Emergent properties of bio-physical self-organization in streams

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Summary

Self-organization is increasingly recognized as an important regulating process in several ecosystem types. Many studies of self-organization in biology have focused on the emergent effects of self-organized spatial patterns on biological properties, such as enhanced productivity or resilience to disturbances. Despite its prevalence in biological theory, self-organization is not yet considered extensively in geophysical studies. Most studies do not fully incorporate the interactive bio-physical feedbacks between biological and physical processes. For this reason, it is unknown if self-organization has emergent effects on both physical and biological properties. In this thesis, using submerged aquatic macrophytes in streams as a model system, I study the emergent properties of self-organization – resulting from the two-way interaction between plant growth and flow redistribution – for both hydrological and ecological processes. Specifically, I study the role of self-organization of aquatic macrophytes in terms of regulation or river flow (velocities and depth), biological interactions (*inter*-specific effects on growth and dispersal, and *intra*-specific effects on spatial patterning) and resource uptake. My study combines field experiments and field observations, laboratory flume experiments and mathematical models.

In Chapter 2, I examine whether self-organization, resulting from the two-way interaction between plant growth and flow redistribution, has emergent properties for stream-level hydrodynamic conditions. The results of a combined mathematical modelling and empirical study suggest that this self-organization process creates heterogeneity in plant biomass and water flow. In turn, it stabilizes both flow velocities and water levels under varying discharges, with multiple ecosystem benefits. Therefore, my results reveal an important link between plant-driven self-organization processes of streams and the ecosystem services they provide in terms of water flow regulation and habitat diversity.

The regulation of water flow by submerged aquatic macrophytes studied in Chapter 2 point to important implications of plant-driven hydrodynamic heterogeneity for species interactions and biodiversity. Consequently, in Chapter 3 I explore the link between self-organization and facilitation. Model and field data suggest that self-organized pattern formation promotes plant species coexistence in lotic communities by creating a 'landscape of facilitation'. Here, multiple new niches arise for species adapted to a wide range of hydrodynamic conditions. Model predictions are confirmed by field observations of species coexistence and transplantation experiments supporting the hypothesis of facilitation. This study therefore highlights that understanding of the way in which competition and facilitation interact in many ecosystems is crucial for successful management of their biodiversity.

The self-organization process described in Chapter 2 and 3 is based on the divergence of water flow around vegetation patches. Divergence of physical stress is a common mechanism underlying the patchy distribution of foundation species in many ecosystems. Yet, it is still unknown if the mechanisms underlying self-organized spatial pattern formation are important for facilitation of species establishment. Retention of vegetative propagules by existing vegetation is an important bottleneck for macrophyte establishment in streams. Water flow is both the dispersal vector of plant propagules and the stress factor that leads to vegetation patchiness. In Chapter 4, I study how this flow divergence mechanism affects facilitation through propagule retention within existing macrophyte patches, using mesocosm, flume and field studies. My study suggests that feedbacks between patch reconfiguration and water movement, leading to self-organization, can facilitate the establishment of macrophyte species during dispersal and primary colonization.

In Chapter 5, I test if existing spatial patchiness of macrophytes, resulting from the two-way interaction between vegetation and hydrodynamics, affects vegetation occurrence through *intra*-specific facilitation. Field manipulation experiments reveal that vegetation patches in streams organize themselves in V-shapes to minimize hydrodynamic and drag forces, resembling the flight formation adopted by migratory birds. My findings highlight that bio-physical interactions shape the way organisms position themselves in landscapes exposed to physical flows.

In Chapter 6, I explore the emergent effects of self-organized spatial patchiness due to different species on resource uptake. Many studies of plant-hydrodynamic feedbacks deal with monospecific canopies. However, natural landscapes are a diverse community composed of patches of different species with contrasting traits. These patches potentially influence each other through their hydrodynamic effects, for instance affecting the uptake of resources that is crucial for productivity. My findings suggest that patches of macrophyte species interact with each other through facilitation of resource uptake, by influencing turbulence. This was tested in racetrack flume experiments combining hydrodynamic measurements and ^{15}N labelled ammonium incubations. My study reveals the importance of turbulence as an agent of interaction between different species. Moreover, the findings suggest that interactions between heterogeneous, multispecific patchy vegetation are crucial to understand aquatic ecosystem functioning and services of nutrient load reduction.

In conclusion, my research highlights the crucial emergent effects of self-organization for a range of physical and biological properties in ecosystems. This study reveals a previously unexplored link between self-organized biological patterns and ecosystem services such as flow regulation, habitat and species diversity. Understanding the regulating functions of spatial self-organization is essential to maintain the valuable ecosystem services it supports. In many ecosystems, bio-physical interactions are still approached in a static way that does not fully incorporate the dynamic feedbacks. Future empirical and modelling studies in other biogeomorphic landscapes should aim to further include these reciprocal feedbacks. This will increase our understanding of the full range of emergent properties of spatial patterning in ecosystems, and the wider applicability of the conclusions presented here. The findings of this thesis also suggest how bio-physical interactions can be used to guide the management and restoration of aquatic ecosystems. Hence, our fundamental research questions on self-organization can be closely linked to applied research. Such linkage is valuable to guide the management and conservation of ecosystems.