \left(\frac{\partial \varphi_i(t, \mathbf{0}, \mathbf{y}, 0)}{\partial y_j} \right)_{i,j=1,\cdots,k}.$$

(V) Function $\varpi(t, \mathbf{x}, \mathbf{y}, \varepsilon)$ is continuous at $\varepsilon = 0$ uniformly in $(t, \mathbf{x}, \mathbf{y}) \in I \times S_R$. Functions $\varpi(t, \mathbf{x}, \mathbf{y}, \varepsilon)$, $\varpi_t(t, \mathbf{x}, \mathbf{y}, 0)$, $\varpi_\mathbf{x}(t, \mathbf{x}, \mathbf{y}, 0)$ and $\varpi_\mathbf{y}(t, \mathbf{x}, \mathbf{y}, 0)$ are bounded on $I \times S_R$.

The last two assumptions concern the stability required of the solutions of the degenerated system (2.7) and the boundary layer problem (2.8). Hoppensteadt used the two following classes of functions

$$\mathfrak{K} := \{d : [0, \infty) \to [0, \infty);\ d(0) = 0,\ \text{strictly increasing and continuous}\}$$

$$\mathfrak{S} := \{\sigma : [0, \infty) \to [0, \infty);\ \lim_{t \to \infty} \sigma(t) = 0,\ \text{strictly decreasing and continuous}\}$$

We note $\phi(t, t_0, \hat{z})$ the solution of a given differential equation fulfilling $\phi(t_0) = \hat{z}$.

(VI) The zero solution of the initial value problem (2.10) is uniform-asymptotically stable, meaning that, if $\mathbf{y} = \phi(t, t_0, \mathbf{y}_0)$ is the solution of system (2.10), there exist $d \in \mathfrak{K}$ and $\sigma \in \mathfrak{S}$ such that

$$\|\phi(t, t_0, \mathbf{y}_0)\| \leq d\left(\|\mathbf{y}_0\|\right)\sigma(t - t_0) \tag{2.11}$$

for $\|\mathbf{y}_0\| \leq R$ and $0 \leq t_0 \leq t < \infty$. (cf [39]).

(VII) The zero solution of the boundary layer problem (2.8) is uniform-asymptotically stable uniformly in the parameters $(\alpha, \boldsymbol{\beta}) \in I \times S_{R_{\mathbf{y}}}$. That is, if $\mathbf{x} = \psi(s, \mathbf{x}_0, \alpha, \boldsymbol{\beta})$ is the solution of the boundary layer problem (2.8), there exist $e \in \mathfrak{K}$ and $\rho \in \mathfrak{S}$ such that

$$\|\psi(s, \mathbf{x}_0, \alpha, \boldsymbol{\beta})\| \leq e\left(\|\mathbf{x}_0\|\right)\rho(s) \tag{2.12}$$

for $\|\mathbf{x}_0\| \leq R$, $0 \leq s < \infty$ and $(\alpha, \boldsymbol{\beta}) \in I \times S_{R_{\mathbf{y}}}$.

Keeping functions ϖ and φ as general ones of class $\mathcal{C}^2$ implies that none of these conditions can be removed, as Hoppensteadt shows by means of appropriate examples [52]. Under these conditions, the following result holds:

Theorem 2.1.2 *Let the conditions (I) through (VII) be satisfied. Then for sufficiently small* $\|\mathbf{x}_0\| + \|\mathbf{y}_0\|$ *and* ε *the solution of the perturbed system* (2.6) *exists for* $t_0 \leq t < \infty$*, and this solution converges to the solution of the degenerate system* (2.7) *as* $\varepsilon \to 0$ *uniformly on all closed subsets of* $t_0 < t < \infty$*.*

Thanks to theorem 2.1.2 we are able to study the general system (2.6) through the less dimensional system (2.10). Even if of different nature, in order to keep parallelism between the aggregation techniques in the autonomous case and these developed here in, we will refer to system (2.10) as the *aggregated problem*.

2.1.3 Contents of this chapter.

In this chapter we use the Hoppensteadt theorem 2.1.2 for extending the approximate aggregation methodology available for autonomous two time scales ordinary differential equation systems of the form of (2.1) to some nonautonomous cases. We point out that conditions (I) up to (VII) are hard to be checked. The goal of this chapter consist in describing general classes of nonautonomous two time scale systems such that these 7 conditions can be replaced by 2 easy-to-check and biologically meaningful conditions.

Let us describe the aforementioned classes of systems we will deal with. Our study concerns with systems of one of the following forms

$$\begin{cases} \dfrac{d\mathbf{n}}{d\tau} = \mathbf{f}_i(\varepsilon\tau, \mathbf{n}) + \varepsilon\, \mathbf{s}(\varepsilon\tau, \mathbf{n}), \\ \mathbf{n}(\tau_0) = \mathbf{n}_0, \end{cases} \tag{2.13}$$

or

$$\begin{cases} \dfrac{d\mathbf{n}}{d\tau} = \mathbf{f}(\tau, \mathbf{n}) + \varepsilon\, \mathbf{s}(\tau, \mathbf{n}), \\ \mathbf{n}(\tau_0) = \mathbf{n}_0, \end{cases} \tag{2.14}$$

which can be expressed in the corresponding slow-fast form

$$\begin{cases} \dfrac{d\mathbf{x}}{d\tau} = \mathbf{F}(\varepsilon\tau, \mathbf{x}, \mathbf{y}) + \varepsilon\, \mathbf{S}(\varepsilon\tau, \mathbf{x}, \mathbf{y}), & \mathbf{x}(\tau_0) = \mathbf{x}_0, \\ \\ \dfrac{d\mathbf{y}}{d\tau} = \varepsilon\, \mathbf{G}(\varepsilon\tau, \mathbf{x}, \mathbf{y}), & \mathbf{y}(\tau_0) = \mathbf{y}_0. \end{cases} \tag{2.15}$$

or

$$\begin{cases} \dfrac{d\mathbf{x}}{d\tau} = \mathbf{F}(\tau, \mathbf{x}, \mathbf{y}) + \varepsilon\, \mathbf{S}(\tau, \mathbf{x}, \mathbf{y}), & \mathbf{x}(\tau_0) = \mathbf{x}_0, \\ \\ \dfrac{d\mathbf{y}}{d\tau} = \varepsilon\, \mathbf{G}(\tau, \mathbf{x}, \mathbf{y}), & \mathbf{y}(\tau_0) = \mathbf{y}_0, \end{cases} \tag{2.16}$$

being all the functions involved in the previous ordinary differential equation systems of class $\mathcal{C}^2$. Regarding systems (2.14) and (2.16), we ask functions $\mathbf{F}, \mathbf{S}$ and $\mathbf{G}$ involved therein to be asymptotically autonomous; see section 2.3 for further information. On the other hand, functions involved in systems (2.13) and (2.15) are supposed to be periodic functions of time τ with the same period. Thus, the term $\varepsilon\tau$ modulates somehow the length of this period; see section 2.2 for more details.

This chapter is organized as follows. Section 2.2 deals with a class of systems of the form of (2.15) and is based on [66] and [67]. After establishing the corresponding version of theorem 2.1.2, we analyze alternative conditions assuring the stability condition given by (2.11). Finally, we apply this results to the study of two different models. On the one hand, we analyze a two patches periodic Lotka-Volterra predator-prey type model and a refuge for prey. On the other hand, we consider a two patches periodic multi strain SIS epidemic model based upon [65]. In both cases displacements between patches stand for the fast process.

In section 2.3 we analyze systems of the form of (2.16). We establish the corresponding version of theorem 2.1.2 and we apply this results to the study of a nonautonomous asymptotically autonomous eco-epidemic system generalizing that addressed in [9]. This model consist on a Lotka-Volterra predator-prey model coupled with an epidemic process. Namely, predators are affected by an epidemic which stands for the fast process.

2.2 Slowly varying periodic dynamics.

Due to Earth movements; rotation around its axes and translation around the Sun, many environmental conditions change periodically. Just think that everybody has experienced daily or seasonally periodicity. It is realistic considering populations inhabiting periodic environments, meaning that parameters describing environmental conditions are periodic in time.

We carry on the approximate aggregation of systems of the form

$$\left\{\begin{array}{l}\dfrac{d\mathbf{n}}{d\tau}=\mathbf{f}(\varepsilon\tau,\mathbf{n})+\varepsilon\mathbf{s}(\varepsilon\tau,\mathbf{n}),\\ \mathbf{n}(\tau_0)=\mathbf{n}_0\end{array}\right. \tag{2.17}$$

where $\mathbf{n}=(n_1,\cdots,n_N)\in\Omega_N\subset\mathbb{R}^N$, an open bounded nonempty set, $\mathbf{f}=(f_1,\cdots,f_N)$, $\mathbf{s}=(s_1,\cdots,s_N)\in\mathcal{C}^2(\mathbb{R}\times\Omega_N)$ are periodic functions of time with the same period. To perform its approximate aggregation, we assume that the previous system can be written in the slow-fast form (2.15) by means of an appropriate change of variables $\mathbf{n}\in\mathbb{R}^N\longrightarrow(\mathbf{x},\mathbf{y})\in\mathbb{R}^{N-k}\times\mathbb{R}^k$,

$$\left\{\begin{array}{ll}\dfrac{d\mathbf{x}}{d\tau}=\mathbf{F}(\varepsilon\tau,\mathbf{x},\mathbf{y})+\varepsilon\mathbf{S}(\varepsilon\tau,\mathbf{x},\mathbf{y}), & \mathbf{x}(\tau_0)=\mathbf{x}_0,\\ \\ \dfrac{d\mathbf{y}}{d\tau}=\varepsilon\mathbf{G}(\varepsilon\tau,\mathbf{x},\mathbf{y}), & \mathbf{y}(\tau_0)=\mathbf{y}_0.\end{array}\right. \tag{2.18}$$

We point out that the independent variable of system (2.18) is τ while functions $\mathbf{F},\mathbf{S}$ and $\mathbf{G}$ involved in (2.18) depend on $\varepsilon\tau$ and are periodic on τ. We refer to this fact by saying that these functions are "slowly periodically varying", meaning that the closer to zero is ε, the larger is the corresponding period.

2.2.1 An aggregation theorem.

System (2.18), which we recall for the convenience of the reader,

$$\begin{cases} \dfrac{d\mathbf{x}}{d\tau} = \mathbf{F}(\varepsilon\tau, \mathbf{x}, \mathbf{y}) + \varepsilon\mathbf{S}(\varepsilon\tau, \mathbf{x}, \mathbf{y}), & \mathbf{x}(\tau_0) = \mathbf{x}_0, \\ \\ \dfrac{d\mathbf{y}}{d\tau} = \varepsilon\mathbf{G}(\varepsilon\tau, \mathbf{x}, \mathbf{y}), & \mathbf{y}(\tau_0) = \mathbf{y}_0, \end{cases}$$

obviously falls into those considered by Hoppensteadt (see (2.6) keeping in mind that $t = \varepsilon\tau$). The following result is the version of theorem 2.1.2 corresponding to system (2.18).

Theorem 2.2.1 *Consider system* (2.18), *where* $\mathbf{F}$, $\mathbf{S}$, $\mathbf{G} \in \mathcal{C}^2(I \times \mathbb{S}_R)$,

$$\mathbb{S}_R := \left\{(\mathbf{x}, \mathbf{y}) \in \mathbb{R}^{N-k} \times \mathbb{R}^k;\ \|\mathbf{y} - \mathbf{y}_0\| \leq R,\ \|\mathbf{x} - \mathbf{x}^*(t, \mathbf{y})\| \leq R,\ t \in I_0\right\}$$

with $R > 0$ *a positive constant,* $\mathbf{y}_0$ *and* $\mathbf{x}^*(t, \mathbf{y})$ *to be defined,* $I_0 = [t_0,\ t_0 + \omega]$, $I = [t_0, \infty)$, $\mathbf{F}$, $\mathbf{S}$ *and* $\mathbf{G}$ *are periodic functions of time with the same period* ω. *Assume that*

(C1) There exists an unique continuum of equilibria $\mathbf{x}^*(\alpha, \boldsymbol{\beta})$ *(see remark 2.2.2), with* $\alpha \in I$ *and* $\boldsymbol{\beta} \in \mathbb{R}^k$ *such that* $\|\boldsymbol{\beta} - \mathbf{y}_0\| \leq R$ *for system*

$$\frac{d\mathbf{x}}{ds} = \mathbf{F}(\alpha, \mathbf{x}, \boldsymbol{\beta}), \tag{2.19}$$

known as boundary layer system, such that the real part of the eigenvalues of $J_{\mathbf{x}}\mathbf{F}(\alpha, \mathbf{x}^*(\alpha, \boldsymbol{\beta}), \boldsymbol{\beta})$ *is negative (*J *stands for the Jacobian matrix).*

(C2) The aggregated system

$$\frac{d\mathbf{y}}{dt} = \mathbf{G}(t, \mathbf{x}^*(t, \mathbf{y}), \mathbf{y}), \tag{2.20}$$

where $\mathbf{x}^*(\alpha, \boldsymbol{\beta})$ *is that of condition (C1), possesses a periodic solution* $\mathbf{y}^*(t, t_0, \mathbf{y}_0)$ *defined for all* $t \in I$ *which is uniformly-asymptotically stable. We mean that there exists* $R > 0$ *such that for any other solution* $\Phi(t, t_0, \bar{\mathbf{y}}_0)$ *of system* (2.20) *with* $\|\bar{\mathbf{y}}_0 - \mathbf{y}_0\| \leq R$, *there exist functions* $d \in \mathfrak{K}$ *and* $\sigma \in \mathfrak{S}$ *such that*

$$\|\mathbf{y}^*(t, t_0, \mathbf{y}_0) - \Phi(t, t_0, \bar{\mathbf{y}}_0)\| \leq d\left(\|\mathbf{y}_0 - \bar{\mathbf{y}}_0\|\right)\sigma(t - t_0). \tag{2.21}$$

Then, there exists $0 < \rho \leq R$ *such that for each* $\varepsilon > 0$ *small enough and each initial condition* $(\bar{\mathbf{x}}_0, \bar{\mathbf{y}}_0)$ *such that* $\|(\bar{\mathbf{x}}_0, \bar{\mathbf{y}}_0) - (\mathbf{x}_0, \mathbf{y}_0)\| < \rho$ *the corresponding solution* $(\mathbf{x}_\varepsilon(t, t_0, \bar{\mathbf{x}}_0),\ \mathbf{y}_\varepsilon(t, t_0, \bar{\mathbf{y}}_0))$ *of the original system* (2.17) *verifies*

$$\lim_{\varepsilon \to 0} (\mathbf{x}_\varepsilon(t, t_0, \bar{\mathbf{x}}_0),\ \mathbf{y}_\varepsilon(t, t_0, \bar{\mathbf{y}}_0)) = (\mathbf{x}^*(t, \mathbf{y}^*(t, t_0, \mathbf{y}_0)), \mathbf{y}^*(t, t_0, \mathbf{y}_0))$$

uniformly on closed subset of $[t_0, \infty)$.

Proof.– The proof consists in checking hypotheses (I) up to (VII) in the Hoppensteadt theorem.

(I) and (II) hold because of the regularity of functions $\mathbf{F}$, $\mathbf{S}$ and $\mathbf{G}$.

(III) We have asked for this at condition (C1) of the statement of the theorem.

(IV) Notice that $\varphi(t, \mathbf{x}, \mathbf{y}, \varepsilon) = \mathbf{G}(t, \mathbf{x}, \mathbf{y})$ and, in particular, it does not depend on ε. Clearly, functions $\varphi(t, \mathbf{x}^*, \mathbf{y}, 0) = \mathbf{G}(t, \mathbf{x}^*, \mathbf{y})$ and $\varphi'_{\mathbf{y}}(t, \mathbf{x}^*, \mathbf{y}, 0) = \mathbf{G}'_{\mathbf{y}}(t, \mathbf{x}^*, \mathbf{y})$ are bounded on $I \times \mathbb{S}_R$ as functions $\mathbf{G}$ and $\mathbf{G}'_{\mathbf{y}}$ are periodic on t and $\mathbf{x}^*$ and $\mathbf{y}$ vary on a compact set.

Let us fix $\eta > 0$. For each $t \in I$ and $\mathbf{y} \in \mathbb{R}$ such that $\|\mathbf{y} - \mathbf{y}_0\| \leq R$ function $\mathbf{G}(t, \cdot, \mathbf{y})$ is continuous in $\mathbf{x}$ at $\mathbf{x} = \mathbf{x}^*(t, \mathbf{y})$. Thus, there exists $\delta(t, \mathbf{y})$ such that

$$\|\mathbf{x} - \mathbf{x}^*(t, \mathbf{y})\| < \delta(t, \mathbf{y}) \Rightarrow \|\mathbf{G}(t, \mathbf{x}, \mathbf{y}) - \mathbf{G}(t, \mathbf{x}^*(t, \mathbf{y}), \mathbf{y})\| < \eta.$$

Notice that δ is continuous on t and $\mathbf{y}$. Besides, we recall that $\mathbf{G}$ is ω-periodic on t. Therefore, for each $\mathbf{y}$ fixed such that $\|\mathbf{y} - \mathbf{y}_0\| \leq R$ we can choose $\delta(\cdot, \mathbf{y})$ to be ω-periodic on t and we define

$$0 < \delta(\mathbf{y}) := \min \{\delta(t, \mathbf{y});\ t \in [t_0, t_0 + \omega]\} = \min \{\delta(t, \mathbf{y});\ t \in I\}.$$

In fact, as $\mathbf{y}$ varies on the compact set $\|\mathbf{y} - \mathbf{y}_0\| \leq R$, there exists $0 < \delta$ defined as $\delta := \min \{\delta(\mathbf{y});\ \|\mathbf{y} - \mathbf{y}_0\| \leq R\}$ whit the desired property.

(V) Analogous to (IV).

(VI) We have asked for in condition (C2).

(VII) This is contained in condition (C1).

■

Remark 2.2.2 *Theorem 2.2.1 is also true if there exist finitely many continuum of equilibria of the form* $\mathbf{x}^*(\alpha, \boldsymbol{\beta})$ *which are suitably isolated; meaning that if there exist* $\mathbf{x}_i^*(\alpha, \boldsymbol{\alpha}, \boldsymbol{\beta})$ *such that* $\mathbf{F}(\alpha, \mathbf{x}_i^*(\boldsymbol{\beta}), \boldsymbol{\beta}) = 0$ *for* $i = 1, 2$*, then*

$$\|\mathbf{x}_1^*(\alpha, \boldsymbol{\beta}) - \mathbf{x}_2^*(\alpha, \boldsymbol{\beta})\| > R$$

for all α *and* $\boldsymbol{\beta}$*, being* $R > 0$ *that from theorem 2.2.1.*

In the general case checking condition (2.21) could be difficult. Taking advantage of the periodic feature of system (2.18) the following result provides us with easy-to-check conditions implying condition (2.21)

Proposition 2.2.3 *Assume that the aggregated system* (2.20) *possesses a periodic solution* $\mathbf{y}^*(t)$*. Consider the linearization of system* (2.20) *around* $\mathbf{y}^*(t)$

$$\mathbf{z}' = \mathbf{G}_{\mathbf{y}}(t, \mathbf{x}^*(\mathbf{y}^*), \mathbf{y}^*)\mathbf{z}. \tag{2.22}$$

Then, any of the following conditions assures that $\mathbf{y}^*(t)$ *is uniformly asymptotically stable in the sense of condition (C2):*

1. *The characteristic multipliers of system* (2.22) *are in modulus less than one.*

2. *Condition* (2.21) *holds for the zero solution of system* (2.22)*.*

Proof.–

1. Let us note $\mathbf{y}^*(t) = \mathbf{y}^*(t, t_0, y_0^*)$ the periodic solution of system (2.20) and $\boldsymbol{\Phi}(t) = \boldsymbol{\Phi}(t, t_0, w_0)$ any other solution of system (2.20), respectively. We define $z(t) := \boldsymbol{\Phi}(t) - \mathbf{y}^*(t)$ and we seek for suitable functions $d \in \mathcal{K}$ and $\sigma \in \mathcal{S}$ such that the stability condition stated in (2.21) holds. In fact, considering the variational problem around $\mathbf{y}^*(t)$, we get that $\mathbf{z}$ is the solution of

   $$\frac{d\mathbf{z}}{dt} = \mathbf{G}_{\mathbf{y}}(t, \mathbf{x}^*(\mathbf{y}^*), \mathbf{y}^*)\mathbf{z} + f(t, \mathbf{z}), \tag{2.23}$$

   where $f(t, \mathbf{z}) = o(|\mathbf{z}|)$ uniformly in t because function $\mathbf{G}$ is periodic on t. Matrix $\mathbf{G}_{\mathbf{y}}(t, \mathbf{x}^*(\mathbf{y}^*), \mathbf{y}^*)$ is periodic and a classical theorem due to Liapunov (see, for instance, theorem 2.2.6 in [30]) assures the existence of a transformation of variables $\mathbf{z} = P(t)\mathbf{w}$ such that system (2.23) becomes

   $$\frac{d\mathbf{w}}{dt} = A\mathbf{w} + \hat{f}(t, \mathbf{w}), \tag{2.24}$$

where A is a matrix with constant entries and $\hat{f}(t, \mathbf{w}) = o(|\mathbf{w}|)$ uniformly in t because function $P(t)$ is continuously differentiable regular matrix periodic on t with period ω or 2ω. The eigenvalues of A are the characteristic exponents of system (2.22). If all the characteristic multipliers are in modulus less than 1, then all of the characteristic exponents have negative real parts (see, for instance, (2.2.13) in [30]). Therefore, condition 1 implies that the real part of all the eigenvalues of A is strictly negative. The variation constants method applied to system (2.24) yields

$$\mathbf{w}(t) = e^{(t-t_0)A}\mathbf{w}(t_0) + \int_{t_0}^{t} e^{(t-s)A}\hat{f}(t, \mathbf{w})ds. \tag{2.25}$$

As the real part of the eigenvalues of A is strictly negative, there exist positive constants ξ and K such that

$$\left\| e^{(t-t_0)A} \right\| \leq K e^{-\xi(t-t_0)} \qquad t \geq t_0,$$

which yields

$$\|\mathbf{w}(t)\| \leq \|\mathbf{w}(t_0)\| K e^{-\xi(t-t_0)} + \int_{t_0}^{t} \bar{K} e^{-\xi(t-s)} \left\| \hat{f}(t, \mathbf{w}) \right\| ds. \tag{2.26}$$

Besides, the fact that $\hat{f}(t, \mathbf{w}) = o(\|\mathbf{w}\|)$ yields the following. Given $\varepsilon > 0$ there exists $\delta > 0$ such that $\|\mathbf{w}\| \leq \delta$ implies

$$\frac{\left\| \hat{f}(t, \mathbf{w}) \right\|}{\|\mathbf{w}\|} \leq \frac{\varepsilon}{\bar{K}}.$$

Therefore, if $\|\mathbf{w}\| \leq \delta$, it follows that

$$\|\mathbf{w}(t)\| \leq \|\mathbf{w}(t_0)\| K e^{-\xi(t-t_0)} + \varepsilon \int_{t_0}^{t} e^{-\xi(t-s)} \|\mathbf{w}(s)\| ds.$$

Multiplying the previous inequality by $e^{\xi t}$ yields

$$\|\mathbf{w}(t)\| e^{\xi t} \leq \|\mathbf{w}(t_0)\| K e^{\xi t_0} + \varepsilon \int_{t_0}^{t} e^{\xi s} \|\mathbf{w}(s)\| ds. \tag{2.27}$$

Let us see now that for $\|\mathbf{w}(t_0)\| < \delta/K$ and $\varepsilon < \xi$ we have

$$\|\mathbf{w}(t)\| \leq \|\mathbf{w}(t_0)\| K e^{-(\xi-\varepsilon)(t-t_0)}. \tag{2.28}$$

We define

$$R(t) := \int_{t_0}^{t} \varepsilon\, e^{\xi s} \left\| \mathbf{w}(s) \right\| ds.$$

Direct calculations and (2.27) yield

$$\begin{aligned} R'(t) - \varepsilon\, R(t) &= \varepsilon\, e^{\xi t} \left\| \mathbf{w}(t) \right\| - \varepsilon \textstyle\int_{t_0}^{t} \varepsilon\, e^{\xi s} \left\| \mathbf{w}(s) \right\| ds \\ &= \varepsilon \left(\left\| \mathbf{w}(t_0) \right\| K e^{\xi t_0} + \varepsilon \textstyle\int_{t_0}^{t} e^{\xi s} \left\| \mathbf{w}(s) \right\| ds \right) \\ &\quad -\varepsilon \textstyle\int_{t_0}^{t} \varepsilon\, e^{\xi s} \left\| \mathbf{w}(s) \right\| ds \\ &\leq \varepsilon K\, e^{\xi t_0} \left\| \mathbf{w}(t_0) \right\| \end{aligned}$$

which implies

$$R(t) \leq R(t_0) e^{\varepsilon(t-t_0)} + \int_{t_0}^{t} \varepsilon K\, e^{\xi t_0} e^{\varepsilon(t-s)} \left\| \mathbf{w}(t_0) \right\| ds.$$

Moreover, $R(t_0) = 0$ and, using the previous inequality in (2.27) we get

$$\begin{aligned} \left\| \mathbf{w}(t) \right\| e^{\xi t} &\leq \left\| \mathbf{w}(t_0) \right\| K e^{\xi t_0} + \textstyle\int_{t_0}^{t} \varepsilon K\, e^{\xi t_0} e^{\varepsilon(t-s)} \left\| \mathbf{w}(t_0) \right\| ds \\ &= \left\| \mathbf{w}(t_0) \right\| K e^{\xi t_0} \left(1 + \textstyle\int_{t_0}^{t} \varepsilon\, e^{\varepsilon(t-s)} ds \right) \\ &= \left\| \mathbf{w}(t_0) \right\| K e^{\xi t_0}\, e^{\varepsilon(t-t_0)}. \end{aligned}$$

Finally, rearranging terms gives rise to

$$\left\| \mathbf{w}(t) \right\| \leq \left\| \mathbf{w}(t_0) \right\| K e^{-\xi(t-t_0)} e^{\varepsilon(t-t_0)}.$$

Thus, defining

$$d(\left\| \mathbf{y}_0^* - \mathbf{\Phi_0} \right\|) := K \left\| \mathbf{w}(t_0) \right\| = K \left\| \mathbf{y}_0^* - \mathbf{\Phi_0} \right\|$$

and

$$\sigma(t - t_0) := e^{-(\xi-\varepsilon)(t-t_0)}$$

finishes the proof.

2. It is straightforward.

■

2.2.2 Periodic predator-prey system with fast autonomous migrations.

Patchy environments enable a tool for simulate environmental heterogeneity. Given a predator-prey community inhabiting in a patchy environment and considering that individual displacements between patches are faster than community interactions yields a two time scales model.

Since the pioneering works of Lotka [60], [61] and Volterra [103] in predator-prey models, many work has been done. In particular, much efforts focus to ascertaining appropriate *functional responses* for the models to accurately describe reality. In ecology, a functional response is the intake rate of a consumer as a function of food density. Besides, it is associated with the quantitative response; the reproduction rate of a consumer as a function of food density.

The most used functional responses (as Holling type [51] ones) are function of prey density and do not consider predator interference which, according to field data [34], has turn out to be relevant.

Summing up we have the basic ingredients of this section. We begin with the construction of an spatially distributed two time scales predator-prey model with functional response of Beddington [15] DeAngelis [28] type, which takes into account predators interference. Then, using the methodology developed in section 2.2.1, we derive reduced model to simplify the study of the original one. After doing so, we perform a detailed analysis of the aggregated system, pointing out which information about the complete system can be recovered from the study of the reduced system through theorem 2.2.1 and proposition 2.2.3.

Construction and reduction of the system.

We consider a predator-prey model inhabiting an heterogeneous ambient. We simulate heterogeneity by considering a patchy environment and letting individuals migrate between patches. By the sake of simplicity we consider a two patches environment. Prey population at patch $i = 1, 2$ is noted by n_i. Prey migrate from patch i at a constant rate m_i. Predators p stay confined in the second region. Migrations are understood as individual movements between different zones of the habitat. Thus, we consider migrations to be faster than local dynamics which, in addition, are supposed to depend on time periodic functions. The first patch is taken to be a refuge for prey and the equation for n_1 is of logistic type. In the second patch prey and predators interact. These interactions are described by a classical predator-prey system with prey logistic growth in absence of predators, predator exponential decay in absence of prey and a particular functional response of the following form:

$$f(t,x,y) = \frac{a(t)x}{1+c(t)y}, \tag{2.29}$$

(x and y stand for prey and predator densities) where the upper bounding predators feeding mechanism is limited to predators interference. From the pioneering works of Beddington [15] and DeAngelis [28] it is known that predators interference is a relevant mechanism in predator-prey interactions. In Skalsky and Gilliam [96] it is presented statistical evidence from nineteen predator-prey systems that three predator-dependent functional responses (Beddington-DeAngelis, Crowley-Martin and Hassel-Varley) can provide better descriptions of predator feeding over a range of predator-prey abundances. It is found that no single functional response best describes all of the data sets, but a common feature of the three proposed functional responses is that all of them include predator interference. From a phenomenological point of view, functional response (2.29) is the simplest one keeping predator interference.

In addition, compared with expression (2.29), the Beddigngton-DeAngelis functional response contains an extra term $b(t)x$ (known as "handling" term) in the denominator. This term represents a mechanism to upper bounding predators feeding rate when there is food superabundance. On the other hand, we notice that this cannot be the case in our model because prey, $x(t)$, local dynamics in the no-refuge region is driven by equation

$$\frac{dx}{dt} = r_2(t)x\left(1-\frac{x}{K_2(t)}\right) - \frac{\phi_2(t)\ x}{1+c(t)y}\ y$$

which solutions are bounded from above by the solutions, $n(t)$, of the periodic logistic equation

$$\frac{dn}{dt} = r_2(t)n\left(1-\frac{n}{K_2(t)}\right)$$

which are bounded. Thus, in our model the aforementioned upper bounding mechanism is not crucial and we decided to use the simplified form (2.29) of Beddington-DeAngelis functional response.

All those settings are represented by means of the following system of nonautonomous ordinary differential equations:

(2.30)

$$\begin{cases} \dfrac{dn_1}{d\tau} = -m_1n_1 + m_2n_2 + \varepsilon r_1(\varepsilon\tau)n_1\left(1 - \dfrac{n_1}{K_1(\varepsilon\tau)}\right), \\[2ex] \dfrac{dn_2}{d\tau} = m_1n_1 - m_2n_2 + \varepsilon\left(r_2(\varepsilon\tau)n_2\left(1 - \dfrac{n_2}{K_2(\varepsilon\tau)}\right) - \dfrac{\phi_2(\varepsilon\tau)\ n_2}{1 + c(\varepsilon\tau)p}\ p\right), \\[2ex] \dfrac{dp}{d\tau} = \varepsilon\left(-\lambda_3(\varepsilon\tau)p + \dfrac{\phi_3(\varepsilon\tau)\ n_2}{1 + c(\varepsilon\tau)p}\ p\right), \end{cases}$$

where the functions r_j, λ_3, c, ϕ_{j+1}, $K_j \in \mathcal{C}^2$, for $j = 1, 2$, are positive, bounded away from zero and periodic with the same period ω. These functions depend on the slow time unit $t = \varepsilon\tau$. On the other hand, ε is a small positive parameter representing the ratio between the time scales. As usual, r_i (i=1,2) and λ_3 stand for the respective net growth rates, K_i (i=1,2) is the carrying capacity, ϕ_i (i=1,2) measures the effect of captures in prey and predator populations and c is related with the time elapsed engaging with other predators. We will set $c = 1$, so that we keep the effect of interferences between predators but simplify the system (which already depends on many parameters). Summing up, system (2.30) matches with system (2.13) and we seek for an appropriate change of variables leading system (2.30) into its slow-fast form.

It is apparent that, at $\varepsilon = 0$, there exists an stable manifold of equilibria for the fast dynamics which are stable but not asymptotically stable. Thus, condition (C1) fails. In this context, according with [6], using the global variable

$$n(\tau) = n_1(\tau) + n_2(\tau), \tag{2.31}$$

allow us to write system (2.30) in the appropriate slow-fast form. Let us now introduce frequencies as

$$\nu_i(\tau) = n_i(\tau)/n(\tau), \qquad i = 1, 2. \tag{2.32}$$

In terms of ν_1 and n system (2.30) reads as follows

$$(2.33)\quad \begin{cases} \varepsilon\dfrac{d\nu_1}{dt} &= m_2 - (m_1+m_2)\nu_1 + \varepsilon(1-\nu_1)\left[r_1(t)\left(1-\dfrac{\nu_1\, p}{K_1(t)}\right)\nu_1\right. \\ & \left. -r_2(t)\left(1-\dfrac{(1-\nu_1)\,p}{K_2(t)}\right)+\dfrac{\phi_2(t)p}{1+p}\right], \\ \dfrac{dn}{dt} &= \left[r_1(t)\left(1-\dfrac{\nu_1\, n}{K_1(t)}\right)\nu_1\right. \\ & \left. +r_2(t)\left(1-\dfrac{(1-\nu_1)\,n}{K_2(t)}\right)(1-\nu_1)-\dfrac{\phi_2(t)(1-\nu_1)p}{1+p}\right]n, \\ \dfrac{dp}{dt} &= \left[-\lambda_3(t)+\dfrac{\phi_3(t)(1-\nu_1)\,n}{1+p}\right]p, \end{cases}$$

provided $t=\varepsilon\tau$. We refer to ν_1 as the fast variable and to n, p as slow variables.

The following result is straightforward:

Lemma 2.2.4 *Consider the boundary layer problem* (2.19)

$$(2.34)\qquad \frac{d\nu_1}{ds} = m_2 - (m_1+m_2)\nu_1$$

associated with system (2.33)*. It holds that*

$$(2.35)\qquad \nu_1^* := \frac{m_2}{m_1+m_2} = \nu_1^*(n,p),$$

fulfills condition (C1) in theorem 2.2.1.

From now on, we note $z' = dz/dt$. Thus, the *aggregated system* reads:

$$(2.36)\qquad \begin{cases} n' = (a(t)-b(t)n)\,n - \dfrac{c(t)\,n}{1+p}\,p, \\ p' = -\lambda(t)p + \dfrac{f(t)\,n}{1+p}\,p, \end{cases}$$

where

$$(2.37)\qquad \begin{aligned} &\nu_2^* = 1-\nu_1^*, \qquad \lambda(t)=\lambda_3(t), \qquad a(t)=r_1(t)\nu_1^*+r_2(t)\nu_2^*, \\ &b(t)=\frac{r_1(t)(\nu_1^*)^2}{K_1(t)}+\frac{r_2(t)(\nu_2^*)^2}{K_2(t)}, \quad c(t)=\phi_2(t)\nu_2^*, \quad f(t)=\phi_3(t)\nu_2^*. \end{aligned}$$

Analysis of the aggregated system.

In this section we carry out the study of system (2.36). For further purposes, we recall that the functions defined in (2.37) are periodic, positive and bounded away from zero, thus, they achieve strictly positive minimum and maximum, which we note with subindex L and M, respectively:

$$\left\{\begin{array}{ll} a_L \leq a(t) \leq a_M & b_L \leq b(t) \leq b_M \\ c_L \leq c(t) \leq c_M & \lambda_L \leq \lambda(t) \leq \lambda_M \\ f_L \leq f(t) \leq f_M & \end{array}\right. \tag{2.38}$$

System (2.36) always admits the trivial solution $(n(t), p(t)) = (0, 0)$ for all $t \geq t_0$. Moreover, if we let $p(t) = 0$, then system (2.36) simplifies in

$$n' = (a(t) - b(t)n)\, n, \qquad n(t_0) = n_0, \tag{2.39}$$

which was studied in [38], where it is shown that if $a(t) > 0$ and $b(t) > 0$ are periodic functions with common period ω, then there exists an unique positive periodic solution $n_0^*(t)$ for (2.39) which is globally asymptotically stable. We will refer to $(n_0^*(t), \mathbf{0})$ as the semi-trivial solution of system (2.36). Later on, we will relate the existence of an asymptotically stable positive periodic solution of system (2.36) with the stability of the semi-trivial solution. Both positive semi-axes are invariant sets for system (2.36).

Next, we describe the behavior of the solutions of the general system (2.30) in terms of the solutions of the corresponding boundary layer problem and aggregated system. In particular, we provide with conditions for the existence and stability of positive and semi-trivial periodic solutions of system (2.36) and apply theorem 2.2.1 and proposition 2.2.3.

Finding periodic solutions of periodic systems and deciding about its stability may become a difficult task. The following lemmas will be used later on. The firs one is a straightforward application of the Andronov Poincaré theorem and provides with sufficient conditions for the existence of such a solutions. The second one concerns ascertaining the stability of the zero solution of a planar periodic linear system.

Lemma 2.2.5 *Consider the ordinary differential equations system*

$$\frac{d\mathbf{y}}{dt} = \mathbf{H}(t, \mathbf{y}) \tag{2.40}$$

where $\mathbf{y} \in \mathbb{R}^N$ *and function* $\mathbf{H} = (h_1, \cdots, h_N) \in \mathcal{C}^1(\mathbb{R} \times \mathbb{R}^N)$ *is periodic on* t *with period* $\omega > 0$. *The existence of a bounded compact simply connected positively invariant region* $\mathcal{R}$ *for the solutions of system* (2.40) *implies the existence of a periodic solution for system* (2.40).

Proof.– Let us consider the ω-operator φ_ω defined by

$$\begin{array}{rcl} \varphi_\omega : \mathcal{R} & \rightarrow & \mathcal{R} \\ \mathbf{y}_0 & \mapsto & \varphi_\omega(\mathbf{y}) = \varphi(t_0 + \omega, t_0, \mathbf{y}_0). \end{array}$$

This operator maps each initial value $\mathbf{y}_0$ on the region $\mathcal{R}$ into the value $\varphi(t_0 + \omega, t_0, \mathbf{y}_0)$ at time $t = t_0 + \omega$ of the solution of system (2.20) starting at $t = t_0$ at the initial value $\mathbf{y}_0$. This is a continuous map and by Brouwer's fixed point theorem this operator has, at least, one fixed point. This means that there exists (at least) a solution φ of system (2.20) such that

$$\varphi(t_0 + \omega, t_0, \mathbf{y}_0) = \varphi(t_0, t_0, \mathbf{y}_0).$$

Let us define $\xi(t) = \varphi(t + \omega)$. We recall that $\mathbf{x}^*(\alpha, \boldsymbol{\beta}) = \mathbf{x}^*(\alpha + \omega, \boldsymbol{\beta})$, which follows from the fact that function $\mathbf{F}$ is ω periodic on t. Then,

$$\begin{aligned} \xi'(t) &= \varphi'(t + \omega) \\ &= \mathbf{H}(t + \omega, \mathbf{x}^*(t + \omega, \varphi(t + \omega)), \varphi(t + \omega)) \\ &= \mathbf{H}(t, \mathbf{x}^*(t, \xi(t)), \xi(t)) \end{aligned}$$

Thus, $\xi(t)$ is a solution of system (2.20) such that $\xi(t_0) = \varphi(t_0 + \omega) = \varphi(t_0)$. Because of the uniqueness of solutions, $\varphi(t) = \xi(t) = \varphi(t + \omega)$, that is, $\varphi(t)$ is a periodic solution of system (2.20) with period ω, which is globally defined.

■

Lemma 2.2.6 *Let* $b_{ij}(t)$, *where* $i, j = 1, 2$, *be strictly positive periodic functions with period* ω. *Then, the zero solution of system*

$$\left\{ \begin{array}{l} z_1' = -b_{11}(t) z_1 - b_{12}(t) z_2 \\ z_2' = b_{21}(t) z_1 - b_{22}(t) z_2 \end{array} \right. \tag{2.41}$$

is uniformly asymptotically stable in the sense of Hoppensteadt.

Proof.– We recall that $b_{ij}(t)$, for $i,j=1,2$, are periodic positive functions. Let us note the minimum and the maximum of each $b_{ij}(t)$, for $i,j=1,2$, as $0<b_{ij}^L$ and $0<b_{ij}^M$, respectively. Before proceeding, we recall a simple fact. Consider system

$$Z'(t)=BZ(t), \tag{2.42}$$

where B is given by

$$\begin{pmatrix} -b_{11} & -b_{12} \\ b_{21} & -b_{22} \end{pmatrix}, \tag{2.43}$$

with $b_{ij}>0$, $i,j=1,2$ positive real numbers. It is well known that tr$(B)<0$ and det$(B)>0$ imply that the real part of the eigenvalues of (2.43) is strictly negative. Thus, the zero solution of system (2.42) is uniformly asymptotically stable with respect to the initial values. We mean that, given initial values Z_0, there exist positive constants K, $\alpha\in\mathbb{R}_+$ such that

$$\|e^{Bt}Z_0\|\leq Ke^{-\alpha t} \qquad \forall Z_0;\ Z_0\leq K. \tag{2.44}$$

Getting back to our problem, let us note

$$Y(t)=\begin{pmatrix} y_1(t) \\ y_2(t) \end{pmatrix} \qquad\qquad Z(t)=\begin{pmatrix} z_1(t) \\ z_2(t) \end{pmatrix}.$$

The study of the stability of the zero solution of system (2.41) is carried out by means of a comparison method. Namely, given a solution of system (2.41) we build up appropriate bounding linear systems with constant coefficient similar to (2.42). The solutions of these bounding systems are upper and lower bounds for the solution of system (2.41).

For this purpose, we use appropriate choices of b_{ij}^L and b_{ij}^M for constructing each bounding system, depending on the sign of y_1 and y_2. Without lost of generality (see comments before (2.44)), let us begin assuming that $y_1(t_0)=y_1^0>0$ and $y_2(t_0)=y_2^0>0$. Then, in a neighborhood of t_0, it follows that

$$\begin{gathered} -b_{11}^My_1(t)-b_{12}^My_2(t)\leq y_1'(t)\leq -b_{11}^Ly_1(t)-b_{12}^Ly_2(t) \\ b_{21}^Ly_1(t)-b_{22}^My_2(t)\leq y_2'(t)\leq b_{21}^My_1(t)-b_{22}^Ly_2(t) \end{gathered} \tag{2.45}$$

Let us consider the following bounding systems
(2.46)

$$\left\{\begin{array}{l} Z'(t)=B_LZ(t), \\ z_1(t_0)=y_1^0, \\ z_2(t_0)=y_2^0, \end{array}\right. \qquad \left\{\begin{array}{l} Y'(t)=B(t)Y(t), \\ y_1(t_0)=y_1^0, \\ y_2(t_0)=y_2^0, \end{array}\right. \qquad \left\{\begin{array}{l} W'(t)=B_MW(t), \\ w_1(t_0)=y_1^0, \\ w_2(t_0)=y_2^0, \end{array}\right.$$

where $B(t)$ is that of equation (2.56) and B_L and B_M are given by

$$(2.47)\qquad B_L = \begin{pmatrix} -b_{11}^M & -b_{12}^M \\ b_{21}^L & -b_{22}^M \end{pmatrix} \qquad B_M = \begin{pmatrix} -b_{11}^L & -b_{12}^L \\ b_{21}^M & -b_{22}^L \end{pmatrix}$$

the Comparison theorem yields

$$(2.48)\qquad z_1(t) \le y_1(t) \le w_1(t), \qquad z_2(t) \le y_2(t) \le w_2(t), \qquad t \ge t_0$$

at least while $z_1(t)$, $z_2(t)$, $w_1(t)$, $w_2(t)$ are kept positive, lets say, in an interval $I_0 := [t_0,\, t^*)$, with $t^* > t_0$ (it may happen that $t^* = +\infty$).

Then, it follows that $Z(t)$ and $W(t)$ decrease exponentially fast, and so does $Y(t)$ in I_0. It may happen that one of the components become zero after a transient time, that is, $t^* < +\infty$. Let us assume, without lost of generality, that $y_1(t^*) = 0$ and $y_2(t^*) > 0$. We recall that $\|Y(t^*)\| < \|Y(t_0)\|$. To carry on approaching the zero solution, let us replace the bounding systems (2.46) by other ones from t^* on.

It is straightforward that there exists $\varepsilon > 0$ such that $y_1(t) < 0$, $y_2(t) > 0$ and $\|Y(t)\| < \|Y(t_0)\|$ for all $t \in [t^*, t^* + \varepsilon/2]$. Thus, let us note

$$t_1 = t^* + \varepsilon/2 \qquad y_1^1 = y_1(t_1) \qquad y_2^1 = y_2(t_1).$$

Considering

$$(2.49)\ \left\{\begin{array}{l} Z'(t) = B_L Z(t) \\ z_1(t_1) = y_1^1, \\ z_2(t_1) = y_2^1, \end{array}\right. \qquad \left\{\begin{array}{l} Y'(t) = B(t)Y(t) \\ y_1(t_1) = y_1^1, \\ y_2(t_1) = y_2^1, \end{array}\right. \qquad \left\{\begin{array}{l} W'(t) = B_M W(t) \\ w_1(t_1) = y_1^1, \\ w_2(t_1) = y_2^1, \end{array}\right.$$

where $B(t)$ is that of equation (2.56) and B_L and B_M are now given by

$$(2.50)\qquad B_L = \begin{pmatrix} -b_{11}^L & -b_{12}^M \\ b_{21}^M & -b_{22}^M \end{pmatrix} \qquad B_M = \begin{pmatrix} -b_{11}^M & -b_{12}^L \\ b_{21}^L & -b_{22}^L \end{pmatrix}$$

Despite of the change in the coefficients corresponding with z_1 and w_1, the left and right hand side systems (2.49) fit in comments made at the beginning of the proof. Therefore, we can repeat the previous argument, so that $Y(t)$ keeps approaching zero for $t \in [t^*, t^* + K)$ for certain $K > 0$.

Summing up, previous argument is independent on the sign of $y_1(t)$ and $y_2(t)$, so that it holds whatever the sign of $y_1(t)$ and $y_2(t)$ is. On the other hand, $Y(t)$ approaches uniformly exponentially fast the zero solution because of the nature of the bounding solutions.

■

Proposition 2.2.7 *Consider the aggregated system* (2.36)

$$\begin{cases} n' = (a(t) - b(t)n)\, n - \dfrac{c(t)\, n}{1+p}\, p, \\ p' = -\lambda(t)p + \dfrac{f(t)\, n}{1+p}\, p, \end{cases}$$

where the coefficients are defined in (2.37)*. If condition*

$$0 < \frac{\lambda_M}{f_L} < \frac{a_L}{b_M} \tag{2.51}$$

holds, then the aggregated system (2.36) *posses at least one positive periodic solution* $(n^*(t), p^*(t))$ *which is uniformly asymptotically stable in the sense of Hoppensteadt.*

Proof.– The proof is decomposed in two steps. First, we find a convex invariant region $\mathcal{R}$ for system (2.36). Applying lemma 2.2.5 yields the existence of $(n^*(t), p^*(t))$. Then, following corollary 2.2.3 we linearize around $(n^*(t), p^*(t))$ and a suitable change of variables allow us to use lemma 2.2.6 to finish the proof.

Step 1. Existence of a positive periodic solution.
With the help of bounds (2.38), direct calculations yield curves bounding regions of the fist quadrant where the sign of n' and p' are constant. Namely

$$\begin{cases} n < \dfrac{1}{b_M}\left[a_L - c_M \dfrac{p}{1+p}\right] \Rightarrow 0 < n' \\ n > \dfrac{1}{b_L}\left[a_M - c_L \dfrac{p}{1+p}\right] \Rightarrow 0 > n' \\ p < \dfrac{f_L}{\lambda_M} n - 1 \Rightarrow 0 < p' \\ p > \dfrac{f_M}{\lambda_L} n - 1 \Rightarrow 0 > p' \end{cases} \tag{2.52}$$

Figure 2.1 shows such a curves.

Depending on the relative position of the nulclines of the bounding equations (2.52) we can find different scenarios. We seek for a positively invariant, convex region $\mathcal{R}$ bounded away from the axes. We will build a rectangular region $\mathcal{R}$ thus, we shall find $r_i \in \mathbb{R}$, $i = 1, \cdots, 4$ such that $\mathcal{R} := [r_1, r_2] \times [r_3, r_4]$. Keeping in mind that $n = (a_L - c_m)/b_M$ is an asymptotic (vertical) line to $n'_+(n)$, we can place r_1 anywhere in $(0, (a_L - c_m)/b_M)$. Moreover, as $n'_+(n) < n'_-(n) < a_M/b_L$,

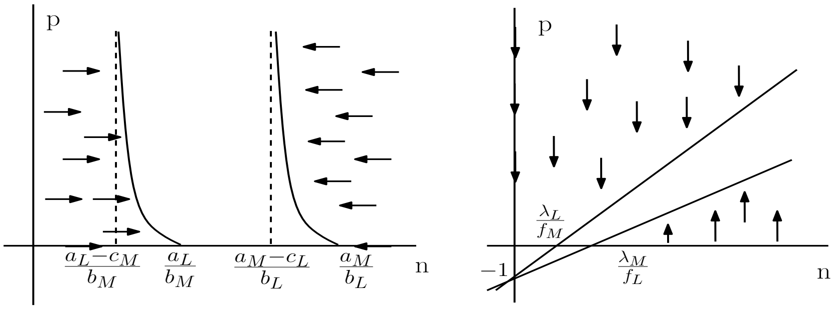

Figure 2.1: Left and right: regions where the sign of n' and p' is constant. The curves are noted, from left to right, $n'_+(n)$, $n'_-(n)$, $p'_-(n)$ and $p'_+(n)$.

we can choose $r_2 \geq a_M/b_L$. On the other hand, we recall that $0 < \lambda_M/f_L < a_L/b_M$ holds. Thus, the curve $p = p'_+(n)$ meets the vertical line $n = a_L/b_M$ at $\bar{p} > 0$ and we can let $r_3 \in (0, \bar{p})$. Finally, as $p'_-(n) > p'_+(n)$ for $n \geq 0$, if $\bar{\bar{p}}$ is the intersection between $p'_-(n)$ and $n = a_M/b_L$, choosing $r_4 \geq \bar{\bar{p}}$ yields $\mathcal{R}$. We have found lower and upper bounds for the vertex $r_i \in \mathbb{R}$, $i = 1, \cdots, 4$ of $\mathcal{R}$. From now on, we will refer to $\mathcal{R}$ as the minimal of such a rectangles. From the bounds for the derivatives of $(n(t), p(t))$ given by equation (2.52), the comparison theorem and its construction, it follows that $\mathcal{R} = [r_1, r_2] \times [r_3, r_4]$ is the region we where looking for. Figure 2.2 shows an rectangular closed invariant region $\mathcal{R}$. Using proposition 2.2.5 yields that the (2.36) system has, at least, a positive periodic solution, which is globally defined.

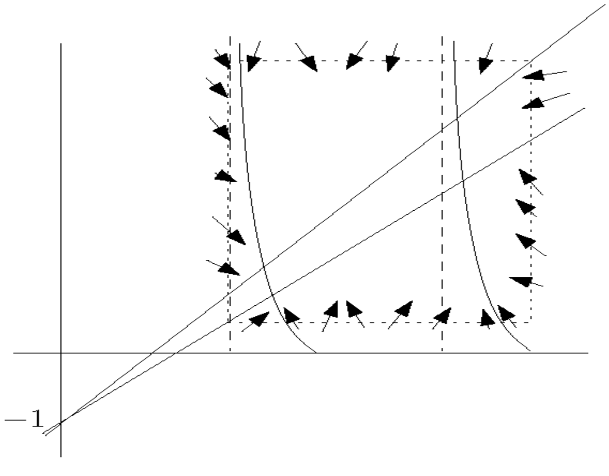

Figure 2.2: The invariant region $\mathcal{R}$.

Step 2. The periodic solution is stable in the sense of condition (C2). In order to assure the attraction of the periodic solution, according to corollary 2.2.3 we will study the stability of the zero solution of the variational problem of (2.36) at $\mathbf{y}^*$ (i.e., we linearize the system at the periodic solution). Thus, we will deal with the system

$$X' = A(t)X \tag{2.53}$$

where

$$A(t) = \begin{pmatrix} a(t) - 2b(t)n_0(t) - \dfrac{c(t)p_0(t)}{1+p_0(t)} & \dfrac{-c(t)n_0(t)}{(1+p_0(t))^2} \\ \dfrac{f(t)p_0(t)}{1+p_0(t)} & -\lambda(t) + \dfrac{f(t)n_0(t)}{(1+p_0(t))^2} \end{pmatrix} \tag{2.54}$$

and $\varphi(t) = (n_0(t),\, p_0(t))$ are the components of the periodic solution. Keeping in mind the fact that

$$\begin{cases} n_0'(t)/n_0(t) = a(t) - b(t)n_0(t) - \dfrac{c(t)p_0(t)}{1+p_0(t)} \\ p_0'(t)/p_0(t) = -\lambda(t) + \dfrac{f(t)n_0(t)}{1+p_0(t)} \end{cases}$$

the change of variables $y_1 = x_1/n_0$, $y_2 = x_2/p_0$ transforms the system (2.54) into

$$Y' = B(t)Y \tag{2.55}$$

where

$$B(t) = (b_{ij}(t)) = \begin{pmatrix} -b(t)n_0(t) & \dfrac{-c(t)p_0(t)}{(1+p_0(t))^2} \\ \dfrac{f(t)n_0(t)}{1+p_0(t)} & \dfrac{-f(t)p_0(t)n_0(t)}{(1+p_0(t))^2} \end{pmatrix}, \tag{2.56}$$

which is equivalent to (2.54). Applying lemma 2.2.6 finishes the proof.

■

The following result is a restatement of proposition 2.2.7 in terms of the complete system (2.30). This corollary explains the behavior if the solutions of the complete system (2.30) in terms of the solutions of the boundary layer problem (2.35) and the aggregated system (2.36).

Corollary 2.2.8 *Consider the general system* (2.30) *and* ν_1^**, the solution of the boundary layer problem* (2.34)*. Let us assume that condition*

$$0 < \frac{\lambda_M}{f_L} < \frac{a_L}{b_M}$$

holds (see (2.37) *for the definition of the coefficients of the previous expression). Consider also* $(n^*(t), p^*(t))$*, the positive periodic solution of the aggregated system* (2.36) *such that* $(n^*(t_0), p^*(t_0)) = (n_0, p_0)$*, whose existence is guaranteed by proposition 2.2.7. We note* $(n_1^\varepsilon(t), n_2^\varepsilon(t), p^\varepsilon(t))$ *the solution of the two time scales system* (2.30) *with initial values* $(\bar{n}_{01}, \bar{n}_{02}, \bar{p}_0)$ *at* $t = t_0$*. Then, there exist constants* $\varepsilon_0 > 0$ *and* $\delta > 0$ *such that for each* $\varepsilon \in (0, \varepsilon_0)$

$$\lim_{\varepsilon \to 0} (n_1^\varepsilon(t), n_2^\varepsilon(t), p(t)) = (\nu_1^* n^*(t), (1 - \nu_1^*) n^*(t), p^*(t))$$

uniformly on closed subintervals of $[t_0, \infty)$ *provided that*

$$\|(\bar{n}_{01}, \bar{n}_{02}, \bar{p}_0) - (\nu_1^* n_0, (1 - \nu_1^*) n_0, p_0)\| < \delta.$$

Proof.– It is a direct consequence of theorem 2.2.1 and proposition 2.2.7.

■

The following results concern the stability of the semi-trivial solution of the aggregated system (2.36). After stating and proving it, we will interpret this result in terms of the general system (2.30).

Proposition 2.2.9 *Let* $(n_0^*(t), 0)$ *be the semi-trivial solution of the aggregated system* (2.36) *and*

$$a_1 := \int_{t_0}^{t_0+\omega} (-\lambda(t) + f(t) n_0^*(t))\, dt. \tag{2.57}$$

If $a_1 < 0$*, then* $(n_0^*(t), 0)$ *is uniformly asymptotically stable in the sense of Hoppensteadt.*

Proof.– Linearizing the aggregated system (2.36) around the semi-trivial solution yields

$$\begin{pmatrix} x_1' \\ x_2' \end{pmatrix} = \begin{pmatrix} a(t) - 2b(t) n_0^*(t) & -c(t) n_0^*(t) \\ 0 & -\lambda(t) + f(t) n_0^*(t) \end{pmatrix} \begin{pmatrix} x_1 \\ x_2 \end{pmatrix} \tag{2.58}$$

This is a linear periodic system and we need calculate the Floquet exponents in order to study its stability. System (2.58) is a diagonal one and can be explicitly solved. The second equation in (2.58) is

$$x_2' = (-\lambda(t) + f(t)n_0^*(t))x_2$$

and its solution is given by

$$x_2(t) = x_2(t_0)\exp\left(\int_{t_0}^{t} -\lambda(s) + f(s)n_0^*(s)ds\right).$$

Replacing this expression into the first equation and solving it we get a fundamental system:

$$\Phi(t) = \left(\begin{array}{cc} \exp\left(\int_{t_0}^{t}(a(s)-2b(s)n_0^*(s))ds\right) & \Phi_{12}(t) \\ 0 & \exp\left(\int_{t_0}^{t} -\lambda(s)+f(s)n_0^*(s)ds\right) \end{array}\right)$$

where $\Phi_{12}(t)$ is a complex expression. Moreover, the Floquet exponents are given by

$$\lambda_1 = \exp\left(\int_{t_0}^{t_0+\omega}(a(s)-2b(s)n_0^*(s))ds\right),$$
$$\lambda_2 = \exp\left(\int_{t_0}^{t_0+\omega} -\lambda(s)+f(s)n_0^*(s)ds\right).$$

On the one hand, $|\lambda_2| < 1$ because of the assumption $a_1 < 0$. On the other hand, $|\lambda_1| < 1$ because $b(s)n_0^*(s) > 0$ and

$$\int_{t_0}^{t_0+\omega}(a(s)-b(s)n_0^*(s))ds = 0.$$

■

In particular, we provide with a condition on the aggregated system (2.36) which implies the exclusion (extinction) of predators in the complete system (2.30) at low predator population densities.

Corollary 2.2.10 *Consider the general system* (2.30), ν_1^*, *the solution of the boundary layer problem* (2.34), $(n_0^*(t),0)$, *the semi-trivial solution of the aggregated system* (2.36) *such that* $(n_0^*(t_0),0) = (\hat{n}_0,0)$ *and* $(n_1^\varepsilon(t), n_2^\varepsilon(t), p(t))$ *is the solution of the two time scales model* (2.30) *with initial values* $(\bar{n}_{01}, \bar{n}_{02}, \bar{p}_0)$ *at*

$t = t_0$. If $a_1 < 0$, where a_1 is that of (2.57), then there exist constants $\varepsilon_0 > 0$ and $\delta > 0$ such that for each $\varepsilon \in (0, \varepsilon_0)$

$$\lim_{\varepsilon \to 0} (n_1^\varepsilon(t), n_2^\varepsilon(t), p^\varepsilon(t)) = (\nu_1^* n_0^*(t), (1 - \nu_1^*) n_0^*(t), 0)$$

uniformly on closed subintervals of $[t_0, \infty)$ provided that

$$\|(\bar{n}_{01}, \bar{n}_{02}, \bar{p}_0) - (\nu_1^* \hat{n}_0, (1 - \nu_1^*) \hat{n}_0, 0)\| < \delta.$$

Proof.– It is a direct consequence of theorem 2.2.1 and proposition 2.2.9.

■

The following is a particular case situation where the previous result holds. Its importance relies in being stated in terms of the maximum and minimum values of the coefficients of aggregated systems.

Corollary 2.2.11 *Let us assume that condition*

$$\frac{a_M}{b_L} < \frac{\lambda_L}{f_M}, \tag{2.59}$$

holds. Consider ν_1^* is that of (2.35), $(n_0^*(t), 0)$ is the semi-trivial solution of the aggregated system (2.36) such that $(n_0^*(t_0), 0) = (\hat{n}_0, 0)$ and $(n_1^\varepsilon(t), n_2^\varepsilon(t), p(t))$ is the solution of two time scales system (2.30) with initial values $(\bar{n}_{01}, \bar{n}_{02}, \bar{p}_0)$ at $t = t_0$. Then, there exist $\varepsilon_0 > 0$ and $\delta > 0$ such that for each $\varepsilon \in (0, \varepsilon_0)$

$$\lim_{\varepsilon \to 0} (n_1^\varepsilon(t), n_2^\varepsilon(t), p^\varepsilon(t)) = (\nu_1^* n_0^*(t), (1 - \nu_1^*) n_0^*(t), 0)$$

uniformly on closed subintervals of $[t_0, \infty)$ provided that

$$\|(\bar{n}_{01}, \bar{n}_{02}, \bar{p}_0) - (\nu_1^* \hat{n}_0, (1 - \nu_1^*) \hat{n}_0, 0)\| < \delta.$$

Proof.– It follows from the proof of proposition 2.2.9. Using the bounds (2.38) for the coefficients we get bounds for the solution

$$x_2^L(t) := x_2(t_0) e^{(-\lambda_M + f_L n_{0L}^*)(t - t_0)} \le x_2(t) \le x_2(t_0) e^{(-\lambda_L + f_M n_{0M}^*)(t - t_0)} =: x_2^M(t).$$

The fact that $\dfrac{a_L}{b_M} \le n_0^*(t) \le \dfrac{a_M}{b_L}$ finishes the proof.

■

Conditions (2.51) and (2.59) state whether predator population is excluded or not. Nevertheless, these conditions do not cover all the possible cases. Thus, we turn out attention to the uncovered cases. Namely, we consider that

$$\frac{a_L}{b_M} < \frac{\lambda_M}{f_L} \qquad \text{and} \qquad \frac{\lambda_L}{f_M} < \frac{a_M}{b_L}. \tag{2.60}$$

These cases can not be studied analytically. Numerical experiments show that, within this case, we can have either a positive solution (coexistence) or a semi-trivial omega limit (predators exclusion) for system (2.30). Thus, either coexistence or exclusion of predators population can happen. We illustrate these facts through two different numerical simulations.

Coexistence. - We set the values of the coefficients of the aggregated system (see figure 2.3) so that condition (2.60) holds. For these coefficient values, we represent, the state variables versus time showing that a positive periodic orbit exists and a phase portrait illustrating the positive periodic orbit. In addition we have included a comparison of the total prey/predator density simulated with the full and the aggregated model. Let us assume that there exists a positive solution for the aggregated system (2.36) for the parameter values listed above. We can go through step two in the proof of proposition 2.2.7 (see lemma 2.2.6) to ensure that, in fact, every positive periodic solution

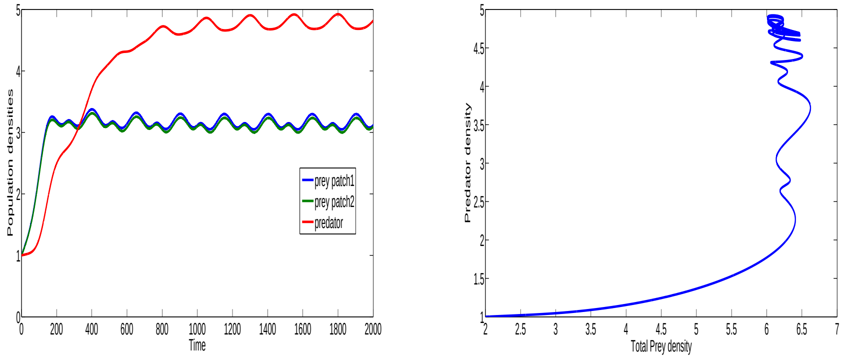

Figure 2.3: Left: state variables vs time: a positive periodic orbit exists. Right: phase portrait of the aggregated model illustrating the positive periodic orbit. Parameter values $m_1 = 1$ $m_2 = 1$, $r_{1L} = 1$, $r_{2L} = 0.1$, $r_{1M} = 3$, $r_{2M} = 2.1$, $\phi_{2L} = 0.1$, $\phi_{3L} = 0.8{*}\phi_{2L}$, $\phi_{2M} = 2.1$, $\phi_{3M} = \phi_{2M}{*}0.8$, $\lambda_{3L} = 0.01$, $\lambda_{3M} = 1.01$, $\omega = 5$, $\varepsilon = 0.02$, $K_{1L} = 5$, $K_{2L} = 1$,$K_{1M} = 9$, $K_{2M} = 5$,

is uniformly-asymptotically stable. Thus, condition (2.21) in (C2) holds and theorem 2.2.1 holds. The simulation in figure 2.4 (keeping the parameter values in figure 2.3) illustrates this fact:

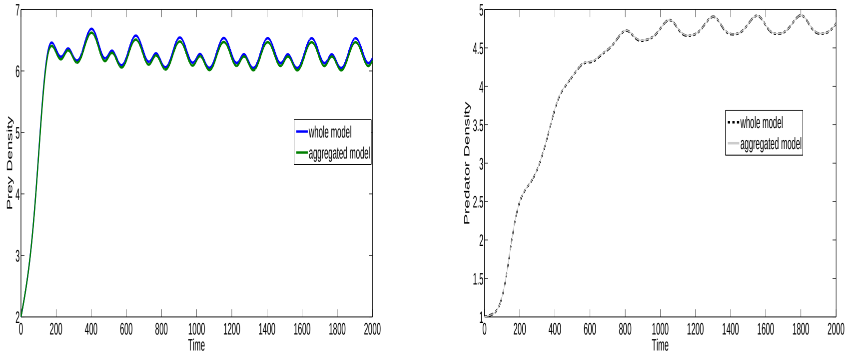

Figure 2.4: Comparison of the total prey density (left) and total predator density (right) simulated with the full and the aggregated model. Parameter values are these of figure 2.3

Predators exclusion. - We set now new values for the coefficients of the aggregated system (see figure 2.5) so that condition (2.60) holds too. Again, for these parameter values, we represent the state variables in front of time showing that the predator can be excluded. Besides, the corresponding phase portrait illustrates the exclusion scenario.

In this case, we could not establish analytically the stability of the semi-trivial. Nevertheless, the simulation in figure 2.6 shows that results obtained with the parameter values stated in figure 2.5 for the general and aggregated system are coherent:

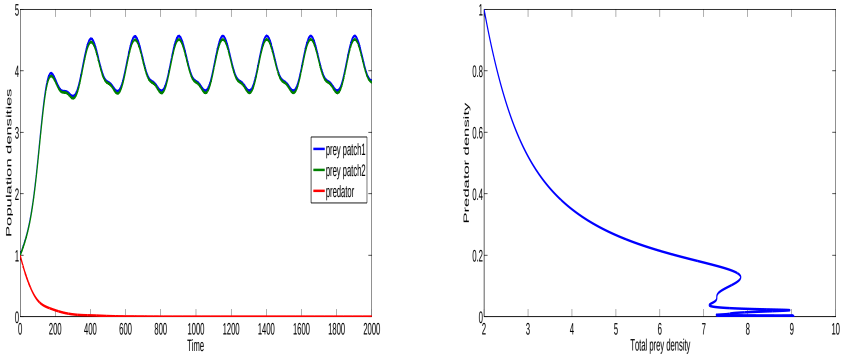

Figure 2.5: Left: state variables vs time: prey permanence; predators extinction. Right: phase portrait of the aggregated model illustrating predators exclusion. Parameter values: $m_1 = 1$, $m_2 = 1$, $r_{1L} = 1$, $r_{2L} = 0.1$, $r_{1M} = 3$, $r_{2M} = 2.1$, $\phi_{2L} = 0.1$, $\phi_{3L} = 0.2 * \phi_{2L}$, $\phi_{2M} = 2.1$, $\phi_{3M} = 0.2 * \phi_{2M}$, $\lambda_{3L} = 0.6$, $\lambda_{3M} = 1.6$, $\omega = 5$, $\varepsilon = 0.02$, $K_{1L} = 5$, $K_{2L} = 1$, $K_{1M} = 9$, $K_{2M} = 5$.

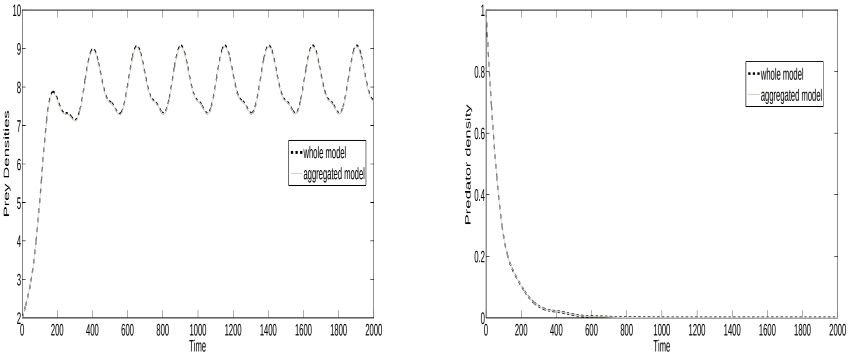

Figure 2.6: Comparison of the total prey density (left) and total predator density (right) simulated with the full and the aggregated model. Parameter values are these stated in figure 2.5.

Conclusions.

Our analysis of the aggregated system yields sufficient conditions for prey predator coexistence and predator exclusion in terms of the relative shape of certain "vital parameters" of the aggregated problem. Namely, comparing

$$\frac{a_L}{b_M} \quad \text{with} \quad \frac{\lambda_M}{f_L} \qquad \text{and} \qquad \frac{\lambda_L}{f_M} \quad \text{with} \quad \frac{a_M}{b_L}$$

In a non spatially distributed system, $a(t)/b(t)$ stands for the carrying capacity of the prey habitat. According to (2.37), it follows that

$$\frac{a(t)}{b(t)} = \frac{(r_1(t)\nu_1^* + r_2(t)\nu_2^*)K_1(t)K_2(t)}{r_1(t)(\nu_1^*)^2K_2(t) + r_2(t)(\nu_2^*)^2K_1(t)}.$$

which is the carrying capacity for the spatially distributed prey population when we consider fast migrations and periodic coefficients at each region. On the other hand, $\lambda(t)/f(t)$ stands for the ratio between predator mortality rate and benefits of captures for predators. Thus, we have stated conditions ensuring the existence of a coexistence state (condition (2.51)) and the exclusion of predators at low population densities (condition (2.59)) in terms of the functions involved in $a(t)/b(t)$ and $\lambda(t)/f(t)$. Summing up:

- There exists an attracting periodic coexistence state if $\dfrac{\lambda_M}{f_L} < \dfrac{a_L}{b_M}$.
- Predators die out at low predator population densities when $\dfrac{a_M}{b_L} < \dfrac{\lambda_L}{f_M}$.
- There exist a range of intermediate cases

  $$\frac{a_L}{b_M} < \frac{\lambda_M}{f_L} \qquad \text{and} \qquad \frac{\lambda_L}{f_M} < \frac{a_M}{b_L}$$

  which are indefinite meaning that both predators exclusion or coexistence can arise.

In the context of the system we are dealing with, coefficients $a(t)$, $b(t)$ and $f(t)$ depend on ν_1^*, which is related with prey migrations. In fact, from the definition of the coefficients (2.38), even small changes in ν_1^* may entail a change in the stability of the semi-trivial solution of the aggregated system and thus, induce the extinction of predators at low predator population density.

2.2.3 Periodic multi-strain epidemics model with periodic fast migrations.

Periodic patterns have been observed in the evolution of many infectious diseases as influenza, pertussis, mumps or chicken-pox. A classical example is the weekly measles reports in England and Wales for the period 1948-1968, [2]. Scientists have focused on explaining these periodic behaviors, finding out a variety of plausible scenarios [49]. Diseases with periodic transmission rates are among the possible explanations. After the pioneering work of Hethcote [48], several authors have pursued his approach studying periodic, or more general nonautonomous, SIS or SEIR models, see [92] for a review.

A central problem in the analysis of nonautonomous epidemic models is defining the reproduction number (the expected number of secondary cases caused by a primary case in a fully susceptible population) which value, greater or lower than 1, characterizes in the autonomous case the existence of an epidemic or the disease eradication, respectively. Ma and Ma [62] suggested defining the reproduction numbers of several periodic SIS and SEIR models through the reproduction numbers of the corresponding averaged systems (the autonomous systems obtained by replacing the time-varying parameters with their long-term time averages) that they denoted $\bar{\mathcal{R}}$. With this definition, they found that the free-disease equilibrium is always reached when $\bar{\mathcal{R}} < 1$ though this is not a necessary condition; they showed, via numerical simulations, that it might happen $\bar{\mathcal{R}} > 1$ together with the number of infected individuals tending to zero. Recently, Martcheva [65] has considered a nonautonomous multi-strain SIS epidemic model with periodic coefficients and has derived reproduction numbers and invasion reproduction numbers (the number of cases strain i will generate when strain j is at equilibrium) which agree with their counterparts in autonomous epidemic models ([62] and [99]); conditions on reproduction numbers ensure local and global stability of the disease-free equilibrium, and conditions on invasion reproduction numbers are shown to yield the local stability of a single-strain periodic solution.

The transmission of an infectious disease is positively related with contacts between individuals. Therefore, migrations in spatially distributed populations become a crucial component of the propagation process of an epidemic disease: it is of interest to study models coupling migrations and epidemic processes. In Kouokam *et al* [56] it is proposed an autonomous system coupling constant migrations and SIRS epidemics local models where migrations rates are considered to be much higher than epidemics rates; the use of aggregation techniques allowed defining the reproduction number corresponding to the complete model through the aggregated (reduced) system and so carrying out a tractable mathematical analysis.

We propose a nonautonomous system coupling migrations and local multi-strain SIS epidemic models similar to that found in [65]. The individuals in the population move between different spatial areas with periodic rates and the coefficients in the local epidemic models are also periodic. The migration process acts at a faster time scale than the epidemic one, being the common period of all rates of the order of the slow time scale.

Next, we present the aforementioned model. Then, applying the reduction procedure described in subsection 2.2.1 we transform the initial spatially explicit model into a particular case of the non-spatialized model treated in [65]. In particular, we are able to define reproduction numbers and invasion reproduction numbers for the complete model through those of the reduced system and to apply the results in [65] to the study of the initial model. That is, analyzing the reduced system we provide with sufficient conditions (in terms of the parameters of the model) for the asymptotic stability of the free disease state and of the single strain state of the original system (2.61). Even if such a conditions are general ones, we study two important particular cases. On the one hand we analyze the effect of fast migrations comparing these stability conditions in an homogeneous patchy environment and in a single patch environment. On the other hand, we study the effect of fast periodic migrations linking two regions where a multi-strain epidemic SIS takes place with different intensities. We illustrate this scenario with numerical simulations.

The model: multi strain SIS epidemic model with fast migrations.

We consider a population inhabiting a p patches environment. Individuals move between patches and an infection evolves within each patch according to a SIS model with multiple strains. Let $S_k(\tau)$ denote the number of susceptible individuals in patch $k = 1, \dots, p$ at time τ. In each patch k the number of individuals infected by strain $j = 1, \cdots, n$ is denoted by $I_{jk}(\tau)$. We assume that migrations act at a faster time scale than the changes of state with respect to infection, so individuals leaving a patch in a particular infection state get to the arrival patch in the same state. The migration rate from patch k to patch i for susceptible is denoted by m_{ik} and for infected by strain j by m^j_{ik}. The ratio of migrations to infection time scales is represented by the small parameter $\varepsilon > 0$. The model takes the form:

(2.61)

$$\left\{\begin{array}{rcl} \dfrac{dS_k}{d\tau} & = & -\displaystyle\sum_{\substack{i=1\\ i\neq k}}^{p} m_{ik}S_k + \sum_{\substack{i=1\\ i\neq k}}^{p} m_{ki}S_i \qquad (k=1,\dots,p;\ j=1,\dots,n) \\ & & +\varepsilon\left[\mu_k\left(S_k + \displaystyle\sum_{j=1}^{n} I_{jk}\right) - \sum_{j=1}^{n}\beta_{jk}S_kI_{jk} - \mu_kS_k + \sum_{j=1}^{n}\gamma_{jk}I_{jk}\right] \\ \dfrac{dI_{jk}}{d\tau} & = & -\displaystyle\sum_{\substack{i=1\\ i\neq k}}^{p} m^j_{ik}I_{jk} + \sum_{\substack{i=1\\ i\neq k}}^{p} m^j_{ki}I_{ji} + \varepsilon\left[\beta_{jk}S_kI_{jk} - (\mu_k+\gamma_{jk})I_{jk}\right] \end{array}\right.$$

The local SIS epidemic model with multiple strains for each patch $k = 1, \dots, p$ is represented by the terms preceded by ε. The mortality rate is the same for all individuals in the same patch and denoted by μ_k. We assume that all newly recruited individuals are susceptible and the recruitment rate equals mortality rate so that in absence of migrations the total population in a patch remains constant. The transmission rate of strain $j = 1, \dots, n$ in patch k is denoted by β_{jk}. Finally we denote γ_{jk} the recovery rate from strain j in patch k.

We are considering two different time scales. All the rates (migration, death, recruitment, transmission and recovery) appearing in the model are assumed to be periodic functions of time and depend on $\varepsilon\tau$.

Reduction of the model: the fast equilibriums and the aggregated problem.

System (2.61) matches with system (2.13) and we seek for an appropriate change of variables leading system (2.30) into its slow-fast form. The choice is straightforward because the total number of susceptible individuals and of individuals infected by each of the different strains are variables that keep constant through migrations, the fast dynamics, and so evolve at the slow time scale, the one that rules the infection process. Let us define:

$$S = \sum_{k=1}^{p} S_k \quad \text{and} \quad I_j = \sum_{k=1}^{p} I_{jk} \quad \text{for} \quad j = 1, \cdots, n.$$

We point out that these variables are kept constant by migrations. We propose the following transformation of variables:

$$\mathbf{n} = (S_1, \dots, S_p, I_{11}, \dots, I_{1p}, \dots, I_{n1}, \dots, I_{np}) \in \mathbb{R}^{p(n+1)}$$

is transformed into $(\mathbf{x}, \mathbf{y}) \in \mathbb{R}^{(p-1)(n+1)} \times \mathbb{R}^{n+1}$ where

$$\mathbf{x} = (S_1, \dots, S_{p-1}, I_{11}, \dots, I_{1\,p-1}, \dots, I_{n1}, \dots, I_{n\,p-1}), \qquad \mathbf{y} = (S, I_1, \dots, I_n).$$

To meet condition (C1) in theorem 2.2.1 we need to impose the condition on migration rates that we present next. Let us call $M = (m_{ki})_{1 \le k,i \le p}$, where $m_{kk} = -\sum_{\substack{i=1 \\ i \ne k}}^{p} m_{ik}$, the matrix of susceptible individuals migration rates and $M^j = (m^j_{ki})_{1 \le k,i \le p}$, where $m^j_{kk} = -\sum_{\substack{i=1 \\ i \ne k}}^{p} m^j_{ik}$, the corresponding matrices of migration rates for individuals infected by strains $j = 1, \cdots, n$. We recall that all these matrices are time dependent.

In what follows we assume that matrices $M(t), M^1(t), \ldots, M^n(t)$ are irreducible for every t.

As a consequence 0 is a simple eigenvalue larger than the real part of any other eigenvalue. The left eigenspace of each of these matrices associated with the eigenvalue 0 is generated by vector $\mathbf{1} := (1, \ldots, 1) \in \mathbb{R}^p$. The right eigenspace is generated by vectors

$$\boldsymbol{\nu}(t) = (\boldsymbol{\nu}^1(t), \ldots, \boldsymbol{\nu}^p(t)), \tag{2.62}$$

$\boldsymbol{\nu}^1(t) = (\nu_1^1(t), \ldots, \nu_p^1(t))$, ..., $\boldsymbol{\nu}^n(t) = (\nu_1^n(t), \ldots, \nu_p^n(t))$, respectively, which we choose to have positive entries that sum up to 1 and so they are unique.

The entries of these eigenvectors, $\boldsymbol{\nu}(t)$ and $\boldsymbol{\nu}^j(t)$ $(j = 1, \cdots, n)$, represent the stable proportions that the distribution among patches of the different types of individuals would attain, at the fast time scale, if the migration process were the only change affecting the population.

The assumption of matrices $M(t), M^1(t), \ldots, M^n(t)$ being irreducible for every t together with the fact that the dependence on t is periodic yield straightforwardly that condition (C1) in theorem 2.2.1 is met. Moreover, to obtain the aggregated system (2.20) we just need to sum up in system (2.61) the corresponding equations to each of the global variables, S and I_j $(j = 1, \cdots, n)$, performing the following substitutions to introduce the equilibria obtained from the boundary layer system:

$S_k = \nu_k(t)S$ and $I_{jk} = \nu_k^j(t)I_j$ for every $j = 1, \cdots, n$ and $k = 1, \cdots, p$.

Finally, the corresponding aggregated system (2.63) becomes

$$\begin{cases} \dfrac{dS}{dt} = \displaystyle\sum_{j=1}^{n} \mu_j^*(t)I_j - \sum_{j=1}^{n} \beta_j^*(t)SI_j + \sum_{j=1}^{n} \gamma_j^*(t)I_j, \\[2ex] \dfrac{dI_j}{dt} = \beta_j^*(t)SI_j - \left(\mu_j^*(t) + \gamma_j^*(t)\right) I_j, \\[2ex] S(t_0) = S_0 = \displaystyle\sum_{k=1}^{p} S_{k,0}, \quad I_j(t_0) = I_{j,0} = \sum_{k=1}^{p} I_{jk,0}, \ j = 1, \cdots, n, \end{cases} \tag{2.63}$$

provided that

$$\mu_j^*(t) = \sum_{k=1}^{p} \mu_k(t)\nu_k^j(t), \qquad \gamma_j^*(t) = \sum_{k=1}^{p} \gamma_{jk}(t)\nu_k^j(t), \tag{2.64}$$

$$\beta_j^*(t) = \sum_{k=1}^{p} \beta_{jk}(t)\nu_k(t)\nu_k^j(t).$$

Reproduction number for spatially distributed SIS models.

According to our settings, total population $N(t) := S(t) + \sum_{j=1}^{n} I_j$ verifies

$$N'(t) = 0.$$

Without lost of generality, we assume that total population is constant and normalized to one, that is, we set

$$S(t) + \sum_{j=1}^{n} I_j(t) = 1.$$

Using theorem 2.2.1 allow us to rescue some results in [65] for the spatially distributed two time scales system (2.61). Because of the nature of Hoppensteadt results, we can recover information concerning periodic solutions of the aggregated system which are stable in the sense of (2.21). System (2.63) was analyzed in [65]. In the following paragraphs we reformulate those results in [65] in terms of the system (2.61) aided by theorem 2.2.1 and according to our settings.

Given an ω-periodic function, we note $\langle f(t)\rangle := \frac{1}{\omega}\int_r^{r+\omega} f(s)ds$. Then, we define the *global reproduction numbers* as

$$\mathcal{R}_j^* := \frac{\langle \beta_j^*(t)\rangle}{\langle \mu_j^*(t)\rangle + \langle \gamma_j^*(t)\rangle} \qquad j = 1, \cdots, N \tag{2.65}$$

These global reproduction numbers are defined (see comment after theorem 2.2.12 as well) in terms of the coefficients of the aggregated problem. As we will see in theorems 2.2.12 and 2.2.14, $\mathcal{R}_j^*$ are related with the stability of the free disease state and the single strain state of the spatially distributed system (2.61).

The coefficients involved in (2.65) (see its definition (2.64)) depend on the equilibrium of the boundary layer system. Therefore, migration rates have an influence on the value of the global reproduction numbers.

In the sequel we label the solutions of the complete system (2.61) with a super index ε in order to stress the fact that such a system can be seen as a family of systems parameterized by ε.

Theorem 2.2.12 *Consider* $\boldsymbol{\nu}(t)$ *given by* (2.62) *and*

$$(S_1^\varepsilon(t),\cdots,S_p^\varepsilon(t);I_{11}^\varepsilon(t),\cdots,I_{1p}^\varepsilon(t);\cdots;I_{n1}^\varepsilon(t),\cdots,I_{np}^\varepsilon(t)),$$

the solution of the complete system (2.61) *with initial values at* $t=t_0$

$$(S_1^{0\varepsilon},\cdots,S_p^{0\varepsilon};I_{11}^{0\varepsilon},\cdots,I_{1p}^{0\varepsilon};\cdots;I_{n1}^{0\varepsilon},\cdots,I_{np}^{0\varepsilon}).$$

If $\mathcal{R}_j^*<1$ *for* $j=1,\cdots,n$ *then there exist* $\delta>0$ *and* $\varepsilon_0>0$ *such that for* $\varepsilon\in(0,\varepsilon_0)$ *it follows that*

$$\lim_{\varepsilon\to 0}(S_1^\varepsilon(t),\cdots,S_p^\varepsilon(t),I_{11}^\varepsilon(t),\cdots,I_{np}^\varepsilon(t))=(\boldsymbol{\nu}(t);0,\cdots,0) \tag{2.66}$$

uniformly in closed subintervals of $I=[t_0,\infty)$*, provided that*

$$\text{dist}\left((S_1^{0\varepsilon},S_2^{0\varepsilon},I_{11}^{0\varepsilon},\cdots,I_{np}^{0\varepsilon}),(\boldsymbol{\nu}(t_0);0,\cdots,0)\right)<\delta.$$

Proof.– It is a direct consequence of proposition 2.1 in [65] and theorem 2.2.1 herein.

■

In this context, the reproduction numbers (2.65) are nothing but the Floquet multipliers of the variational system corresponding to system (2.63) with respect to the free disease solution $\mathcal{E}_0$. Therefore, $\mathcal{R}_j^*$ are related with the stability of $\mathcal{E}_0$ and with the eradication of the epidemic.

Sometimes, in multiple strain epidemics, one of these strains manages to persist while the others die out. This fact (a sort of competitive exclusion) is known as single strain solution. The global reproduction numbers are related with the existence of such a solution for the aggregated problem;

Proposition 2.2.13 *Assume that* $\mathcal{R}_i^*>1$*. Then, there exists a single strain periodic solution* $\mathcal{E}_i=(0,\cdots,0,\xi_i,0,\cdots,0)$ *for the aggregated system* (2.63)*.*

Proof.– It is a direct consequence of theorem 3.1 in [65].

■

The stability of the periodic single strain solution and the exclusion of any other strain are, of course, related. The stability of $\mathcal{E}_i$ depends on the Floquet multipliers of the variational system with respect to the single strain solution, which are called invasion reproduction numbers (see [65]). We define the *global invasion reproduction number* of the strain $j = 1, \cdots, n$, $j \neq i$ at the single strain equilibrium of strain i as

$$\hat{\mathcal{R}}_j^{*i} := \frac{\left\langle \beta_j^*(1-\xi_i) \right\rangle}{\left\langle \mu_j^* \right\rangle + \left\langle \gamma_j^* \right\rangle} \tag{2.67}$$

Besides, the coefficients of the global invasion reproduction numbers depend on migration rates and, thus, extend those defined in [65] to the two time scales spatially distributed framework.

Theorem 2.2.14 *Consider $\boldsymbol{\nu}(t)$ and $\boldsymbol{\nu}^j(t)$, for $j = 1, \ldots, p$, given by (2.62) and the solution of the complete system (2.61) $(S_1^\varepsilon(t), \cdots, S_p^\varepsilon(t); I_{11}^\varepsilon(t), \cdots, I_{np}^\varepsilon(t))$ with initial value at $t = t_0$ $\boldsymbol{\Phi}(t_0) := (S_1^{0\varepsilon}, \cdots, S_p^{0\varepsilon}; I_{11}^{0\varepsilon}, \cdots, I_{np}^{0\varepsilon})$. If*

$$\mathcal{R}_i^* > 1, \qquad \text{and} \qquad \hat{\mathcal{R}}_j^{*i} < 1, \ \forall j \neq i,$$

then, there exist $\delta > 0$ and $\varepsilon_0 > 0$ such that for $\varepsilon \in (0, \varepsilon_0)$ it follows that

$$\begin{gathered}\lim_{\varepsilon \to 0}(S_1^\varepsilon(t), \cdots, S_p^\varepsilon(t); I_{11}^\varepsilon(t), \cdots, I_{np}^\varepsilon(t)) = \\ (\boldsymbol{\nu}(t)(1-\xi_i(t)), 0, \cdots, 0, \boldsymbol{\nu}^i(t)\xi_i(t), \cdots, 0)\end{gathered} \tag{2.68}$$

uniformly in closed subintervals of $[t_0, \infty)$, provided that

$$\text{dist}\left(\boldsymbol{\Phi}(t_0), (\boldsymbol{\nu}(t_0)(1-\xi_i(t_0)), 0, \cdots, 0, \boldsymbol{\nu}^i(t_0)\xi_i(t_0), 0, \cdots, 0)\right) < \delta.$$

Proof.– It is a direct consequence of theorem 4.1 in [65] and theorem 2.2.1.

■

Figuring out a relation between reproduction number at patch k of strain j in absence of migrations

$$\mathcal{R}_{jk} := \frac{\langle \beta_{jk}(t) \rangle}{\langle \mu_k(t) \rangle + \langle \gamma_{jk}(t) \rangle}, \qquad k = 1, \cdots, p,$$

the corresponding invasion reproduction number at patch k of strain j in absence of migrations

$$\hat{\mathcal{R}}_j^k := \frac{\langle \beta_{jk}(t)(1-\xi_{ik}(t))\rangle}{\langle \mu_{jk}(t)\rangle + \langle \gamma_{jk}(t)\rangle}, \qquad k = 1, \cdots, p,$$

(both $\mathcal{R}_{jk}$ and $\hat{\mathcal{R}}_j^k$ were defined in [65] as $\mathcal{R}_j$ and $\hat{\mathcal{R}}_j$ as it was just one patch) and their global counterparts $\mathcal{R}_j^*$, $\hat{\mathcal{R}}_j^{*k}$ should provide a comprehension of the global outcome of the epidemic process in terms of its local behavior. Unfortunately, we could not derive such a general relation; there are too many parameters involved in the definitions in the spatially distributed case. In the sequel we analyze two different cases with its own interest. We show that periodic fast migrations can induce behaviors different from those expected when patches are isolated. Thus, we extract some conclusions related with having considered time scales and fast migrations when handling epidemic models.

The role of fast migrations. In order to understand the role of migrations, we consider that epidemics behave exactly the same in all patches, that is

$$\left\{ \begin{array}{r} \beta_{j1}(t) = \cdots = \beta_{jp}(t), \\ \gamma_{j1}(t) = \cdots = \gamma_{jp}(t), \\ \mu_1(t) = \cdots = \mu_p(t). \end{array} \right. \tag{2.69}$$

Keeping in mind this configuration, we proceed to compare $\mathcal{R}_j^*$ and $\mathcal{R}_{jk}$. We note $\mathcal{R}_{jk}$ by $\mathcal{R}_j$ to stress the fact that local reproduction numbers are equal at every patch, as the corresponding epidemic parameters are the same everywhere. According with condition (2.69) we note β_j, γ_j and μ the corresponding parameter values (we have dropped the subindex labeling each region because of condition (2.69)).

Theorem 2.2.15 *Let us assume conditions* (2.69)*. Then, it follows that*

$$\mathcal{R}_j^* < \mathcal{R}_j, \qquad j = 1, \cdots, n.$$

In addition,

$$\mathcal{R}_j^* < 1 < \mathcal{R}_j, \qquad j = 1, \cdots, n \tag{2.70}$$

if, and only if,

$$\langle \beta_j(t) \sum_{h=1}^{p} \nu_h(t)\nu^h(t)\rangle < \langle \mu(t)\rangle + \langle \gamma_j(t)\rangle < \langle \beta_j(t)\rangle\,. \tag{2.71}$$

Proof.– Thanks to (2.69), it follows that

$$\mathcal{R}_{jk} = \frac{\langle \beta_{jk}(t)\rangle}{\langle \mu_{jk}(t)\rangle + \langle \gamma_{jk}(t)\rangle} = \frac{\langle \beta_j(t)\rangle}{\langle \mu(t)\rangle + \langle \gamma_j(t)\rangle} \qquad k = 1, \cdots, p.$$

On the other hand, we get from (2.64) and (2.69) that

$$\mu_j^*(t) = \sum_{k=1}^{p} \mu_k(t)\nu_k^j(t) = \mu(t)\sum_{k=1}^{p} \nu_k^j(t) = \mu(t)$$

$$\gamma_j^*(t) = \sum_{k=1}^{p} \gamma_{jk}(t)\nu_k^j(t) = \gamma_j(t)\sum_{k=1}^{p} \nu_k^j(t) = \gamma_j(t)$$

which implies

$$\mathcal{R}_j^* = \frac{\langle \beta_j^*(t)\rangle}{\langle \mu_j^*(t)\rangle + \langle \gamma_j^*(t)\rangle} = \frac{\langle \beta_j^*(t)\rangle}{\langle \mu(t)\rangle + \langle \gamma_j(t)\rangle}$$

in addition

$$\begin{aligned} \beta_j^*(t) &= \textstyle\sum_{k=1}^{p} \beta_{jk}(t)\nu_k(t)\nu_k^j(t) \\ &= \beta_j(t)\sum_{k=1}^{p} \nu_k(t)\nu_k^j(t) < \beta_j(t) \end{aligned}$$

because $\nu_k(t)$, $\nu_k^j(t) \in [0, 1]$ and $\sum_{k=1}^{p} \nu_k(t) = 1 = \sum_{k=1}^{p} \nu_k^j(t)$ for all t and j. Finally, condition $\mathcal{R}_j^* < 1 < \mathcal{R}_{jk}$ is equivalent to

$$\frac{\langle \beta_j(t)\sum_{k=1}^{p} \nu_k(t)\nu_k^j(t)\rangle}{\langle \mu(t)\rangle + \langle \gamma_j(t)\rangle} < 1 < \frac{\langle \beta_j(t)\rangle}{\langle \mu(t)\rangle + \langle \gamma_j(t)\rangle}$$

which is still equivalent to

$$\langle \beta_j(t)\sum_{k=1}^{p} \nu_k(t)\nu_k^j(t)\rangle < \langle \mu(t)\rangle + \langle \gamma_j(t)\rangle < \langle \beta_j(t)\rangle$$

■

Theorem 2.2.15 provides conditions for $\mathcal{R}_j^* < 1 < \mathcal{R}_j$ to hold. On the one hand, condition $1 < \mathcal{R}_j$ implies that, *in absence of migrations*, the free disease equilibrium is unstable at each patch and an endemic disease scenario arises at each region (see [65]), while condition $\mathcal{R}_j^* < 1$ (see theorem 2.2.12) for the aggregated system implies that the free disease state is stable when fast migrations exists and the disease is globally eradicated.

This result suggest fast migrations as a process that stimulates stability for the free disease state, at least according with the conditions stated in theorem 2.2.12.

Asymmetric patches. Now we let disease behave different in each patch. Namely, we assume that regions can be grouped in two disjoint sets according with the following: transmission rates are larger at regions of the first subgroup, while recovery rates are larger at patches of the second subgroup. We mean that the disease has stronger incidence in patches belonging to subgroup 1 than in those belonging to subgroup 2. Without lost of generality, we restrict ourselves to a two patches environment, thus, we consider the following conditions

$$\left\{\begin{array}{c} \beta_{j2}(t) < \beta_{j1}(t), \\ \gamma_{j1}(t) < \gamma_{j2}(t), \\ \mu_1(t) = \mu_2(t) \equiv \mu(t). \end{array}\right. \qquad j = 1, \cdots, n. \tag{2.72}$$

Then, direct calculations yield

Theorem 2.2.16 *Whenever* (2.72) *holds, it follows that*

$$\mathcal{R}_{j2} < \mathcal{R}_j^* < \mathcal{R}_{j1}, \qquad j = 1, \cdots, n. \tag{2.73}$$

Proof.– This proof is similar to that of theorem 2.2.15. According with (2.64) and (2.72) it follows that

$$\mu_j^*(t) = \sum_{k=1}^{2} \mu_k(t)\nu_k^j(t) = \mu(t),$$

$$\gamma_{j1}(t) \leq \gamma_j^*(t) = \sum_{k=1}^{2} \gamma_{jk}(t)\nu_k^j(t) \leq \gamma_{j2}(t)$$

and

$$\beta_{j1}(t) \leq \beta_j^*(t) = \sum_{k=1}^{2} \beta_{jk}(t)\nu_k(t)\nu_k^j(t) \leq \beta_{j2}(t),$$

which concludes the proof.

■

Let us discuss the implications of relation (2.73). As in the symmetric patches case, considering fast migrations allows the complete model to exhibit a global behavior qualitatively different from what is expected *when individuals do not migrate*. On the one hand, relation (2.73) allows

$$\mathcal{R}_{i2} < \mathcal{R}_i^* < 1 < \mathcal{R}_{i1}. \tag{2.74}$$

Thus, *in absence of migration*, strain i persists at region 1 while this strain dies out at the second region. Nevertheless, migrations induce the extinction of strain i at both regions. It is not difficult to obtain necessary and sufficient conditions for condition (2.74) to hold (see the proof of theorem 2.2.15). We do not include such expression because it is not as compact as (2.71).

On the other hand, from (2.73), let us assume that $\mathcal{R}_{i2} < 1 < \mathcal{R}_i^* < \mathcal{R}_{i1}$. If both patches were isolated, according to [65], strain i can not persist at path 2. Nevertheless, if, in addition, $\mathcal{R}_j^* < 1\ \forall j \neq i$, $\mathcal{R}_i^* > 1$ and $\hat{\mathcal{R}}_j^{*i} < 1\ \forall j \neq i$, the proposition 2.2.13 applies and strain i also persists in patch 2.

In figure 2.7 we illustrate the case in which one of the strains is excluded and the other coexists (through individuals infected by this strain) with susceptible individuals. We point out the agreement between both the aggregated system (in green) and the original system (in blue), which increases as $\varepsilon \to 0$.

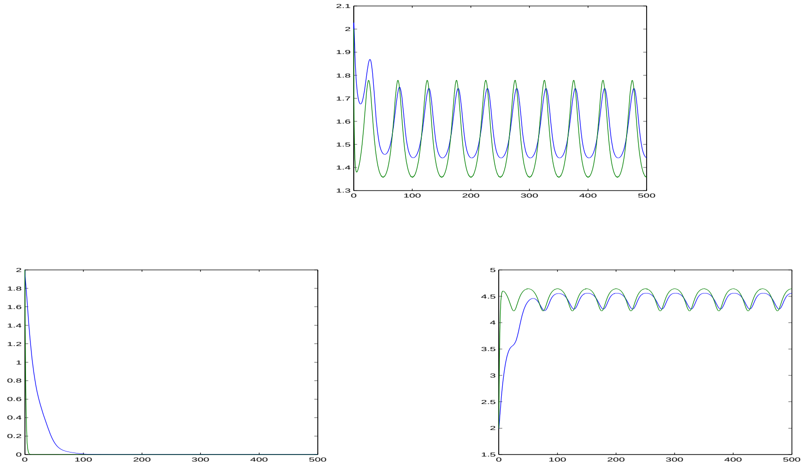

Figure 2.7: We consider two patches and two strain. Top, bottom left and bottom right figures display the solutions to the complete (blue) and the aggregated model (green) corresponding to the total number of susceptible and infected by strain 1 and infected by strain 2, resp. One of the strain is excluded and the other one coexists with the susceptible. Parameters: $m_1(t) = 1 + 0.1\cos(t)$, $m_2(t) = 2m_1(t)$, $m_{11}(t) = 1 + 0.5\cos(t) = m_{21}(t)$, $m_{12}(t) = 2 + \cos(t)$, $m_{22}(t) = 2 + 0.5\cos(t)$, $\mu_1(t) = 1 + 0.2\cos(t) = \mu_2(t)$, $\beta_{11}(t) = 1 + 0.5\cos(t)$, $\beta_{21}(t) = 2 + \cos(t)$, $\beta_{12}(t) = 0.4 + 0.2\cos(t)$, $\beta_{22}(t) = 0.5 + 0.2\cos(t)$, $\gamma_{11} = 0.2 + 0.1\cos(t)$, $\gamma_{21} = 0.25 + 0.2\cos(t)$, $\gamma_{12} = 0.1 + 0.1\cos(t)$, $\gamma_{22} = 0.15 + 0.1\cos(t)$, $\varepsilon = 0, 1$.

2.3 Asymptotically autonomous systems.

In this section we deal with another category of two time scales nonautonomous ordinary differential equation systems.

Some environmental conditions change with time but do not variate following periodic patterns. Among other possible behaviors, we find systems containing time depending parameters which stabilize "quickly". This idea can be described through nonautonomous models, let say $y' = f(t, y)$, and such that there exists the limit $g(y) = \lim\limits_{t\to\infty} f(t, y)$. If this limit is uniform on compacts set, the corresponding system is known as asymptotically autonomous systems. From the pioneer works of Markus [64] and Thieme [98], several authors (see [58] and references therein) have focused on such kind of systems to answer control problems. The interest is focused on ascertaining which dynamical properties of the nonautonomous system are kept by its limit system $y' = f(y)$. In terms of control problems, the management of the system concerns the control of such a limit.

On the other hand, this assumption fits in the framework of two time scale systems considering nonautonomous systems whose coefficients evolve (somehow) according with the fast time unit. We carry on with the approximate aggregation of systems of the form

$$\frac{d\mathbf{n}}{d\tau} = \mathbf{f}(\tau, \mathbf{n}) + \varepsilon \mathbf{s}(\tau, \mathbf{n}) \tag{2.75}$$

where $\mathbf{n} = (n_1, \cdots, n_N) \in \Omega_N$, where $\Omega_N \subset \mathbb{R}^N$ is a open bounded nonempty set and $\mathbf{f} = (f_1, \cdots, f_N)$, $\mathbf{s} = (s_1, \cdots, s_N) \in \mathcal{C}^2(I \times \Omega_N)$, where $I = [t_0, \infty)$.

2.3.1 An aggregation theorem.

As we did before, we assume that an appropriate transformation of variables $\mathbf{n} \in \mathbb{R}^N \longrightarrow (\mathbf{x}, \mathbf{y}) \in \mathbb{R}^{N-k} \times \mathbb{R}^k$ is available so that problem (2.75) can be written in the slow-fast form, namely

$$\begin{cases} \dfrac{d\mathbf{x}}{d\tau} = \mathbf{F}(\tau, \mathbf{x}, \mathbf{y}) + \varepsilon \mathbf{S}(\tau, \mathbf{x}, \mathbf{y}), \\[2ex] \dfrac{d\mathbf{y}}{d\tau} = \varepsilon \mathbf{G}(\tau, \mathbf{x}, \mathbf{y}), \end{cases} \tag{2.76}$$

where where $\mathbf{x}$, $\mathbf{y}$ stand for the fast and slow variables, respectively. This case was not explicitly covered in [52] but the same proof applies for. It turns out that writing system (2.76) in terms of the slow variable yields

$$
\begin{cases}
\varepsilon \dfrac{d\mathbf{x}}{dt} = \mathbf{F}(t/\varepsilon, \mathbf{x}, \mathbf{y}) + \varepsilon \mathbf{S}(t/\varepsilon, \mathbf{x}, \mathbf{y}), \\
\\
\dfrac{d\mathbf{y}}{dt} = \varepsilon \mathbf{G}(t/\varepsilon, \mathbf{x}, \mathbf{y}),
\end{cases}
\tag{2.77}
$$

It is apparent that an extra condition is needed in order to get the corresponding boundary layer problem and aggregated system. The natural condition is asking for the existence of the limit when we let $\varepsilon \to 0$, as collected in the following definition:

Definition 2.3.1 *A function $\mathbf{H} \in \mathcal{C}(\mathbb{R} \times \mathbb{R}^N)$ is said to be asymptotically autonomous, if there exists a function $\bar{\mathbf{H}} \in \mathcal{C}(\mathbb{R}^N)$ such that the limit*

$$\lim_{\xi \to \infty} \mathbf{H}(\xi, \mathbf{z}) = \bar{\mathbf{H}}(\mathbf{z})$$

exists and it is locally uniform (that is, uniform on compact sets of the $\mathbb{R}^N$).

Theorem 2.3.1 *Consider system (2.77) with $\mathbf{F}$, $\mathbf{S}$, $\mathbf{G} \in \mathcal{C}^2(I \times \mathbb{S}_R)$ asymptotically autonomous, where $I = [t_0 \infty)$ and*

$$\mathbb{S}_R := \left\{(\mathbf{x}, \mathbf{y}) \in \mathbb{R}^{N-k} \times \mathbb{R}^k ;\ \|\mathbf{y} - \mathbf{y}_0\| \leq R,\ \|\mathbf{x} - \mathbf{x}^*(\mathbf{y})\| \leq R\right\},$$

with $R > 0$, $\mathbf{y}_0$ and $\mathbf{x}^*(\mathbf{y})$ to be defined. Thus, for all $\mathbf{H} \in \{\mathbf{F}, \mathbf{S}, \mathbf{G}\}$ there exists a function $\bar{\mathbf{H}} \in \mathcal{C}^2(\mathbb{S}_R)$ such that the limit

$$\lim_{\xi \to \infty} \mathbf{H}(\xi, \mathbf{x}, \mathbf{y}) = \bar{\mathbf{H}}(\mathbf{x}, \mathbf{y})$$

is uniform on compact sets of $\mathbb{S}_R$. Assume the following conditions.

(C1) There exists an unique continuum of equilibria $\mathbf{x}^*(\boldsymbol{\beta})$ (see remark 2.3.2), with $\boldsymbol{\beta} \in \mathbb{R}^k$ and $\|\boldsymbol{\beta} - \mathbf{y}_0\| < R$, for equation

$$\frac{d\mathbf{x}}{ds} = \bar{\mathbf{F}}(\mathbf{x}, \boldsymbol{\beta})$$

such that the real parts of the eigenvalues of $J_{\mathbf{x}}\bar{\mathbf{F}}(\mathbf{x}^*(\boldsymbol{\beta}), \boldsymbol{\beta})$ are negative and bounded away from zero uniformly in $\boldsymbol{\beta}$ (J stands for the Jacobian matrix).

(C2) The aggregated problem

$$\frac{d\mathbf{y}}{dt} = \bar{\mathbf{G}}(\mathbf{x}^*(\mathbf{y}), \mathbf{y}) \tag{2.78}$$

where $\mathbf{x}^*(\alpha, \boldsymbol{\beta})$ is that of condition (C1), possesses a solution $\mathbf{y}^*(t, t_0, \mathbf{y}_0)$ defined for all $t \in I$ which is uniformly-asymptotically stable. We mean that there exists $R > 0$ such that for any other solution $\Phi(t, t_0, \bar{\mathbf{y}}_0)$ of system (2.20) with $\|\bar{\mathbf{y}}_0 - \mathbf{y}_0\| \leq R$, there exist functions $d \in \mathfrak{K}$ and $\sigma \in \mathfrak{S}$ such that

$$\|\mathbf{y}^*(t, t_0, \mathbf{y}_0) - \Phi(t, t_0, \bar{\mathbf{y}}_0)\| \leq d\left(\|\mathbf{y}_0 - \bar{\mathbf{y}}_0\|\right) \sigma(t - t_0). \tag{2.79}$$

Then, there exists $R > 0$ such that and each $(\bar{\mathbf{x}}_0, \bar{\mathbf{y}}_0) \in \mathbb{R}^{N-k} \times \mathbb{R}^k$ such that $\|(\bar{\mathbf{x}}_0, \bar{\mathbf{y}}_0) - (\mathbf{x}_0, \mathbf{y}_0)\| < R$ and each $\varepsilon > 0$ small enough, the corresponding solution $(\mathbf{x}_\varepsilon(t, t_0, \bar{\mathbf{x}}_0),\, \mathbf{y}_\varepsilon(t, t_0, \bar{\mathbf{y}}_0))$ of the general system (2.77) verifies

$$\lim_{\varepsilon \to 0} (\mathbf{x}_\varepsilon(t, t_0, \bar{\mathbf{x}}_0),\, \mathbf{y}_\varepsilon(t, t_0, \bar{\mathbf{y}}_0)) = (\mathbf{x}^*(\mathbf{y}^*(t_0, \mathbf{y}_0)),\, \mathbf{y}^*(t, t_0, \mathbf{y}_0))$$

uniformly on closed subset of $[t_0, \infty)$.

Proof.– The proof consist in showing that conditions (C1), (C2) and those required in the statement of the theorem fulfill conditions (I) up to (VII) stated in the main result of [52].

(I) It holds because of the regularity of functions $\mathbf{F}$, $\mathbf{S}, \mathbf{G}$.

(II) Idem.

(III) According to our settings, $\varpi(t, \mathbf{x}(t, \mathbf{y}), \mathbf{y}, 0) = \bar{\mathbf{F}}(\mathbf{x}^*(\mathbf{y}), \mathbf{y})$ and (C1) assures the existence of such an isolated (continuum of) equilibrium.

(IV) We recall that function $\bar{\mathbf{G}}$ does not depend on ε. We fix $\eta > 0$ and consider

$$\|\mathbf{G}(t/\varepsilon, \mathbf{x}, \mathbf{y}) - \bar{\mathbf{G}}(\mathbf{x}^*(\mathbf{y}), \mathbf{y})\|.$$

It is apparent that

$$\|\mathbf{G}(t/\varepsilon, \mathbf{x}, \mathbf{y}) - \bar{\mathbf{G}}(\mathbf{x}^*(\mathbf{y}), \mathbf{y})\|$$

$$\leq \|\mathbf{G}(t/\varepsilon, \mathbf{x}, \mathbf{y}) - \bar{\mathbf{G}}(\mathbf{x}^*(\mathbf{y}), \mathbf{y})\| + \|\bar{\mathbf{G}}(\mathbf{x}^*(\mathbf{y}), \mathbf{y}) - \bar{\mathbf{G}}(\mathbf{x}, \mathbf{y})\|$$

On the one hand, the fact that

$$\lim_{\xi\to\infty} \mathbf{G}(\xi,\mathbf{x},\mathbf{y}) = \bar{\mathbf{G}}(\mathbf{x},\mathbf{y})$$

is locally uniform means that there exists $\xi_0 > 0$ such that for all $\xi > \xi_0$ it follows that

$$\sup \|\mathbf{G}(\xi,\mathbf{x},\mathbf{y}) - \bar{\mathbf{G}}(\mathbf{x},\mathbf{y})\| < \eta/2 \qquad \forall(\mathbf{x},\mathbf{y}) \in \mathbb{S}_R.$$

Moreover, as $t_0/\varepsilon < t/\varepsilon$ for all $t > t_0$, there exists $\delta_0 > 0$ such that $0 < \varepsilon < \delta_0/2$ implies $t_0/\varepsilon > \xi_0$ and, thus,

$$\sup_{S_R} \|\mathbf{G}(t/\varepsilon,\mathbf{x},\mathbf{y}) - \bar{\mathbf{G}}(\mathbf{x},\mathbf{y})\| < \eta/2 \qquad \forall(t,\mathbf{x},\mathbf{y}) \in I \times \mathbb{S}_R.$$

On the other hand, function $\bar{\mathbf{G}}$ is continuous in $\mathbf{x}$ and $\mathbf{y}$ varies in a compact set. For each fixed $\mathbf{y}$ there exists $\delta = \delta(\mathbf{y})$ such that $\|\mathbf{x} - \mathbf{x}^*(\mathbf{y})\| < \delta(\mathbf{y})$ implies

$$\|\bar{\mathbf{G}}(\mathbf{x}^*(\mathbf{y}),\mathbf{y}) - \bar{\mathbf{G}}(\mathbf{x},\mathbf{y})\| < \eta/2.$$

In fact, there exists

$$0 < \hat{\delta} := \min\{\delta(\mathbf{y});\ \|\mathbf{y} - \mathbf{y}_0\| \le R\}$$

and choosing $\delta = \min\left\{\delta_0, \hat{\delta}\right\}$ yields the result we were looking for.

(V) Similar to (IV).

(VI) This condition is among the hypotheses asked for in the statement of the theorem.

(VII) The (C1) condition asks for the existence of $\Delta > 0$ such that

$$\max\left\{\mathrm{Re}\,(\lambda(\boldsymbol{\beta}))\,;\ \lambda(\boldsymbol{\beta}) \in \sigma\left(J\bar{\mathbf{F}}(\mathbf{x}^*(\boldsymbol{\beta}))\right);\ \|\boldsymbol{\beta} - \mathbf{y}_0\| \le R\right\} \le -\Delta < 0,$$

where $\sigma\left(J\bar{\mathbf{F}}(\mathbf{x}^*(\boldsymbol{\beta}))\right)$ stands for the spectrum of the linearization of $\bar{\mathbf{F}}$ about the equilibrium $\mathbf{x}^*(\boldsymbol{\beta})$.

■

Remark 2.3.2 *Theorem 2.3.1 is also true if there exist finitely many continuum of equilibria of the form $\mathbf{x}^*(\boldsymbol{\beta})$ which are suitably isolated; meaning that if there exist $\mathbf{x}_i^*(\boldsymbol{\beta})$ such that $\mathbf{F}(\mathbf{x}_i^*(\boldsymbol{\beta}),\boldsymbol{\beta}) = 0$ for $i = 1, 2$, then*

$$\|\mathbf{x}_1^*(\boldsymbol{\beta}) - \mathbf{x}_2^*(\boldsymbol{\beta})\| > R$$

for all and $\boldsymbol{\beta}$, being $R > 0$ that from theorem 2.3.1.

In the autonomous case, the concept of uniformly asymptotically stability (see condition (C2) in theorem 2.3.1) can be easily characterized for constant solutions (i.e., equilibrium points) as shown in the following proposition.

Proposition 2.3.3 *Assume that system* (2.78) *has an equilibrium point* $\mathbf{y}^*$*. Then,* $\mathbf{y}^*$ *is asymptotically uniformly stable if the real part of the eigenvalues of the linearization of* $\mathbf{G}$ *about* $\mathbf{y}^*$ *is strictly negative.*

Proof.– It follows easily mutatis mutandis from the proof of proposition 2.2.3.

■

2.3.2 Asymptotically autonomous predator-prey system with epidemic disease for predators.

Eco-epidemiology is a research area that studies the interactions between community and epidemic processes. Despite its youth, it is rapidly becoming a field of study in its own rights. Anderson and May [3] were the first to consider a predator-prey model where prey species was infected by some disease. Since then, many authors have proposed and studied different predator-prey models in the presence of disease, mainly affecting preys [16], [25], [74] and [50] but also affecting predators [40], [41] and [102]. Recently, Bairagi and Chattopadhyay have summarized the state of the art in eco-epidemiology [13]. Among other questions, in [13] they point out the problem of dealing with (nonautonomous) periodic eco-epidemiological systems, which, to the best of our knowledge, have not still been treated. Besides, nonautonomous asymptotically autonomous eco-epidemic models seem not to be treated either.

We present a generalization of the autonomous model studied in [9]. In that paper, Auger *et al.* considered a Lotka-Volterra predator-prey model as a slow process. This community system was coupled with a SIR epidemic affecting the predators. Both the mass action and the frequency-dependent transmission law (see [69] for a survey of pathogen transmission models) were considered and compared. We deal with the nonautonomous asymptotically autonomous version of the aforementioned model when the frequency-dependent transmission law occurs. We explore the possibility of using an epidemic process for handling predator population size, that is, we consider asymptotically autonomous coefficients to simulate the effect of human handling of the disease through slight modifications (in time) of disease parameters. We extend this "control" to the whole model assuming the parameters defining community relations to be asymptotically autonomous too.

Next, we set up a nonautonomous version of the eco-epidemic model found in [9] which, in fact, fits in system (2.76). Then, using the reduction procedure developed in this section, we are able to recover those results obtained in [9] and recycle them to explain the behavior of the nonautonomous original system.

Nonautonomous asymptotically autonomous predator-prey system with disease affecting predators.

As we have already said, we present a prey predator community system in which predators are affected by an epidemic process. On the one hand, we consider a classic Lotka-Volterra model with logistic growth in absence of predators

$$\tag{2.80} \begin{cases} \dfrac{dx}{dt} = r(s)x\left(1 - \dfrac{x}{K(t)}\right) + a(t)xy \\[2ex] \dfrac{dy}{dt} = -\mu(t)y + b(t)xy \end{cases}$$

were x and y stand for prey and predator densities, parameters are time depending functions and have the usual meaning; r and μ stand for corresponding the growth net rates, $K > 0$ stands for the carrying capacity, a and b measure the effect of encounters between preys and predators (respectively, the damage for preys and the benefit for predators). It is usually assumed that $b(t) = e\,a(t)$.

On the other hand, the most usual transmission law considered in the literature is the mass action law. However, several more complex functions relating disease transmission to the densities of susceptible and infected hosts have also been proposed [69]: frequency-dependent transmission (known as well as standard incidence law), power relationship, negative binomial, Holling like, asymptotic transmission, and many others. In this case, we consider the asymptotic transmission law (see [1], [46], [69] [82] for further information in the asymptotic transmission law), that is:

$$(2.81)\qquad \begin{cases} \dfrac{ds}{dt} = \gamma(t)r - \beta(t)\,\dfrac{si}{s+i} \\[2ex] \dfrac{di}{dt} = \beta(t)\,\dfrac{si}{s+i} - \delta(t)i \\[2ex] \dfrac{dr}{dt} = \delta(t)i - \gamma(t)\,r \end{cases}$$

where s, i and r stand for the densities of susceptible, infected and recovered individuals. The epidemiological parameters γ, β, and δ depend on time and represent, respectively, the rate at which predators loss immunity, the infection rate and the recovery rate of infected predators.

Al the coefficients involved in systems (2.80) and (2.81) are supposed to have limit when $s \to \infty$ which, in the end, will yield an asymptotically autonomous system. For further purposes, we note

$$\bar{z} := \lim_{s\to\infty} z(s) \qquad \forall\, z(s) \in \{\beta(s),\, \delta(s),\, \gamma(s),\, \mu(s),\, \mu'(s),\, a(s),\, b(s),\, K(s)\}\,.$$

Finally, we couple (2.80) and (2.81) and separate the time scales; the epidemic process is considered to be faster when compared with community relations. This may be the case when transmission rate is very high. For this purpose let us consider ε, a parameter close to zero. Coupling (2.80) and (2.81) yields the so-called *complete system*:

$$(2.82)\qquad \begin{cases} \dfrac{dn}{d\tau} &= \varepsilon\left[r(\tau)n\left(1 - \dfrac{n}{K(\tau)}\right) - a(\tau)n(S+I+R)\right] \\[2ex] \dfrac{dS}{d\tau} &= \gamma(\tau)R - \dfrac{\beta(\tau)SI}{S+I} + \varepsilon\left[-\mu(\tau)S + b(\tau)nS\right] \\[2ex] \dfrac{dI}{d\tau} &= \dfrac{\beta(\tau)SI}{S+I} - \delta(\tau)I + \varepsilon\left[-\mu(\tau)I - \mu'(\tau)I + b(\tau)nI\right] \\[2ex] \dfrac{dR}{d\tau} &= \delta(\tau)\,I - \gamma(\tau)\,R + \varepsilon\left[-\mu(\tau)R + b(\tau)nR\right] \end{cases}$$

Here, we have noted prey density by n while S, I and R stand for susceptible, infected and recovered predators, respectively. We point out that we have chosen a non lethal disease, but even if the infection is not mortal, it has a negative effect in the long time life of infected individuals, which is included through μ' in the slow part of the third equation in(2.82).

Now, we apply the aggregation result stated in this section in order to study system (2.82) by means of a reduced one. Getting back to (2.82), the corresponding boundary layer problem reads as follows

$$\begin{cases} \dfrac{dS}{ds} = \bar{\gamma} R - \bar{\beta}\, \dfrac{SI}{S+I} \\[2ex] \dfrac{dI}{ds} = \bar{\beta}\, \dfrac{SI}{S+I} - \bar{\delta} I \\[2ex] \dfrac{dR}{ds} = \bar{\delta}\, I - \bar{\gamma}\, R. \end{cases} \tag{2.83}$$

We point out that epidemics described by system (2.83) do not consider births or deaths. Thus, total predator population $p = S + I + R$ is kept constant in (2.83). This assumption will be coherent with the consideration that epidemics evolve much faster than community processes, where demography takes place. According with lemma 4.1 in [9], which we reproduce for the convenience of the reader, it follows that

Lemma 2.3.4 *System* (2.83) *may posses two different equilibrium:*

- *If* $\bar{\beta} > \bar{\delta}$ *the so-called* disease-endemic equilibrium,

  $$S_* = \frac{\bar{\gamma}\bar{\delta}p}{\bar{\gamma}\bar{\beta} + (\bar{\beta} - \bar{\delta})\bar{\delta}} \qquad I_* = \frac{\bar{\gamma}(\bar{\beta} - \bar{\delta})p}{\bar{\gamma}\bar{\beta} + (\bar{\beta} - \bar{\delta})\bar{\delta}} \qquad R_* = \frac{\bar{\delta}(\bar{\beta} - \bar{\delta})p}{\bar{\gamma}\bar{\beta} + (\bar{\beta} - \bar{\delta})\bar{\delta}}$$

  which is asymptotically stable.

- *otherwise (that is, if* $\bar{\beta} \leq \bar{\delta}$*) the non-negative equilibrium is*

  $$S_* = p, \qquad I_* = 0, \qquad R_* = 0$$

  known as free disease equilibrium *is also asymptotically stable.*

Let us introduce new variables, the global variable p, and the frequencies, defined as follow

$$p = S + I + R, \qquad \mathcal{S} := \frac{S}{p} \qquad \mathcal{I} := \frac{I}{p} \qquad \mathcal{R} := \frac{R}{p}$$

The global variable p stands for the total density of predators, as we have already said. Writing system (2.82) in terms of these new variables, according with theorem 2.3.1 the corresponding aggregated system is the following

$$
(2.84) \qquad \begin{cases} \dfrac{dn}{dt} = \bar{r}n\left(1-\dfrac{n}{\bar{K}}\right) - \bar{a}np, \\[2ex] \dfrac{dp}{dt} = -\hat{\mu}p + \bar{b}np, \end{cases}
$$

where

$$
\hat{\mu} = \begin{cases} \bar{\mu} & \text{if } \bar{\beta} < \bar{\delta}, \\[2ex] \bar{\mu} + \bar{\mu}'\mathcal{I}_* & \text{if } \bar{\beta} > \bar{\delta}, \end{cases}
$$

We are ready to proceed with the study of the aggregated problem. The sub indexes $_{fde}$ and $_{ede}$ will refer to the free disease equilibrium and the endemic disease equilibrium, respectively.

Theorem 2.3.5 *Let us consider* $(n^\varepsilon(t), S^\varepsilon(t), I^\varepsilon(t), R^\varepsilon(t))$*, the solution of system* (2.82) *with initial values* $(n_0^\varepsilon, S_0^\varepsilon, I_0^\varepsilon, R_0^\varepsilon)$ *and assume that* $\bar{K} > \hat{\mu}/\bar{b}$*. We have that,*

- *If* $\bar{\beta} < \bar{\delta}$*, then there exist* $\delta_1 > 0$ *and* $\varepsilon_1 > 0$ *such that for* $\varepsilon \in (0, \varepsilon_1)$ *it follows that*

$$
\lim_{\varepsilon\to 0}(n^\varepsilon(t), S^\varepsilon(t), I^\varepsilon(t), R^\varepsilon(t)) = \left(\frac{\bar{\mu}}{\bar{b}}, \frac{\bar{r}}{\bar{a}}\left(1-\frac{\hat{\mu}}{\bar{b}\bar{K}}\right), 0, 0\right) =: \Psi_{fde}
$$

  uniformly in closed subintervals of $I = [t_0, \infty)$*, provided that*

$$
\operatorname{dist}\left((n_0^\varepsilon, S_0^\varepsilon, I_0^\varepsilon, R_0^\varepsilon), \Psi_{fde}\right) < \delta_1.
$$

- *If* $\bar{\beta} > \bar{\delta}$ *there exist* $\delta_2 > 0$ *and* $\varepsilon_2 > 0$ *such that for* $\varepsilon \in (0, \varepsilon_2)$ *it follows that*

$$
\lim_{\varepsilon\to 0}(n^\varepsilon(t), S^\varepsilon(t), I^\varepsilon(t), R^\varepsilon(t))
$$

$$
= \left(\frac{\hat{\mu}}{\bar{b}}, \frac{\bar{r}}{\bar{a}}\left(1-\frac{\hat{\mu}}{\bar{b}\bar{K}}\right)\mathcal{S}_*, \frac{\bar{r}}{\bar{a}}\left(1-\frac{\hat{\mu}}{\bar{b}\bar{K}}\right)\mathcal{I}_*, \frac{\bar{r}}{\bar{a}}\left(1-\frac{\hat{\mu}}{\bar{b}\bar{K}}\right)\mathcal{R}_*\right) =: \Psi_{ede}
$$

  uniformly in closed subintervals of $I = [t_0, \infty)$*, provided that*

$$
\operatorname{dist}\left((n_0^\varepsilon, S_0^\varepsilon, I_0^\varepsilon, R_0^\varepsilon), \Psi_{ede}\right) < \delta_2.
$$

Proof.– Straightforward calculations yield the result.

■

Theorem 2.3.6 *Let us consider* $(n^\varepsilon(t), S^\varepsilon(t), I^\varepsilon(t), R^\varepsilon(t))$*, the solution of system* (2.82) *with initial values* $(n_0^\varepsilon, S_0^\varepsilon, I_0^\varepsilon, R_0^\varepsilon)$*. If* $\bar{K} < \hat{\mu}/\bar{b}$ *then there exist* $\delta > 0$ *and* $\varepsilon_0 > 0$ *such that for* $\varepsilon \in (0, \varepsilon_0)$ *it follows that*

$$\lim_{\varepsilon \to 0}(n^\varepsilon(t), S^\varepsilon(t), I^\varepsilon(t), R^\varepsilon(t)) = (\bar{K}, 0, 0, 0)$$

uniformly in closed subintervals of $I = [t_0, \infty)$*, provided that*

$$\text{dist}\left((n_0^\varepsilon, S_0^\varepsilon, I_0^\varepsilon, R_0^\varepsilon), (\bar{K}, 0, 0, 0)\right) < \delta.$$

Proof.– Straightforward calculations yield the result.

■

Conclusions.

Our results show not only that predator population size is larger in the free disease state than in the endemic scenario, but also that prey population is larger in the endemic scenario than in the free disease.

In addition, the corresponding sizes depend on these parameters governing epidemics. Then, epidemics seems to be a suitable mechanism for controlling prey and predator populations size.

2.4 Conclusions and perspectives.

The departure point of this chapter are the approximate aggregation techniques described by Auger *et al.* (see [6] and references therein) concerning two time scales systems of the form

$$\frac{d\mathbf{n}}{d\tau} = \mathbf{f}(\mathbf{n}) + \varepsilon\, \mathbf{s}(\mathbf{n}), \tag{2.85}$$

admitting a change of variables $\mathbf{n} \mapsto (\mathbf{x}, \mathbf{y})$ such that system (2.85) becomes

$$\begin{cases} \varepsilon \dfrac{d\mathbf{x}}{dt} = \mathbf{F}(\mathbf{x}, \mathbf{y}) + \varepsilon\, \mathbf{S}(\mathbf{x}, \mathbf{y}), \\ \dfrac{d\mathbf{y}}{dt} = \mathbf{G}(\mathbf{x}, \mathbf{y}), \end{cases} \tag{2.86}$$

where $t = \varepsilon\tau$. Functions $\mathbf{f}$ and $\mathbf{F}$ stand for the fast dynamics while functions $\mathbf{s}$ and $\mathbf{S}$ and $\mathbf{G}$ concern the slow process. In this chapter we develop a methodology for the approximate aggregation of nonautonomous two time scales systems similar to (2.85).

Our results are based on a theorem due to F.C. Hoppensteadt [52] concerning singular perturbations on the infinite interval. We notice that functions involved in the equations studied by Hoppensteadt are of class $\mathcal{C}^2$ while those involved in the equations of the autonomous aggregation result presented in section 2.1.1 are of class $\mathcal{C}^1$ on its respective domains. However, this is not a real restriction in usual applications, where these functions can be chosen as regular as needed.

Hoppensteadt theorem states conditions allowing the study of certain dynamical properties of nonautonomous two time scale systems analyzing two related and simpler systems; the boundary layer problem and the aggregated system, both systems being less dimensional than the original system. Using this theorem, the existence of solutions for the aggregated system and boundary layer problem (stable in the sense of sense (2.12) and (2.11), resp) allows one to describe a curve uniformly attracting the solutions of the complete system on closed subintervals of $[t_0, \infty)$.

Hoppensteadt theorem is a general one but, as a counterpart, it holds under seven restrictive and complicated to be checked hypotheses. Five of them are regularity conditions concerning those functions involved in the system and the other two conditions are stability requirements for the solutions of the boundary layer problem and the aggregated system. Roughly, our results point out that when considering periodic (section 2.2) or asymptotically autonomous systems (section 2.3), all these conditions can be replaced by much simpler ones which enhances the applicability of this classic theorem.

In section 2.2 we consider systems of the form

$$\frac{d\mathbf{n}}{d\tau} = \mathbf{f}(\varepsilon\tau, \mathbf{n}) + \varepsilon\, \mathbf{s}(\varepsilon\tau, \mathbf{n}), \tag{2.87}$$

where functions $\mathbf{f}$ and $\mathbf{s}$ are periodic function of τ. We assume the existence of a change of variables $\mathbf{n} \mapsto (\mathbf{x}, \mathbf{y})$ such that system (2.87) becomes

$$\begin{cases} \varepsilon \dfrac{d\mathbf{x}}{dt} = \mathbf{F}(t, \mathbf{x}, \mathbf{y}) + \varepsilon\, \mathbf{S}(t, \mathbf{x}, \mathbf{y}), \\ \dfrac{d\mathbf{y}}{dt} = \mathbf{G}(t, \mathbf{x}, \mathbf{y}), \end{cases} \tag{2.88}$$

where $t = \varepsilon\tau$ and functions $\mathbf{F}$, $\mathbf{S}$ and $\mathbf{G}$ are periodic function of time t with the same period. We show that precisely being a periodic system allows to simplify those hypothesis in the Hoppensteadt theorem. In theorem 2.2.1 we show that the regularity conditions imposed in the Hoppensteadt theorem on the function involved in the system automatically hold for periodic systems. In addition, in proposition 2.2.3 we show that, when dealing with periodic systems, the Hoppensteadt stability condition on the periodic solution of the reduced system can be established using Floquet theory, that is, through a linearized system. We use these results to analyze two different two time scales population models.

In a first application we analyze a two patches periodic Lotka-Volterra predator-prey type model with a refuge for prey. We include predator interference, which has been proven to be relevant when fitting models to real data. Considering prey displacements between the refuge and the interacting regions to be faster than local predator-prey interactions allows us to study the three dimensional system by means of a two dimensional one. We obtain different conditions (in terms of the coefficients of the model) for the existence and the stability of the semi-trivial solution (predator population become extinct) or the non trivial positive solution (predator-prey coexistence) in terms of certain "vital" parameters derived from the study of the aggregated model, which is a sort of carrying capacity for coexistence of the spatially distributed system.

In a second application we consider a spatially distributed periodic multi strain SIS epidemic model. We allow epidemic heterogeneity considering a patchy environment (with an arbitrary number of patches) where epidemic parameters could take different values at each patch. We let susceptible and infected individuals to move around patches with periodic displacement rates. Considering that individual movements are much faster than epidemic processes, we build up a two dimensional (thus, aggregated) system describing the asymptotic behavior of the original model. In this way, we are able to define coherent reproduction numbers and invasion reproduction numbers of the spatially distributed nonautonomous model through the aggregated system. Comparing these reproduction numbers with their non spatially distributed counterparts we show that adequate periodic fast migration rates entail persistence or eradication of epidemic strains in regions where, in absence of migrations, the contrary is expected.

In section 2.3 we address another kind of two time scales nonautonomous systems. Therein we deal with systems of the form

$$\frac{d\mathbf{n}}{d\tau} = \mathbf{f}(\tau, \mathbf{n}) + \varepsilon\, \mathbf{s}(\tau, \mathbf{n}), \tag{2.89}$$

such that the aforementioned change of variables $\mathbf{n} \mapsto (\mathbf{x}, \mathbf{y})$ exists and where functions $\mathbf{f}$ and $\mathbf{s}$ are asymptotically autonomous on τ. Now the asymptotically autonomous feature of the system allow us to drastically simplify those conditions for the Hoppensteadt theorem to hold, as shown in theorem 2.3.1. In addition, in proposition 2.3.3 we proof that the Hoppensteadt stability conditions on the solution of the aggregated system reduces to checking the sign of the real part of the eigenvalues of an appropriate linear system. The reduction procedure is illustrated by means of an application to an eco-epidemiologic model.

We consider a Lotka-Volterra predator-prey model as a slow process. This community system is coupled with a SIR epidemic model following the frequency-dependent transmission law affecting predators. Both processes are modeled by means of asymptotically autonomous functions thus, extending the results achieved in [9] for the autonomous counterpart of this model. We show that predator population size is larger in the free disease state than in the endemic scenario while prey population size is smaller when there is no epidemics. In case of endemic epidemics, both predator and prey population size depend on the epidemic parameter values. Thus, epidemics are a suitable mechanism for controlling populations size.

We point out that combining theorems 2.2.1 and 2.3.1 allow us to study two time scales models combining periodic and asymptotically autonomous features, which will permit analyzing more realistic and general models.

Regarding perspectives, because of the nature of the Hoppensteadt theorem, those results related with invariant regions or unstable solutions found for the aggregated system can not be read in terms of the general system (using the Hoppensteadt theorem). In this sense, it is of interest searching for alternative mathematical tools complementing those developed herein.

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Scientific production

In this section we summarize the scientific production related with this thesis. We list published or submitted research papers and talks or posters presented in conferences of scientific meetings during the preparation of this thesis.

Published or submitted papers with results achieved during the preparation of this thesis

- M. Marvá, E. Sánchez, R. Bravo de la Parra and L. Sanz. *Reduction of slowfast discrete models coupling migration and demography*. Journal of Theoretical Biology. Volume 258. 2009. 371–379.

- M. Marvá, R. Bravo de la Parra, E. Sánchez and L. Sanz. *Aplicaciones a la ecología de la agregación aproximada de variables en sistemas dinámicos discretos*. UAH Obras colectivas. Ciencias 04. 2009.

- T. Nguyen Huu, P. Auger, C. Lett and M. Marvá. *Emergence of global behavior in a host-parasitoid model with density-dependent dispersal in a chain of patches*. Ecological Complexity. Volume 5, Issue 2. 2008. 9–21.

- M. Marvá, R. Bravo de la Parra and J.-C. Poggiale. *Approximate aggregation of a two time scales periodic multi-strain sis epidemic model: a patchy environment with fast migrations*. Submitted.

- M. Marvá, J.-C. Poggiale and R. Bravo de la Parra. *Reduction of slow-fast periodic systems: fast migrations in a predator-prey community*. Submitted.

- M. Marvá, R. Bravo de la Parra and P. Auger. *Reproductive numbers for non autonomous periodic two time scales spatially distributed SIS*. Submitted.

Talks delivered at conferences or scientific meetings whose contents are related with those of this thesis.

- M. Marvá, R. Bravo de la Parra and J.-C. Poggiale. Approximate aggregation of nonautonomous two time scales spatially distributed system. III Conference on Computational and Mathematical Population Dynamics. CMPD3 Bordeaux, France June 2010.
- M. Marvá, J.-C. Poggiale and R. Bravo de la Parra. Reduction of nonautonomous ordinary differential equations system with two time scales. Laboratory of Marine Microbiology, Geochemistry and Ecology. Centre of Oceanography. University Aix-Marseille II. Marseille, France June 2009.
- M. Marvá, R. Bravo de la Parra, E. Sánchez and L. Sanz. Agregacin aproximada de variables. Aplicaciones a la ecologa. II Jornadas Jóvenes Investigadores. Alcalá de Henares, Spain December 2008.
- M. Marvá, R. Bravo de la Parra, E. Sánchez and L. Sanz. Some applications of the approximate reduction of non-linear discrete models with two time scales. IX Journes d'Analyse Numrique et d'Optimisation. JANO8 Mohammedia, Morocco December 2008.

Posters presented at conferences or scientific meetings whose contents are related with those of this thesis.

- M. Marvá, R. Bravo de la Parra and P. Auger. Approximate aggregation of non-autonomous systems with two time scales. III International Conference Socit Francophone de Biologie Thoriche. SFBT10. Tunez, Tunicia July 2010.
- CMPD3 M. Marvá, R. Bravo de la Parra, P. Auger and M.A. Zavala. Individual behavior in a structured population: reduction of a discrete system coupling hawk-dove tactics and demography III Conference on Computational and Mathematical Population Dynamics. CMPD3 Bordeaux, France June 2010.
- M. Marvá, R. Bravo de la Parra, E. Sánchez and L. Sanz Approximate reduction of non-linear discrete models with two time scales. II Conference on Computational and Mathematical Population Dynamics CMPD2. Campinas, Brazil July 2007.