General Introduction

Monique de Jager
The simplicity of complex patterns

It is amazing how simple things in life can create immense complexity. With a few simple rules, complex patterns can arise from the interactions between individuals. When I was in Japan, I visited the world’s most crowded crossing in Shibuya, Tokyo (Fig. 1.1A). Although it seemed impossible to cross the street in such a vast mass of people, I actually found it quite effortless to make it to the other side of the road. Looking back, I remember making a few simple decisions. I tried to find my way using a path of least resistance, which meant that I avoided collisions with fellow crossers and followed anyone walking before me that was going in the same direction as I was trying to go. After crossing the street, I climbed the stairs of one of the tall buildings right next to the crossing for a bird’s eye view of the scramble that was taking place down below. At first I saw a complex mixture of pedestrians, but when I looked closer I could see patterns emerging during the crossover activity. I noticed that most people were using the same simple rules as I had earlier, and thereby they formed these large strings interlacing at the crossroad (Fig. 1.1B). Simply by crossing the street at a crowded location, we can see spatial patterns emerging from the straightforward actions of and interactions between individuals.

The most fascinating thing about the interactions responsible for the emergence of spatial patterns is how the success of one individual within the pattern depends on the actions of others. Just imagine that you are crossing a busy street, where cars turn into blazing menaces that will run you over once their light turns green. If you would be the sole pedestrian crossing this busy street, you simply cross at the sight of your green light and you will reach the other side in plenty of time. However, the situation becomes more complicated when the intersection is full of pedestrians. Those who are crossing in the same direction as you won’t much affect your chances of reaching the other side in time, but the people traversing in the opposite direction might hamper your cross-over. The spatial pattern that is generated will affect the probability that you run into fellow crossers, and hence influences the ability of individuals to safely cross the street. Thus, spatial patterns that emerge from interactions between individuals will affect survival and fitness, and may thereby influence evolutionary processes.
Figure 1.1: Although the street-crossing behavior at Shibuya crossing, Tokyo, appears a pedestrian’s pandemonium (A), spatial patterns emerge when we separate the people that are going in opposite directions (B), using a different color for those who are crossing to this side of the street (in blue) than for the those who are walking in the other direction (in yellow).
Surprisingly, evolutionary processes have seldom been investigated in studies on self-organized pattern formation (but see Hogeweg & Takeuchi, 2003; Kéfi et al., 2008; Xavier et al., 2009). Yet, a feedback between pattern formation and evolutionary adaptation of the pattern-generating traits likely exists. For instance, picture a fish population trying to arrive at their spawning grounds safely. Because individuals that try to stay close to conspecifics decrease their risk of being predated, more of these fish have a chance to reproduce than those who swim freely (Partridge 1982; Partridge et al., 1983; Parrish et al., 2002; Hemelrijk & Hildenbrandt, 2012). If schooling behavior is a heritable trait, the frequency of fish that school will be higher in the next generation, which generates a larger school and hence decreases predation risk even further for those fish that school together. This process repeats itself: schooling behavior again becomes more frequent in the next generation, producing an even larger, safer school, and so on. Here, the pattern-generating behavior – schooling – creates a spatial structure which influences the survival success of these individuals, thereby altering the pattern-generating behavior of the individuals in the next generation and, in turn, the emergent spatial structure. I believe that this feedback between ecology and evolution is of great importance for understanding both species traits and ecosystem functioning in natural systems with self-organized patterns.

The feedbacks between ecological pattern formation and evolutionary adaptation of self-organizing traits are not only of importance for street-crossing behavior or schooling of fish, but may also be vital in the wide prevalence of self-organized complexity throughout nature (Fig. 1.2). For instance, regular spatial patterns can emerge from individuals’ self-organizing traits, such as movement, cooperation, and facilitation, in ecosystems as diverse as ribbon forests (Fig. 1.2C), coral reefs (Fig. 1.2D), arid bush lands, tidal wetlands, peat lands, and mussel beds (Klausmeier, 1999; Mistr & Bercovici, 2003; Rietkerk et al., 2004a; Rietkerk et al., 2004b; Van de Koppel et al., 2005; Van de Koppel & Crain, 2006; Van de Koppel et al., 2008; Eppinga et al., 2009). In arid bush lands, for example, plants locally ameliorate their environment, which facilitates the settlement and survival of seedlings and thereby gives rise to spatially clustered patches of vegetation (Klausmeier, 1999). Another example involves mussels actively aggregating into
labyrinth-like patterns, which simultaneously decreases dislodgement risk and food competition (Van de Koppel et al., 2008). The shared key feature in all self-organized systems is that structures larger than the organism develop from the local interactions between individuals, without any underlying templates or superior control. By means of self-organized pattern formation, organisms can strongly influence the ecosystem, thereby affecting environmental conditions as well, which in turn feeds back on the organisms’ fitness. Although the ecology of self-organized pattern formation has been researched for a wide range of ecosystems, feedback between ecology and evolution has seldom been considered in these ecosystems (but see Kéfi et al., 2008).

The apparent shortage of knowledge on eco-evolutionary feedbacks in self-organized ecosystems created a great opportunity for me to investigate this subject in my dissertation. In the past seven years, I have examined many aspects of self-organized patterning in young mussel beds, using both ecological experiments and eco-evolutionary models. With mussel beds as a model system, I will use the next five chapters to explore the dynamics and importance of eco-evolutionary
feedbacks in self-organized ecosystems. In the remainder of this introduction, I give more detail on self-organized pattern formation in mussel beds and the main traits responsible for self-organization in ecosystems – movement and cooperation.

Making the bed

Most of the work that I present in this thesis stems from mesocosm experiments, field experiments, and individual-based models that all involve mussel beds as a model system. These allow me to study the interaction between self-organization and evolutionary adaptation in spatially patterned ecosystems. When thinking about large-scale regular patterns in ecosystems, a mussel bed might not be the first habitat that comes to mind. Yet, mussel beds are an ideal system for studying self-organized complexity, as I will explain in the following paragraphs.

First, mussels actively move into a regular spatial pattern. Whereas self-organizing plant species are only dispersed as seeds before they settle, young mussels make use of their one foot and drag themselves along the sediment in search of conspecifics (Maas Geesteranus, 1942). They search for the perfect compromise between food availability and safety. On the one hand, mussels need sufficient algae on which to grow and live, yet on the other hand, they ought to be safely attached to neighboring mussels to decrease wave stress and predation risk (Van de Koppel et al., 2005; Van de Koppel et al., 2008). Aggregating into labyrinth-like patterns helps mussels to achieve this compromise and allows them to exist under conditions that would otherwise be lethal (Van de Koppel et al., 2008). The movement of mussels into regularly patterned beds is an exciting self-organizing trait, which considerably affects the ecosystem’s spatial structure.

Second, mussels cooperate with neighboring conspecifics, without any familiarity between them. Studies on cooperation in other self-organized ecosystems show that short-range dispersal is a prerequisite for local facilitation to evolve (Kéfi et al., 2008). Whereas local dispersal is frequently regarded as a necessity for cooperation and facilitation, many cooperative organisms disperse over a wide range. Mussels, for example, settle down in a completely mixed mussel bed; yet they cooperate with others by attaching their byssus threads – a glue-like substance that can fasten two mussels together – to any random neighbor within
their well-mixed population. So far, the evolution of cooperation in spatially patterned populations with wide-ranging dispersal remains elusive, but mussel beds are a perfect model system to investigate this problem as well as its effect on self-organized patterning. Furthermore, the combination of aggregative movement and between-mussel attachment lends itself to a novel study of feedback between self-organization and the joint evolution of two traits (movement and cooperation).

Third, one of the most useful features of mussels is the ease at which they provide data. A simple camera is sufficient to take snapshots of individual-level pattern formation at the scale of meters. Mussels are not too particular on where they create patterns; they will even produce strings in a bucket. Using a seawater-filled tank and a webcam, we can follow mussel movement and pattern formation with little effort. Mussels create patterns within 8 hours, which is much faster than self-organization in most other ecosystems (for instance, self-organized pattern formation in arid systems takes decades; Barbier et al., 2008). Data on between-mussel cooperation is also easily obtained using simple tools; the tweezers that are ideally suited for plucking eyebrows are also of great use when counting byssal attachments, nail polish does the trick when mussels are in need of individual identification, and cable ties are of good use for immobilizing mussels and preventing them from cooperating. Even the shape of a mussel – which is roughly oval – can be nicely approximated with circular individuals in agent-based models. In sum, the size and shape of the individuals and pattern, and the speed of pattern formation make mussel beds a great ecosystem to study the feedback between spatial pattern formation and the evolution of self-organizing traits.

A movement to aggregate

Active movement is frequently used by mobile organisms to aggregate with nearby conspecifics. For instance, birds fly into flocks of all shapes and sizes, fish swim close to each other to create dense schools, cockroaches move into aggregations, and ants carry their dead around and stock them onto massive ant piles (Theraultaz et al., 2003; Jeanson et al., 2005; Hemelrijk & Hildenbrandt, 2012). Similar to the strolling of pedestrians at a crowded crossing (Moussaïd et al., 2009), the movement patterns of these aggregating animals also shape their large-scale spatial distribution and influence the organisms’ efficiency and fitness. An individual can
improve its survival chances by adopting a movement strategy that allows it to move more rapidly to its preferred location. For example, being able to reach a group faster decreases predation risk, as aggregations provide cover, increase vigilance and information spreading, and can create a dilution effect (Treherne & Foster, 1981; Krause, 1994; Parrish & Edelstein-Keshet, 1999). Similar to the fish schooling example, the more effective movement types become increasingly frequent in the population and promote the generation of self-organized patterns.

The ability to aggregate into a patterned population initially requires that organisms are capable of finding each other. In the simplest case, conspecifics are within reach or viewing distance, which allows individuals to move in a straight line to join a neighbor and the crowd (as most natural populations are patchily distributed). However, finding others is far more complicated when the individual does not have any information about their neighbors’ whereabouts. In this case, straight-line movement might not be efficient, since the individual may as well move in the wrong direction and miss the opportunity to turn and set another course. In this case, it might be advantageous to make random turns once in a while, allowing the individual to search in a closer range to its previous location. This arbitrary movement into random directions is what constitutes a random search strategy, where random steps and turning angles that are both drawn from particular frequency distributions can increase one's search efficiency when information about the environment is insufficient (Viswanathan et al., 2000).

The classic example of such random movement is the Brownian walk, where the steps between random turns are of approximately the same length. Oddly enough, the main theory on Brownian motion finds its origin in the movement of pollen grains under a microscope. When Robert Brown struggled to examine pollen seeds in a petri dish, he initiated his investigation of the movements that impeded his original research. He discovered that these pollen grains randomly move around, with move lengths drawn from an exponential frequency distribution (Brown, 1828). Later on, Albert Einstein recommenced research on Brownian motion and mathematically explained how colliding water particles actively changed the position of pollen grains. Using his study on Brownian motion, Einstein demonstrated that these collisions could describe the
diffusion of dissolved particles (Einstein, 1905; Langevin, 1908). Following the wide applicability of diffusion in physics, movement patterns resembling Brownian motion were detected in the movement trajectories of many animal species. As Brownian motion is presumed to be an adequate, simple model, it has become the default template for describing animal movement (Skellam, 1951; Turchin, 1998; Okubo & Levin, 2002).

Recently, another random movement strategy – the Lévy walk – has been frequently observed in nature (Shlesinger & Klafter, 1986; Viswanathan et al., 1996; Ramos-Fernandez et al., 2004; De Knegt et al., 2007; Sims et al., 2008). A Lévy walk is a scale-free movement strategy that encompasses a long-tailed step length distribution, i.e. large steps occur more frequently than expected from Brownian movement (Clauset et al., 2009). This movement strategy was named after Paul Pierre Lévy, a French mathematician who is famous for his discovery of the Lévy distribution (Mandelbrot, 1982). Lévy walks have been observed in myriad terrestrial and marine species, including ants, albatrosses, spider monkeys, goats, and marine predators (Shlesinger & Klafter, 1986; Viswanathan et al., 1996; Ramos-Fernandez et al., 2004; De Knegt et al., 2007; Sims et al., 2008).

Some random movement strategies exceed others in their effectiveness for finding resources, such as food, shelter, or mates; however, some may require greater intellect. Imagine searching for Easter eggs in a large field. When Easter eggs are scarce and difficult to find in the high grass, you must put effort into searching if you wish to indulge yourself with chocolate. There are a number of strategies you could follow. First, you could systematically search the field by browsing one row of grass after the other (Fig. 1.3A). Although this strategy will guarantee success, it does require that you remember exactly where you have been before and is therefore the most intellect-demanding strategy (Viswanathan et al., 2011). A second strategy would be to start off in one direction and switch to a local search when you encounter an egg (the Easter bunny is likely to drop eggs in clusters, as is often the case with food items; Fig. 1.3B; Benhamou, 2007). After not finding anything for some time, you again switch to straight line movement until the next egg is found. Because this strategy requires an active shift between two random search modes, it is quite complex (Reynolds, 2008). A third strategy looks
fairly complicated; yet is the simplest of all. You move in one random direction for some time, then turn in another random direction and make a couple of steps, and so on (Fig. 1.3C). The trick here is to pick your step lengths from a power law frequency distribution, which is a step length distribution with a heavy tail that ensures you to make many small steps that are occasionally alternated by very long moves (in other words, a Lévy walk; Viswanathan et al., 1999). The upside of this strategy is that you do not need to remember where you have been before, or how long it has been since you have encountered anything. However, for many ecologists, the strategy appears too simple (Benhamou, 2007; Jansen et al., 2012).

As all search strategies have benefits and downsides, which movement strategy is most efficient under particular circumstances is much debated (James et al., 2011; Jansen et al., 2012). Especially in the case where organisms are searching in heterogeneous, patchy environments where food, shelter, or mates are scarce, ecologists tend to be divided in two opposing parties (Benhamou, 2007; Reynolds, 2008; Jansen et al., 2012). Some ecologists consider Lévy walks to be most efficient and therefore most prominent in patchy environments (Viswanathan et al., 1999; Bartumeus et al., 2002; de Jager et al., 2011; de Jager et al., 2014). Theoretical studies on search efficiency demonstrate that Lévy movement outcompetes simple Brownian movement in heterogeneous, patchy environments (Viswanathan et al., 1996). Opposing this group are those who believe that organisms actively switch between two or more search modes using a Composite Brownian walk (Benhamou, 2007; Jansen et al., 2012). A Composite Brownian walk comprises multiple Brownian walks with different mean step lengths into one movement strategy. Observed movement patterns that deviate from simple Brownian motion are often treated as either being the consequence of an interaction between Brownian movement and ecological encounters (Hastings et al., 2005), or as multiple Brownian walks combined in a Composite Brownian walk (Benhamou, 2007; Jansen et al., 2012). Although composite Brownian walks were found to give a better representation of movement patterns observed in nature than simple Lévy walks (Jansen et al., 2012; De Jager et al., 2012b), switching between multiple movement modes adds an extra level of complexity to the behavior. Presently, the debate continues.
Figure 1.3: Three different methods to search for resources (such as Easter eggs). (A) Strategically browsing the area enables you to find all the Easter eggs; yet, it is also the most memory-demanding strategy. (B) Alternatively, one could switch between straight line movement until an egg is found and a local search at the site of the discovered egg. (C) A strategy that does not make use of your memory is to randomly draw step lengths from a certain step length frequency distribution. In between the steps, turns into random directions are made.
Optimizing one's random search strategy is not just a matter of finding the most efficient strategy to use in a certain environment, but also involves how this movement strategy in turn affects the environment. Whenever the environment affects an organism's behavior, the altered behavior can in turn influence that of others. Take for instance my example of the busy crossing. If one person moves a little to the left during his cross-over because he cannot move forward, others might have to adjust their walking direction to prevent a collision with this left-going individual. Certain movement strategies used by street-crossing pedestrians or other moving organisms can become less efficient due to the response of adjacent individuals on their crowded environment. Especially in self-organized systems, the movement of one individual affects the efficiency of the search strategy of others. As most of these interactions have not been considered in previous research, much remains unknown about the functioning of different movement strategies during self-organization. Furthermore, evolution of these movement strategies has been disregarded in earlier studies and, moreover, eco-evolutionary feedback with respect to movement strategies remains unstudied. Especially in self-organized ecosystems, the movement strategy used by individuals may have large implications for the development of the spatial population structure. As the emergent structure in turn affects the selection pressures for the individual organisms, evolutionary adaptation of movement behavior to self-generated conditions is expected to occur. In Chapter 2 of this thesis, I investigate how Lévy walk movement strategies can evolve from the feedback between mussel movement and self-organized mussel bed formation.

An active response to environmental cues is not necessary for a change in an organism's movement pattern. For example, an intended step can be prematurely stopped because the organism can go no further due to a physical obstruction. In natural systems, organisms can interact with one another by consuming resources, predaing each other, or simply encountering one another. These interactions can change an intended search strategy and generate a completely new movement pattern. A number of empirical studies have observed how the movement pattern of microzooplankton, goats, marine predators, and albatrosses changed from Lévy-like movement in resource-poor environments to Brownian motion in denser locations (Bartumeus et al., 2003; De Knegt et al., 2007;
Humphries et al., 2010; Humphries et al., 2012). When we recall how Einstein (1905) demonstrated that Brownian motion of dissolved particles was caused by collisions between these particles and water molecules, we can easily imagine that observed Brownian patterns in the movement of organisms might also be the result of ecological ‘collisions’. Until now, however, it is often hypothesized that the observed switch from Lévy-like to Brownian movement is an active response of an animal to changes in resource availability, because an active switch between Lévy and Brownian movement is assumed to increase the animal’s search efficiency. In Chapter 3 of my thesis, I experimentally demonstrate that observed Brownian movement patterns in dense mussel beds are the consequence of the interaction between an intrinsic Lévy walk and frequent collisions with neighboring conspecifics. I prove this principle with a simple argument and further show that actively switching between Lévy and Brownian motion does not improve one’s ability to locate resources.

To settle the debate on whether organisms are using a Lévy walk or a Composite Brownian walk, I have been exploring ways to distinguish between these two movement strategies. I figured that environmental cues, such as the presence of food or other resources, might trigger the switch from one movement mode to another in a Composite Brownian walk. As resources are often patchily distributed, an efficient Composite Brownian walk would consist of a local search in the presence of resources and a straight-line leap between food patches. Lévy walks are not controlled by switches induced by environmental cues but are always fully random, despite the presence or absence of resources. Hence, one can imagine that with Lévy-like movement patterns, clusters of small steps are not only found near food patches but also in free space. In contrast, clusters of steps should be associated with resource distributions in Composite Brownian walks. We use this idea to investigate whether mud snails (Hydrobia ulvae) are making use of Lévy-like movement or a Composite Brownian walk, by examining clusters of steps on and off food patches in Chapter 4 of this thesis.

Patterns of Cooperation

A crucial component of many forms of self-organization in ecosystems is local positive feedback, which is often generated by facilitative or cooperative
interactions between organisms. Moving into a self-organized pattern would be pointless if aggregation did not help you in any way. For instance, if mussels are not attached to their neighbors within the pattern, they risk becoming dislodged by wave action or predation (Hunt & Scheibling, 2001; Zardi et al., 2006). Hence, creating a pattern without profiting from some sort of cooperation that the pattern offers is not advantageous. Both cooperation, where one individual helps another at its own expense, and facilitation, where the benefit to others is an accidental byproduct, aid in ameliorating the environment locally. In numerous species, cooperation between individuals is a common process; yet, understanding how cooperation has evolved remains a major challenge. For instance, I have seen young elephants helping one another by giving a little push on a climb up a steep slope, leaving the assisting youngster vulnerable on the dry river bed. Why did this elephant help the other? Assisting another might come at a great cost, and it remains uncertain whether the other will do anything in return. Evolutionarily speaking, cooperation can only evolve when cooperating individuals gain a fitness advantage over uncooperative conspecifics; therefore, cooperators should in the end benefit from their own generosity.

There is a Dutch saying that comes to mind when thinking of cooperation in spatially heterogeneous systems: ‘better to have a good neighbor than a far friend’. This saying is quite true; since you will interact more frequently with those nearby than with distant individuals. Regularly cooperating with ‘good neighbors’ will be more profitable than the rare cooperation with a faraway friend. Without spatial segregation of cooperative interactions, everyone will randomly interact with each other, and this has been shown to result in the demise of cooperation in the first models of evolutionary game theory (Maynard-Smith, 1982; Axelrod, 1984). However, when individuals are placed within a spatial structure, cooperate only with close neighbors, and locally disperse their offspring, cooperation is able to evolve (Nowak & May, 1992; Skyrms & Pemantle, 2000; Ishibuchi & Namikawa, 2005; Kun et al., 2006; Langer et al., 2008; Szamado et al., 2008). In these models of cooperation, staying close to related individuals increases ones chance that its relatives will assist it, provided that cooperation has a genetic basis. Furthermore, helping family members indirectly benefits an individual’s fitness, as they share some of that individual’s genes (Hamilton, 1963). This inclusive fitness concept is
habitually regarded as an essential and sufficient explanation for the evolution of cooperation.

Until now, research on the evolution of cooperation in spatially complex populations has overlooked at least two issues. First, many cooperative species disperse over a wide range and are therefore not interacting more frequently with relatives than with unrelated conspecifics. For example, various marine invertebrates that later in life interact with sessile neighbors have a suspended larval stage – where they can drift over large distances – before settling on a surface (Godfrey & Kerr, 2009). In most studies, the positive effect of spatial structure on the evolution of cooperation is attributable to the increased chance of cooperating with relatives; how this process works in populations with wide-ranging dispersal remains elusive. In Chapter 5 of this thesis, I investigate the effect of spatial patterning on the evolution of between-mussel attachment in self-organized mussel beds, where mussels settle down in regular spatial patterns after being suspended during their larval stage.

The second neglected issue is that spatial structure can itself result from cooperation between organisms. For example, without the between-mussel cooperation of attaching byssus threads to neighbors, spatial patterns in mussel beds have little chance to persist. Moreover, the spatial structure that is generated by organisms and their interactions can lead to the formation of groups. When the ability to achieve a collective goal differs between these groups, group-level selection can occur (Van Boven & Weissing, 1999; Traulson & Nowak, 2006; Thompson 2000; Kohn, 2008; Burton et al., 2012; Molleman et al., 2013). For instance, picture a group of people in a rowing boat. To get across the sea and safely to land, one needs to cooperate with boat members. Whether the boat will return safely from the voyage depends on the paddling efforts of everyone on board. Hence, a group-level survival process is taking place; either everyone will return or nobody at all. At the same time, individual-level fitness differences between the boat members can arise when some people are putting more effort in rowing than others. Someone who rows too enthusiastically might die of a heart attack and thereby is eliminated by an individual-level selection process. By contrast, groups of lazy boatmen that all perish from hunger and thirst are killed
by a group-level selection process. When taken together, the group-level and individual-level processes will combine as multilevel selection (Wilson & Sober, 1994; Sober & Wilson, 1998; Thompson, 2000; Okasha, 2006; Wilson & Wilson, 2007; West et al., 2008), where an individual’s fitness depends on the paddling skills and efforts of the group and on that individual’s own investment in rowing the boat. Hence, with the emergence of self-organized structures from the actions of and interactions between individuals, an additional level of selection may arise next to simple individual-level selection.

Self-organized ecosystems are likely to be influenced by multilevel selection. The additional level of selection that emerges from self-organization can create a feedback between pattern formation and the evolution of self-organizing traits. Yet, how multilevel selection affects the evolution of cooperation and thereby influences spatial pattern formation in self-organized ecosystems remains unknown. In Chapter 6 of this thesis, I investigate the effect of multilevel selection on the joint evolution of aggregative movement and between-mussel cooperation in self-organized mussel beds. Subsequently, I examine how the feedback between multilevel selection and mussel bed formation will influence the development of spatial patterns in mussel populations.

The conclusions drawn from the studies considered in Chapters 2 to 6 are summarized in the General Discussion. In this final chapter, I discuss how the results of my research on animal movement, between-mussel cooperation, eco-evolutionary processes, and emergent spatial complexity can change our perspective on self-organized ecosystems. Specifically, I highlight the importance of investigating eco-evolutionary feedbacks within these systems, which is necessary for drawing reliable conclusions from models as well as from observations of natural processes.