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Biophysical self-organization of coastal wetlands

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Chapter 6

General Discussion

Chapter 6 - General Discussion

Synthesis

Coastal wetlands, such as tidal flats and marshes, provide crucial ecosystem services including biodiverse habitats (e.g., Gedan et al., 2009) and flood protection for densely populated coastlines (e.g., Nicholls et al., 1999; Barbier et al., 2008; Zhu et al., 2020). The spatial structure of coastal wetlands varies greatly from location to location. The tidal channel systems that dissect wetlands form an illustrative example of this structural diversity, as they range in morphology from simple parallel channels (e.g., Allen, 1987; Gouleau et al., 2000; Williams et al., 2008) to elaborated branching networks (e.g., Rinaldo et al., 1999; Vandenbruwaene et al., 2013; Kearney and Fagherazzi, 2016). As tidal channels transport water, sediment and biota, their network morphology strongly affects wetland functioning and resilience to, e.g., sea-level rise (e.g., Morris et al., 2004; Loder et al., 2009; Hughes, 2012). Therefore, my thesis aims at understanding the emergence of spatial complexity in coastal wetlands and the effect of complexity on landscape functioning. My research is inspired by Earth's geological past, given that the development from spatially simple (e.g., Schumm, 1968; Tomescu and Rothwell, 2006; Noffke, 2009) to complex (Davies and Gibling, 2010; Gibling and Davies, 2012) channel systems has been recorded in the fossil record, from the Precambrian (more than 541 million years ago) to the present. Geological records indicate that this landscape complexification has occurred in synchrony with the evolution of sediment-stabilizing organisms (biostabilizers) from primitive microbial mats to more evolved plants (Davies and Gibling, 2010; Gibling and Davies, 2012). Whereas my thesis is focused at the landscape-building role of biostabilizers in modern-day wetlands, my findings may also shed light on the way in which life can shape a planetary surface over billions of years.

In this thesis, I performed field measurements, lab experiments and mathematical modelling to understand how spatial complexity arises in coastal wetlands due to biogeomorphic feedbacks between sediment-stabilizing organisms (algal mats, plants), sedimentary processes and hydrodynamics. Firstly, I found that spatially simple channel patterns can arise from scale-dependent (locally positive, distally negative) feedbacks, which leads to the spontaneous emergence of spatial order, i.e., spatial self-organization (Chapter 2). Whereas this process is a widely accepted explanation for regular patterning in present-day ecosystems, I here showed that the origin of biophysical self-organization might date back to the Precambrian, i.e., prior to the evolution of complex life on Earth. Secondly, I identified a single self-organization mechanism that can explain the entire range from simple to complex network architectures in tidal marshes (Chapter 3). This mechanism consists of a recursion of scale-dependent feedbacks, which is triggered when the underlying feedback is strong enough. I showed that feedback strength is directly related to sediment strength. Thirdly, I found that primitive algal mats can actively increase

sediment strength by forming a dense filamentous mesh, which induces a biogeomorphic feedback loop that explains the formation of elevated, algal-covered ridge bedforms with enhanced sediment strength (Chapter 2 and 4). The establishment of marsh vegetation is facilitated by the presence of these algal bedforms (Chapter 5). The biogeomorphic feedback cycle between biostabilizer (algal or plant) growth, sediment strength and bedform elevation, makes channelized (patterned) wetlands highly resilient to deteriorating environmental conditions. However, the same feedbacks also inhibits the establishment of a biostabilizing ecosystem, such that mudflats can remain bare and topographically smooth even when mudflat elevation is high enough for ecosystem establishment (Chapter 5). Hence, there is an elevation range that supports the co-existence of two alternative states, i.e., a patterned biostabilizer ecosystem and a homogeneous bare mudflat, and tipping points exist where critical transitions (ecosystem collapse or emergence) between these alternative wetland states can take place. Given the drastic implications of tipping point behavior for wetland conservation and restoration projects, I looked for early warning indicators to predict such state shifts. I found that the spatial complexity of channel networks does not only enhance ecosystem productivity (Chapter 3), but also is a clear indicator of the resilience of wetlands to critical state shifts (Chapter 5). Collectively, my findings might further improve the design of wetland restoration projects, stimulating the transition from conventional to nature-based flood protection of densely populated coastlines worldwide.

In this final chapter, I will discuss the broader implications of my thesis (Figure 6.1). I will first focus on primitive biostabilizers (biofilms, algal mats): what is their importance nowadays, how did they shape the sedimentary landscape on early Earth, and how could primitive life be detected on other planets? I will then discuss how my findings can help to explain the hand-in-hand diversification of life and landscapes through geological time, and how the mechanisms I identified could advance complexity science. Finally, I will look ahead to the future of coastal wetlands: how could my findings contribute to successful restoration efforts, and what role could spatial wetland patterns play therein?

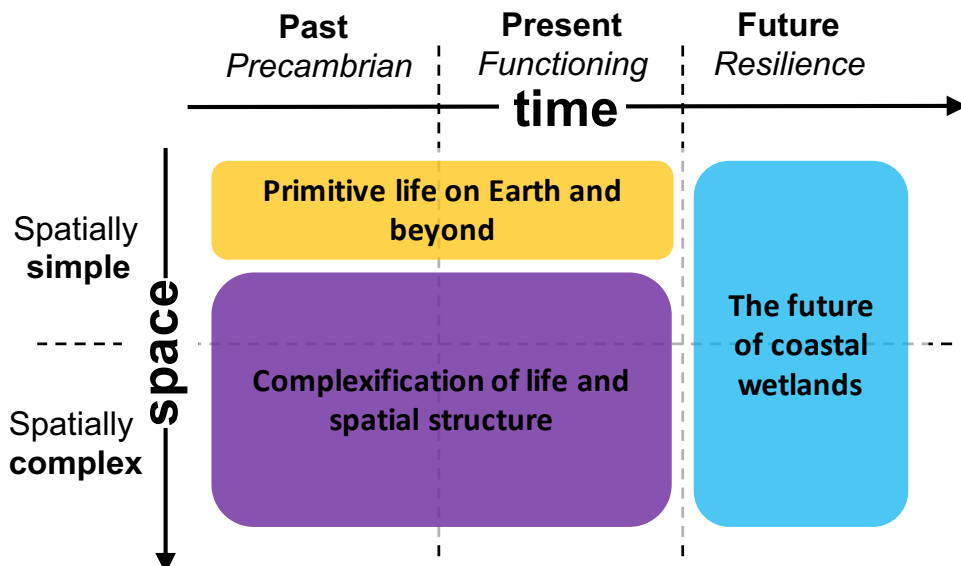


Figure 6.1. Schematized overview of the main implications of my thesis, organized along the dimensions space (spatial complexity of coastal wetlands) and time (geological origin, present functioning and future development).

Primitive life on Earth and beyond

The importance of primitive biota in modern evolved ecosystems

Complex organisms like marsh plants and mangroves are often considered to be the key ecosystem engineers in coastal wetlands. However, in my thesis I show that very primitive biota, i.e., the filamentous mat-forming algae *Vaucheria* sp., can rapidly colonize tidal flats (e.g., Van den Bergh et al., 2005; Van den Neucker et al., 2007) and induce biogeomorphic feedbacks (Chapter 4) which create elevated topographic relief composed of strengthened sediments and that persist stably for years in a row (Chapter 2), thereby forming substrates that facilitate plant growth (Chapter 5). Although microbial biofilms can also form a protective “skin layer” (e.g., Le Hir et al., 2007) that leads to the formation of sedimentary bedforms (e.g., Weerman et al., 2010), the presence of such bedforms is often reported to be seasonal (e.g., Weerman et al., 2012) as the biostabilizing effect disappears as soon as a biofilm gets disturbed (e.g., de Brouwer et al., 2000). The algal filaments of *Vaucheria*, however, can penetrate the sediment several centimeters deep (Gallagher and Humm, 1981), providing internal sediment strength (Chapter 4). This might explain the persistence of their bedforms and the consequent effect facilitating effect on vegetation (e.g., Cao et al., 2018; Fivash et al., 2020). My findings therefore indicate that the windows of opportunity for seedling establishment are not merely dependent on the temporal reduction of physical disturbances (e.g., Balke et al., 2014), but that the ecosystem engineering effect of primitive biota could lead to a “widening” of the windows of opportunity for more complex ecosystem engineers. The facilitative effect of *Vaucheria* on salt marsh

growth (Chapter 5) is in contrast with the negative impact that macroalgal can have (related to soil aeration and biogeochemistry) on marsh vegetation (e.g., Underwood, 1997; Watson et al., 2015; Wasson et al., 2017). Future work is needed to see whether *Vaucheria*'s facilitative effect on marsh establishment is shared by other primitive (microbial or macroalgal) biostabilizers. In any case, our findings clearly illustrate that primitive lifeforms can fulfill an essential pioneering role during coastal wetland development.

Primitive ecosystem engineering on early Earth

Our findings that modern analogues of Precambrian microbialites are self-organized (Chapter 2, 4, 5) has implications for our understanding of how life evolved on Earth. Most previous studies on microbialites do not go into detail about the mechanism behind patterning (e.g., Andres and Reid, 2006). Many microbialites are regularly patterned, which cannot be explained by random perturbations (Noffke, 1999), but instead could be explained by self-organization through scale-dependent feedbacks (Rietkerk and van de Koppel, 2008). If indeed these ancient bedforms were formed by self-organization (Chapter 2), the underlying positive feedbacks (Chapter 4) could have induced tipping point-behavior in these ancient wetland ecosystems (Chapter 5). This implies that self-organized or autogenic dynamics may be recorded in the rock record (e.g., Purkis et al., 2016), which may influence the interpretation of these paleo-environments based on microbialite stratigraphy (Logan et al., 1964; Jerzykiewicz and Sweet, 1988; Harzhauser et al., 2014; Lettéron et al., 2017). These findings might be relevant for the paleo-reconstruction of other fossilized depositional systems as well (e.g., Purkis et al., 2016; McNeil et al., 2020).

Finding primitive life on other planets

Coupled to the study of primitive life on early Earth is the quest for life on other planets. Channels on the surface of Mars and other planets may indicate the former presence of water (e.g., McKay, 1997; Fassett and Head, 2005; Salese et al., 2020). However, spatially simple and complex channel systems can also evolve without the presence of life (e.g., Allen, 1987; O'Brien et al., 2000; Rodriguez-Iturbe and Rinaldo, 1997). Therefore, it is the question whether the influence of life could be recognized based on sedimentary bedforms (e.g., Cady et al., 2003; Cady and Nofke, 2009). My thesis shows several clues to this question. Firstly, the scaling properties between water depth and channel spacing might be modified by biota (Chapter 2). Whereas, in parallel channel systems without biotic involvement, shallowing water depths generally yield more closely spaced channels (Franca and Lemmin, 2006; Carling et al., 2009), I found an increased channel spacing instead, most likely related to biological processes (Chapter 2). Such scaling relations could be retrieved on other planets by using remote sensing techniques. Secondly, I found that biostabilizers increase the steepness of channel banks (Chapters 2) and with that, the complexity of the channel network (Chapter 3). However, these are relative measures that require an abiotic "reference" state to be compared with. Given the absence of such information for other planets, mathematical

models like those introduced in Chapter 3 and 5 might provide a solution, after they have been parameterized based on the physical conditions (or estimates thereof) for other planets.

Complexification of life and spatial structure

Explaining the co-evolution of biostabilizers and sedimentary landscapes

I identified a unifying mechanism, recursion of the scale-dependent feedback, to explain a broad range of spatial patterns, from simple to complex (Chapter 3). The same principle might also explain the geological evolution from simple to complex fluvial styles (Davies and Gibling, 2010; Gibling and Davies, 2012). Whereas the Precambrian was characterized by simple biostabilizers (e.g., Noffke, 2008) with a relatively small ecosystem engineering potential that were thus susceptible to the topography-smoothing effect of soil creep (Perron et al., 2009; 2012), the evolution of roots enabled vegetation to actively increase sediment strength, thereby reducing soil creep (e.g., Murray and Paola, 2003; Mariotti et al., 2016) and strengthening their biogeomorphic feedback, which enabled scale-dependent feedback recursion and hence the formation of more complex channel networks (Chapter 3). The recursion mechanism that I identified in my thesis might also explain why drainage networks in present-day wetlands are more efficient when vegetation biomass increases (Kearney and Fagherazzi, 2016) and could be applicable to explain the formation of spatially complex networks in other systems too, such as terrestrial, fluvial or glacial drainage channels, as well as vascular and neural networks.

Advancing complexity science and models

I have shown that spatial self-organization reaches far beyond the realm of simple, regularly spaced patterns that it is typically associated with (e.g., Rietkerk and van de Koppel, 2008). Moreover, self-organization is typically associated with a coarsening process, i.e., where smaller-scale interactions give rise to larger-scale structure. The opposite process, where finer-scale structures emerge from a larger-scale pattern, is known as “downward causation” and is believed to be important in complex systems in, e.g., biological, physical, social and neurosciences (e.g., Campbell, 1974; Bishop, 2008; Flack, 2017). Nonetheless, downward causation has received considerably less scientific attention than the process of emergence (e.g., Klausmeier, 1999; Kondo, 2002; Rietkerk and van de Koppel, 2008; Liu et al., 2014a; Tarnita et al., 2017; Han et al., 2020). The mechanism we identified, whereby multi-scale patterns arise when a scale-dependent feedback acts recursively at increasingly finer scales (Chapter 3) illustrates that complex patterns can arise due to iterative interactions between coarsening (emergence) and refinement (downward causation). These findings indicate that downward causation may be an essential process to consider, in order to understand spatial complexity. We provide a clear-cut example and mathematical framework (Chapter 3, 5) to study the coupling between emergence and downward causation.

In order to mathematically model the formation of spatially complex channel patterns, I introduced a model that dynamically couples biological processes to both a sediment balance and a dynamic water flow field, whilst ensuring high computational efficiency in order to simulate multi-scale pattern formation at a fine spatial scale (Chapter 3, 5). Existing models either had a high computational efficiency but were lacking scale-dependent feedbacks (Rinaldo et al., 1999; D’Alpaos et al., 2005; Kirwan and Murray 2007), or did account for scale-dependent feedbacks but not for dynamic water flow (e.g., van de Koppel et al., 2005; Liu et al., 2012; 2014a,b), or modelled pattern formation in only one spatial dimension (Weerman et al., 2010). Self-organization models with biological-hydrodynamic interactions have been introduced recently (Cornacchia et al., 2020), but the interaction with sediment dynamics is not represented therein. Finally, highly realistic models that include bio-sedimentary-hydrodynamic interactions and scale-dependent feedbacks and a realistic tidal forcing (e.g., Temmerman et al., 2007; Schwarz et al., 2014) are computationally too expensive to simulate the formation of multi-scale channel patterns. Although several processes, including tidal forcing and sediment transport, have been strongly idealized in the model that I introduced (Chapter 3, 5), it fills in this modelling “niche” and could be readily modified to simulate the multi-scale organization in other spatially complex ecosystems, including coral reefs (Mistr and Bercovici, 2003), mussel beds (Liu et al., 2014b), seagrasses (Kendrick et al., 2005) and mangrove forests (Horstman et al., 2015).

The future of coastal wetlands

Optimizing wetland restoration

Wetland restoration and conservation projects are undertaken worldwide to compensate for wetland losses due to climate change and (other) anthropogenic stressors (e.g., Wolters et al., 2005; Mossman et al., 2012; Lawrence et al., 2018; Oosterlee et al., 2019; Temmink et al., 2020). It had been found before that the establishment of vegetation seedlings depends on windows of opportunity where establishment thresholds can be overcome (e.g., Balke et al., 2011; 2013; 2014). To overcome these thresholds, engineering interventions are sometimes taken in restoration projects, such as the placement of breakwaters or fences to reduce wave impact and enhance sedimentation (e.g., Van Cuong et al., 2015), the creation of artificial channels or heterogeneity (e.g., Lawrence et al., 2018) to improve soil drainage and the placement of artificial hard structures to provide substrate for settlement (e.g., Fivash et al., 2020; Temmink et al., 2020). However, my findings show that biological processes induced by algal mats can also improve the establishment chance of vegetation (Chapter 5). Because these algae induce their own biogeomorphic feedbacks (Chapter 4) and can establish and grow rapidly (e.g., Van den Bergh et al., 2005; Van den Neucker et al., 2007), it requires smaller effort to facilitate the growth of these primitive algae, rather than to intervene to facilitate vegetation establishment. In designing coastal restoration projects, it is therefore recommended to choose a location where such algae occur naturally; possibly (and

when this does not lead to the introduction of invasive species) the establishment of these biostabilizers could be triggered by transplanting or inoculating small algal patches. Besides, slight topographic heterogeneities could already be enough to initiate the biogeomorphic feedbacks that these algae induce (Chapter 4). When conventional engineering measures are taken after all, e.g., the creation of artificial drainage channels, it could be beneficial to follow the channel spacing (wavelength) that is found naturally on nearby tidal flats (Chapter 2), as mimicking natural self-organized architecture may improve restoration success (e.g., Silliman et al., 2015; Temmink et al., 2020). Alternatively, artificial creation of spatially complex drainage networks may improve soil drainage (Chapter 3) and thereby sediment strength, which might ultimately lead to more productive tidal marshes that are more resilient to sea level rise (Chapter 5).

Using wetland patterns as indicator for ecosystem development

Finally, my findings indicate that coastal wetlands can exhibit alternative stable states that co-exist under the same external conditions (Chapter 5). The existence of alternative ecosystem states is typically associated with the threat of critical transitions leading to unexpected ecosystem collapse (e.g., Scheffer et al., 2001; Barbier et al., 2006; van Belzen et al., 2017). However, the existence of a vegetated, channelized wetland state as an alternative to the bare and unchanneled mudflat state (Chapter 5) also provides an opportunity for ecosystem restoration. In line with earlier findings (e.g., Rietkerk et al., 2004; Barbier et al., 2006; Weerman et al., 2012; Kéfi et al., 2014), I found that self-organized spatial patterns contain information about the proximity to a tipping point. While the biomass of an ecosystem engineer is too low to induce biogeomorphic feedbacks, this ecosystem engineer remains practically absent (e.g., Corenblit et al., 2007). However, I showed that a range of environmental conditions can exist where growth conditions are sufficient for the ecosystem engineer to build up biomass, but where spatial heterogeneity is still lacking to trigger a scale-dependent feedback and hence self-organization (e.g., Rietkerk and van de Koppel, 2008). This range could be detected during restoration projects with the use of remote sensing techniques (biomass and spatial heterogeneity therein could be detected within the visible light spectrum or with NDVI-cameras; topographic relief could be measured with laser scanners, LIDAR or drone-based structure from motion techniques). When a restoration site is in this range of environmental conditions, only a minimal disturbance (the creation of some topographic relief or the transplantation of some algal patches) would – in theory – be sufficient to trigger the scale-dependent feedbacks that can cause a shift to a vegetated, channelized wetland. These theoretical findings (Chapter 5) should be tested in the field and might contribute to a higher wetland restoration success (Wolters et al., 2005; Mossman et al., 2012; Lawrence et al., 2018), ultimately contributing to nature-based coastal protection in the global changes experienced worldwide (e.g., Nicholls et al., 1999; Barbier et al., 2008; Temmerman et al., 2013; Arkema et al., 2013).