The emergent properties of spatial self-organization
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Theoretical studies highlight that the presence of self-organized spatial patterns can have important emergent effects on the functioning of ecosystems. For instance, spatial patterns in arid systems, in the form of regular striped patterns, are predicted to increase the water harvesting capacity of the vegetation, and thereby increase primary productivity (Pringle et al., 2010). Similar emergent properties have been advanced for patterned ecosystems such as for example peat lands, mussel beds, and intertidal mudflats. Yet, most of these studies present models based on presumed pattern-forming processes and study the effects of these processes on the functioning of ecosystems under idealized conditions (Rietkerk and Van de Koppel, 2008, for review). Moreover, only a limited palette of possible mechanisms is often considered, and the possibility of alternative mechanisms leading to similar spatial patterns is often neglected. However, although alternative mechanism may lead to very similar spatial patterns, they nevertheless may affect ecosystem functioning in a completely different way. This emphasizes the need for a carefull consideration of the processes behind spatial pattern formation in ecosystem.

An essential prediction of many self-organizing models is that the patterns make ecosystems more stable and robust to disturbances (Sole and Bascompte, 2006; van de Koppel et al., 2005). On the other hand, self-organized ecosystems may lose their current state when a critical tipping point is surpassed (Rietkerk et al., 2004). This emphasizes the need to fully understand the dynamical behaviour of self-organized systems, and in particular how they respond to changing conditions. How ecosystems are
self-organized and how much complexity can arise from local interactions are two central questions in this thesis, which are addressed to unravel the self-organization phenomenon and to predict how it affects ecosystem functioning.

In this thesis, I have studied alternative mechanisms explaining self-organization pattern formation in mussel beds, and addressed how these mechanisms affect mussel bed functioning. Existing understanding of spatial self-organization in ecosystems is for a large part based on Turing’s activator-inhibitor principle (Turing, 1952), which affects demographic process of population growth and mortality. However, this principle falls short, for instance, in explaining pattern formation observed to occur at the scale of individual mussels, where activator-inhibitor processes are not apparent. Using mussel bed ecosystems, I have studied a new mechanism—phase separation—to explain small-scale self-organization in mussels, a mechanism that is unrecognised so-far in ecology. Secondly, as self-organized mussel beds display two scales of pattern formation, one governed by demographic processes and the other by behavioural processes, I have studied how these two processes interact to shape the functioning of mussel beds in terms of its productivity and resilience to disturbances. Below, I give a detailed account of my findings, and discuss how, in general terms, they affect our current understanding of spatial self-organization in ecological systems.

**Alternative mechanisms of pattern formation**

Although studies have advanced our understanding of the mechanisms behind self-organized patterns in natural ecosystems, little evidence has been reported that considers the validity of the proposed mechanisms and the validity of possible alternative mechanisms, in explaining spatial patterns in a same ecosystem. In chapter 2, I examine the effect of two potential ecological mechanisms for pattern formation in mussel beds, and address how these two mechanisms affect ecosystem functioning, in terms of productivity and ecological resilience. For both mechanisms, field evidence can be found in the literature in support of them. The first mechanism involves a reduced mussel loss rate at high density owing to mutual protection between the mussels, which is based on a previous model proposed by van de Koppel (van de Koppel et al., 2005). The
second mechanism is based on novel experimental evidence, indicating that mussels feed more efficiently on top of hummocks. Both are able to explain the observed patterns, but they nevertheless lead to different effects on ecosystem functioning. Hence, I argue that we should carefully consider the predicted implications and emergent properties of spatial self-organization when the mechanisms underlying self-organization are not completely understood and not based on experimental study.

The models worked out in chapter 2 describe that two possible interactions could in principle account for mussel bed formation, but our conclusions can be easily extended to a more general context. Similarly, alternative mechanisms have been proposed for a wide range of ecosystems. For patterned arid ecosystems, both root competition and surface water flow potentially explain pattern formation, while this has not been tested in the field experiments (Klausmeier, 1999; Rietkerk et al., 2002). In a similar way, a number of alternative mechanisms have recently been proposed to explain patterning in peatlands (Eppinga, 2009; Eppinga et al., 2009). In ecology, it is often difficult to obtain conclusive experimental evidence for the (relative) contribution of specific processes involved in self-organization patterns.

To provide in-depth understanding of the causality of the emergent properties of self-organized systems, it is interesting to examine the different ecological processes that can generate activator-inhibitor dynamics. The activator-inhibitor principle is based on the universal interaction between a substance (activator) that promotes its own production and that diffuses on a short range, and a rapidly diffusing antagonist (inhibitor) that depresses the effect of the promoter over a longer range. Yet, there are several different types of interactions that can lead to pattern activator-inhibitor-like interactions in biology and ecological systems (Meinhardt et al., 2003). The first potential mechanism for pattern formation is the activator-depleted substrate process, where depletion of a substrate acts as the inhibiting process, such as for example in semi-arid regions, where depletion of (surface) water acts as an inhibitor to vegetation growth, as proposed by Klausmeier in 1999 (Klausmeier, 1999). A second alternative mechanism for pattern formations is inhibition via a process that destroys the activator, where the inhibitor may slow down or locally remove the activator from the system. Future studies on pattern formation in ecosystems should consider these possible alternative configurations of activating and
inhibiting processes when modelling spatial self-organization.

**Phase separation**

When explaining the formation of regular patterns in ecology, ecological theory generally points at Turing’s activator-inhibitor principle, where the interplay between an activator and an inhibitor causes spatial variation in the net growth or reaction of the involved species (Turing, 1952; Klausmeier, 1999; Rietkerk et al., 2002). As mentioned in chapter 1, this principle is based on population level mechanisms such as birth, or death processes, from hereon referred to as demographic processes. In contrast, recent experimental evidence indicates that movement may be an important process causing self-organization pattern formation, in particular at short time scale (van de Koppel et al., 2008; de Jager et al., 2011; Viswanathan et al., 2011; Folmer et al., 2012). In chapter 3, building on data from laboratory experiments, I have derived a model to demonstrate that this movement-driven pattern formation in mussel beds is mathematically equivalent to the Cahn-Hilliard model (Cahn and Hilliard, 1958) for phase separation in physics (Emmerich, 2008; Bray, 2002). Although the long-term development of the patterns was found to deviate from the standard prediction of the Cahn-Hilliard model, our experimental data was well consistent with theoretical predictions during the early stages of pattern formation.

The phase separation mechanism is different from the activator-inhibitor principle in two important aspects. Firstly, there are no activator and inhibitor species in the model because there is only one involved species. Second, this new mechanism is based on density-dependence of movement rather than growth and mortality processes (i.e., demographic processes). My work suggests that a broader array of possible processes should be considered in explaining spatial self-organization in ecosystems, where both mobility behavior and demographic processes may occur simultaneously. An in-depth discussion on the evidence, within ecology, for both the phase separation and the classical activator-inhibitor principles is presented in chapter 6, where I describe a broader survey of self-organization patterns arising from density-dependent movement speed or probability, and distinguished their differences.
Application of the phase separation principle in other ecological systems

Current understanding of ecological dispersal advances that movement or diffusion leads to dissipation rather than aggregation of species, where the diffusive flux is proportional to the gradient of density or concentration (Groot and Mazur, 1962)). This concept of diffusion is widely used in biology and ecology. Our experiments in mussels, however, demonstrate that density-dependent movement may also cause aggregation, leading to the formation of patterns. This phenomenon does not only occur in mussels, but also explains the aggregative behavior of ants (Camazine et al., 2003; Theraulaz et al., 2002), bacteria (Cates et al., 2010; Fu et al., 2012) and fish schools (Anderson et al., 2012), as I discuss in chapter 6. A central question is how to generalize density-dependent movement behavior in ecological systems? So far, evidence linking to this topic is scarce (Theraulaz et al., 2002). Most recently, a lab experiment suggests that aggregative movement behavior may be attributed to social interactions, aimed to reduce predation risk (Ioannou et al., 2012), where chances of predation are strikingly lower when the prey use collective motion. Further studies are needed to reveal the universality of my results that movement not only leads to dissipation but can also explain pattern formation in ecosystems.

Interestingly, a recent study shows that the spatial distributions of flocking foragers depend on the balance of conspecific interference and attraction (Folmer et al., 2012; Folmer, 2012), where flocking patterns arise from local interactions. This observation suggests that the phase separation principle may apply to a wide range of contexts, for instance explaining the spatial distribution of foraging animals. Density-dependent movement plays a pivotal role in explaining spatial organization in biology, from the scale of cells to entire organisms (Fu et al., 2012; Bitume et al., 2013). For instance, in animal populations, ordered flocks and shoals emerge via individuals altering their movement with respect to their neighbors.

Multiple-scale patterns in ecology

Most studies that investigate the formation of self-organized spatial patterns focus on purely demographic processes (Hassell et al., 1991; Klausmeier, 1999; Pascual and Guichard, 2005; van de Koppel et al., 2005; Eppinga
et al., 2009; van der Heide et al., 2010b; Dakos et al., 2011) or purely behavioral processes (Couzin et al., 2002; Theraulaz et al., 2002; van de Koppel et al., 2008; Cavagna et al., 2010; Sumpter, 2010; Vicsek and Zafeiris, 2012). However, in real natural ecosystems, spatial complexity commonly involves the interplay of behavior, population dynamics and ecosystem processes at various spatial scales. Interactions between multiple self-organization processes have mostly been neglected in both theoretical and experimental studies.

Recently, patterns occurring at two distinctly different spatial scales have been reported in mussel beds by van de Koppel et al (van de Koppel et al., 2008, 2005). They found two distinct different spatial patterns resulting from different ecological mechanism. Here, small-scale net-shaped patterns originate from behavioral processes, while larger-scale pattern result from demographic processes (see chapter 2 and Figure 7.1). Hence, a novel type of self-organized spatial pattern, here called a nested pattern, is created by combining behavioral and ecological processes. This kind of complex nested pattern was observed, beyond mussel beds, also in seagrass ecosystems and coral reefs. How this spatially complex interplay between animal behavior and ecological processes affects ecosystem functioning is badly unknown.

Figure 7.1: The conceptual model integrates both mussel behavior (clump formation), and competitive and facilitative interactions (band formation).
One of the big challenges for ecological theory is to understand how complexity affects the functioning of ecological systems. In chapter 4, I integrated mussel behavior and demographic processes into a single model of self-organization in mussel beds. The model results suggest that combining behavioral with demographic self-organization dramatically increased both the rate of pattern development and the resilience of the system to disturbance. This implies that restoration schemes that take into account both behavioral and demographic processes of self-organization will likely be more successful than the ones that focus on a single spatial scale. Hence, combining multiple mechanisms of self-organization in mathematical models may not only provide insight in the processes underlying spatial complexity, but can also help to restore these often very valuable ecosystems.

Heterogeneity and the emergent properties of patterns

Theoretical models highlight two important emergent effects of pattern formation on ecosystem functioning (Rietkerk et al., 2004; van de Koppel et al., 2005). On the one hand, by optimizing facilitative (activating) interactions between organisms, patterns improve productivity, and allow organisms to survive under conditions that are otherwise too inhospitable for growth or survival. On the other hand, it makes the system vulnerable to dramatic changes once these facilitative interactions are overwhelmed. When conditions degrade below a so-called tipping point, the system may switch to an alternative, degraded state, from which it is difficult to recover. Hence, despite of its positive effect on production, self-organization can lead to non-linear dynamics in the face of changing conditions.

Most models on self-organized pattern formation presume idealized homogeneous conditions, where for instance the initial distribution and influx of resource are the same over the entire simulated domain. However, these conditions are rarely met in real ecosystems, especially at large spatial scales. For instance, rainfall, temperature and nutrition in the soil can vary because of landscape features. The effects of large-scale spatial heterogeneities in background conditions have for the most, not been studied in theoretical models and field examinations. Yet, field observations suggests that most mussel beds on intertidal flats exhibit remarkable gradients in the properties of the patterns. In chapter 5, I present
a model that considers the effects of more realistic environmental settings where tidal waters enter the tidal flat from the seaward side. This causes depletion of the algae in the water, leading to heterogeneity in the properties of the spatial patterns, similar to what was observed on real mussel beds.

Of course, it is natural to ask what the effects are of this self-induced spatial heterogeneity on functioning of mussel bed ecosystems, and specifically on the emergent properties of pattern formation. Our results suggest that large-scale spatial heterogeneity will strikingly alter ecosystem dynamics. Specially, heterogeneity can eliminate the possibility of alternative states and the tipping behavior it can cause, and no increase of productivity is predicted to emerge as a consequence of spatial self-organization, when a self-organizing model is compared to models where the self-organization process has been blocked. These results put in question the emergent properties predicted to result from spatial self-organization, specifically for mussel beds. Whether these conclusion are also valid for other patterned ecosystem remains an urgent question for the field of spatial self-organization.

Concluding remark

Spatial complexity is one of the last frontiers of ecological theory. Many populations and ecosystems exhibit a complex spatial structure, much of which is generated by interactions between the organisms themselves in a process called spatial self-organization. This thesis has highlighted how various mechanisms of self-organization, involving animal behavior, demographics, and habitat modification, act and interact to determine the shape and functioning of an ecological system. In many ecosystems, spatial self-organized complexity has in the past century been constrained and degraded by human interference. Our analysis suggests that complexity occurring at multiple organizational levels (or spatial scales) is an important determinant of the resilience of ecosystems. Moreover, human-induced reduction of spatial complexity might be an important cause for the prevalence of tipping points in many current ecosystems. Can spatial patterns be used as a template for the restoration of populations that have collapsed as a consequence of human interference? This important question remains to be answered in the future.