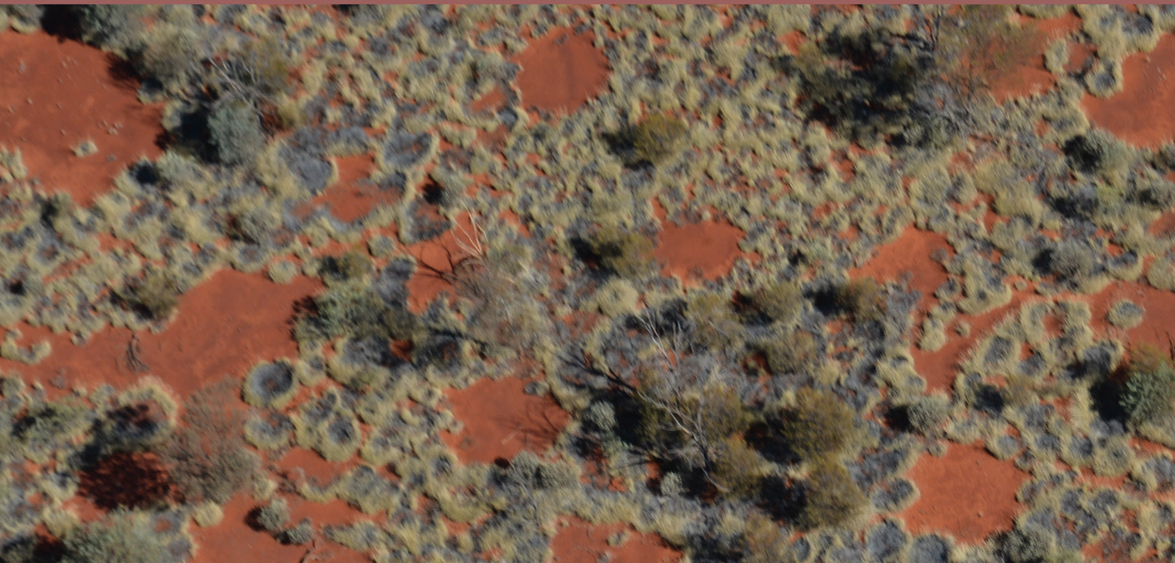
Nonlinear Physics of Ecosystems



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Nonlinear Physics of Ecosystems

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Cover image: Vegetation patterns in an arid landscape. Courtesy of Kevin Sanders.

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To my wife, Liora, and my children, Elia and Omri,

and

to the memory of my parents,

my father, Yehoshua, who fervently believed in human progress through science and continued to support my scientific inclination even after witnessing the results of igniting hydrogen in my home lab,
and
my mother, Shoshana, who was a wholehearted artist, but her skepticism and analytical thinking would have well suited the soul of a scientist.

Patterns of shapes and colors (Shoshana Meron).

Contents

Preface

A significant part of this book is based on a graduate course on pattern formation which I have been teaching during the past two decades in the Physics Department at Ben-Gurion University. Another significant part of the book reflects the activities of my research group and the interactions with a few close colleagues, throughout this period on pattern formation problems and their applications to ecology. The book has also benefited from numerous joint meetings with Prof. Moshe Shachak's ecology group. These meetings helped to establish a common language, understandable to both physicists and ecologists, which I have used in the book.

The book is primarily intended for graduate students and researchers in nonlinear and interdisciplinary physics, geophysics, biomathematics, mathematical ecology, and ecohydrology. However, a broader readership, including ecologists in general and physical geographers, may also benefit from the book. The book chapters are intentionally divided into three parts: an overview of pattern formation and spatial ecology as disparate research fields that are yet strongly related to one another (Part I), an advanced account of pattern formation theory (Part II), and applications of pattern formation theory to ecological problems (Part III). Readers who are not mathematically oriented may skip Part II, which is pretty technical, and use the basic introduction to pattern formation theory and modeling in Part I to follow the ecological applications of pattern formation theory described in Part III. A fairly good understanding of model results can be achieved without dwelling on their mathematical derivation.

Many studies that are related to the topics addressed in the book are not cited, and I apologize for that. The book is not intended to provide a review of the proliferating studies at the interface between pattern formation and spatial ecology; it is rather intended to introduce the concepts and tools of pattern formation theory and demonstrate their utility in ecological research using selected problems in spatial ecology. It therefore includes representative references rather than citations to all relevant studies.

The content of the book is a result of many collaborations with colleagues and students. I am indebted to Christian Elphick, from whom I learnt more about asymptotic expansions and perturbation theory than from any course or textbook. I am also indebted to Moshe Shachak, who introduced me to the field of spatial ecology and kept updating me with new relevant studies; I particularly benefited from his integrative approach to the field. Special thanks go to Aric Hagberg and Jost von Hardenberg for most enjoyable and fruitful long-term collaborations, and to Golan Bel for the very productive recent collaboration. The outcomes of these interactions fill up many pages in this book. Special thanks go also to Harry Swinney, Anna Lin and other members of the experimental Austin group. The long and fruitful collaboration with this top group helped me realize the importance of confronting theory with experiment and has provided many joyful moments, especially when matching between the two has been achieved. Last but not least, I would like to thank Yagil Osem, Antonello Provenzale, Hezi Yizhaq, and Yair Zarmi for the most productive interactions, the outcomes of which constitute important parts of the book.

First and foremost, however, this book describes the work of graduate students I have been advising and co-advising throughout the years: Arik Yochelis, Erez Gilad, Efrat Sheffer, Assaf Kletter, Rotem Manor, Adam Lampert, Jonathan Nathan, Yair Mau, Lev Haim, Shai Kinast, Paris Kyriazopoulos, and Yuval Zelnik. Their capacity to study new topics and methods, their commitment to hard work, and the often surprising ideas and results they came up with made this book possible.

I would also like to thank all people who helped me in preparing the manuscript through helpful suggestions and corrections or figure preparation: Yair Zarmi, Moshe Shachak, Isaak Rubinstein, Ruhama Lipow, Michele Herman, Yuval Zelnik, Yair Mau, Lev Haim, and Marco Cusmai. Finally, I would like to thank Luna Han, a senior editor of the Taylor & Francis publishing group, for her helpful comments and patience, and my wife, Liora, for her help in designing the cover page and for her enthusiastic and continuous encouragement.

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About the author

Ehud Meron is a professor of physics in the Blaustein Institutes for Desert Research and the Physics Department at Ben-Gurion University of the Negev. His research interests include nonlinear dynamics and pattern formation theory with applications to fluid dynamics and chemical reactions, modeling complex systems, and spatial ecology with a focus on desertification and biodiversity dynamics. Professor Meron has been collaborating with ecologists since the year 2000 in an effort to assimilate the concepts of pattern-formation theory into ecological research, and this book is part of that effort.

Chapter 1

Introduction

1.1 An emerging new scientific discipline

Scientific research is generally conducted within well established disciplines of "normal science" [162] with few cross-disciplinary interactions. Periods of time in which two disparate scientific disciplines begin to interface with one another are rather the exception. Such is the case with spatial ecology and pattern formation, a research field that centers on the nonlinear dynamics of spatially extended systems and the self-appearance of spatial patterns. Field observations in arid and semi-arid regions during the past decade [317, 309, 63, 101] have revealed nearly periodic vegetation patterns that are familiar from a variety of other pattern-formation contexts, including fluid dynamics, chemical reactions and nonlinear optics [56]. A few examples of such patterns are shown in Figure 1.1. They consist of vegetation spots in an otherwise bare area devoid of vegetation (panel (a)), vegetation stripes (panel (b)), or barren gaps in vegetated areas (panel (c)). The understanding that vegetation patchiness is not merely dictated by environmental heterogeneities, but may also be a result of self-organization driven by pattern-forming instabilities of uniform states, has led to a surge of empirical and theoretical studies using the conceptual framework of pattern-formation theory [169, 155, 325, 128, 255, 256, 29, 212].

The relevance of pattern-formation theory to spatial ecology has been pointed out earlier [275, 173, 172], and has motivated modeling studies in various ecological contexts [259, 307, 209, 40, 293, 15, 190, 341, 220]. However, of all contexts, self-organized vegetation patchiness in water-limited systems stands out in providing the best case study, so far, for applying pattern-formation theory to spatial ecology. One reason for that is the wide scope of observed vegetation patterns and the good correspondence to model predictions. These observations not only include nearly periodic spot, stripe and gap patterns, but also a wide variety of non-periodic patterns (see Figures 10.12, 10.17 and 10.19). Another reason is the wide scope of ecological problems that

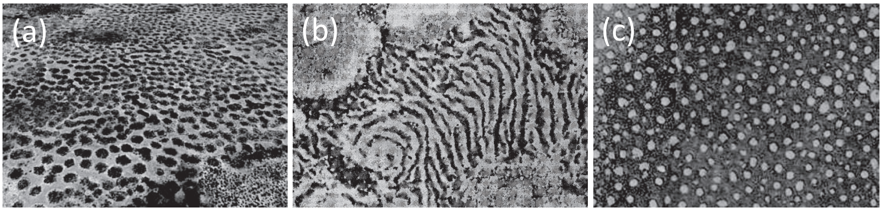

FIGURE 1.1: Aerial photographs of nearly periodic vegetation patterns in nature: (a) a spot pattern in Zambia (from [29]), (b) a stripe pattern in Niger (from [317]), (c) a gap ("fairy circle") pattern in Namibia (courtesy of S. Getzin).

can be addressed, including outstanding questions such as desertification, biodiversity loss and their implication for ecosystem function.

The increasing interest in dryland vegetation has motivated pattern formation studies in wetland vegetation too [85, 46], and in a few other marine ecosystems, such as mussels beds [178]. In all these cases pattern formation results from non-uniform instabilities of uniform states in which the growth of spatially structured modes leads to patterned states. However, pattern formation may also result from uniform instabilities that give rise to a multiplicity of stable uniform states, as patterns consisting of spatial domains occupied by different states are then possible. As will be shown in Part II of this book, such systems can show a wide variety of persistent patterns, including stationary labyrinthine patterns, rotating spiral waves, and spatiotemporal chaos. A multiplicity of stable states has been found in studies of tidal marshes [197], plankton systems [262, 261] and coastal vegetation [140], and is likely to be found in many more marine or marine-related ecosystems. These systems all lend themselves to pattern formation studies.

The main thesis we pursue here is that inasmuch as concepts of nonlinear dynamics, such as multi-stability of steady states, tipping points, oscillations and chaos, have already been integrated into ecological research, pattern formation concepts should be integrated too. The latter include the concepts of a non-uniform instability, periodic stripe and hexagonal patterns, traveling waves, front dynamics, spatial resonances and others. The need to integrate these concepts should be expected on general grounds, as ecosystems are nonlinear spatially extended systems, like all other pattern forming systems in nature, but can also be motivated using concrete examples, as we discuss in the next section.

1.2 Pattern formation—a missing link in ecological research

Much effort is focused in ecology on understanding the reciprocal relationships between the abiotic environment, biodiversity, and ecosystem function [180]. We argue that these relationships are very often mediated by pattern-formation processes as Figure 1.2 schematically illustrates. Pattern formation is directly linked to any of the three components (small dotted arrows). It is linked to the abiotic environment because environmental stresses often induce spatially patterned states. It is linked to biodiversity because it may induce self-organized heterogeneity of biomass and resources that affect inter-specific interactions[1]. It is also linked to ecosystem function since pattern formation can affect water-use efficiency and biomass production, or imply different rates and pathways of nutrient change.

These links form indirect causal relationships between the abiotic environment, biodiversity and ecosystem function through various pattern formation processes (solid arrows in Figure 1.2). The impact of climate change on species diversity through pattern transitions that change inter-specific interactions is an example of an indirect relation between the abiotic environment and biodiversity. A possible example of an indirect relation between biodiversity and ecosystem function is spatial self-reorganization of a community in an alternative stable state of different productivity, and an example of an indirect relation between the abiotic environment and ecosystem function is gradual regime shifts involving cascades across different pattern states.

The pattern formation links depicted in Figure 1.2 involve processes occurring on different length scales and across different organization levels. Figure 1.3 illustrates an example of a series of such processes in the context of dryland vegetation. The processes described are motivated by model studies to be presented in detail in Part III. Local biomass-water feedbacks, involving water transport toward vegetation growth points, can induce spatial instabilities that lead to vegetation pattern formation at the landscape scale. Environmental changes at the landscape scale, such as drought or spate, can induce transitions to a variety of other alternative stable patterns. Associated with these transitions are changes in the spatial soil-water distributions, which, in turn, affect inter-specific interactions at local scales. In woody-herbaceous systems these interaction changes can result in transitions from competition to facilitation and, consequently, in community-structure changes.

The scenario described above includes bottom-up processes whereby plant-plant interactions, mediated by the limiting water resource at the local scale, give rise to the emergence of periodic patterns at the landscape scale. It also

[1]The term *inter-specific* interaction refers to the interaction between individuals of different species, in contrast to the term *intra-specific* interaction, which refers to interactions between individuals of the same species.

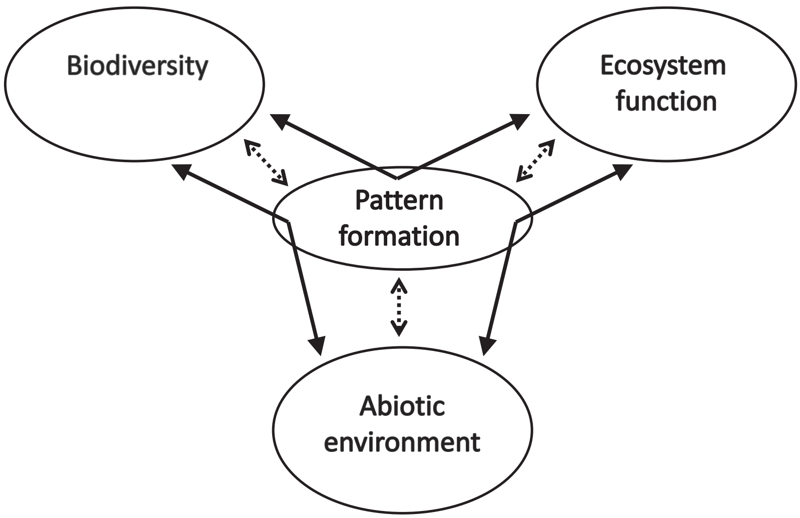

FIGURE 1.2: Pattern formation processes induce indirect causal relationships between the abiotic environment, biodiversity and ecosystem function. The dotted arrows represent different manners by which pattern formation is linked to these three components, and the solid arrows represent compositions of these manners that form indirect relationships between the three components (see the text for examples).

includes top-down processes, in which species-interactions at local scales are affected by pattern changes at the landscape scale. These processes not only involve disparate length scales, but also different levels of organization, starting at the organism level, with species traits that give rise to spatial instabilities, proceeding to the population level, through vegetation pattern formation, and to the community level, through changes in inter-specific interactions.

This example also highlights the integrative role pattern formation can play in ecological research. Ecology, as an empirical science, has branched into different research fields according to the hierarchical levels and spatio-temporal scales that the empirical studies have addressed. As a result, many subdisciplines have emerged, such as population ecology, community ecology, ecosystem ecology[2], and landscape ecology. By bridging over different organization and trophic levels, and over different length and time scales, studies of pattern formation in ecology can contribute to the integration of these subdisciplines.

[2]Ecosystem ecology is a subfield of ecology dealing with the flow of energy and matter through biotic and abiotic ecosystem components. The term is somewhat misleading in that it refers to specific aspects of ecosystems, rather than to all aspects as the term suggests.

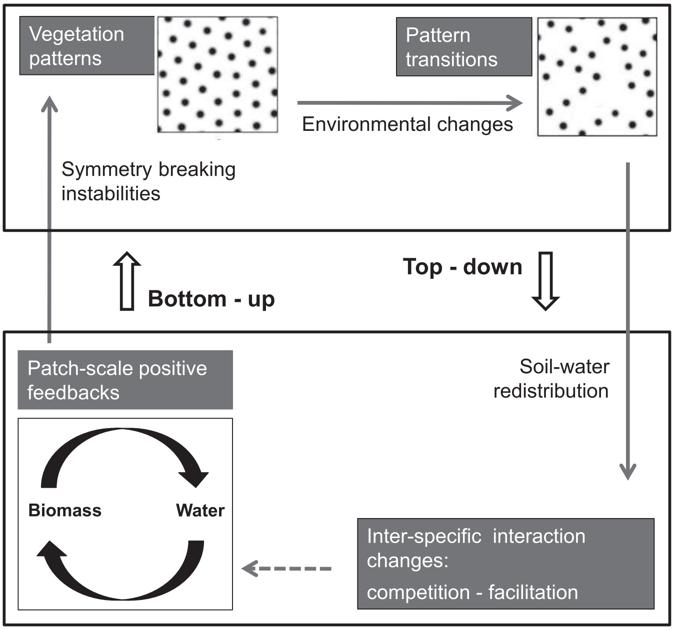

FIGURE 1.3: Pattern formation can link phenomena that occur on different length scales and organization levels - an illustration with a dryland-vegetation example. Local biomass-water feedbacks (lower frame) induce vegetation pattern formation at the landscape scale (upper frame; dark spots represent vegetation patches). Environmental changes at the landscape scale induce transitions to other alternate stable vegetation patterns (upper frame). These pattern transitions change the local soil-water distributions and thereby affect inter-specific interactions (lower frame). In woody-herbaceous systems these interaction changes may induce transitions from competition to facilitation. In other systems they may feed back on vegetation pattern formation (dashed arrow).

1.3 Purpose and scope of the book

The purpose of this book is to assimilate the concepts and methods of pattern formation theory into ecological research and, thereby, to contribute to the development of the newly emerging interdisciplinary research field at the interface between spatial ecology and pattern formation. Much of the book revolves around the diagram shown in Figure 1.2, and the elucidation of various links between pattern formation, on one hand, and the abiotic environment, biodiversity and ecosystem function, on the other hand. We focus on dryland vegetation as a case study, but the general approach is applicable to other ecological contexts, including marine ecosystems. The book is by no means intended to be comprehensive. It is rather intended to demonstrate the utility of pattern formation theory in ecological research and to highlight outstanding open problems that can be handled with this approach, along with the progress that has already been made on selected problems.

Being an interdisciplinary field in its infancy, a significant part of the book is devoted to the introduction of pattern formation theory. The introduction is made at two levels; an elementary level that requires basic knowledge of linear algebra and ordinary differential equations, and a more advanced level which also requires familiarity with partial differential equations. The elementary-level introduction is included in Part I of the book, which is devoted to an overview of pattern formation and spatial ecology as strongly related disparate research fields. The advanced introduction is presented in Part II of the book, and includes descriptions of analytical tools and applications of these tools to the study of general mechanisms of pattern formation and pattern dynamics.

There are several related topics which were left aside. We focus on deterministic dynamics, largely ignoring stochastic aspects, such as demographic noise in small populations [28] and noise-induced patterns [34, 268, 253]. A few pattern formation topics have not been considered, including front propagation into an unstable state [73], which is relevant to species invasion problems [289], and pattern formation in excitable media [211], which has been studied in the context of phytoplankton ecosystems [311, 189]. The presentation of mathematical methods has also been limited to the most common ones. For example, we refer to, but do not describe the derivation of phase equations far from the onset of instabilities [226, 136], nor do we describe free boundary-layer analysis, leading, for example, to kinematic descriptions of curved fronts [20, 119, 121] and spiral waves [124]. Finally, although numerical methods are crucial tools for studying nonlinear spatially extended systems we left a detailed description of these methods outside the scope of this book, as this topic is well covered in the literature.

Part I

Overview

Chapter 2

Spatial self-organization

2.1 Natural and laboratory realizations of pattern formation

The term "pattern formation" refers to processes by which positive feedbacks operating at small spatial scales give rise to self-organization at large scales that results in stationary or time-dependent spatial patterns. Numerous examples of such processes have been found and studied in various fields of science, including fluid dynamics, chemical kinetics, nonlinear optics and geophysics. Much of our understanding of pattern formation phenomena derives from controlled laboratory experiments conducted on simple model systems. Following a brief description of patterns in nature and some of their characteristic features (Section 2.1.1), we introduce two experimental model systems, the Rayleigh–Bénard thermal convection system (Section 2.1.2) and the Belouzov–Zhabotinsky chemical reaction (2.1.3). Both systems show a variety of pattern formation phenomena and have played important roles in uncovering general mechanisms of pattern formation and dynamics.

2.1.1 Patterns in nature

A common feature of spatially extended nonequilibrium systems is the possible emergence of ordered patterns with characteristic length scales. Plenty of natural examples of this phenomenon exist, including cloud streets, sand ripples, stone patterns and vegetation patterns (Figure 2.1). A fascinating aspect of these pattern-formation phenomena is that the order is not imposed by any external factor; it rather results from positive feedbacks operating at small scales, that give rise to self-organization and pattern formation at large scales. We will discuss these phenomena in two specific physical contexts shortly, but some of the underlying principles can already be stated. A uniform force that drives a uniform system out of equilibrium can break the spatial uniformity of the system and induce spatially periodic patterns. The transition to the patterned state is not gradual; spatial variability appears only beyond a critical force strength. We call such a phenomenon a *symmetry breaking instability*. Although we generally cannot prove the emergence of patterns in nature from symmetry breaking instabilities, we often do make this association, relying on experimental studies of model systems and on mathematical analyses of model equations.

Another principle of pattern formation relates to the universal nature of these phenomena, that is, to the observations of similar patterns, such as stripes, hexagons and spiral waves, in completely different physical contexts. Stripe patterns, for example, appear in clouds, in dryland vegetation and in animal coat patterns, although the mechanisms responsible for these patterns are obviously specific to the system in question, and differ from one another. The universality of pattern formation phenomena is tightly related to the symmetry breaking instabilities that induce patterns; different systems that go through the same type of instability behave similarly close to the instability threshold.

Pattern formation is an example of an emergent property [3], that is, a property that appears at the system level, e.g., the level of clouds, sand dunes, or patchy landscapes, and often has no meaning at the level of the system's constituents—the water molecules, sand grains, or plants. At the system level, patterns are affected by global forces, such as temperature, wind, and rainfall, and the resulting pattern dynamics may feed back on small-scale processes (Figure 1.3). Studying pattern formation and pattern dynamics is therefore significant for understanding bottom-up and top-down cross-scale processes in complex natural systems.

2.1.2 The Rayleigh–Bénard system

A classical experimental model for pattern formation is the Rayleigh–Bénard (RB) system of thermal convection [44, 24]. Consider a fluid at rest that is heated from below. If the temperature difference between the bottom and the top of the fluid compartment is smaller than some critical value,

FIGURE 2.1: Patterns in nature. From left to right: cloud stripes, sand ripples on a dune [13], stone patterns [151] and grass patterns [325].

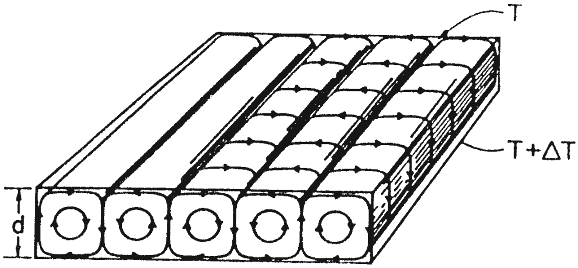

FIGURE 2.2: Schematic representation of convection rolls in the Rayleigh–Bénard system. The fluid compartment is of depth d with temperature at the bottom $T_{\rm bot} = T + \Delta T$ higher than that at the top $T_{\rm top} = T$. From [56].

$\Delta T = T_{\rm bot} - T_{\rm top} < \Delta T_C$, the fluid remains at rest and the heat transfer upward proceeds by molecular conduction. However, when $\Delta T > \Delta T_C$ a convection sets in, generating ordered parallel fluid rolls as illustrated in Figure 2.2. The number of rolls is approximately determined by the ratio of the length of the fluid compartment to its height, the so-called *aspect ratio*.

Why does the rest state of the fluid become unstable beyond a certain temperature difference? Imagine a fluctuation in which a fluid particle[1] at some height has a temperature which is slightly higher than the surrounding fluid at that height. Because of thermal expansion the fluid particle will have a lower density than that of the surrounding fluid (i.e., will be lighter) and will tend to move upward. As it moves upward the surrounding fluid becomes yet colder and the buoyancy force upwards increases. This is a positive feedback between the height of the fluid particle and the buoyancy force; the higher the

[1]By a "fluid particle" we mean a parcel of fluid which is very small on a macroscopic scale, but still very large on a microscopic scale.

particle's position the stronger the force and the stronger the force the higher the particle's position. Besides the buoyancy force there are also processes that act to stabilize the rest state. Fluid viscosity induces transfer of linear momentum from the upward moving fluid particle to its neighborhood, thus reducing its momentum and speed. In addition, thermal conduction induces diffusion of heat from the fluid particle to its colder neighborhood, thus reducing the buoyancy force that drives the fluid particle upward. The instability therefore sets in at a critical temperature difference, ΔT_C, at which these stabilizing factors just balance the destabilizing buoyancy force.

The instability can be induced by varying other parameters that affect the buoyancy force or the stabilizing factors: the coefficient of thermal expansion, α, the thermal diffusivity, κ, the fluid's kinematic viscosity, ν, the gravitational acceleration, g, and the hight of the fluid layer, d. The instability can be induced, for example, by increasing α which strengthens the buoyancy force, or by decreasing κ and ν, which weakens the stabilizing factors. The effects of all parameters are lumped together in a single dimensionless parameter, the so called Rayleigh number R, given by [44]

$$R = \frac{\alpha g \Delta T d^3}{\kappa \nu} \,. \tag{2.1}$$

The instability sets in as R exceeds a threshold value R_c. In practice, the Rayleigh number is generally increased by heating the bottom of the fluid compartment, i.e., by increasing ΔT. The roll patterns that form beyond the instability point can be visualized by the shadowgraphy method. This method makes use of the fact that the index of refraction varies weakly with temperature; warmer (colder) fluid regions have a lower (higher) index of refraction. Since the temperature varies periodically across the rolls, so does the refraction index. Passing a beam of light through the fluid layer results in a pattern of alternating bright and dark stripes. The bright stripes correspond to regions of cold fluid flowing downward, that act as converging lenses because of the higher refraction index. Figure 2.3 shows examples of roll patterns observed with the shadowgraphy method.

2.1.3 The Belouzov–Zhabotinsky reaction

The Rayleigh–Bénard system is an example of an experimental pattern-formation model associated with fluid motion. Chemical reactions provide another type of experimental pattern-formation model. A classical example is the oscillatory Belousov–Zhabotinsky (BZ) reaction [90], a catalytic oxidation reaction of malonic acid in an acidic bromate solution. A nice aspect of this reaction is that the oscillations are clearly visible to the bare eye because of the different colors associated with the two oxidation states of the catalyst. The mechanism of this reaction has been worked out by Field et al. [91] and contains many elementary reactions. A reduced model (the Oregonator), consisting of only five reaction steps, captures many qualitative aspects of the

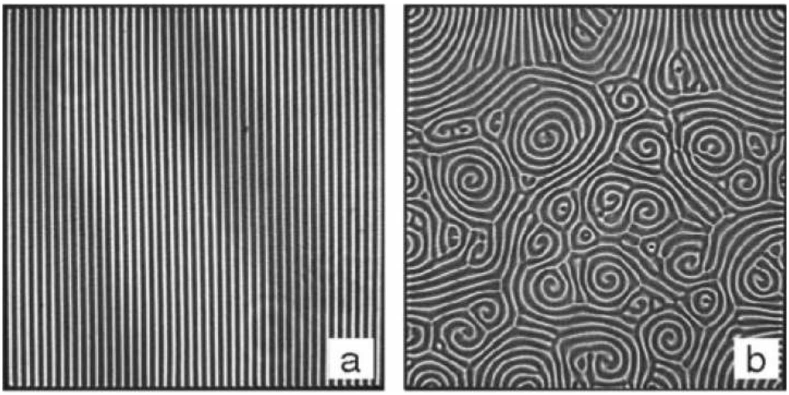

FIGURE 2.3: Regular (a) and chaotic (b) roll patterns in a Rayleigh–Bénard convection experiment. From [24].

BZ reaction dynamics [92]. The five reaction steps are:

$$A + W \rightarrow U + P\,, \tag{2.2a}$$
$$U + W \rightarrow 2P\,, \tag{2.2b}$$
$$A + U \rightarrow 2U + 2V\,, \tag{2.2c}$$
$$2U \rightarrow A + P\,, \tag{2.2d}$$
$$B + V \rightarrow hW\,. \tag{2.2e}$$

where $A = BrO_3^-$ (bromate ions), $W = Br^-$ (bromide ions), $U = HBrO_2$ (bromous acid), $P = HOBr$ (hypobromous acid), V is the oxidized form of the catalyst (e.g., cerium Ce^{4+}), $B = CH_2(COOH)_2$ (malonic acid), and h is a stoichiometric coefficient (note that this simple model is not stoichiometrically balanced). The key steps in this reaction scheme are (2.2b) and (2.2c). Both steps compete for U, but while U is consumed in (2.2b) it is autocatalytically produced in (2.2c). An initial access of W eliminates U in step (2.2b) before step (2.2c) becomes significant. However, as W drops down step (2.2c) takes over. This step involves a positive feedback (U accelerates the growth of itself), which leads to fast exponential production of U. The production of U is accompanied by the production of V, which changes the color of the solution. The growth of U is slowed down in step (2.2d) which, together with step (2.2e), brings the system to the starting point and to the initiation of a new cycle. The chemical composition needed to initiate the reaction consists of an acidic aqueous solution containing bromate ions (e.g., potassium bromate), malonic acid, bromide ions (e.g., potassium bromide), and a metal catalyst in a reduced form (e.g., cerium Ce^{3+}).

The BZ reaction is an example of an *activator-inhibitor* system. In such a system, the activator is a substance that "activates" the growth of itself and of another substance–the inhibitor. The inhibitor inhibits the growth of the

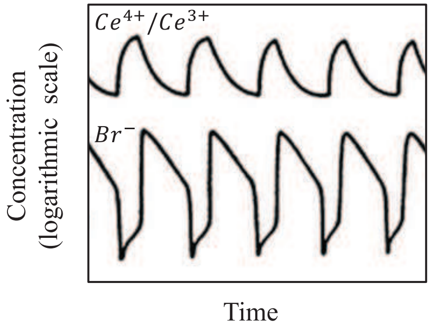

FIGURE 2.4: Relaxation oscillations in the BZ reaction. Shown are time signals of $\log{[Ce^{4+}]}/[Ce^{3+}]$ (top) and $\log{[Br^-]}$ (bottom). The oscillation period is of the order of $10^2 s$. Adopted from [91].

activator and often the growth of itself too. In the BZ reaction U plays the role of the activator and V the role of the inhibitor. Quite often the activator changes on a time-scale significantly shorter than that of the inhibitor. The oscillatory dynamics then involve alternate phases of slow and fast concentration changes as Figure 2.4 shows. Oscillations that involve two distinct time scales are often called "relaxation oscillations" [296]. In spatially extended systems with diffusive coupling such oscillations can give rise to traveling-wave phenomena; diffusion of the activator to its neighborhood, before it is damped by the inhibitor, can induce its growth there and therefore its spatial spread. Sufficiently fast inhibitor diffusion, on the other hand, can give rise to stationary patterns; the fast inhibitor diffusion away from an activated domain prevents the local decay of the activator and also the activator's spread to the highly inhibited neighborhood of this domain. In the BZ reaction the activator changes on a time scale much shorter than that of the inhibitor, and the inhibitor diffusion is sufficiently slow to allow for traveling waves.

Early pattern formation experiments in the BZ reaction were made in closed systems (petri-dish experiments) with the inevitable approach to a stationary, uniform equilibrium state. Even in these simple experiments striking traveling-wave phenomena, such as spiral waves, have been observed [331]. More recent experiments have utilized open systems which are continuously fed with fresh chemicals so as to keep the system at a fixed distance from equilibrium [299, 17]. A typical experimental setup consists of a thin reactor layer containing an inert gel or a porous glass that allow diffusion of the reactants but damp convection. The reactor layer is in diffusive contact with one or two stirred reservoirs which are continuously fed with fresh reagents. The reaction dynamics can be controlled by varying the flow rates of chemical reagents, such as bromate or malonic acid, into the reservoirs. The advantage of this type of setup is that it allows conducting long experiments which are needed in studying instability phenomena.

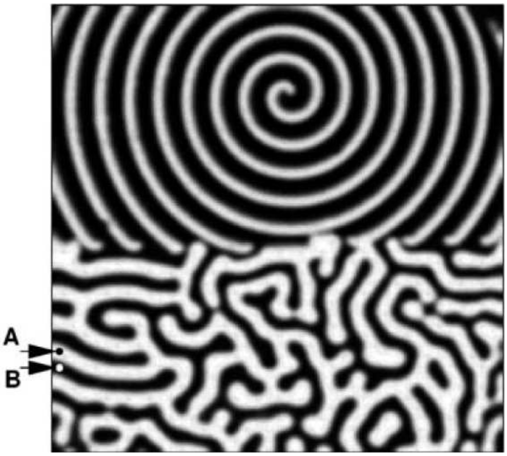

FIGURE 2.5: Patterns in a reactor of the light sensitive BZ reaction whose lower half is subjected to periodic illumination at twice the natural frequency of the oscillatory reaction. The unforced reaction (upper half) shows a rotating spiral wave, while the forced reaction shows a labyrinthine standing-wave pattern. The labels A and B denote points that oscillate out of phase. From [241].

Various modifications of the BZ reaction have been studied. One type of modification is the replacement of the metal catalyst, Ce^{3+}, by other metal ions such as Fe^{2+}, Mn^{2+} and Ru^{2+}. Of particular significance is the use of ruthenium (Ru^{2+}) as the catalyst. This modification makes the chemical kinetics sensitive to light, and allows studying the effects of forcing the chemical oscillations by periodic illumination in time or in space or in both. Experiments on the light-sensitive BZ reaction, subjected to time-periodic, spatially uniform illumination, have shown resonant responses similar to those found in periodically forced oscillators [177]. That is, denoting the oscillation frequency of the unforced system by ω_0, and the forcing frequency by ω_f, resonance bands have been found in which the oscillation frequency of the forced system, ω, locks to a rational fraction of the forcing frequency, $\omega = (n/m)\omega_f$, in a range of ω_f around ω_0 (whose width increases with the forcing amplitude). Various resonances $(\omega_f : \omega) = (m : n)$ have been found in the experiments, revealing part of a Farey tree hierarchy of resonances[2] [74, 108] as Figure 8.1 shows. The forcing, however, can also induce new spatial patterns. A striking example is shown in Figure 2.5, where spiral waves in the unforced reaction destabilize to standing-wave labyrinthine patterns when a sufficiently strong uniform forcing with a frequency $\omega_f \approx 2\omega_0$ is applied. A detailed discussion

[2] In a Farey tree of resonances, between any two resonances $(i : j)$ and $(k : l)$ there is an intermediate resonance $(i + k) : (j + l)$.

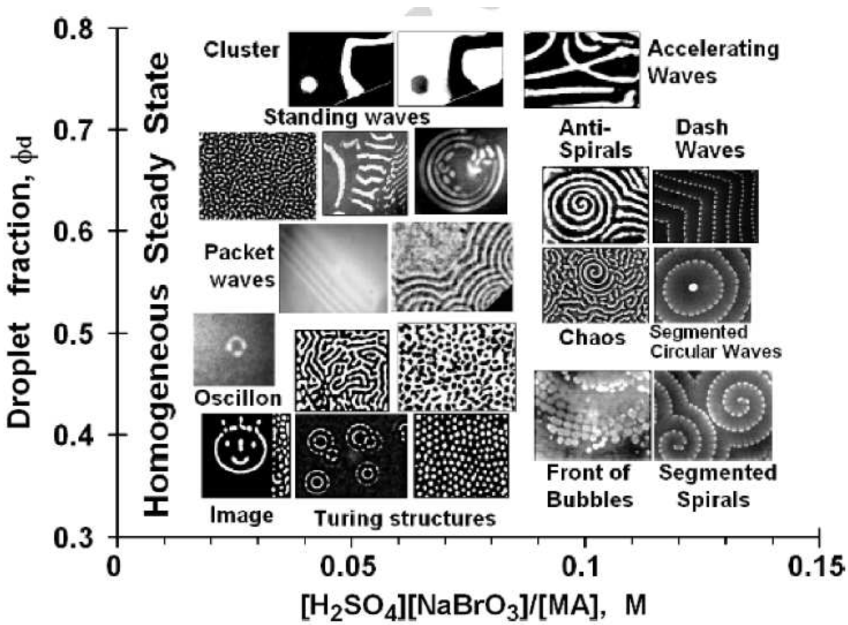

FIGURE 2.6: Patterns observed in the BZ-AOT reaction. From [321].

of periodically forced, spatially extended oscillatory systems is presented in Chapter 8.

Another interesting modification of the BZ reaction is a water-in-oil microemulsion system with nanometer-sized droplets of water surrounded by monolayers of a surfactant (aerosol OT or AOT) and dispersed in oil (octane) [321]. Since most reagents of the BZ reaction are polar, they reside in the water droplets and diffuse at a relatively slow rate characteristic of entire droplets. Some key intermediates, however, are non-polar and therefore escape into the oil and diffuse much faster. This property of the BZ-AOT reaction allows for stationary patterns and a wide variety of traveling wave patterns not observed in the original BZ reaction, as Figure 2.6 shows.

2.2 Pattern-forming systems as dynamical systems

Pattern-forming systems are often described by small sets of fields; the velocity and temperature fields in thermal convection, the concentrations of key species in chemical reactions, biomass and resource fields in patchy landscapes, and so on. Quite often approximate dynamical equations for these fields are known. For relatively simple systems the dynamical equations are derivable from first principles. This is the case with simple fluids that satisfy the Navier–Stokes equations [44], or with electromagnetic radiation in dielectric materials that satisfies the Maxwell equations [229]. More complex systems generally involve some degree of modeling. Pattern-forming chemical reactions, for example, are described by reaction-diffusion models that simplify the complex chemical kinetics of these reactions. Pattern-forming ecosystems require a yet higher degree of modeling (see Chapter 9). We will refer to the set of dynamical equations that describe a pattern forming system as a *dynamical system.*

In what follows we distinguish between small and large pattern forming systems using the concept of *dimension* of a dynamical system (Section 2.2.1). Small pattern forming systems are governed by small numbers of independent degrees of freedom and can be described by small sets of nonlinear ordinary differential equations or "low-dimensional" dynamical systems. The theory of low-dimensional dynamical systems is well developed and is described in many textbooks [296, 165, 163]. We briefly describe it here (Sections 2.2.2, 2.2.3, 2.2.4, and 2.2.5) focusing on concepts that are essential for understanding the presentation of pattern formation theory in Part II and the applications to spatial ecology in Part III.

2.2.1 Dimension and size of a pattern-forming system

The dynamical equations of pattern-forming systems represent infinitely many degrees of freedom; formally, any point in space contributes at least one degree of freedom. However, because of the dissipative nature of these systems, the number of independent degrees of freedom reduces dramatically in the course of time. The asymptotic[3] independent degrees of freedom generally represent slow modes, such as modes that begin to grow at instability points, but may describe faster processes as well, such as transitions between slowly evolving states. We define the *dimension* of a pattern-forming system as the number of independent degrees of freedom that describe the (asymptotic) long-term dynamics of the system.

The dimension of a pattern-forming system strongly depends on its physical size. The size is determined relative to a typical length in the system, such as the wavelength of a periodic pattern. Thus, a small (large) aspect-ratio Rayleigh–Bénard (RB) system that fits in a few (many) pairs of rolls, is an example of a small (large) system. The dynamics of small pattern-forming systems, just above the instability of the equilibrium state, involve a small number of independent degrees of freedom. The tremendous reduction in the number of degrees of freedom in this case is mathematically accounted for by the center manifold theorem [114], but can be intuitively understood using the example of a small RB system. The roll pattern that sets in at the instability

[3]Throughout the book we will use the term "asymptotic" to refer to long times unless otherwise is stated.

point represents the first spatial mode for which the buoyancy force just overcomes all dissipative processes. All other modes describe significantly different spatial structures for which the dissipative processes still dominate the buoyancy force in some range above the instability point. These modes decay to zero unless they are nonlinearly coupled to the growing mode. In that case they do show up but do not represent independent degrees of freedom. As the system becomes larger, more pairs of rolls fit in, and the difference between adjacent modes (i.e., modes describing n and $n+1$ pairs of rolls) becomes smaller. As a result, more modes can grow and the dimension of the system increases.

The independent degrees of freedom of a pattern forming system near an instability point are often represented by the amplitudes of the modes that begin to grow at that point. Consider, for example, a chemical system that goes through an instability to a stationary periodic pattern with a wavelength λ. The concentrations, $c_i(x,t)$ $(i=1,...,n)$, of the chemical species that participate in the reaction, can be approximated, near the instability point, by

$$c_i(x,t) \approx \alpha_i u(t) \cos(k_0 x + \phi)\,, \tag{2.3}$$

where the cosine term represents the spatial mode that starts growing at the instability point, with $k_0 = 2\pi/\lambda$ and ϕ being its wavenumber and phase, $u(t)$ is a slowly varying amplitude of that mode, and the factors α_i are constants. The amplitude u represents the independent degree of freedom that describes the long-term dynamics of the system in some parameter range close to the instability point in which k_0 is the only mode to grow[4]. In small systems, i.e., systems whose size L is comparable to λ ($L \sim \lambda$), this parameter range can be significant and the long-term dynamics are captured by a single degree of freedom—the amplitude of the growing mode k_0. However, in large systems ($L \gg \lambda$) this range can become diminishingly small, because there are many other modes with wavenumbers close to k_0. At any finite range beyond the instability point the asymptotic dynamics are described by a set of independent degrees of freedom representing a band of modes centered around k_0. We postpone the discussion of large systems to Chapters 5 and 6 and consider in the rest of this section small systems that are describable by low-dimensional dynamical systems.

2.2.2 Basic concepts of low-dimensional dynamical systems

Low-dimensional systems are generally described by small sets of nonlinear ordinary differential equations or ODEs:

$$\dot{\mathbf{u}} = \mathbf{f}(\mathbf{u};\lambda)\,, \tag{2.4}$$

where $\mathbf{u} = (u_1(t),...,u_n(t))$ is a vector of real valued state variables, representing the independent degrees of freedom, $\lambda = (\lambda_1,...,\lambda_m)$ is a set of parameters,

[4]Note that the number of independent degrees of freedom is not determined by the number of chemical species n, but rather by the number of modes that grow at the instability point.

$\mathbf{f} = (f_1(\mathbf{u};\lambda), ..., f_n(\mathbf{u};\lambda))$ is a non-linear vector function of the state variables, and the dot represents the time derivative ($\dot{u} = du/dt$)[5].

The space spanned by the state variables $\mathbf{u}$ is called *phase space*. The temporal evolution of the system, $\mathbf{u}(t)$, from an initial value, $\mathbf{u}(0)$, traces a trajectory in phase space. Trajectories of this kind can be viewed as "stream lines" of a *flow* in phase space, determined by the specific form of $\mathbf{f}(\mathbf{u})$.

In general, the first objective in studying equations of this kind is identifying steady-state solutions and studying their stability properties. In the phase space of the system such solutions are represented by points and are often referred to as *fixed points*. We say that a steady-state solution, $\mathbf{u_s} = (u_{s1}, ..., u_{sn})$ of (2.4) is *linearly stable* if any infinitesimally small perturbation of $\mathbf{u_s}$ decays in time[6]. Conversely, a steady-state solution $\mathbf{u_s}$ is *linearly unstable* if there exists a small perturbation of $\mathbf{u_s}$ that grows in time. To study the linear stability of $\mathbf{u_s}$ we consider an infinitesimal perturbation of that solution, which we denote by $\delta\mathbf{u} = (\delta u_1, ..., \delta u_n)$, and insert the perturbed form $\mathbf{u}(t) = \mathbf{u_s} + \delta\mathbf{u}(t)$ into (2.4). Linearizing around $\mathbf{u_s}$ we obtain

$$\dot{\delta\mathbf{u}} = \mathbf{J}\delta\mathbf{u}\,, \tag{2.5}$$

where $\mathbf{J}$ is the Jacobian matrix whose (i,j) entry is $\partial f_i/\partial u_j|_{\mathbf{u}=\mathbf{u_s}}$. The solution $\mathbf{u_s}$ is linearly stable when the eigenvalues of $\mathbf{J}$ all have negative real parts, for in that case any perturbation $\delta\mathbf{u}$ decays exponentially in time. It is linearly unstable if the largest real part of all eigenvalues is positive[7].

An instability of a steady-state solution generally takes the system to a new steady-state solution or to a time-periodic solution. We refer to such instabilities as to *stationary instability* and *oscillatory instability*, respectively. In two-dimensional systems steady-state and time-periodic are the only possible asymptotic solutions. In higher dimensional systems chaotic dynamics are possible too [296]. In the following two subsections we analyze a few examples of stationary and oscillatory instabilities and use them to introduce additional concepts of dynamical systems.

2.2.3 Stationary instabilities

Many of the concepts to be introduced here can be explained using the following one-dimensional system and variants thereof:

$$\dot{u} = f(u;\lambda) = \lambda u - u^3\,. \tag{2.6}$$

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[5] Readers unfamiliar with ODEs are referred to Ref. [165] or to any other textbook on ODEs

[6] The theory of dynamical systems defines a few forms of stability [107]. The definition given here amounts to *asymptotic stability* in which points near $\mathbf{u_s}$ converge to it directly. Weaker forms of stability include quasi-asymptotic stability in which nearby points eventually converge to $\mathbf{u_s}$, but not necessarily in a direct manner. This weaker form of stability occurs, for example, in excitable systems [211].

[7] The reader is referred to Ref. [165] for a brief introduction to the concepts of matrices and eigenvalues.