

REVIEW

The influence of local- and landscape-scale processes on spatial self-organization in estuarine ecosystems

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Summary

Complexity theory proposes that spatial self-organization, the process whereby small-scale, localized interactions among the components of a system generate complex spatial structures at large spatial scales, explains the formation of autogenic spatial patterns in ecosystems. We question this premise by reviewing three estuarine ecosystems – mussel beds, mudflats and salt marshes – where self-organization has been put forward to explain spatial patterns. Our review highlights that these self-organized estuarine systems are shaped by the combination of small-scale interactions between ecological and physical processes on the one hand, and large-scale physical forcing on the other. More specifically, local interactions generate patchiness at small spatial scales, whereas landscape forcing determines the shape and orientation of these patches in the landscape. We present a framework that illustrates how self-organized ecosystems are shaped by interactions between organisms and physical processes occurring at multiple spatial scales. Moreover, the present review of estuarine systems underlines that scale-dependent feedbacks are capable of explaining spatial patterns that are much more complex than the regular patterns to which they have been applied so far.

Key words: mudflat, mussel bed, salt marsh, self-organization, spatial pattern.

Introduction

Many estuarine ecosystems are characterized by striking spatial patterns. From the air, mussel beds can reveal stunning banded patterns that remain regular over an extensive spatial range (Fig. 1A). In mudflats, diatoms can generate patchy landscapes of elevated hummocks covered by dense diatom biofilms (Fig. 1B). Salt marshes reveal fractal-like creek structures along which vegetation patterns are aligned (Fig. 1C). Recent research has suggested that organisms within these spatial patterns do not simply follow landscape features, but that an intricate interaction between ecological and physical processes is a central explanation for the observed landscape complexity (Klausmeier, 1999; Van de Koppel et al., 2005; Temmerman et al., 2007; Weerman et al., 2010). Similar spatial patterns have been observed all over the world, in systems ranging from arid bush lands to boreal peat lands (Rietkerk and Van de Koppel, 2008).

Complexity theory proposes that small-scale, localized interactions between components of a system can generate spatial patterns at larger spatial scales through a process called spatial self-organization, even in the absence of external, landscape-scale forcing (Levin, 1998). So what characterizes these ‘local’ interactions? In estuarine systems, organisms experience the direct and indirect effects of the tidal water. Whereas water motion from currents and waves is an important supply of resources such as, for example, food and oxygen, it also imposes a force that can dislodge organisms. Especially wave action during storm events can impose a strong disturbing force. Many organisms have special adaptations or strategies to cope with these mechanical forces. Salt marsh plants form dense clumps in which the effects of water flow are diverted. Mussels form mats by binding to each other using byssus threads,

preventing dislodgement by waves and water flow (Waite and Broomell, 2012). Other organisms dig into the sediment, only to come out when the tidal flow has subsided. These adaptations invoke a wide range of ecological, physical and biomechanical interactions, which can have a profound influence on how estuarine communities are organized. Many communities are characterized by strong aggregation of the organisms, as is found in mussel beds, oyster beds, diatom biofilms and salt marshes. The spatial structure of these intertidal communities was found to be determined by the interplay of positive and negative interactions within the system (Gascoigne et al., 2005; Van de Koppel et al., 2005; Van de Koppel et al., 2008; Weerman et al., 2010). A reoccurring feature is that intraspecific positive interactions act on a local scale: organisms can resist mechanical forces by clumping directly to neighbouring individuals, which for instance protects against wave action or stimulates sedimentation. Negative interactions, however, such as competition for algae, predominate at a somewhat larger spatial scale. The resultant of these interactions at different scales is that positive interactions predominate at short distances from any individual, whereas negative interactions mainly occur at larger distances. This scale-dependent interplay between positive and negative interactions has been found to explain the formation of spatial complexity in estuarine systems such as mussel beds and mudflats, but occurs similarly in other patterned ecosystems all over the world (Rietkerk and Van de Koppel, 2008).

We question the premise of complexity theory that self-organized spatial patterns are primarily shaped by local interactions at scales below that of the observed spatial patterns. Results from a number of spatially self-organized systems lead us to propose that the shape of many self-organized spatial patterns is often determined by a

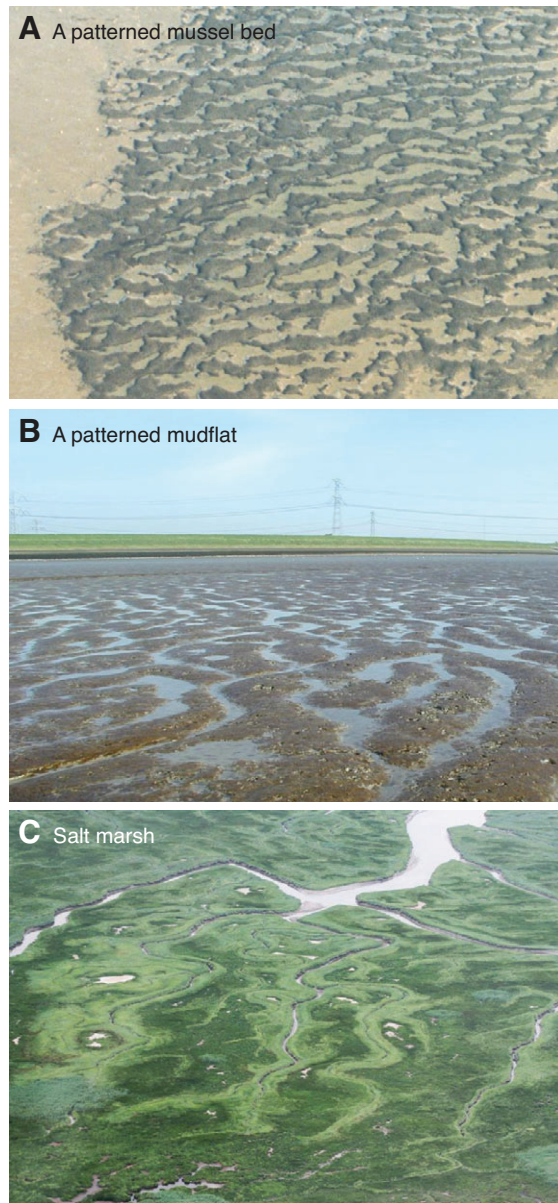


Fig. 1. Self-organized spatial patterns as observed in estuarine ecosystems. (A) Representation of a banded mussel bed, of scale approximately 100 m across (Van de Koppel et al., 2005). (B) A regular spatial pattern on the Kapellebank mudflat in the Westerschelde, The Netherlands (Weerman et al., 2010). (C) Creek patterns in a salt marsh in the drowned land of Saeftinghe, The Netherlands. Source: Chiel Jacobusse, Het Zeeuwse Landschap.

combination of local interactions and large-scale physical forcing. We therefore hypothesize that small-scale interactions between organisms and physical processes can break the symmetry of an ecosystem to initiate pattern, in terms of a concentration or aggregation of individuals in clusters of a particular scale. How these feedbacks scale up to determine ecosystem structure and functioning is determined by the physical constraints on organism–environment feedback set by the landscape. Hence, our hypothesis implies that both local and landscape-level processes shape self-organized spatial patterns in ecosystems.

Here, we review three estuarine ecosystems that illustrate how physical constraints at large spatial scales determine the spatial complexity of an estuarine ecosystem. First, we use mussel beds to

show how the physical setting shapes spatial patterns that basically originate from an ecological interaction. Second, we discuss a diatom-covered mudflat ecosystem where interactions between the physical process of water drainage and increased sedimentation by benthic diatoms generate a regular physical landscape. Finally, we discuss how a scale- and density-dependent feedback induced by salt marsh vegetation interacts with the physical settings to generate a complex salt marsh landscape. Our examples demonstrate that, despite their complexity, estuarine habitats are shaped by simple interactions between biology and physics operating at both local and landscape scales.

Mussel beds

Mussel beds on soft sediment often have a patchy appearance, where dense aggregations of mussels alternate with nearly bare sediment (Snover and Commito, 1998; Gascoigne et al., 2005). When viewed from the air, the seemingly haphazard patchiness reveals itself as being strikingly patterned: elongated mussel patches are aligned in a regular fashion perpendicularly to the incoming flood direction. In particular in young mussel beds that have not gone through their first winter, regular patterning is strong and consistent over extensive ranges. Older mussel beds can have a more fractal appearance, likely owing to the disturbing effects of strong wave action due to storms.

Can we explain the formation of regular patterns in mussel beds from the ecology of mussels? Mussels are filter feeders that occur on concentrated beds in a wide range of temperate intertidal systems. Mussels aggregate to form tight mats in which they bind themselves together using byssus threads. In these mats, they are better protected against predation and wave dislodgement (Bertness and Grosholz, 1985; Hunt and Scheibling, 2001; Hunt and Scheibling, 2002), generating a direct positive interaction between neighbouring mussels through byssus connection. Being filter feeders, however, mussels also interact by depleting the algae in the lower water layers (Bertness and Grosholz, 1985; Newell, 1990; Svane and Ompi, 1993), which can generate strong competition for food. Competition can act at large spatial scales as the water flows over the mussel bed. Models have shown that this interplay between facilitation through byssus connections on a small spatial scale and competition for algae at a larger spatial scale generates spatial self-organization within mussel beds that can explain the observed regular spatial patterns in mussel beds (Van de Koppel et al., 2005).

The above-described approach views pattern formation between mussels as being to a large extent an ecological process. However, comparison of mussel beds in different tidal conditions reveals the effects of the large-scale physical setting in which a mussel bed can be found. If water flow is minimal, as is for instance the case in the limfjorden in Denmark, no consistent patterning is found at scales above 1 m (Ysebaert et al., 2009). By contrast, in intertidal areas with strong tidal currents, mussel beds typically form banded patterns. Integral to these banded patterns are the physical constraints set by the flow rate causing the banded patterns to be aligned perpendicularly to the flood direction, as the incoming floods carry most of the algae. Hence, the spatial pattern in mussel beds results from the interplay of small-scale ecological feedbacks and the physical constraints imposed by tidal flow, which in turn is determined to a large extent by the topography of the intertidal landscape.

Mudflat ecosystems

A close interaction between biology, hydrodynamics and geomorphology generating a spatially patterned landscape is found

in patterned, diatom-covered mudflat ecosystems. On intertidal mudflats, spatial patterns can develop in the form of diatom-covered hummocks alternating with water-filled hollows where diatom density is much lower. Diatoms can form thick biofilms through the excretion of extracellular polymeric substances (EPSs), which form a smooth film on top of the sediment, trapping fine-grained sediment particles and preventing them from being eroded by the shear stress imposed by the tidal currents. As a result, sediment accumulates underneath these biofilms, generating proto-hummocks on which thick biofilms can persist. However, this results in water diverting away from these hummocks and accumulating in the hollows, which face increasing water levels as they receive the drainage water remaining on the tidal flat after the tides have receded (Fig. 2). In this remaining water layer, EPSs dissolve, reducing the integrity of the biofilm, and making the sediment more vulnerable to erosion. As a consequence of this interplay between diatom biofilm growth, sediment accumulation and erosion, and water drainage, a regular landscape of hummocks develops interspersed with gullies that form a drainage network. Hence, also in this mudflat, the interplay between ecological and physical processes can explain self-organized patterns (Weerman et al., 2010).

Although local diatom–sedimentation feedbacks form the central mechanisms behind the observed patterns, the spatial characteristics of this hummock-and-hollow landscape are set by the physical constraints determined by the landscape. If the tidal flat covers a large area and is very flat, water flow can be very high once the system submerges, and near-linear patterns of ridges and runnels emerge parallel to the flow direction, as is observed in the Marenne-Oléron tidal flats in France (Laima et al., 1999) or the Humber estuary in England (Blanchard et al., 2000). When flow rates are much reduced, more roundish patterns become prominent, as was described in the Kapellebank tidal flat in the Westerschelde, The Netherlands (Weerman et al., 2010). Again, although at their

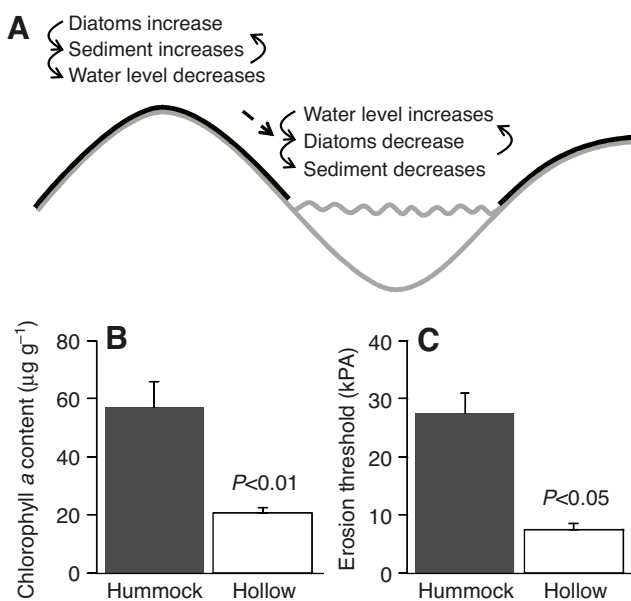


Fig. 2. (A) Schematic representation of how the interaction between diatom growth, sediment accumulation and water diversion generate a positive feedback that can explain the formation of regularly spaced patches covered by a diatom biofilm. (B) The difference in the diatom densities, as reflected by the density of chlorophyll, and (C) the difference in erosion threshold, between hummocks (modified from Weerman et al., 2010).

heart the mudflat patterns are generated by a feedback that involves organisms, physical constraints imposed by the landscape determine their final shape.

Salt marsh ecosystems

Among the most striking spatially patterned ecosystems found in estuaries are salt marshes. Salt marshes are shaped by drainage creeks that form feather-shaped networks removing the tidal water from the marsh during ebb periods. At the banks of the creeks, increased sedimentation of sandy particles causes the formation of elevated levees. The elevated marsh platform that forms owing to increased sedimentation in between the creeks hence gets bounded by levees, forming a basin. As a consequence, the areas in between these levees drain less efficiently, generating a landscape with clear variation in waterlogging of the soil (Allen, 2000). Hence, in salt marshes, variation in elevation and water logging are the main drivers of salt marsh vegetation patterns, which can persist for extended periods of time (Bertness, 1999; Allen, 2000).

At first glance, the vegetation can appear to follow just the variation in landscape properties. A typical property of salt marshes, however, is that the landscape itself is mostly biogenic – for example, the formation of salt marsh geomorphology is largely the result of a close interaction between biology, hydrodynamics and geomorphology (Allen, 2000). Salt marsh vegetation attenuates both wave energy and water flow, which in turn prevents erosion and stimulates the settlement of fine-grained sediment. As a consequence, salt marshes typically increase in elevation during their development and can accumulate extensive amounts of sediment (Kirwan et al., 2010). This results in a decrease of the influence of tidal flow and of salt water, and as a consequence the marsh becomes more benign to plant growth (Allen, 2000).

Sediment accumulation on salt marshes does not occur homogeneously over space. Initially, sediment-stabilizing plants such as *Spartina anglica* or *Puccinellia maritima* establish in isolated patches, which develop dome-shaped hummocks over time owing to increased sedimentation. Water flow gets diverted around these hummocks, where water flow rates increase, generating increased erosion, especially in high-energy environments (Fig. 3A) (Bouma et al., 2007). Divergence of water flow around expanding vegetation patches finally results in the formation of creek networks as the patchy salt marsh pioneer zone develops into a mature marsh (Fig. 4) (Temmerman et al., 2007). Hence, similar to mussel beds and diatom-covered mudflats, the interaction between plant growth, hydrodynamics and geomorphology that underlies salt marsh formation is scale dependent, changing in nature from increased sedimentation within vegetation tussocks to increased erosion at some distance.

An important question is why salt marshes reveal a much more complex spatial structure compared with other estuarine systems, despite the underlying interaction between plants and sedimentation being a similar scale-dependent feedback as that found in mussel beds and mudflats. First, the feedback processes that characterize plant–sediment interactions are strongly density dependent (Fig. 3B,C). In low-density tussocks, plant density is insufficient to divert the water flow, and hence no positive feedback develops locally, and the trembling of individual shoots in the flow might even cause increased erosion and plant dislodgement (Bouma et al., 2009). Hence, at very low density, feedbacks are predominantly negative. As density increases, the flow rate of the water is reduced as water flow is diverted laterally or over the vegetation, increasing sedimentation (Bouma et al., 2009). This effect introduces threshold dynamics, where salt marsh plants have

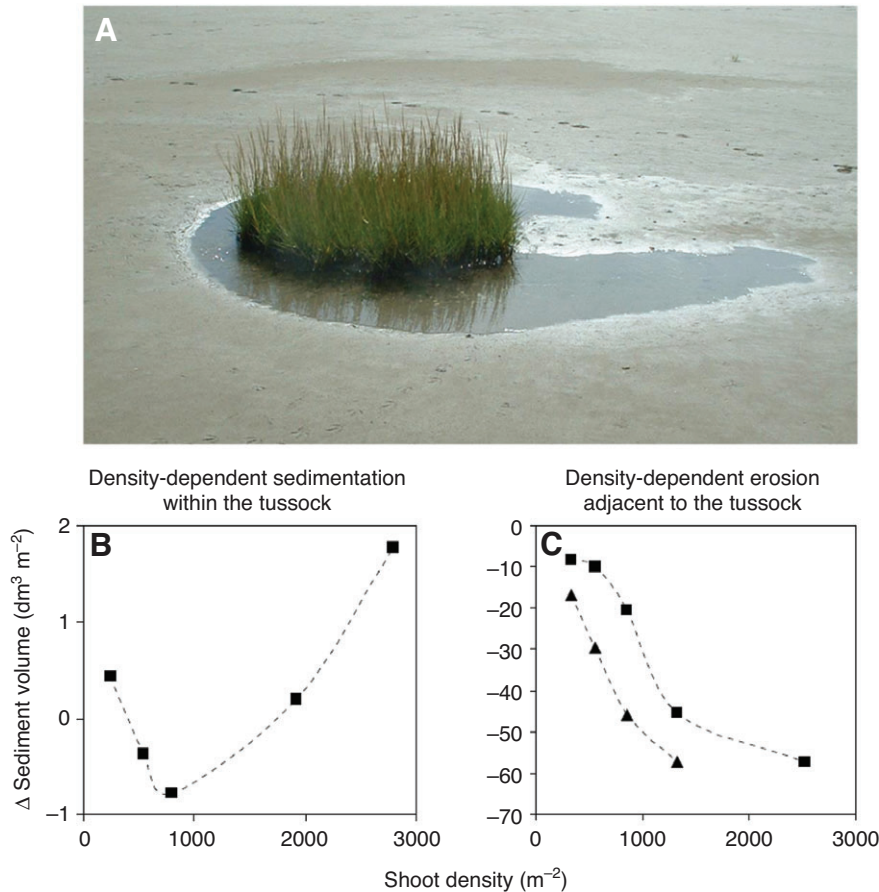


Fig. 3. (A) A single tussock of *Spartina alterniflora* demonstrates that the interaction between *Spartina* and sedimentation is both scale and density dependent. (B) Density-dependent sedimentation within the tussock. Graph showing the relationship between the local density and net sedimentation within a tussock of *Spartina*, revealing a clear density dependence. (C) Density-dependent erosion adjacent to the tussock. Graph showing the relationship between the intra-tussock density of shoots and erosion next to the tussock (modified from Bouma et al., 2009).

difficulty establishing, whereas clumps of marsh plants can persist and expand (Van Wesenbeeck et al., 2008). As a consequence, salt marsh pioneer zones are characterized by extensive patchworks, which slowly expand at their edges and can easily take decades to develop into semi-closed vegetation. Second, estuarine marshes are bounded primarily by terrestrial environments, with less than 30% of marsh boundaries bounded by open water. This has important implications for the spatial structure of salt marshes. When not bounded by coastline, marshes develop a semi-regular spacing of creeks alternating with dense vegetation (Temmerman et al., 2007). Hence, under these conditions, salt marshes conform to the regularity that is predicted by models with a scale-dependent interaction of positive and negative feedback. When salt marshes are enclosed by coastline, models of marshes predict more complex feather-shaped drainage canals, or fractal shapes if erosion is a dominant process (D'Alpaos et al., 2007; Kirwan and Murray, 2007). This suggests that the complexity that salt marsh ecosystems can exhibit results not so much from the underlying complexity in governing processes but from a simple interaction between vegetation and morphological processes put into a physically constraining landscape setting.

Scaling up local interactions between organisms and the physical world

A central premise in spatial ecology is that small-scale interactions explain patterns that occur at broad spatial scales, in a process called spatial self-organization (Levin, 1992; Wootton, 2001). This premise has been applied to a wide range of self-organized ecosystems, such as patterned arid bush lands, boreal peat lands and seagrass beds (Rietkerk and Van de Koppel, 2008). In this paper,

we argue that, to explain the patterns observed in self-organized ecosystems, processes occurring at small spatial scales as well as those occurring at the landscape scale need to be considered (Fig. 5). Small-scale processes occurring at the individual level are crucial in explaining the formation of aggregations of animals or patches of vegetation. These processes cause small inhomogeneities in the distribution of organisms to increase and develop into clear aggregations, clusters or patches (a symmetry-breaking instability in mathematical terms). The combined studies reviewed in this paper demonstrate, however, that subsequently landscape-level features such as the strength and direction of the tidal water flow or the slope of the underlying landscape shape these patterns and determine the patterns as we see them – as being dotted or banded, regular or fractal shaped. Landscape-scale processes thereby shape and constrain these self-organized spatial patterns. Hence, localized interactions, in combination with landscape-level constraints, determine the development of self-organized patterns. When physical constraints are minimal, relatively simple spatial patterns can develop, like the striped patterns that are observed in mussel beds and mudflat systems. When landscape settings constrain the formation of spatial structure, and multiple processes interact, more-complex spatial structures can form, as is found in salt marshes.

Although we support our argument using three patterned ecosystems that we ourselves are most acquainted with (i.e. mussel beds, mudflats and salt marsh ecosystems), the insights obtained are by no means limited to estuarine systems. For example, in patterned arid bush land, the general slope of the landscapes dictates whether surface runoff of rain is directional, which in turn determines whether vegetation patterns are banded ('tiger bush') or

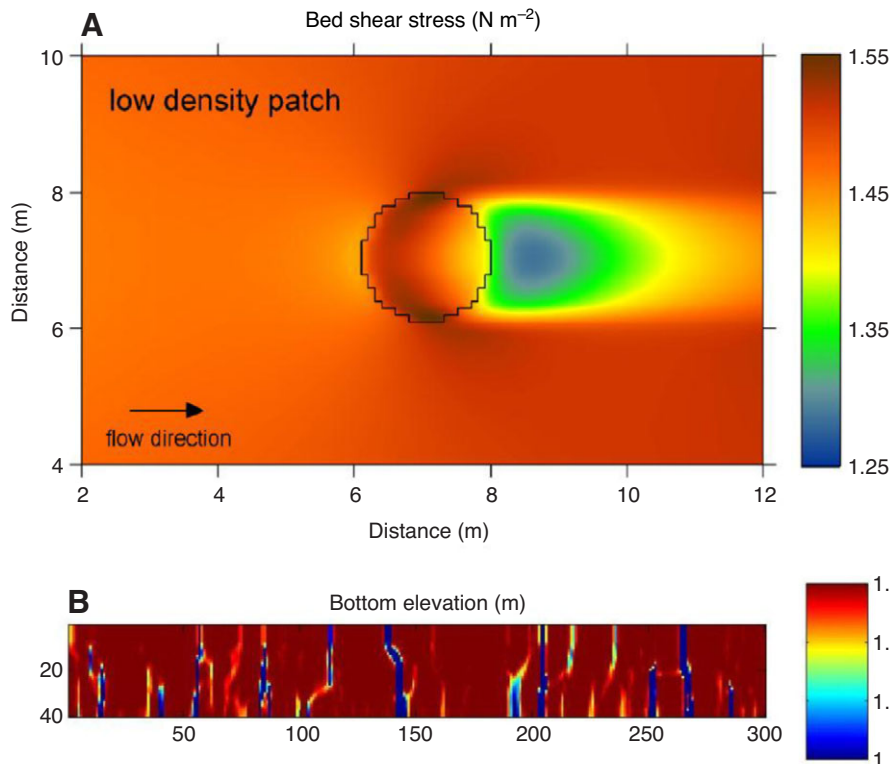


Fig. 4. A spatially explicit model of the interaction between *Spartina* vegetation, hydrodynamics and sedimentation processes. (A) Representation of the changes in the water flow field induced by a single, round tussock of *Spartina* (modified from Bouma et al., 2007). (B) A regular landscape of creeks alternating with vegetation-covered salt marsh plateaus develops after 30 years as a result of scale-dependent feedback between sedimentation and plant growth (modified from Temmerman et al., 2007).

have a dotted or labyrinth shape ('leopard bush') (Klausmeier, 1999; Rietkerk et al., 2002). Boreal peat land can develop ribbon-shaped vegetation patterns that are aligned perpendicularly to the direction of water drainage through the peat land, a process that is dictated by the landscape (Rietkerk et al., 2004). Hence, the influence of landscape-scale processes on pattern formation can be distinguished in patterned systems all over the world, and we hypothesize that it is a general feature of self-organized ecological systems.

Conclusions

From this review of the processes that govern the development of spatial structure in mussel beds, mudflats and salt marshes, it becomes evident that a close interplay between ecological and

physical interactions plays a large part in causing the spatial complexity that characterizes estuarine communities. Underlying this complexity are sometimes very simple interactions between organisms and physical processes such as tidal water flow and sedimentation, which trigger self-organization processes and generate patterns at larger spatial scales. The complexity of these spatial patterns, however, not only follows from the self-organization process, but is co-determined by physical constraints that characterize the estuarine environment – directional tidal flow of sea water and constraining coastline features. More importantly, our review of estuarine systems emphasizes that scale-dependent feedbacks are capable of explaining spatial patterns that are much more complex than the regular patterns to which they have thus far been applied.

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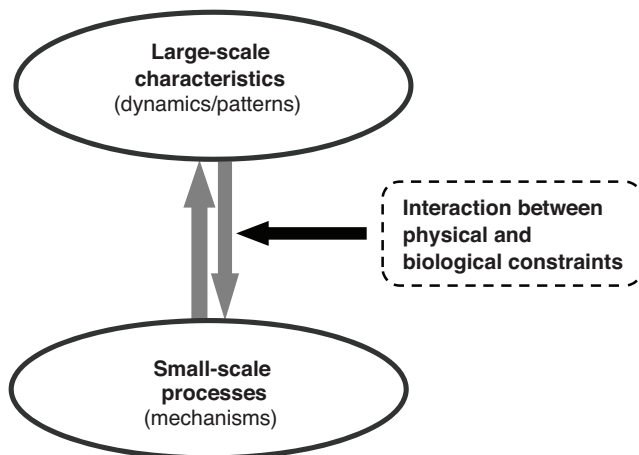


Fig. 5. A schematic representation of how the interplay of local interactions and physical forcing from the landscape generate spatial pattern and structure in ecosystems.

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