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Emergent properties of bio-physical self-organization in streams

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Chapter 7

General discussion

In this thesis, I investigated the emergent properties of self-organization of submerged macrophytes in streams – resulting from the two-way interaction between plant growth and water flow – in terms of physical properties, biological interactions and resource uptake (Figure 7.1). This self-organization process has important emergent properties for stream-level hydrodynamic conditions (Chapter 2). Specifically, vegetation stabilizes local flow velocities and reach-scale water levels under varying discharge, providing multiple ecosystem services in terms of flow regulation and habitat diversity (Chapter 2). Consequently, model and field data suggest that such plant-driven hydrodynamic heterogeneity promotes plant species coexistence in lotic communities, by creating a ‘landscape of facilitation’ where a multitude of new niches arise for species adapted to a wide range of contrasting flow conditions (Chapter 3). My findings indicate that such ‘landscape of facilitation’ may establish based on macrophyte propagule retention during dispersal and primary colonization (Chapter 4). Moreover, bio-physical interactions affect the processes of vegetation occurrence through *intra*-specific interactions: vegetation patches in streams organize themselves in V-shapes to minimize hydrodynamic and drag forces, resembling the flight formation adopted

by migratory birds (Chapter 5). Finally, self-organized spatial patchiness due to species mixtures also leads to emergent effects on nutrient uptake, a crucial ecosystem function in streams. Flume experiments suggest that patches of macrophyte species interact with each other through facilitation of resource uptake, by influencing turbulence. The latter has implications for aquatic ecosystem functions and services such as nutrient load reduction (Chapter 6).

In this chapter, I will discuss the implications of the main findings of this thesis and how they contribute to advance the field of self-organization. Specifically, the focus will be on the implications of physical emergent properties, species interactions and resource uptake for self-organization theory. Finally, I will provide an outlook on ecosystem functioning and management implications, focusing on alternative stable states, river restoration and management (Figure 7.1).

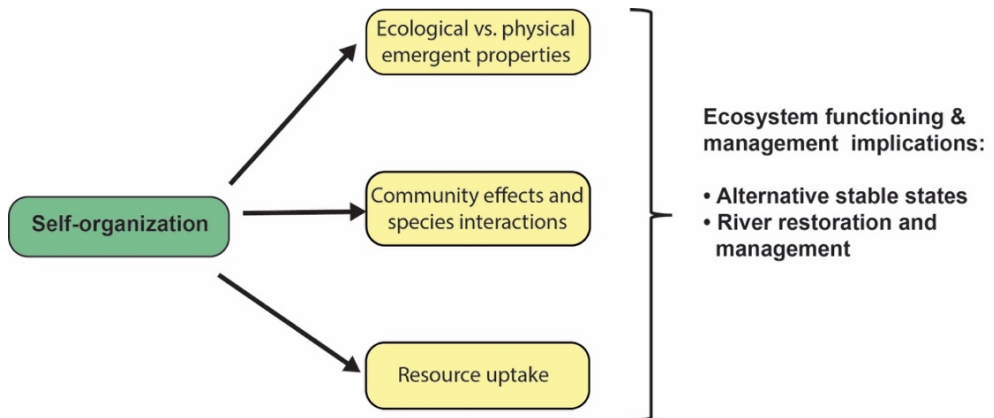


Figure 7.1: Overview of the main themes and implications related to the findings of this thesis, in terms of advancing self-organization theory from both a fundamental and an applied perspective.

Implications for self-organization theory: from ecological to physical emergent effects

Self-organized patterns emerge across landscapes worldwide (Rietkerk and Van de Koppel 2008) and have important implications for the functioning of the ecosystems in which they are found. However, most of the emergent effects of self-organization explored so far focused on the biological properties, such as enhanced productivity and resilience through spatial patterning (van de Koppel et al. 2005; Pringle et al. 2010). This study advances self-organization theory by revealing that self-organization also has crucial emergent effects in terms of physical variables, at both local and larger scales (Chapter 2), next to the previously known effects on biological properties. Present findings suggest to shift from the view that physical variables in landscapes are a direct function of physical processes (Rinaldo et al. 1993; Rigon et al. 1994; Rodríguez-Iturbe and Rinaldo 2001), to understanding that the physical environment can be largely controlled by the interaction between biological and physical processes. Compared to previous studies integrating reciprocal bio-physical interactions (Kirwan and Murray 2007; Temmerman et al. 2007), my study goes forward by suggesting that the physical characteristics of the landscape can be an emergent property of biological-physical self-organization. Hence, these reciprocal feedbacks should be integrated in future models of biogeomorphic landscapes to fully investigate the emergent properties of spatial patterning in ecosystems.

Our coupled modelling-empirical study revealed that the mechanism behind the flow regulation by macrophytes is the readjustment of total vegetation cover to changing discharge (Chapter 2). Yet, the total cover of vegetation does not provide information about the actual spatial distribution of vegetation patterns (Chapter 5), or how the spatial patterns will reorganize when abiotic stress increases. Investigating changes in patch size over time could highlight whether typical sizes (width, length) exist in landscapes dominated by physical flows, and how their size and/or shape adapts to increasing environmental stress. Moreover, quantifying the spatially heterogeneous distributions of vegetation is important to estimate reach-scale flow resistance (Bal et al. 2011a), which is the relevant scale for flood management (Nepf 2012). Repeated testing of patch-size distributions at different incoming discharge could be combined with other measures of spatial

reorganization, such as mean patch size or spatial autocorrelation (Kéfi et al. 2007; Kéfi et al. 2011; Weerman et al. 2012). This type of knowledge on patch dynamics would increase our understanding of how spatial patterns are structured by the interplay of biological and physical processes (Chapter 5), and advance their use as indicators of ecosystem state to improve both conservation and management practices (Rietkerk et al. 2004b; Kéfi et al. 2007; Weerman et al. 2012).

Exciting new lines of research should consider the effects of self-organization on other geomorphic processes that shape landscapes, such as sediment transport (Larsen and Harvey 2010; Corenblit et al. 2011). Our study suggests that plant-flow feedbacks regulate river flow velocities (Chapter 2). Interestingly, this implies that sediment dynamics may be regulated in a similar way, with constant sediment transport and retention rates despite changes in physical forcing and biological properties (e.g. discharge and vegetation cover). This would provide a new perspective of macrophytes, from important retentive structures that promote sedimentation (Schulz et al. 2003), to agents that simultaneously enhance both sedimentation and erosion processes. Potentially, this might also affect the temporal evolution of river bed topography. Another interesting aspect to consider is the time scale of physical and biological adjustments. For instance, it is unclear whether the sediment retained within vegetation patches is released immediately when vegetation cover is lost (Schulz et al. 2003; Cotton et al. 2006). This would have important implications for patterns of nutrient retention and any following erosion and transport of sediment in rivers. Therefore, self-organized biological patterns are much more important than previously thought for earth-surface processes, and can enhance our understanding of the role of organisms as geomorphic agents (Butler 1995; Corenblit et al. 2015).

Species interactions in self-organized landscapes

Most studies of self-organization do generally not consider species interactions. Previous studies typically focused on a single species at a landscape setting, analysing both scale-dependent effects of local facilitation and large-scale competition (Rietkerk and Van de Koppel 2008; van Wesenbeeck et al. 2008; Schoelynck et al. 2012). However, self-organization also has important effects on bottlenecks for species establishment. While the recently developed ‘Window of

Opportunity' concept reveals the importance of periods free of physical disturbances for species establishment (Balke et al. 2011), my study suggests that a combination of biological and physical variables can influence the windows of opportunity for establishment (Chapter 4). Through self-organization, existing vegetation can facilitate other plant species by retaining their propagules. This interaction allows propagules to pass one of the physical thresholds to establishment, but is conditional upon propagule traits, flow velocities and pre-existing vegetation traits and cover. This knowledge is particularly relevant in physically stressed environments, where primary colonization is challenging due to forces that act to dislodge seedlings and propagules (Bouma et al. (2009a); Balke et al. (2011); Chapter 4 & 5).

Integrating species interactions within self-organization theory may also shed light on its effects on trophic interactions and food web structure. Self-organization creates conditions for a wider number of species to coexist (Chapter 3), and can alter community structure (Christianen et al. 2016). However, spatial patterns in many ecosystems are under increasing threat due to global change. Arid ecosystems are prone to transitions into deserts (Rietkerk et al. 2004b; Scheffer et al. 2009). Coastal ecosystems are threatened and degrading worldwide (Hoegh-Guldberg and Bruno 2010). In addition, human interference is making ecosystems more homogeneous, reducing their spatial structural complexity through damming, channel straightening, or mowing of natural vegetation (Poff et al. 2007; Spieles 2010). As self-organized heterogeneity supports a wide range of species, losing the habitat complexity it provides can result in the loss of many other species that depend on it and are connected by trophic interactions. The non-trophic interactions that characterize self-organization are not yet fully integrated into studies of food web dynamics (Kéfi et al. 2012). Hence, an interesting topic for future studies would be to investigate the consequences of the loss of self-organized heterogeneity for all the related species it can support, in terms of food web structure and stability.

Although spatial patterns are created by a single species, they are likely inserted into a 'matrix' of other species, creating a heterogeneous and diverse community (Chapter 3 & 6; Donadi et al. (2013)). Yet, very few studies so far have investigated how feedback interactions with physical stressors, such as water flow,

are affected by heterogeneous species distributions (Adhitya et al. 2014; Weitzman et al. 2015), and what the implications are for species interactions. My findings suggest that patches of different species can interact, and specifically facilitate each other, by having contrasting effects on hydrodynamic conditions (e.g. mean velocity and turbulence; Chapter 6). The role of turbulence as an agent of species interactions has been relatively neglected in studies of facilitation. In fact, most previous studies focused on facilitation driven by flow stress reduction (Bruno 2000; Donadi et al. 2013). My data suggest that increased flow energy and turbulence can also play a role in facilitation, and deserve further attention. However, patches likely interact when they are at relatively short distances from each other, i.e. where their hydrodynamic effects are strongest. Thus, species traits and their spatial patch organization add other dimensions of complexity to flow-vegetation interactions. To bring this field forward, some next steps would be to collect more detailed hydrodynamic measurements across heterogeneous species landscapes, varying both positions and distances between patches. Future studies could also explore interactions among a wider range of species with contrasting traits. As community diversity is a fundamental characteristic of natural environments, understanding physical flows across bio-diverse landscapes with many species will get us to a more realistic understanding of the implications of bio-physical interactions.

Effects of self-organization on ecosystem function of resource uptake

The emergent effects of self-organization on ecosystem functioning have been increasingly investigated in both theoretical and empirical studies (van de Koppel et al. 2005; Pringle et al. 2010; Liu et al. 2012; de Paoli et al. 2017). In aquatic ecosystems, spatial patchiness due to self-organization has important emergent effects on the ecosystem function of nutrient uptake (Chapter 6). My findings indicate that spatial patchiness of vegetation creates heterogeneity in hydrodynamic conditions and thereby plays a role in resource use. Specifically, dense vegetation patches decouple turbulence from local flow velocity, creating heterogeneously distributed regions where either mean flow velocity or turbulence are high. The non-locally generated turbulence due to large, dense patches influences the downstream fluxes of nutrients for other species and facilitates their

uptake rates (Chapter 6). This turbulence-driven facilitation of resource uptake implies that patchy, biodiverse landscapes could maximize the ecosystem function of nutrient load removal. A similar conclusion on the importance of heterogeneity for resource use was reached in a study on stream biofilm (Singer et al. 2010). This suggest the crucial role of self-organized heterogeneity in supporting ecosystem functioning, and provides a warning against the ongoing homogenization of ecosystems (Poff et al. 2007).

Alternative stable states in submerged aquatic vegetation

Self-organized patterned ecosystems are vulnerable to sudden dramatic shifts towards alternative, degraded ecosystem states once a tipping point in environmental stress is exceeded (May 1977; Rietkerk and van de Koppel 1997; Scheffer et al. 2001; van de Koppel et al. 2001). Understanding the response of natural ecosystems to abiotic changes is therefore a priority for their future persistence and conservation.

This study suggests that self-organization can make vegetation more resistant and resilient to changing discharge regimes (Chapter 2), for instance due to global change (Houghton et al. 2001) and land use change in river catchments (Foley et al. 2005; Palmer et al. 2008). However, we observed so far that vegetation is able to readjust to varying discharge when these changes are gradual over time. It is currently unknown how vegetation will respond to peak events of discharge, and whether it would it still be able to maintain its regulatory function on water velocities and levels. To understand how ecosystems will respond to a future governed by global change, we should not only evaluate its sensitivity to the intensity of these disturbances, but also its response to gradual versus abrupt abiotic changes.

The model presented in Chapter 2 hints at the possibility of two stable states in aquatic communities, one where vegetation is patterned versus a bare state where vegetation cannot survive. In the vegetated state, plants can gradually adapt to varying external conditions (i.e., discharge). However, when close to the critical threshold, even small perturbations can shift the system to the alternative state (Van Nes and Scheffer 2007). Our model predicts that once the system is in the degraded (unvegetated) state, vegetation can recover if discharge decreases to

much lower values than the level at which the shift occurred, indicating hysteresis (Scheffer et al. 2001; Scheffer et al. 2009). This implies that natural or human disturbances at high discharge might shift the system towards the alternative unvegetated state, where the regulatory functions provided by vegetation are lost and from which vegetation recovery is hindered. Previous studies showed that nutrient addition can reduce the mechanical resistance of vegetation (La Nafie et al. 2012; Lamberti-Raverot and Puijalon 2012). It might be speculated that, under eutrophication, the critical threshold at which the system shifts to the unvegetated state might be at much lower levels of environmental stress than we would expect. This could occur due to plant tissues being already weakened by high nutrient loads and thus less resistant to hydrodynamic stress. Exploring the combined effects of multiple stressors on critical thresholds in ecosystems is a potentially interesting question for future cross-ecosystem studies, involving organisms exposed to similar stressors in other ecosystems (e.g. aquatic streams, salt marshes, seagrass beds).

Implications for management and restoration of aquatic ecosystems

Aquatic macrophytes are important foundation species in lotic environments (Carpenter and Lodge 1986). Macrophytes improve river water quality (Sculthorpe 1967), they affect sediment patterns (Sand-Jensen 1998; Madsen et al. 2001), remove nutrients (Bal et al., 2013; Chapter 6) and provide habitat diversity for many other species, such as invertebrates or fish (Haslam 1978; Baattrup-Pedersen et al. 2003; Franklin et al. 2008). Despite the awareness of the multiple ecological benefits provided by macrophytes, river management practices usually focus on vegetation removal. These management actions aim to reduce the risk of overbank flooding, as vegetation is generally considered a nuisance that increases hydraulic resistance and raises water levels (Dawson 1979; Flynn et al. 2002; Sukhodolova 2008; Sukhodolov and Sukhodolova 2009). Here, I discuss the implications of my main findings on the self-organizing interaction between plant growth and hydrodynamics for management and restoration of aquatic ecosystems.

Our study puts forward a surprising new perspective on stream management, where interactions between plant growth and flow redistribution lead to self-

regulation of vegetation abundance (Chapter 2). As the plant-flow feedback creates an upper limit for vegetation expansion in the river bed, the continuity of water transport in the unvegetated channelled flow areas is preserved throughout the annual flow regime. Also, plants maintain flow habitat requirements at low discharges by raising water levels, but their effect on water levels declines as discharge increases (Chapter 2, Figure 2.3). At high discharge, flexible aquatic macrophytes tend to flatten near the river bed (Chapter 2, Figure 2.6), creating much lower hydraulic resistance than it would be expected from measuring vegetation resistance at peak cover during summer. This finding suggests that the increased flood risk by vegetation may only occur under a certain set of conditions, for instance at highest macrophyte cover during the peak of the growing season where the system is suddenly exposed to prolonged periods of high rainfall. As anthropogenic impact in the form of stream management contributes to disturb a system that is already disturbed by natural perturbations, the frequency of such actions should be limited to prevent ecosystem degradation (Baatrup-Pedersen et al. 2003). Hence, a change of perspective might be needed in current management strategies, where vegetation is valued for the wide range of ecosystem functions and flow-regulating services it provides, rather than mainly regarding it as a flow obstacle that might cause flooding.

Together with the buffering of water velocities and levels, the self-organization process described in Chapter 2 points to important implications for the maintenance of habitat diversity in stream ecosystems. While increasing flow diversity, the patchy vegetation creates heterogeneity in sediment characteristics. Thus, both areas of finer, nutrient-rich sediment within the vegetation and clean gravels in the unvegetated channels are preserved, which can support a diverse invertebrate community (Wharton et al. 2006). Moreover, the low-flow regions within the plant patches create areas for fish cover, nursery and refuge from predation, while the faster flowing clean gravels are ideal feeding and spawning grounds (Kemp et al. 2011). By increasing water levels during periods of low discharge, vegetation can support other species in multiple ways. First, it can maintain more mesohabitats by maximising wetted channel width and stream cross-sectional area. Secondly, it minimises longitudinal disconnection that might occur during drying of the river. Finally, higher water depths allow water temperatures to be lower in summer, hence holding greater dissolved oxygen levels

for the aquatic community (Carpenter and Lodge 1986). In dryland ecosystems, habitat modification by key self-organizing species can in a similar way create habitats for many other species (Gilad et al. 2004), promoting species coexistence and diversity (Nathan et al. 2013). Hence, the creation and maintenance of habitat diversity by aquatic vegetation suggests it is a crucial component of both physical regulatory functions and biodiversity in streams.

The findings of this thesis suggest future strategies to maximize vegetation colonization in restoration projects. Species interactions could be used to facilitate other plant species in their first stages of establishment and growth. The aquatic macrophyte *Callitriche platycarpa* provides a wide range of facilitative effects on both the establishment and growth of other species (Chapter 3, 4 & 6). Due to its high density and canopy architecture, this species acts as a strong ecosystem engineer, altering both local flow velocities and turbulence (Chapter 3 & 6; Schoelynck et al. (2012); Schoelynck et al. (2013)). Hence, to maximize plant species diversity, *Callitriche* is a high priority target species to be reintroduced in streams. Due to the challenges of seedling and propagule establishment in running waters (Bouma et al. (2009a); Balke et al. (2014); Chapter 5), transplantation of bigger clumps might be more efficient (Silliman et al. 2015). Once *Callitriche* is established and forms self-organized patterns, it will form a 'landscape of facilitation' (Chapter 3), providing contrasting flow conditions and habitat requirements for other species. Also, given that an upstream source of propagules is available, it can efficiently trap the propagules of other macrophytes (Chapter 4), allowing them to pass one of the thresholds for successful colonization. Due to its similar effects of flow modification and habitat creation (Chapter 2; Cotton et al. (2006); Wharton et al. (2006)), *Ranunculus penicillatus* is an equally important species to be preserved and reintroduced where possible. Ecosystem functions could also be maximized by making use of species interactions, as more diverse landscapes can increase the capacity of ecosystems for nutrient load removal (Chapter 6).

Taken together, the fundamental research questions investigated in this thesis highlight geo-biological self-organization as an exciting field for future studies, where self-organized biological patterns are increasingly considered for their emergent effects on physical processes. Moreover, these findings can be translated

into novel insights that might be used for applied questions. In the face of changing climate and anthropogenic impacts, such linkage from fundamental to applied is increasingly needed to guide the management and conservation of ecosystems.

