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Emergent properties of bio-physical self-organization in streams

Loreta Cornacchia

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The research presented in this thesis was carried out at the Department of Estuarine and Delta System of the Royal Netherlands Institute for Sea Research (NIOZ-Yerseke), and the Conservation Ecology Group, part of the Groningen Institute for Evolutionary Life Sciences (GELIFES), of the University of Groningen (The Netherlands). This research was supported by the European Union's Seventh Framework Programme FP7-PEOPLE-2012-ITN under grant agreement N. 316546. Printing of this thesis was financially supported by NIOZ and University of Groningen.

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Back cover: Channel along the Rhône river, near Flévieu (France) (photo by Loreta Cornacchia)

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Prof. M.G. Kleinhans

Table of Contents

Chapter 1

General introduction

All interactions between species and their abiotic environment, as well as between species themselves, occur in a spatial setting. Due to the complexity of integrating the spatial context of species interactions, early theoretical models generally focused on presumed mean field conditions, ignoring the spatial heterogeneity that is prevalent in many populations (Lotka 1926; Volterra 1926). However, no community is truly homogeneous as assumed in these classical studies. This became soon apparent in the famous experiments by Gause (1932), showing that two species competing for the same resource cannot coexist in laboratory conditions if other ecological factors are constant, while they would persist in natural habitats. Later, Huffaker (1958) showed that coexistence was not possible in small homogeneous habitats, but was promoted in spatially complex habitats. Since then, there has been growing interest in the field of spatial ecology (Levin 1992; Tilman and Kareiva 1997). The importance of spatial processes and heterogeneity has been recognized in theoretical models or empirical studies on annual plants (Hutchinson 1953; Levin 1970; Koch 1974; Armstrong and McGehee 1976; Holt 1984; Tilman 1994; Amarasekare 2003). By providing multiple niches and diverse ways of exploiting environmental resources, structurally complex physical habitats increase species diversity (MacArthur and MacArthur 1961). Hence, spatial heterogeneity can provide a solution to the paradox of the plankton, where hundreds of species can grow and coexist on only a few limiting resources (Hutchinson 1961).

Along with the recognition of the importance of spatial heterogeneity, a closely related topic in spatial ecology is the spatial structure of organisms and communities. That is, understanding the spatial organization in the distribution of organisms and what determines it. Classical ecological theory assumes that abiotic conditions determine the distribution of organisms (Clements 1916), for instance following underlying gradients in environmental stress (Colman 1933; Stephenson and Stephenson 1949). However, it was noted already by Darwin (1881) that species themselves can in turn influence abiotic conditions. Through time, this topic has received increasing attention, and different terms have been suggested to indicate the role of organisms that can modify the abiotic environment and species distributions (Ellison et al. 2005). One of the most general terms to indicate organisms that can modify their physical environment is ecosystem engineers (Jones et al. 1994). Ecosystem engineers cause physical changes in biotic or abiotic material through their action (*allogenic engineers*, like beavers) or through their own physical structure (*autogenic engineers*, like forest trees, submerged macrophytes and corals) (Jones et al. 1997). Some examples of ecological effects of ecosystem engineers are modulation of abiotic forces or concentration of resources (Jones et al. 1994). By modifying the environment, ecosystem engineers can also make it more suitable for other species in a community. In this way, ecosystem engineering can lead to facilitation for other species (Wright et al. 2002; Bruno et al. 2003; Borthagaray and Carranza 2007; Brooker et al. 2008; McIntire and Fajardo 2014), as will be discussed in the next chapters.

Spatial self-organization

Many engineering organisms can have such a strong effect on their environment that they lead to the emergence of striking spatial patterns in species distributions, through the process of self-organization (Rietkerk and Van de Koppel 2008). Here, the organisms create positive feedbacks for their own survival or growth (Wilson and Agnew 1992). When positive feedbacks are linked to a negative feedback at somewhat larger scales (Lejeune et al. 1999; van de Koppel et al. 2005), this can lead to the formation of spatial patterns, even in the absence of underlying environmental heterogeneity. Both the mechanism and implications of self-organized spatial patterns for ecosystems will be discussed in more detail in the following paragraphs.

Scale-dependent feedbacks have been proposed as an explanatory principle for the occurrence of patterning in many different systems (Rietkerk and Van de Koppel 2008), both biological and physical. There, a local positive feedback due to stress reduction or resource concentration promotes growth, but a large-scale negative feedback of increased stress or depleted resources limits their further expansion or growth. This mechanism of regular pattern formation is largely based on the activator-inhibitor principle, which was first proposed by Turing in chemical systems (Turing 1952). Self-organized patterns have important implications for the ecological functions of these ecosystems, but also for their persistence and stability against stress and disturbance (Rietkerk et al. 2004b; Pringle et al. 2010; Liu et al. 2014; de Paoli et al. 2017). Moreover, with the current rates of global change and human alteration of natural ecosystems (Houghton et al. 2001), they may be exposed to increasingly stressful environmental conditions. Hence, understanding both the mechanisms and the emergent effects of self-organization is essential for adequate management and conservation of these diverse and ecologically valuable ecosystems.

Self-organization in biology

Self-organization is increasingly recognized as an important regulating process in many ecosystems where organisms interact with their environment (Rietkerk and Van de Koppel 2008). Examples of self-organization in nature range from arid systems (Klausmeier 1999; von Hardenberg et al. 2001; Rietkerk et al. 2002), to mussel beds (van de Koppel et al. 2005; Liu et al. 2014), diatoms on tidal flats (Weerman et al. 2010) and peatlands (Swanson and Grigal 1988; Rietkerk et al. 2004a). Many studies of self-organization in biology have focused on the emergent properties of self-organized spatial patterns in terms of ecosystem functioning and stability (van de Koppel et al. 2005; Solé and Bascompte 2006; Scheffer et al. 2009; Pringle et al. 2010; Liu et al. 2012). For instance, spatial patterns increase productivity of mussel beds, compared to homogeneously distributed mussels (van de Koppel et al. 2005). In arid systems, patterned vegetation can concentrate and optimize water resources, increasing primary productivity (Pringle et al. 2010) and allowing vegetation to survive under aridity conditions that would otherwise be too stressful for its growth (Rietkerk et al. 2002). Self-organization is also predicted to promote species coexistence, increasing biodiversity (Nathan et al. 2013). Finally, spatial patterns affect ecosystem stability in various ways. On one hand, they increase the resilience of ecosystems to disturbance (Pascual and Guichard 2005; van de Koppel et al. 2005; Liu et al. 2014; de Paoli et al. 2017). On the other hand, patterned ecosystems are more vulnerable to sudden dramatic shifts towards an alternative, degraded ecosystem state once a tipping point in environmental stress is exceeded (Scheffer et al. 2001; Rietkerk et al. 2004b; Kéfi et al. 2010).

Despite the abundance of studies on self-organized patterning in natural ecosystems, most of the emergent effects of self-organization known so far focused on the biological properties, such as enhanced productivity or resilience to disturbances (van de Koppel et al. 2005; Pringle et al. 2010). While physical processes are often crucial and accounted for in these works, the biophysics of the system tend to be simplified (Rietkerk et al. 2002; van de Koppel et al. 2005). Consequently, the potential emergent effects of self-organization in terms of physical properties are generally overlooked.

Self-organization in geoscience

Despite of its prevalence in biological theory, self-organization is not as prevalent as a theoretical framework in geophysical studies (Rinaldo et al. 1993; Rigon et al. 1994; Rodríguez-Iturbe and Rinaldo 2001; Baas 2002). Organisms are considered mostly as a source of flow resistance. Benthic organisms (plants and animals) are generally assumed to increase surface roughness and dissipate energy of air or water flows (Corenblit et al. 2011), reducing flow speeds and promoting sediment deposition (Stallins and Parker 2003). For this reason, vegetation in fluvial and coastal environments (e.g. freshwater streams, dunes, marshes) is often parameterized through flow resistance (Nardin and Edmonds 2014), or as variations in bottom shear stress (D'Alpaos et al. 2005). Because it is regarded as a relatively static entity that does not grow or expand dynamically over time

(Marjoribanks et al. 2016), the effects that physical forcing in turn has on vegetation growth tend to be ignored. Field surveys (Cotton et al. 2006; Wharton et al. 2006) and models (Naden et al. 2006) started to account for changes in flow resistance due to seasonal variations in vegetation cover, but did not fully incorporate the two-way interactions. Hence, while the importance of biota for geomorphic processes has been increasingly recognized (Hickin 1984; Dietrich and Perron 2006; Corenblit et al. 2011), the existence of potential bio-physical feedback mechanisms and of emergent properties in relation to self-organization remains underexplored.

However, a few examples of models that include the reciprocal bio-physical interactions exist. Temmerman et al. (2007) showed that the interplay of vegetation expansion and hydrodynamics drives channel erosion and steers marsh formation and evolution. A similar modelling approach on salt marsh channel initiation is found in Schwarz et al. (2014). Kirwan and Murray (2007) developed a model of tidal marsh evolution that couples sediment transport processes with changes in vegetation biomass, showing that vegetated platforms maintain their elevation relative to rising sea level. Other models on the interactions between geomorphic processes and vegetation growth have highlighted their effects on landscape evolution (Baas 2002; Collins et al. 2004; Istanbulluoglu and Bras 2005; Baas and Nield 2007). Except these few rare cases, there seems to be a disciplinary division where engineers mostly focus on how vegetation affects roughness and decreases physical flows (Kouwen and Unny 1973; Järvelä 2002), and ecologists look at how physical forcing affects vegetation growth (Puijalon and Bornette 2006), morphology (Puijalon and Bornette 2004; Puijalon et al. 2005) and species composition (Riis and Biggs 2003; Franklin et al. 2008). To date, this remains a clear limitation of our understanding of the dynamic, two-way feedbacks between biological and physical processes.

Why are two-way interactions important for the emergent properties of ecosystems?

Interactions between biota and the landscape in which they live occur in a wide range of ecosystems (Dietrich and Perron 2006; Corenblit et al. 2011). Yet, it is unknown if the self-organization process arising from this interaction in turn has emergent effects on both *a)* physical and *b)* biological properties such as species interactions and biodiversity (Gilad et al. 2004). This knowledge gap is important because physical forcing is in itself an important control on biology (Corenblit et al. 2011), and can affect the emergent properties for the whole ecosystem. Physical forcing can determine the growth, expansion, community composition and structure of organisms (Franklin et al. 2008). Hence, without accounting for these dynamical interactions, our understanding of the ecosystem will be incomplete, and any prediction on the emergent properties of spatial patterns will be uncertain or unsupported (Liu et al. 2012). This aspect of the two-way interactions between biological and physical processes was studied using stream aquatic macrophytes as model system.

The model system: submerged aquatic macrophytes in streams

Effects of macrophytes on hydrodynamics and sedimentation

Submerged aquatic macrophytes are important foundation species in rivers and streams (Carpenter and Lodge 1986). They act as ecosystem engineers (Jones et al. 1994) and contribute to the functioning of fluvial ecosystems. They are a fundamental component of nutrient cycles, geochemical patterns and processes in rivers; they naturally purify water and soil, and provide food and refuges for many other species (e.g. fish, invertebrates) (Haslam 1978; Franklin et al. 2008). Macrophytes tend to grow aggregated into well-defined stands due to their interaction with water flow (Figure 1.1), leading to a pseudo-braided distribution on the scale of a stream reach (Dawson 1989; Sand-Jensen and Vindbœk Madsen 1992; Cotton et al. 2006). The interaction between hydrodynamics and individual patches of submerged aquatic macrophytes has been intensively studied (Sand-Jensen and Mebus 1996; Sand-Jensen 1998; Sukhodolov and Sukhodolova 2009). Flow velocities are locally reduced within the macrophyte patches, and accelerated outside of the patches (Schoelynck et al. 2012). Besides their effects on hydrodynamics, submerged macrophytes also locally increase sedimentation (Madsen et al. (2001); Figure 1.2). Sedimentation occurs both directly through effects on reducing water velocity, or indirectly through collision with leaves (Sand-Jensen 1998; Schulz et al. 2003; Hendriks et al. 2008; Peralta et al. 2008). Hence, aquatic macrophytes promote the deposition of finer, nutrient-rich sediment within their patches (Cotton et al. 2006; Wharton et al. 2006).

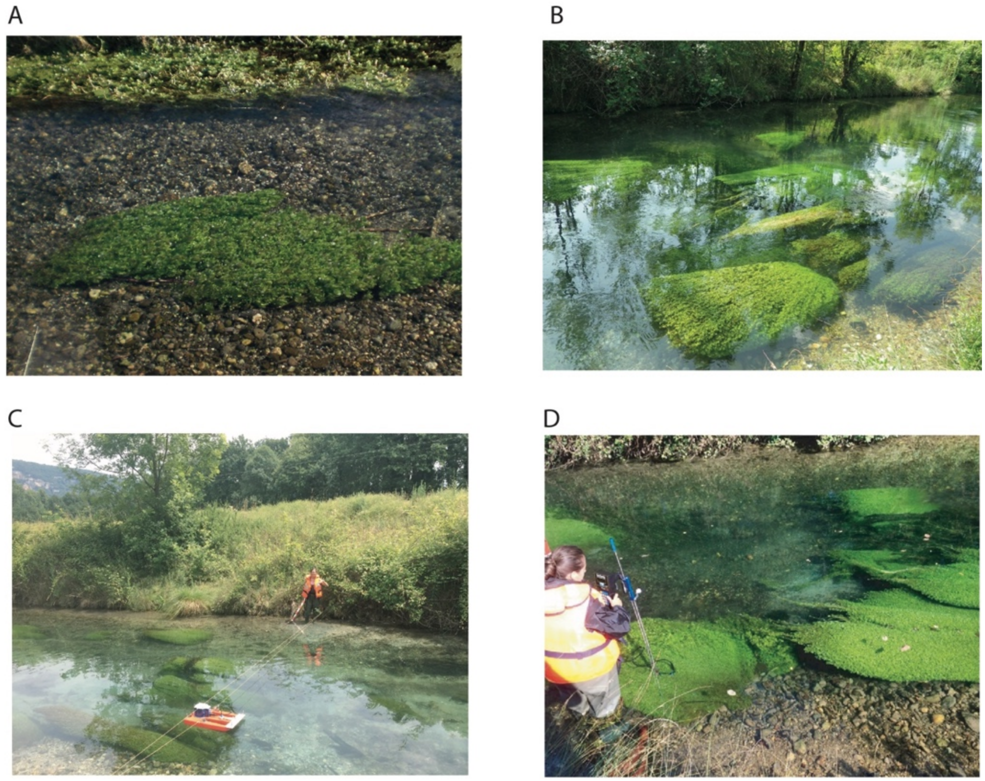

Figure 1.1: Patchy distribution of submerged freshwater macrophytes. (A) Patches of *Veronica anagallis-aquatica* (photo by Sofia Licci). (B – D) Stream reaches dominated by *Callitriche platycarpa.*

Effects of hydrodynamics and sedimentation on macrophytes

While aquatic macrophytes have strong effects on hydrodynamics and sedimentation, hydrodynamics and sedimentation also have important effects on macrophyte communities (Franklin et al. 2008). Currents and drag resulting from currents impose a mechanical stress that reduces plant growth (Puijalon et al. 2011) or establishment, by increasing the risk of plant uprooting at higher velocities (Riis and Biggs 2003). Many macrophyte species show high phenotypic plasticity and altered morphology in response to mechanical stress. For instance, plastic responses include size reduction with increasing hydrodynamic forces

(Puijalon and Bornette 2004; Puijalon et al. 2005; Puijalon and Bornette 2006), or adopting tolerance strategies in response to currents (Puijalon et al. 2011).

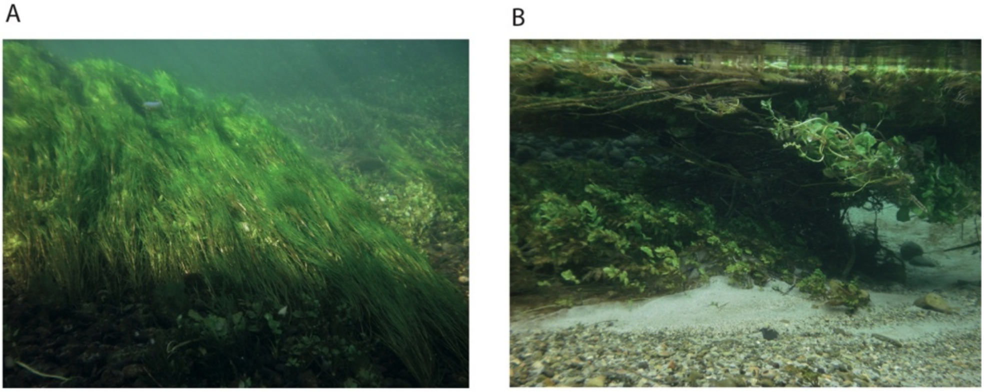

Figure 1.2: Submerged aquatic macrophytes in streams. (A) Patches of flexible submerged macrophytes bend down towards the stream bed when exposed to currents. (B) Fine sediment accumulation within vegetation patches. Photos by Sofia Licci.

Hydrodynamics can also lead to positive effects on macrophytes. Increased flow velocities and turbulence reduce the thickness of the boundary layer and can increase nutrient uptake rates (Thomas et al. 2000; Cornelisen and Thomas 2004; Morris et al. 2008; Bal et al. 2013). Moreover, hydrodynamics mediates the dispersal of seeds and vegetative fragments (hydrochory; Goodson et al. (2001); Goodson et al. (2003); Nilsson et al. (2010); Bornette and Puijalon (2011)). Next to direct hydrodynamic effects, sedimentation can also affect aquatic macrophytes (Madsen et al. 2001). The accumulation of finer, nutrient-rich sediment within the vegetation patches can be beneficial for plant growth (Madsen et al. 2001). On the other hand, high levels of organic matter accumulation have been found to become toxic for plants (Barko and Smart 1983).

With submerged macrophytes as a model system, I have examined the self-organization process arising from hydrodynamic-vegetation interactions. This process was studied in 5 key research questions outlined below.

Outline of the thesis

Self-organized spatial patterning in aquatic macrophytes results from the above-mentioned interactions between vegetation growth, hydrodynamics and sedimentation. By focusing on these reciprocal interactions, I investigate the emergent effects of self-organization of aquatic macrophytes on river flow regulation, biological interactions and resource uptake in a number of chapters (Figure 1.3). In these studies, I combine field and laboratory flume experiments, field observations and mathematical models, at a variety of scales, from the macrophyte patch scale (1 – 3 m) to that of a stream reach (30 – 100 m).

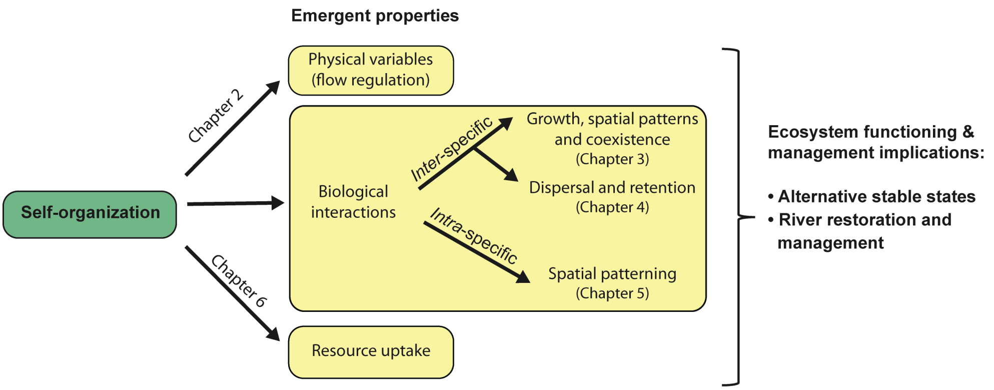

Figure 1.3: Diagram of the main research themes investigated in terms of self-organization and relation with the thesis chapters.

Chapter 2) Does self-organization of aquatic vegetation regulate hydrological variables?

Water flow velocities in rivers are a function of the balance between energy imposed by slope or discharge and the resistance imposed by the river bed. Conventional equations, relating discharge to flow velocity in a channel, assume vegetation cover to be static over time and presume a uni-directional effect of vegetation on water flow (Chow 1959). However, aquatic vegetation does not only influence water velocities, but is also controlled by it (Franklin et al. 2008; Bornette and Puijalon 2011; Puijalon et al. 2011). There is insufficient understanding of the feedbacks operating within the self-organization process in streams and their implications for ecosystem functioning. Understanding how this feedback affects hydraulic resistance is a key question for water regulation in rivers. In particular, there is a trade-off between sustaining water levels in periods of low discharge while managing flood risk.

RQ-chapter 2: *How does self-organization, emerging from the two-way interaction between plant growth and flow redistribution, affect stream hydrodynamic conditions (flow velocities and water levels)? What are the implications for ecosystem functioning and services?*

In this chapter, combining mathematical modelling with an empirical study, I investigate whether aquatic macrophytes are able to regulate flow velocities and water levels under varying discharges, and the implications of this plant-driven self-organization process for ecosystem services in streams.

Chapter 3) Does self-organization create a 'landscape of facilitation' through hydrodynamic heterogeneity?

Environmental heterogeneity plays a crucial role in the coexistence of species (Hutchinson 1953; Levin 1970; Koch 1974; Armstrong and McGehee 1976; Holt 1984; Tilman 1994; Amarasekare 2003). Yet, many ecosystems have limited abiotic heterogeneity but can still host a high number of species. As mentioned above, self-organization can create environmental heterogeneity, even if underlying abiotic conditions are homogeneous (Rietkerk and Van de Koppel 2008). Despite its importance in creating heterogeneity, it is still unknown whether self-organization can promote species coexistence through facilitation. While studies of facilitation focus on interactions between species, they do so only at a local scale (within the patch of the facilitator) (Callaway 1995; Padilla and Pugnaire 2006) or assuming that interactions are homogeneous in space. Instead, studies of self-organization consider these spatially-extended effects, but mostly focus on a single species. Thus, the link between self-organization and facilitation is still unclear. In streams, aquatic macrophytes with different morphologies increase hydrodynamic heterogeneity (Kemp et al. 2000; Gurnell et al. 2006). But the consequences of such plant-driven heterogeneity for interspecific interactions have not yet been explored in experimental or theoretical studies.

RQ-chapter 3: *What is the link between self-organization and facilitation? How do scale-dependent feedbacks under self-organization affect species coexistence and diversity in streams?*

In this chapter, I hypothesize that self-organized pattern formation can create a ‘landscape of facilitation’ that promotes plant species coexistence in streams, by providing new niches for species adapted to a wide range of hydrodynamic conditions. To test this hypothesis, I combined mathematical modelling with field observations of plant spatial aggregation and transplantation experiments.

Chapter 4) Stress-divergence feedbacks, do they matter for facilitation of dispersal and retention?

Divergence of physical stress such as water flow is a common mechanism underlying the self-organized, patchy distribution of foundation species in both fluvial (Schoelynck et al. 2012) and coastal (Van der Heide et al. 2010) aquatic ecosystems. Foundation species or ecosystem engineers create stable conditions for other species and provide much of the structure of a community (Dayton 1972; Jones et al. 1994), hence providing a facilitative interaction. However, despite their patchy distribution at the landscape scale, facilitation between species is usually studied at a local scale of individual patches (Callaway 1995; Padilla and Pugnaire 2006), along physical gradients (Bertness and Callaway 1994; Bertness and Leonard 1997) or in a non-spatial context assuming homogeneous distribution of the facilitator (McKee et al. 2007; Chang et al. 2008; Peterson and Bell 2012; Van der Stocken et al. 2015). It is currently unknown how the two-way interactions between plants and water flow, leading to vegetation patchiness, in turn affect facilitation during species dispersal and colonization.

Retention of plant propagules by existing vegetation is an important bottleneck for macrophyte establishment in streams (Riis and Sand-Jensen 2006;

Riis 2008). Water flow is both one of the main dispersal vectors of plant propagules (Nilsson et al. 2010) and the stress factor that leads to vegetation patchiness (Schoelynck et al. 2012). Water flow stress is an important factor because it can change the vertical structure (canopy architecture) of the vegetation (Schoelynck et al. 2013); if vegetation becomes less of an obstruction due to bending as flow velocity increases, it might trap less propagules. Hence, we aim to study how this water flow divergence mechanism affects propagule retention, which would potentially benefit macrophyte colonization.

RQ-chapter 4: *How do stress-divergence feedbacks in aquatic vegetation affect macrophyte propagule retention during dispersal? What is their relative role, compared with hydrodynamic stress and propagule traits?*

In Chapter 4, I tested the hypothesis that feedbacks between vegetation and water flow, leading to self-organization, are essential for propagule retention during dispersal and primary colonization. Therefore, I carried out flume and field release experiments to reveal the role of spatial vegetation patchiness, propagule traits and hydrodynamic stress on propagule retention.

Chapter 5) Intraspecific effects on patch occurrence: are they important for stream landscape pattern development?

Interactions between vegetation and hydrodynamics are widespread and crucial in many ecosystems (Leonard and Luther 1995; Madsen et al. 2001; Schulz et al. 2003; Bouma et al. 2007). However, while the interactions between existing patches are now relatively understood (Folkard 2005; Vandenbruwaene et al. 2011; Adhitya et al. 2014), we still have limited understanding of how an existing patch can influence the occurrence of others. Vegetation patches increase flow velocity in some adjacent areas, while reducing it directly downstream of the patch (Bouma et al. 2007; Chen et al. 2012; Schoelynck et al. 2012; Meire et al. 2014). As growth and seedling establishment can be challenging due to the physical stress of currents and drag (Vogel 1994; Schutten et al. 2005; Puijalon et al. 2008; Balke et al. 2011; Silinski et al. 2015), an existing patch may create optimal spots where plant occurrence is promoted due to drag reduction. However, it is currently unknown if existing spatial patchiness of macrophytes, resulting from the two-way interaction between vegetation and hydrodynamics, affects the processes of vegetation occurrence through intraspecific interactions. Hence, using submerged macrophytes as a model system, we address the following question.

RQ-chapter 5: *How does hydrodynamic heterogeneity created by existing vegetation patches affect the processes controlling vegetation occurrence? How does it influence long-term stream landscape patchiness?*

Here I tested the hypothesis that vegetation patches in streams organize themselves in V-shapes to minimize hydrodynamic and drag forces, resembling the flight formation adopted by migratory birds. This chapter combines field manipulations of patch inter-distance with temporal field surveys of patch formation to investigate how bio-physical interactions shape the way organisms position themselves in landscapes exposed to physical flows.

Chapter 6) Self-organized patterns: implications for physiological functioning

As mentioned above, feedbacks between vegetation and hydrodynamics are important for the evolution of many landscapes. The interaction between plants and hydrodynamics also mediates other ecosystem functions and processes, such as the uptake of resources by vegetation that is crucial for productivity (Thomas et al. 2000; Morris et al. 2008). While resource uptake has so far been studied mostly in monospecific canopies, natural landscapes are much more heterogeneous and composed of multiple species. Different plant species also show diverse traits that can have contrasting effects on hydrodynamics (Peralta et al. 2008; Bouma et al. 2013), and thereby on their access to resources.

Streams show a patchy distribution of vegetation (Dawson 1989; Sand-Jensen and Vindbœk Madsen 1992; Cotton et al. 2006). These patches can be a mixture of plant species with contrasting traits, which alter hydrodynamics differently (Adhitya et al. 2014). To date, we do not know how different species patches interact with each other to affect the delivery and uptake of resources between neighbouring patches, by altering hydrodynamic conditions. Hence, using patches of two submerged macrophyte species in a flume experiment, I explore the emergent effects of self-organized spatial patchiness due to species mixtures on resource uptake.

RQ-chapter 6: *What are the effects of spatial patchiness due to different species on resource (ammonium) uptake in streams? How does it translate to resource uptake at the channel scale?*

In Chapter 6, I investigate how patches of different species interact with each other by facilitating uptake of resources, through their effects on hydrodynamics. In a racetrack flume experiment combining hydrodynamic measurements and ^{15}N labelled ammonium incubations, I explore the effects of spatial patchiness due to multispecific canopies on ecosystem functions and services of nutrient load reduction.

Finally, in Chapter 7, I will summarize the main findings of my thesis and provide a discussion and perspective for future research. Specifically, I will focus on considering both ecological and physical emergent properties of self-organization, including species interactions in self-organization theory, and the implications of self-organization for resource use. I will then use my findings to provide an outlook on ecosystem functioning and management implications, focusing on alternative stable states and suggestions for river management and restoration.

Chapter 2

Plants regulate river flows and water levels through self-organization

L. Cornacchia, G. Wharton, G. Davies, R.C. Grabowski, S. Temmerman, D. van der Wal, T.J. Bouma, J. van de Koppel

Submitted

Abstract

The importance of vegetation in shaping terrestrial, tidal and fluvial landscapes through its effects on water flow is increasingly recognized. However, many current approaches fail to fully incorporate the interactive bio-physical feedbacks that characterize the interplay between vegetation and water flow. Through a combined mathematical modelling and empirical study, we demonstrate that feedback interactions between vegetation growth and flow redistribution in streams stabilize local flow velocities and reach-scale water levels under varying discharges. The interplay of vegetation growth and hydrodynamics results in a spatial separation of the stream into densely vegetated, low-flow zones divided by unvegetated channels of higher flow velocities. This self-organization process decouples both local flow velocities and water levels from the forcing effect of changing stream discharge. Field data from natural chalk streams support the model predictions and highlight two important stream-level emergent properties: vegetation controls flow conveyance in fast-flowing channels throughout the annual growth cycle, and maintains sufficient water levels to sustain a diverse stream community. Our results provide evidence for an important link between plant-driven self-organization processes characteristic of natural streams and the ecosystem services these streams provide in terms of flow velocity and water level regulation, and maintenance of habitat diversity.

The importance of vegetation in affecting water and air flow and shaping physical landscapes has been widely recognized (Dietrich and Perron 2006; Corenblit et al. 2011). Mountain and hillslope vegetation affect surface runoff, river discharge, erosion rates and the resulting landscape morphology (Collins et al. 2004; Istanbulluoglu and Bras 2005); vegetation steers tidal landscape development (Temmerman et al. 2007; Nardin and Edmonds 2014; Kearney and Fagherazzi 2016) and dune formation (Baas and Nield 2007); and in-stream, riparian and floodplain plants affect the processes and forms of alluvial rivers (Tal and Paola 2007; Gibling and Davies 2012; Gurnell 2014). Water flow velocities in rivers are a function of the balance between energy imposed by slope or discharge and the resistance imposed by the river bed. Within rivers, submerged and marginal aquatic vegetation imparts a resistance to water flow (Green 2005) that affects water velocities in the channel (Sand-Jensen 1998; Cotton et al. 2006; Wharton et al. 2006). Conventional models, relating river discharge to flow velocity, assume vegetation to be an independent resistance factor restricting water flow (Chow 1959). Here, vegetation cover is regarded as a static entity, presuming a uni-directional effect of vegetation on water flow. However, aquatic vegetation is also controlled by water flow; water velocity dictates the presence, density and species composition of aquatic vegetation communities (Franklin et al. 2008; Puijalon et al. 2011). Field surveys (Cotton et al. 2006; Wharton et al. 2006) and models (Naden et al. 2006) have highlighted the impact of seasonal variation in vegetation cover in streams on local water velocities, but often ignore the two-way interaction in the process. Aquatic vegetation typically grows as monospecific patches within streams (Franklin et al. 2008) with a patterning caused by self-organization processes emerging from the divergence of water around vegetation patches (Schoelynck et al. 2012). Self-organization is an important regulating process in several ecosystems (Rietkerk and Van de Koppel 2008), but there is insufficient understanding of the implications of self-organization induced by the interaction between plant growth and water flow for the functioning of stream ecosystems, both in biological and physical terms. Specifically, how this feedback affects hydraulic resistance is a key question for water regulation in rivers in particular the trade-off between sustaining water levels in periods of low discharge while managing flood risk.

In this paper, we combine mathematical modelling and field measurements to reveal how feedback mechanisms between plants and river discharge control flow velocity and water level in stream environments. We present a model that describes the interplay of plant growth and hydrodynamics within a spatially heterogeneous vegetated stream, in which the discharge varies gradually over the year. With this model, we explore how self-organization processes that emerge from this interaction create heterogeneity in plant biomass and water flow, and how in turn this affects stream hydrodynamic conditions. We model an “abstract” stream where we adopt a simplified setting of a single channelized flow area in between two vegetated areas, and focus on the lateral adjustment of the effective width of the channel in response to changing discharge (Figure 2.1A). By only including the essential aspects of the coupling between hydrodynamics and vegetation, our model allows us to investigate the key process of flow velocity and water level regulation by macrophytes. Plant growth is described in the model using the logistic growth equation, and plant mortality due to hydrodynamic stress is assumed to increase linearly with net water velocity (Temmerman et al. 2007). We assume that the lateral expansion of plants through clonal growth can be described by a random walk, and we therefore apply a diffusion approximation (Holmes et al. 1994). Water flow is modeled using depth-averaged shallow water equations in non-conservative form. The effects of friction exerted by the bed and vegetation on flow velocity are represented by the Chézy coefficient, following the approach of Baptist et al. (Baptist et al. 2007), slightly modified to account for bending of flexible submerged macrophytes in response to increased water flow (Verschoren et al. 2016). To test the model predictions on flow regulation by macrophytes, we use field measurements of seasonal variations in macrophyte cover, discharge, water levels and spatial patterns of flow velocities within and around vegetation in two baseflow-dominated chalk streams with seasonal variations in discharge and low flashiness. One was dominated by mixed submerged and emergent vegetation, and the other by submerged vegetation (see Methods).

Our model analysis reveals that the feedback between vegetation growth and local flow velocity creates a self-organization process that allows vegetation cover to readjust in response to changes in discharge (see bifurcation analysis in *Supplementary Information* S1 and Figure 2.4; *Supplementary Information* S2 and

Figure 2.5). At low discharge, the entire stream is homogeneously vegetated (Figure 2.1A). When discharge increases, the stream bifurcates into two spatially separated zones. One is characterized by low to zero vegetation biomass and high flow velocities in the middle of the stream, and the other by high biomass and low flow velocities at the edges of the stream. This is caused by a scale-dependent effect of vegetation on hydrodynamics where increased flow resistance locally reduces flow velocities in the vegetated regions, while water flow is diverted and concentrated outside of the vegetation, thereby inhibiting its expansion. Model predictions generally agree with experimental evidence of the flow divergence effect of vegetation patches (Vandenbruwaene et al. 2011; Schoelynck et al. 2012). With gradually increasing discharge, the area of channelled flow progressively increases and the vegetated portions decrease as plants are uprooted, due to the self-organized adjustment of vegetation cover, until no vegetation can persist and the entire stream becomes unvegetated (Figure 2.1A). The resulting inverse relationship between incoming flow discharge and vegetation cover (Figure 2.1B) is confirmed by the negative relationship observed in the field for both study sites showing that vegetation cover decreases with increasing discharge ($r^2 = 0.77$, $p < 0.0001$, Figure 2.1C) in response to the seasonal pattern of changing hydrology and vegetation growth and die-back.

Our model highlights a number of important properties resulting from self-organizing interaction between vegetation growth and water flow. First, the model predicts that local flow velocities both within the vegetation and in the unvegetated channelled flow area are relatively constant despite changes in discharge (Figure 2.2A). This stability in local flow velocities is the consequence of the adjustment of vegetation cover to increases in overall water discharge, with vegetation expanding when discharge and flow velocities in the channelled area decrease, and retreating due to uprooting when discharge and flow velocities increase. Vegetation readjustment thereby buffers for enhanced water flow velocities that would otherwise result from an increase in discharge (Figure 2.2A). These predictions are supported by field data at the two study sites. Flow velocities within and between vegetation patches are buffered almost completely against changes in discharge. In comparison, when averaged over the cross-section, water velocities show a much stronger response to discharge variations, as a larger volume of water is passing through the channel. However, since the area covered by vegetation decreases with increasing discharge, the widened, high-flow section of the stream accommodates the increased discharge and a four-fold increase in discharge produces only a slight increase in local velocities (Figure 2.2B & C; further details in *Supplementary Information* S3 and Figure 2.6).

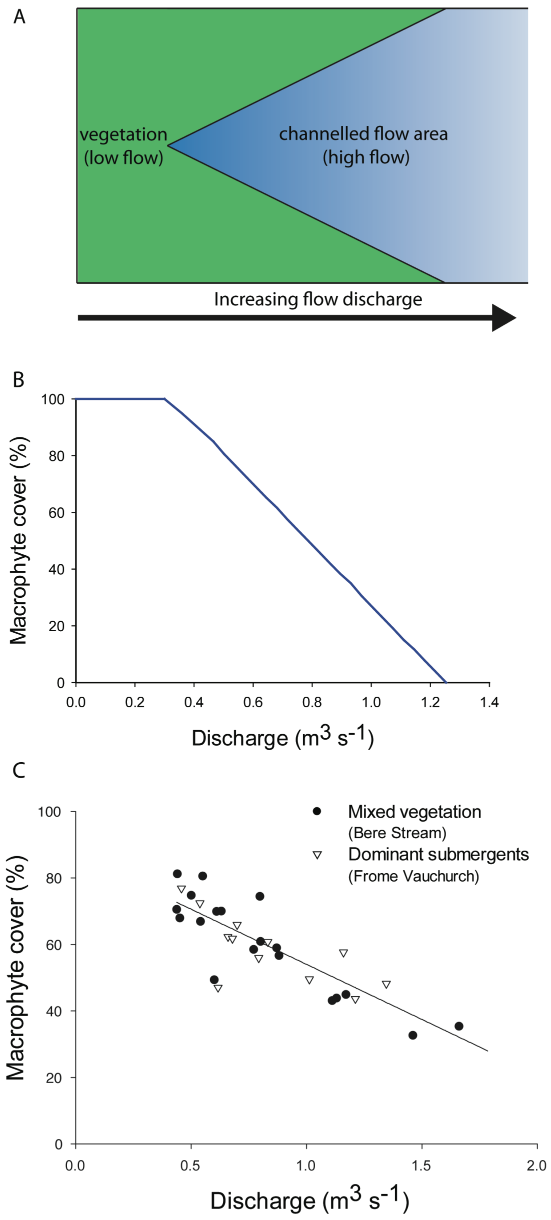

Figure 2.1: Relationship between discharge and macrophyte cover in the model and in two chalk streams. (A) Schematic diagram of the "abstract" stream simulated in the model: the proportion of the stream cross-section that is vegetated adjusts in response to changes in water discharge. In the model, at very low discharge, the entire stream cross-section is homogeneously vegetated. As discharge increases, the stream becomes spatially separated into densely vegetated, low-flow zones, and low-density, high-flow zones; vegetation cover decreases until the stream becomes entirely unvegetated. (B) Relationship between modelled percentage macrophyte cover (fraction of vegetated cells over the whole simulated domain) and discharge. (C) Relationship between macrophyte cover and river discharge as found in the field for both study sites (N = 31) ($r^2 = 0.77$, $p < 0.0001$).

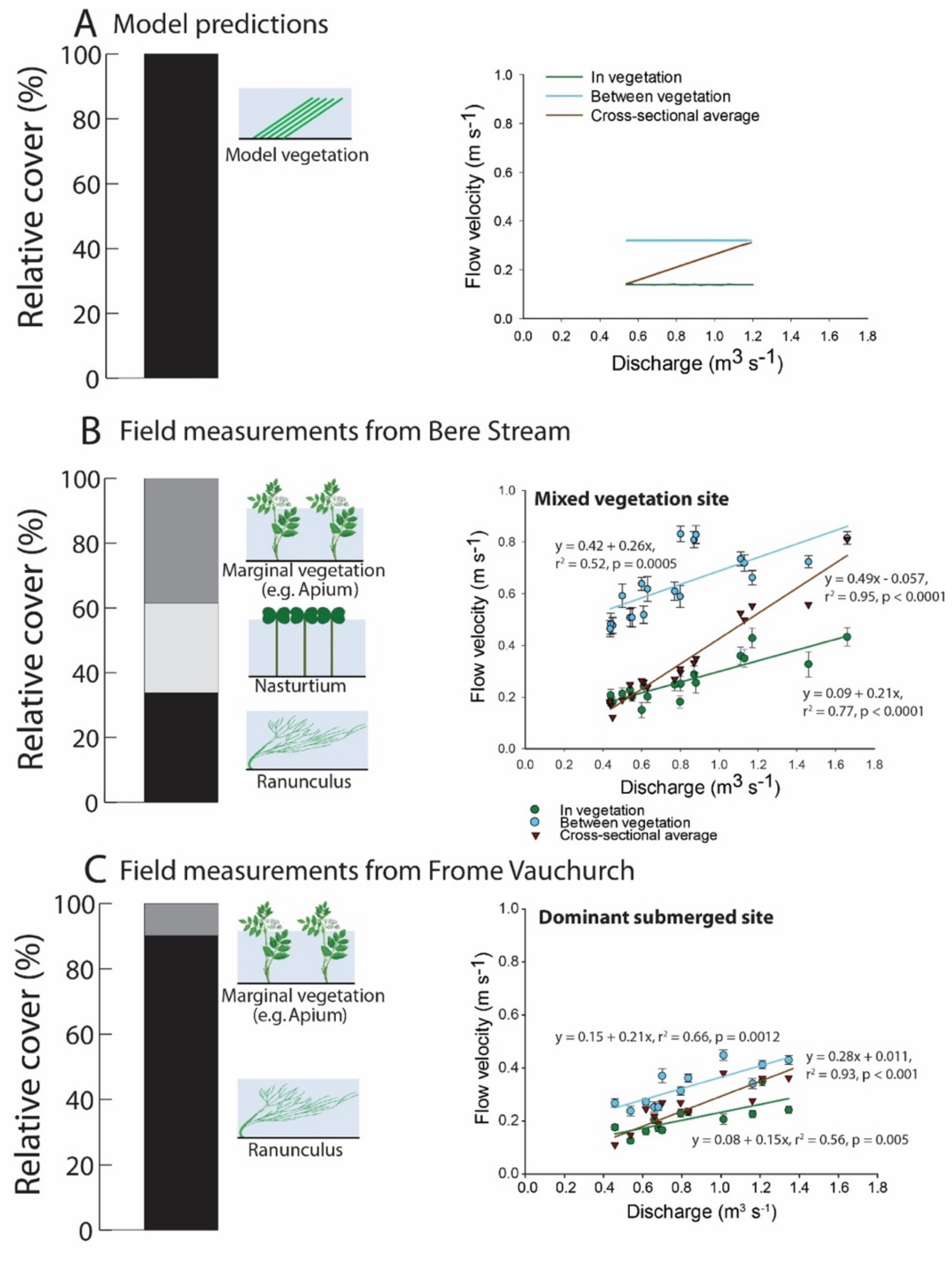

Figure 2.2: (Continued on the following page.)

Figure 2.2: Relationship between discharge and flow velocity in the model and in two chalk streams. (A) *Left:* Schematic representation of the flexible submerged aquatic vegetation considered in the model. *Right:* Model predictions of average flow velocities (m s^{-1}) for increasing values of discharge, calculated within vegetated and unvegetated sections of the channel, and compared with cross-sectional average flow velocities. (B) *Left*: Species composition, expressed as relative macrophyte cover (%) per vegetation type, at the peak of the growing season (July 2008): marginal vegetation (e.g. *Apium*, emergent along the margins), *Nasturtium* (emergent along the margins) and *Ranunculus* (submerged, growing in mid-channel). *Right*: relationship between flow discharge (m^3 s^{-1}) and flow velocity (m s^{-1}) in both vegetated and unvegetated river portions in the mixed vegetation site, compared with the cross-sectional average flow velocity in the stream. (C) *Left:* Species composition, expressed as relative macrophyte cover (%) per vegetation type, at the peak of the growing season (July 2008): marginal vegetation (e.g. *Apium*, emergent along the margins) and *Ranunculus* (submerged, growing in mid-channel). *Right:* relationship between flow discharge (m^3 s^{-1}) and flow velocity (m s^{-1}) in both vegetated and unvegetated river portions in the dominant submerged site, compared with the cross-sectional average flow velocity in the stream.

A second emergent property emanating from the two-way interaction between water flow and vegetation growth is that water levels in the channel are maintained at constant level despite changes in discharge (Figure 2.3A). By increasing hydraulic roughness, vegetation raises water levels compared to an unvegetated stream for a given discharge. This effect is most pronounced at low discharge, where water levels are significantly higher in fully vegetated streams compared to unvegetated streams. As discharge increases, however, vegetation cover decreases, producing strikingly constant water levels, whereas water levels would steadily increase in a homogeneously vegetated channel (Figure 2.3A). These predictions are confirmed by our field measurements of mean water levels from both study sites (Figure 2.3B). In the 'mixed vegetation' site, water levels were on average 0.28 ± 0.04 m, and only increased slightly with discharge, but much less than what would be experienced in an unvegetated stream ($r^2 = 0.54$, $p = 0.0003$; Figure 2.3B). In the River Frome, the site with predominantly submerged plants, water levels were on average 0.39 ± 0.07 m, and did not significantly increase with discharge ($r^2 = 0.06$, $p = 0.44$; Figure 2.3B), in agreement with model predictions. Thus, for both study sites the largest effect of vegetation in raising water levels, relative to an unvegetated stream, occurs at low discharges.

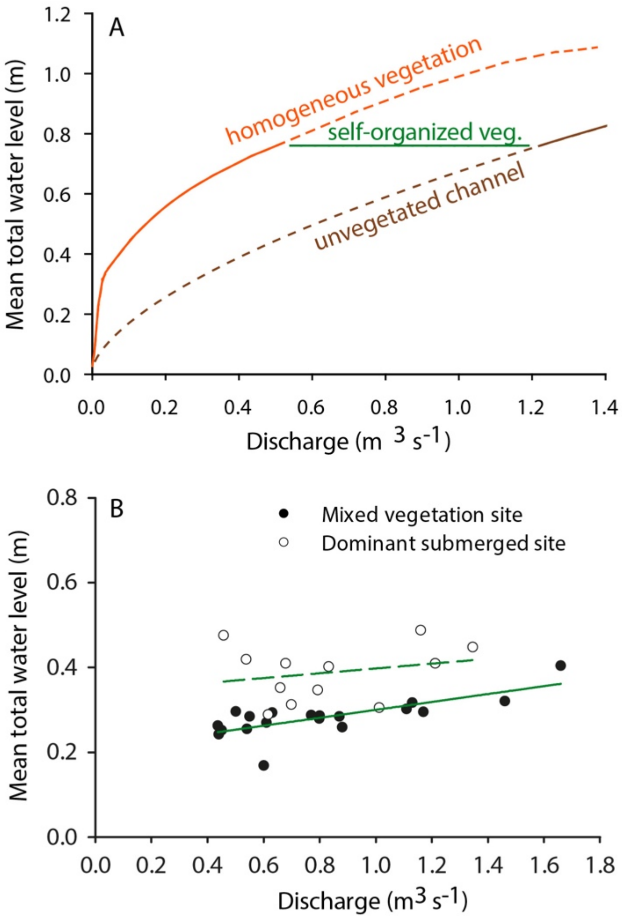

Figure 2.3: Relationship between discharge and mean total water level in the model and in two chalk streams. (A) Model predictions on the relationship between flow discharge (m^3 s^{-1}) and water level (m) in the simulated channel with vegetation homogeneously distributed over the channel bed (*orange line*), with self-organized vegetation (*green line*) and without vegetation (*brown line*). Solid lines indicate the dominant state over the range of discharge, and dashed lines indicate the relationship outside that range. (B) Field measurements on the relationship between flow discharge (m^3 s^{-1}) and mean total water level (m) in the 'mixed vegetation' (*solid green line*) and 'dominant submerged' (*dashed green line*) study sites.

The two-way interaction between water flow and plant growth has important implications for the functioning of the stream as an ecosystem, facilitating biodiversity. By buffering variations in local water flow velocities, vegetation maintains both low-flow-velocity and high-flow-velocity habitats within individual reaches. This self-organized heterogeneity facilitates ecosystem resilience to discharge variations and stream biodiversity (Wharton et al. 2006; Stein et al. 2014), by maintaining a wide range of mesohabitats that provide high-flow areas for feeding and spawning, adjacent to sheltered low-flow areas for nursery, resting and refuge from predation. Moreover, by preserving reach-scale water depths, water temperatures are lowered and can hold greater dissolved oxygen levels (Carpenter and Lodge 1986), and the maintenance of high-flow velocities increases the turbulent diffusion of atmospheric oxygen into the water. Thus, the survival of a wide range of aquatic and riparian organisms is facilitated. This is crucially important during low summer discharge, where there might otherwise not be sufficient water levels to maintain a functioning aquatic community (Hearne and Armitage 1993; Wharton et al. 2006). Finally, the creation of fast flowing areas in between the vegetation maintains flow conveyance and avoids flood risks when in-stream macrophyte growth is abundant, ensures sediment conveyance, maintains river bed permeability by reducing the ingress of fine sediments into river beds (Wharton et al. 2017), and keeps a clean gravel bed as spawning ground for fish (Kemp et al. 2011). Hence, the feedback between water flow and plant growth crucially sustains a wide range of ecosystem services under a variable discharge regime.

Our model results further highlight two additional important biological implications of the flow regulation process resulting from self-organization. *First*, our model predictions indicate that the self-organized vegetation pattern allows vegetation to persist over a wider range of discharge than if it were homogeneously distributed throughout the river bed. Moreover, within a certain range of discharge, the system has two stable states, one where vegetation is patterned and a bare state where vegetation cannot survive (see *Supplementary Information* S1 and Figure 2.4). Hence, removal of vegetation due to human activity or natural disturbances under conditions of high discharge might shift the system towards the alternative unvegetated state, from which vegetation recovery is slow or severely hindered unless discharge is significantly reduced. A *second* implication of our results is that self-organized pattern formation strongly increases macrophyte resilience compared to homogeneously vegetated streams, in terms of a faster recovery of vegetation biomass following for instance a disturbance imposed by strong discharge variations (see *Supplementary Information* S4 and Figure 2.7). This enhanced resistance and resilience of stream ecosystems resulting from self-organization processes is highly important in the light of global change. Intensification of rainfall (Houghton et al. 2001) in combination with land use change in river catchments (Foley et al. 2005; Palmer et al. 2008) may alter hydrologic partitioning and surface runoff, imposing increasingly stressful and variable discharge conditions to stream ecosystems.

Our results, therefore, lead to important considerations for the management of stream ecosystems. In current maintenance strategies, abundant vegetation growth is typically regarded as an obstacle that decreases the capacity of these streams for water conveyance in response to high discharge, with the risk of overbank flooding being increased by vegetation growth and rising water levels (Franklin et al. 2008; Sukhodolov and Sukhodolova 2009). This risk is present in surface runoff-dominated streams, but our study provides a very different perspective and evidence for the value of vegetation in groundwater-fed systems that are characterized by more subtle changes in water discharge. Here, the vegetation itself – through its two-way interaction with hydrodynamics – prevents "choking" of water ways and maintains sufficient water levels for the aquatic ecological community at low discharge. Hence, there might be a need to reconsider current management paradigms for natural streams, where vegetation is appreciated for its regulating functions, and considered an important component of the adaptive capacity of stream ecosystems.

The process of water flow diversion within self-organizing ecosystem is not unique to streams. Similar self-organization processes govern salt marsh pioneer vegetation (Temmerman et al. 2007; Vandenbruwaene et al. 2011), diatom-covered tidal flats (Weerman et al. 2010), and flow-governed peat land ecosystems (Larsen et al. 2007; Rietkerk and Van de Koppel 2008). This points at the universal emergent properties that result from the interplay of vegetation, water flow and drainage, shaping the adaptive capacity of fluvial and intertidal ecosystems and the services these ecosystems deliver in terms of supporting biodiversity. With the current rates of climate change threatening ecosystems worldwide and potentially increasing the frequency and intensity of extreme rainfall events, increased insight into the emergent, regulating properties of spatial self-organization in ecosystems and an understanding of their role in ecosystem resilience will be essential to help maintain these ecosystems in a future governed by global change.

Materials and Methods

Model description

To study how vegetation affects flow velocity and water levels in streams, we constructed a spatially-explicit mathematical model of the interplay of plant growth and water flow through a heterogeneously vegetated stream. The model consists of a set of partial differential equations, where one equation describes the dynamics of plant density (*P*), and where water velocity and water level are described using the shallow water equations. The choice of this type of mathematical model was made to maintain an as-simple-as-possible formulation that yet maintains an essential description of the feedback between hydrodynamics and vegetation dynamics in terms of growth, mortality and vegetative reproduction by lateral expansion.

The rate of change of plant biomass P [g DW m^{-2}] in each grid cell is described by:

$$\frac{\partial P}{\partial t} = rP\left(1 - \frac{P}{k}\right) - m_W P|u| + D\frac{\partial^2 P}{\partial x^2} \tag{2.1}$$

Here, plant growth is described using the logistic growth equation, where r [day^{-1}] is the intrinsic growth rate of the plants and k [g DW m^{-2}] is the plant carrying capacity, that indirectly reflects the mechanisms of nutrient and light competition between the plants (see Franklin et al. (2008) for a review of the main factors controlling macrophyte growth and survival). Plant mortality caused by hydrodynamic stress is modelled as the product of the mortality constant m_W [-] and net water speed $|\boldsymbol{u}| = \sqrt{(u^2 + v^2)}$ [m s^{-1}] due to plant breakage or uprooting at higher velocities (Riis and Biggs 2003; Temmerman et al. 2007; Franklin et al. 2008). We assume that the lateral expansion of plants through clonal growth can be described by a random walk, and we therefore apply a diffusion approximation, where D [m^2 day^{-1}] is the diffusion constant of the plants (Holmes et al. 1994).

Water flow is modeled using depth-averaged shallow water equations in non-conservative form (Vreugdenhil 1989). To determine water depth and speed in both *x* and *y* directions we have:

$$\frac{\partial u}{\partial t} = -g\frac{\partial H}{\partial x} - u\frac{\partial u}{\partial x} - v\frac{\partial u}{\partial y} - \frac{g}{C_d^2}u\frac{|u|}{h} \qquad \textbf{(2.2)}$$

$$\frac{\partial v}{\partial t} = -g\frac{\partial H}{\partial y} - u\frac{\partial v}{\partial x} - v\frac{\partial v}{\partial y} - \frac{g}{C_d^2}v\frac{|u|}{h} \qquad \textbf{(2.3)}$$

$$\frac{\partial h}{\partial t} = -\frac{\partial}{\partial x}(uh) - \frac{\partial}{\partial y}(vh) \qquad \textbf{(2.4)}$$

where u [m s^{-1}] is water velocity in the streamwise (x) direction, v [m s^{-1}] is the water velocity in the spanwise (y) direction, H [m] is the elevation of the water surface (expressed as the sum of water depth and the underlying bottom topography), h [m] is water depth and C_d [$m^{1/2}$/s] is the Chézy roughness coefficient due to bed and vegetation roughness. The effects of bed and vegetative roughness on flow velocity are represented by determining hydrodynamic roughness characteristics for each cover type separately using the Chézy coefficient, following the approach of Straatsma and Baptist (2008) and Verschoren et al. (2016).

The Chézy coefficient within the unvegetated cells of the simulated grid, which we will refer to as C_b in this paper, is calculated using Manning's roughness coefficient through the following relation:

$$C_b = \frac{1}{n}h^{1/6} \qquad \textbf{(2.5)}$$

where n [s/$m^{1/3}$] is Manning's roughness coefficient for an unvegetated gravel bed channel and h [m] is water depth.

The Chézy coefficient for each grid cell occupied by submerged vegetation, which we will refer to as C_d, is calculated using the equation of Baptist et al. (2007) and slightly modified by Verschoren et al. (2016) to account for reconfiguration of flexible submerged macrophytes. Due to the important feedback effects taking place between macrophyte growth and flow velocity (Franklin et al. 2008), we link the hydrodynamic and plant growth model by relating wetted plant surface area to plant biomass, to express vegetation resistance as:

$$C_d = \sqrt{\frac{1}{C_b^{-2} + (2g)^{-1}\, D_c A_w}} + \frac{\sqrt{g}}{k_v} \ln \frac{h}{H_v} \qquad \textbf{(2.6)}$$

where C_b [$\mathrm{m}^{1/2}$/s] is the Chézy coefficient for non-vegetated surfaces (Eq. 2.5), g is acceleration due to gravity (9.81 m s^{-2}), D_c [-] is a species-specific drag coefficient, A_w [m^2 m^{-2}] is the wetted plant surface area (total wetted surface area of the vegetation per unit horizontal surface area of the river (Sand-Jensen 2003; Verschoren et al. 2016)), directly related to plant biomass P through the empirical relationship described for *Ranunculus* in Gregg and Rose (1982), k_v is the Von Kármàn constant (0.41 [-]), and H_v [m] is the deflected vegetation height (further defined below). The equation proposed by Baptist et al. (2007) has been identified as one of the best fitting model to represent the effects of vegetation on flow resistance, for both artificial and real (submerged and emergent) vegetation (Vargas-Luna et al. 2015). However, Eq. (2.6) becomes undefined at low vegetation biomass, therefore we used Eq. (2.5) in all grid cells where biomass P fell below a certain threshold value (see *Supplementary Information* S5 and Figure 2.8 for the identification of the threshold). Deflected vegetation height varies as a function of incoming flow velocity, due to the high flexibility of submerged aquatic vegetation and reconfiguration at higher stream velocities (Sand-Jensen 2003; Schoelynck et al. 2013). Following the approach of Verschoren et al. (2016), H_v is calculated within each vegetated grid cell as the product of shoot length L [m] and the sine of the bending angle α [degrees] (Table 2.1), using an empirical relationship between bending angle and incoming current velocity based on flume experiments performed on single shoots of *Ranunculus penicillatus* (Bal et al. 2011b). In our model, bending angle of a single shoot is used to represent the bending angle of a whole patch, as plants located at the leading edge tend to push the whole canopy towards the stream bed. However, bending of the vegetation in a patch with multiple shoots can be expected to decrease with increasing along-stream distance within the patch, due to flow deceleration effects of the vegetation. Table 2.1 provides an overview of the parameter values used, their interpretations, units and sources. We were able to obtain parameter values from the literature for all parameters except for r, m_W and D, which were estimated based on plausible values. Sensitivity analyses revealed that changes in these parameter values resulted in quantitative but not qualitative changes in model behaviour.

Study sites

Two chalk stream reaches within the Frome-Piddle catchment (Dorset, UK) were chosen for a two-year survey of macrophyte growth and flow velocity patterns. The two study reaches were selected in order to provide a comparison in terms of species richness of aquatic macrophyte cover. One site was selected for its richness in macrophyte cover, while the other was dominated by *Ranunculus* stands. The study reaches were straight sections of 30 m long by 7-9 m wide. In the Bere Stream ('mixed vegetation site') the dominant in-channel aquatic macrophyte was water crowfoot (*Ranunculus penicillatus* subsp. *pseudofluitans*), represented in both floating-leaved and submergent forms. The stream margins were mainly colonized by the emergent macrophyte *Nasturtium officinale* (watercress) in similar proportions (bar plot in Figure 2.2B). Other macrophyte species, such as *Apium nodiflorum* and *Callitriche* sp., were also present in the channel in sparser stands. In the River Frome ('dominant submerged site'), *Nasturtium* was not found and *Ranunculus* was the dominant in-stream macrophyte, representing more than 80% of the total macrophyte cover (bar plot in Figure 2.2C).

Table 2.1: Symbols, interpretations, values, units and sources used in the model simulation.

Symbol	Interpretation	Value	Unit	Source
r	Intrinsic growth rate of plants	1	day^{-1}	Estimated
k	Carrying capacity of plants	200	g DW m^{-2}	Sand-Jensen and Mebus (1996)
m_W	Plant mortality coefficient due to water shear stress	10	Dimensionless	Estimated
D	Diffusion rate of plants	0.00085	$\text{m}^2\ \text{day}^{-1}$	Estimated
n	Manning's roughness coefficient for unvegetated gravel bed	0.025	$\text{s/[m}^{1/3}]$	Arcement and Schneider (1989)
D_c	Drag coefficient	0.5	Dimensionless	Naden et al. (2004)
A_w	Wetted plant surface area	$(814.8 * (P) - 25.05) * 0.0001$	$\text{m}^2\ \text{m}^{-2}$	Gregg and Rose (1982)
α	Plant bending angle	$15.5 * \lvert\boldsymbol{u}\rvert^{-0.38}$	degrees	Bal et al. (2011b)
L	Shoot length	0.5	m	Bal et al. (2011b)

Note: P is plant biomass [g DW m^{-2}]; u is water velocity in the streamwise (x) direction [m s^{-1}]; v is water velocity in the spanwise (y) direction [m s^{-1}].

Field measurements

The two study reaches were mapped throughout two annual growth cycles (July 2008 – July 2010). Field surveys were conducted monthly from July 2008 to July 2009, and bimonthly until July 2010. During each survey, macrophyte distribution and hydrodynamic conditions were mapped along transects that were located at 1-m distance intervals along the 30-m long study reaches. Along each transect, measurement points were located at 0.5 m intervals to measure water depth, macrophyte presence and species, and water flow velocities (m s^{-1}). Total water depth was measured as the depth between the water surface and the surface of the gravel bed, using a reinforced meter rule. The velocity in each position was measured down from the water surface at 60% of the total flow depth with an electromagnetic flow meter (Valeport Model 801) for 30 seconds, to have an estimate of the depth-averaged flow velocity in the water column (Dingman 1984). The average flow velocities for the vegetated and unvegetated sections of the channel were calculated for each survey month, based on the cover type of each measurement point. The relationship between discharge and cross-sectional average velocities were calculated for each survey month as the ratio between the measured discharge (m^3 s^{-1}) and the cross-sectional area (m^2). For comparison, in the main text we present a subset of the monthly measurements from the ‘dominant submerged’ site that fall within the same range of discharge as the ‘mixed vegetation’ site. The full dataset is provided in *Supplementary Information* S3 and Figure 2.6.

Statistical analyses

The mean vegetated and unvegetated flow velocities for each survey month were compared using Kruskal-Wallis one-way tests. The correlations between channel discharge and mean total water level, and between discharge and vegetated and unvegetated flow velocities in the ‘mixed vegetation’ site, were tested with a linear regression model. The correlation between channel discharge and vegetated and unvegetated flow velocities in the ‘dominant submerged’ site was tested with piecewise regression.

Numerical implementation

We investigated vegetation development with two-dimensional numerical simulations using the central difference scheme on the finite difference equations. The simulated area consisted of a rectangular grid of 60 × 30 cells, to simulate a straight channel with rectangular cross-sectional shape and initial bed slope of 0.09 m m^{-1}. Simulations were started by specifying an initial value of inflowing water speed for the streamwise water flow in the x direction and assuming constant flux. The boundary condition downstream was a constant discharge. Periodic boundary conditions were adopted in the cross-stream (y) direction. As flow redistribution processes mostly occur in the cross-stream direction, we assumed that lateral expansion of vegetation would be mainly affected in the direction across, rather than along, the channel. Therefore, we did not account for variation in vegetation cover in the streamwise direction: at the beginning of each simulation, vegetation was set to occupy a fixed amount of the channel bed, in the form of two bands located along the channel margins and each occupying 1/3 of the cross-section.

Appendix 2.A: Supplementary text on model analyses and field measurements

S1 Bifurcation analysis

Our model demonstrates that spatial separation of vegetation into high- and low-density areas is strongly dependent on the water discharge in the stream as a whole. Results of bifurcation analysis with respect to discharge predicts that at low discharge levels, a stable homogeneous equilibrium exists where the entire stream is vegetated (*red line* in Figure 2.4). At this equilibrium, vegetation biomass decreases linearly with increasing discharge, Q, until plants disappear at $Q \geq 0.85$ m^3 s^{-1}. However, at a threshold level QT_1 ($Q = 0.55$ m^3 s^{-1}), the homogeneous equilibrium becomes unstable to spatially heterogeneous perturbations, leading to spatial separation into two zones, one characterized by low vegetation biomass and high flow velocities in the middle of the stream, and one by high biomass and low flow velocities at the edges of the stream. The point QT_1 is the point beyond which the stable heterogeneous pattern of spatial separation develops, similarly to a Turing instability point. Beyond the second point QT_2 ($Q = 0.85$ m^3 s^{-1}), spatial separation into low- and high-biomass zones is needed for vegetation to persist. From the bifurcation points, unstable nonhomogeneous equilibria originate which link up to a stable nonhomogeneous equilibrium. In this stable nonhomogeneous equilibrium (*solid green line* in Figure 2.4), plant cover can persist for a much wider range of discharge values, far beyond the value where homogeneously distributed plants would disappear (QT_2). The stable nonhomogeneous equilibrium exists until the limit point LP ($Q = 1.22$ m^3 s^{-1}), beyond which no vegetation can persist and only a homogeneous state without plants is found. An unstable nonhomogeneous equilibrium occurs within $0.85 < Q < 1.22$ m^3 s^{-1} (*dotted green line* in Figure 2.4). Between these values of discharge, two alternative stable states are found, one characterized by spatial separation of vegetation into high- and low-biomass areas, and the other where vegetation cannot survive. In the graph, the dotted green line represents the threshold biomass under which plant cover will collapse. In general, the model predicts that plant density is higher in the heterogeneous state compared to the homogeneous situation (*green line* vs. *red line* in Figure 2.4), for all parameter values where spatial separation occurs.

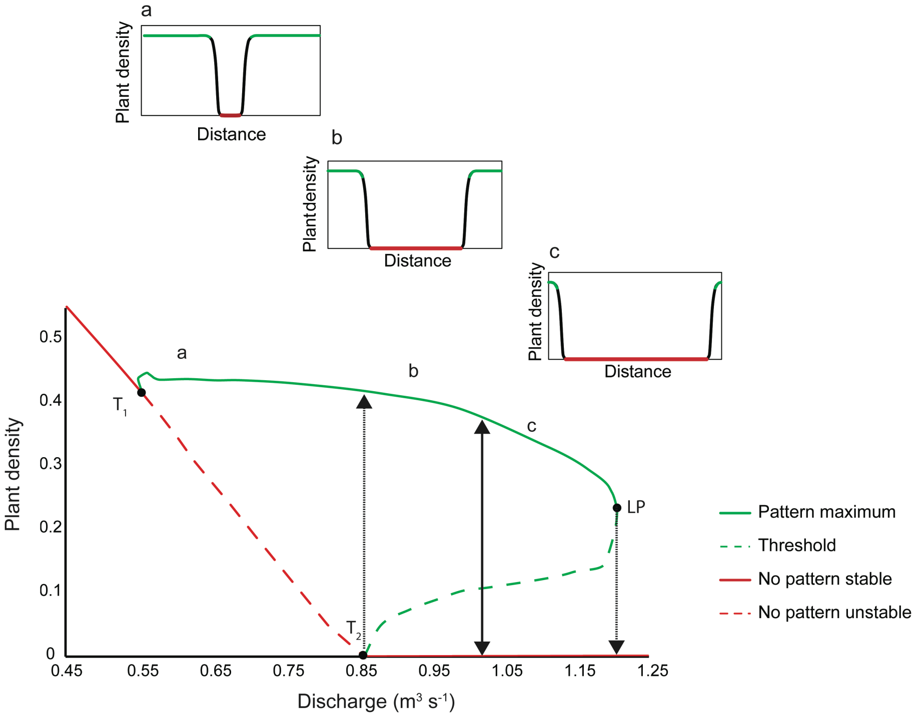

Figure 2.4: Bifurcation diagrams of plant density (P) with changes in discharge (Q). Red lines represent the homogeneous equilibrium, green lines show maximum plant density in the nonhomogeneous (spatially separated) equilibrium. Solid lines represent stable equilibria, whereas dotted lines are unstable equilibria. Beyond the point QT1 (Q = 0.55 m^3 s^{-1}), the stable heterogeneous pattern of spatial separation develops, similarly to a Turing instability point. Beyond QT2 (Q = 0.85 m^3 s^{-1}), spatial separation is needed for vegetation persistence. LP (Q = 1.22 m^3 s^{-1}) is a limit point, beyond which no vegetation persists. The insets show simulated plant density distribution along the model cross-section for Q = 0.60 m^3 s^{-1} (a), Q = 0.91 m^3 s^{-1} (b), and Q = 1.10 m^3 s^{-1} (c).

S2 Testing for regular pattern formation

The formation of regular patterns was tested by increasing the grid size of the simulated domain in the cross-stream direction. We tested the stability of the homogeneous equilibrium to small heterogeneous perturbations before and after the point QT_1 (Q = 0.55 m^3 s^{-1}), which is similar to a Turing instability point. Below this point, we expect heterogeneous perturbations to return to the stable homogeneous equilibrium; however, beyond this point, we expect small perturbations to be amplified, leading to the formation of regular spatial patterns. For simulations performed at Q = 0.525 m^3 s^{-1}, below the point QT_1, heterogeneous perturbations in plant biomass returned to a stable homogeneous equilibrium (Figure 2.5A). For simulations performed at Q = 0.575 m^3 s^{-1}, above QT_1, small perturbations in plant biomass were amplified and led to the formation of regular spatial patterns of vegetation (Figure 2.5B).

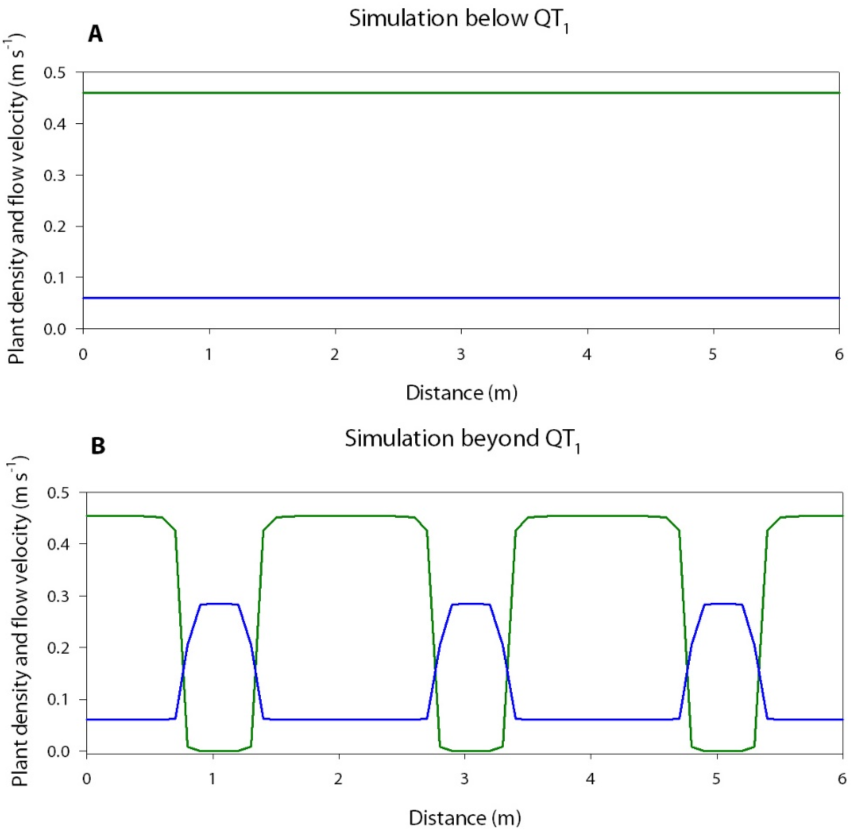

Figure 2.5: Simulated spatial patterns of flow velocity (*blue line*) and vegetation biomass (*green line*) along a model cross-section, performed below (A) and above (B) the threshold in incoming channel discharge QT_1 (Q = 0.55 m^3 s^{-1}), similar to a Turing instability point. Below this point, heterogeneous perturbations in plant biomass return to a stable homogeneous equilibrium. Above this point, small perturbations in plant biomass lead to the formation of regular spatial patterns of vegetation.

S3 Field measurements on river discharge, flow velocities and water levels

The changes in flow velocity patterns with discharge obtained from our field measurements are shown in Figure 2.2. In the ‘mixed vegetation’ site, water flow velocities within open and vegetated areas were significantly different (Kruskal-Wallis test, $P < 0.002$, Figure 2.2B) for all survey months, and discharge was significantly correlated with flow velocity within the stands ($r^2 = 0.77$, $p < 0.0001$) and between them ($r^2 = 0.52$, $p = 0.0005$, Figure 2.2B). Vegetated flow velocities in the ‘dominant submerged’ site (Figure 2.2C) were also significantly lower than unvegetated flow velocities (Kruskal-Wallis test, $p < 0.03$) up to discharges of 1.6 $m^3\ s^{-1}$. Above these values of discharge, vegetated flow velocities tend to become much higher and not significantly different from the unvegetated ones (Kruskal-Wallis test, $P > 0.05$, Figure 2.6). For this site, piecewise regression was used due to the presence of a breakpoint, after which flow velocities rapidly increased. This breakpoint was estimated at 1.5 $m^3\ s^{-1}$. Below the breakpoint, a significant relationship was found between discharge and flow velocity between the stands ($r^2 = 0.66$, $p = 0.0012$) and within them ($r^2 = 0.56$, $p = 0.005$; Figure 2.2C). Above the breakpoint, a significant relationship was found between discharge and flow velocity above the stands and between them ($r^2 = 0.85$, $p = 0.002$, Figure 2.6C), but the linear relationship was very similar to the one for an unvegetated channel. Most importantly, in the two streams as well as in model predictions, the slopes of these relationships are lower than the cross-sectional average flow velocities from each reach survey measurement (Figure 2.2B and C).

The negative relationship between macrophyte cover and discharge observed in the subset dataset of the ‘dominant submerged’ study site (Figure 2.1C) is also consistent with the full dataset ($r^2 = 0.80$, $p < 0.001$, Figure 2.6A). Similarly, the non-significant relationship between discharge and mean total water level for the subset dataset (Figure 2.3B), is also found in the full dataset under a wider range of incoming discharge ($r^2 = 0.03$, $p = 0.50$, Figure 2.6C).

S4 Implications of pattern formation for the resilience of macrophytes to disturbances

We used our model to explore the consequences of pattern formation for the resilience of aquatic macrophytes to disturbances. We imposed a disturbance on patterned vegetation at equilibrium biomass, in which we reduced vegetation density by 50%. In three different simulation runs, we compared the time needed to return to equilibrium. In the first simulation, we reduced the density but we left the patterns intact. In the second simulation, we reduced the density, distributed the remaining biomass equally over the simulated grid, and imposed a deviation in randomly selected cells up to 10% of the biomass. In the third simulation, we reduced the density and homogenized the remaining biomass, removing all spatial variability. We found that recovery to pre-disturbance conditions was quickly reached in the simulation where the patterns were left intact (Figure 2.7, *solid line*). The simulation in which vegetation was randomly redistributed showed a strong delay in its recovery (Figure 2.7, *dotted line*). However, as soon as patterns re-emerged, vegetation could recover to the initial equilibrium values. Finally, in the simulation with vegetation completely homogenized, vegetation density remained low and could not recover to pre-disturbance conditions, as no patterns developed due to the absence of small spatial heterogeneity (Figure 2.7, *dashed line*). Hence, our simulations demonstrate that self-organized pattern formation strongly increases macrophyte resilience compared to homogeneously vegetated streams, in response to disturbances that reduce vegetation biomass.

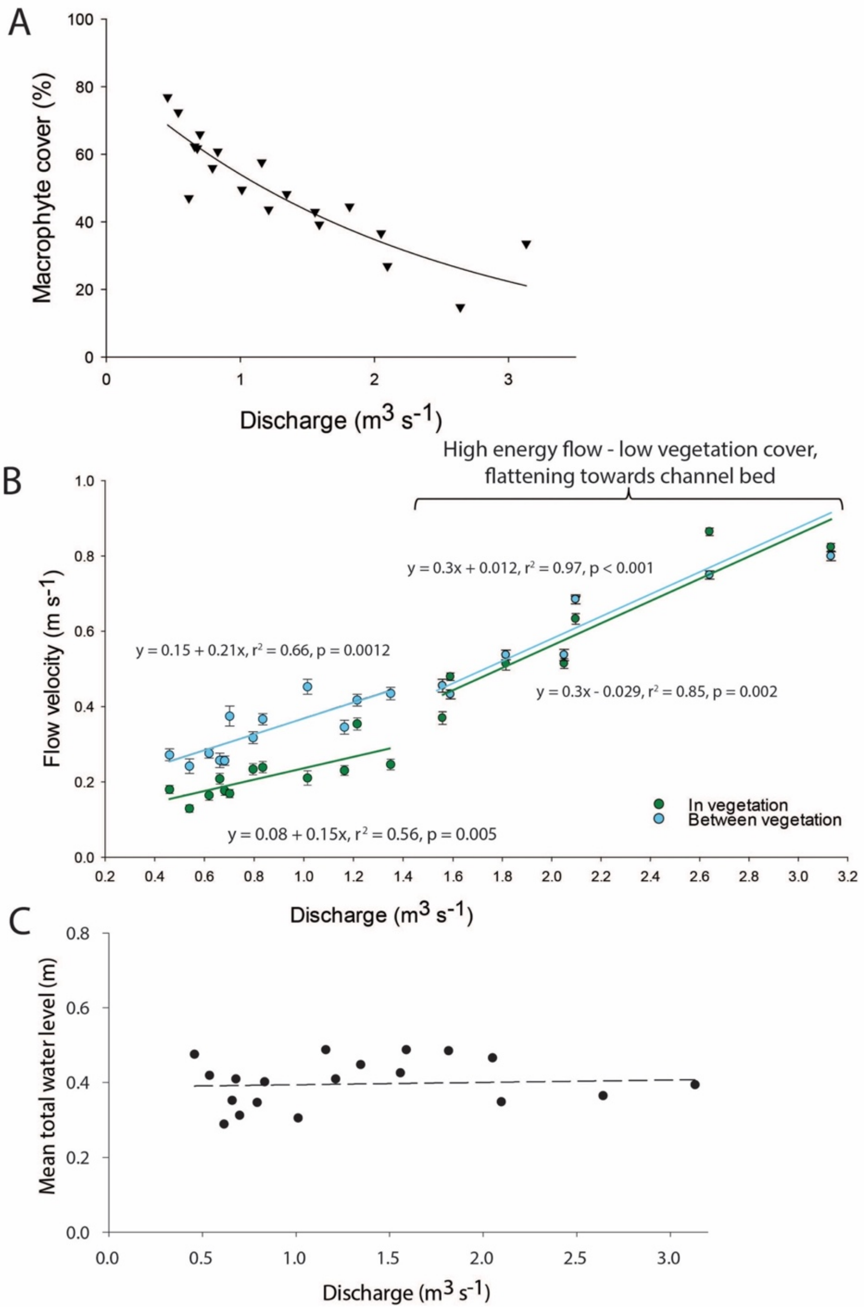

Figure 2.6: Full dataset of measured macrophyte cover (A), flow velocities (B) and mean total water level (C) plotted against channel discharge in the 'dominant submerged' study site.

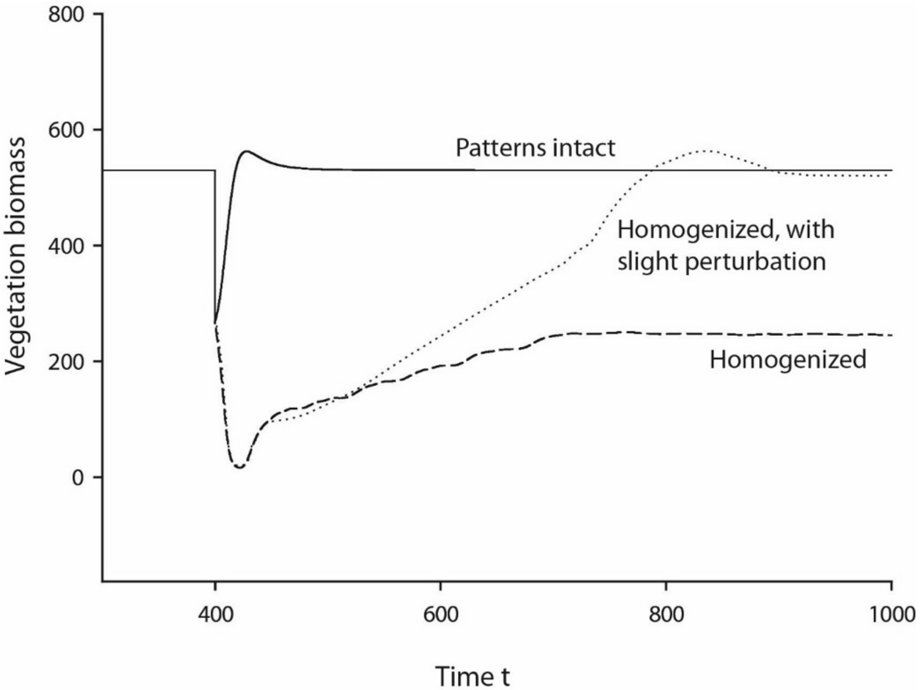

Figure 2.7: Results of three simulations describing the recovery of vegetation in the stream after a disturbance in which 50% of the biomass was removed. The solid line represents a simulation in which the patterns were left intact. The dotted line represents a simulation where the remaining biomass was equally redistributed over the simulated grid, and a deviation was imposed in randomly selected cells up to 10% of the biomass. The dashed line represents a simulation where the remaining biomass was homogenized in space, leaving no spatial variability. Units are dimensionless. Parameters as in Table 1, for $U_{in} = 0.20$ m s^{-1}.

S5 Identifying the biomass threshold for the use of Baptist formula (Eq. 2.6)

The equation proposed by Baptist et al. (2007) has been identified as one of the model approaches that can best represent the effects of vegetation on flow resistance, for both artificial and real vegetation (Vargas-Luna et al. 2015). However, Eq. (2.6) is undefined at low vegetation biomass, as the Chézy coefficient C_d becomes higher than the Chézy coefficient for the bed roughness C_b. Therefore, we used the relationship between biomass P and C_d to identify the threshold value in biomass at which Eq. (2.6) is not valid anymore (Figure 2.8);

hence, Eq. (2.5) instead was used in all grid cells where biomass P fell below this threshold value (i.e. for $P \leq 0.030$).

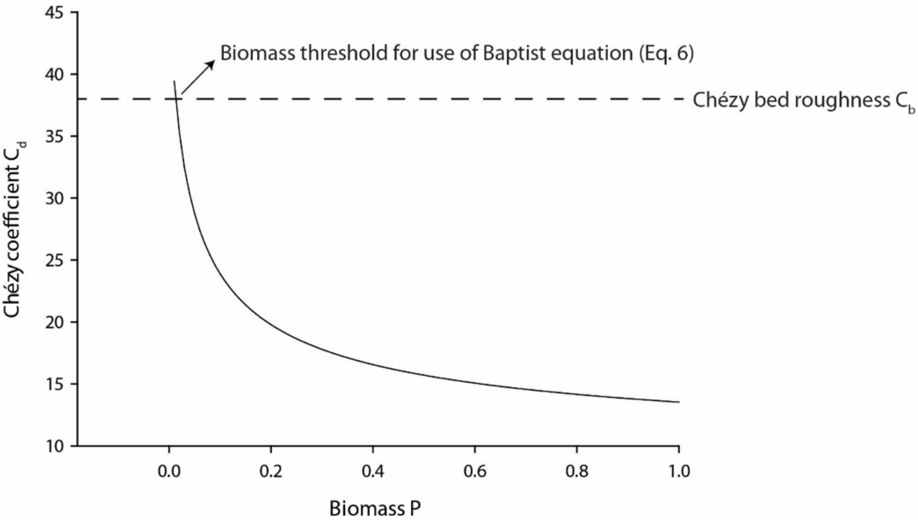

Figure 2.8: Identification of the threshold in biomass P below which the Baptist formula (Eq. 2.6) becomes undefined, and instead Eq. 2.5 is used to calculate the Chézy roughness coefficient. Eq. 2.6 with $C_b = 38\ \text{m}^{1/2}\,\text{s}^{-1}$, $h = 0.76$ m, $H_v = 0.26$ m.

Chapter 3

Landscapes of facilitation: how self-organized patchiness of aquatic macrophytes promotes diversity in streams

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Submitted

Abstract

Spatial heterogeneity plays a crucial role in the coexistence of species. Despite recognition of the importance of self-organization in creating environmental heterogeneity in otherwise uniform landscapes, the effects of such self-organized pattern formation in promoting coexistence through facilitation are still unknown. In this study, we investigated the effects of pattern formation on species interactions and community spatial structure in ecosystems with limited underlying environmental heterogeneity, using self-organized patchiness of the aquatic macrophyte *Callitriche platycarpa* in streams as a model system. Our theoretical model predicted that pattern formation in aquatic vegetation – due to feedback interactions between plant growth, water flow and sedimentation processes – could promote species coexistence, by creating heterogeneous flow conditions inside and around the plant patches. The spatial plant patterns predicted by our model agreed with field observations at the reach scale in naturally vegetated rivers, where we found a significant spatial aggregation of two macrophyte species around *C. platycarpa*. Field transplantation experiments showed that *C. platycarpa* had a positive effect on the growth of both beneficiary species, and the intensity of this facilitative effect was correlated with the heterogeneous hydrodynamic conditions created within and around *C. platycarpa* patches. Our results emphasize the importance of self-organized patchiness in promoting species coexistence by creating a landscape of facilitation, where a multitude of new niches and facilitative effects arise in different locations. Understanding the interplay between competition and facilitation is therefore essential for successful management of biodiversity in many ecosystems.

Introduction

The challenge of understanding species diversity and coexistence is fundamental in community ecology. According to the competitive exclusion principle, two species competing for the same resource cannot coexist if other ecological factors are constant (Gause 1932). However, many natural communities defy the theoretical predictions of low species coexistence, as often a high number of species can be found living on few resources (e.g. 'paradox of the plankton', Hutchinson (1961)). To explain this discrepancy, many of the suggested mechanisms rely on the importance of spatial or temporal heterogeneity (Levin 1970; Koch 1974; Armstrong and McGehee 1976; Holt 1984; Tilman 1994; Amarasekare 2003). Extensive evidence exists that structurally complex physical habitats favour increased species diversity, by providing niches and diverse ways of exploiting environmental resources (MacArthur and MacArthur 1961). Yet, many ecosystems with limited abiotic heterogeneity also host a high number of species. Thus, despite the importance of heterogeneity in space and time for species coexistence, we still lack understanding of how species can coexist in environments where underlying abiotic heterogeneity is low.

In recent decades, there has been increasing evidence that strong interactions between organisms and their environment can create environmental heterogeneity, even under uniform, homogeneous conditions, through the process called *spatial self-organization* (Rietkerk and Van de Koppel 2008). Self-organization processes can generate spatial patterns in ecosystems, through the interaction between local positive and large-scale negative feedbacks (Solé and Bascompte 2006; Rietkerk and Van de Koppel 2008). Examples range from vegetation patches alternating with bare soil areas in arid ecosystems (Rietkerk et al. 2002), tree patterns in Siberian peatlands (Eppinga et al. 2008) to diatoms in homogeneous tidal flats (Weerman et al. 2010). Self-organized patterns can cause strong variability in abiotic conditions in their surroundings. By modifying the abiotic environment, self-organizing species can promote favourable conditions leading to a positive feedback on their own growth (Wilson and Agnew 1992; Rietkerk and Van de Koppel 2008; Kéfi et al. 2016).

Several studies have also focused on the importance of positive interactions that benefit individuals of different species, i.e. interspecific facilitation (Bertness and Callaway 1994; Callaway and Walker 1997). For instance, facilitator species can reduce environmental stress, increasing the realized niche of other species and allowing them to occupy environments that they would normally not inhabit (Bruno et al. 2003; Callaway 2007). Facilitation is in essence based on the same mechanism as self-organization, involving a positive interaction that improves environmental conditions and enhances growth or survival. However, facilitative interactions between two species are mostly considered at a relative local scale, within a tussock or patch of the facilitator species, for instance through "nurse plant effects" in relation to herbivory or drought (Callaway 1995; Padilla and Pugnaire 2006). Instead, studies of self-organization typically focus 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). Therefore, as the link between self-organization and interspecific facilitation remains unclear and has rarely been addressed in the literature (Gilad et al. 2007), we pose the question whether self-organized pattern formation can create a 'landscape of facilitation'.

In lotic aquatic ecosystems, self-organized patchiness has been found to occur in submerged aquatic vegetation due to scale-dependent feedbacks between plant growth, water flow and sedimentation processes (Schoelynck et al. 2012; Schoelynck et al. 2013). Submerged macrophytes often grow as well-defined, streamlined stands composed of either a single species, or a mixture of species. Macrophytes act as ecosystem engineers (Jones et al. 1994), slowing down the water flow within the patches and promoting sediment deposition (Sand-Jensen and Mebus 1996; Sand-Jensen 1998; Wharton et al. 2006), which creates a local positive feedback on their own growth and survival. At the same time, flow velocities increase by about 30% around the patches, creating a large-scale negative feedback on plant growth due to the increased mechanical stress (Puijalon et al. 2011; Schoelynck et al. 2012). In lowland rivers, aquatic macrophytes with different morphologies increase habitat heterogeneity beyond that promoted by hydrodynamic and geomorphological processes alone (Kemp et al. 2000; Gurnell et al. 2006). Despite being suggested by previous observational studies (Jones

1955; Haslam 1978), the consequences of such plant-driven heterogeneity for interspecific interactions have not yet been explored.

We investigated whether self-organized pattern formation in aquatic vegetation promotes the coexistence of different macrophyte species in lotic communities, by generating heterogeneous hydrodynamic conditions and hence creating a 'landscape of facilitation'. First, to demonstrate self-organized pattern formation by the aquatic macrophyte *Callitriche platycarpa* Kütz (various-leaved water starwort), we constructed a spatially explicit mathematical model based on the interaction between plant growth and hydrodynamics. Secondly, we investigated whether such self-organized spatial heterogeneity could promote species coexistence, by modelling the interaction between the pattern-forming species (i.e., facilitator) and two species (i.e., beneficiaries) with different resistance to hydrodynamic stress. Thirdly, to show self-organization and spatial association among species in the field, we compared the model-predicted spatial distribution patterns against field observations on the spatial distribution of two hypothesized beneficiary species (lesser water parsnip, *Berula erecta* (Huds.) Coville and opposite-leaved pondweed, *Groenlandia densa* (L.) Fourr.) around *Callitriche*. Finally, to show that such spatial association provides facilitative interactions, we carried out field transplantations of the two beneficiary species in different locations around patches of the facilitator *Callitriche* as well as on bare sediment, and we investigated if their growth rate, reproduction, and survival correlated with changes in hydrodynamic conditions created by *Callitriche* patches. Our results suggest that species coexistence in streams is promoted by a biophysical feedback process that creates a landscape of facilitation where multiple new niches emerge for species adapted to a wide range of conditions.

Materials and methods

A model of pattern formation for submerged aquatic macrophytes

Model description

To study the emergence of self-organized patterns in aquatic macrophytes and the potential consequences for species coexistence, we constructed a spatially-explicit mathematical model based on the feedback between vegetation and water flow.

The model consists of a set of partial differential equations, where two equations describe the dynamics of plant biomass for the facilitator species f (P_f) and for its beneficiary species b (P_b), and where water velocity in the streamwise and spanwise directions (u and v), and water depth (h) are described using the shallow water equations (Vreugdenhil 1989).

The rate of change of plant biomass per species in each grid cell can be expressed as:

$$\frac{\partial P_i}{\partial t} = r_i P_i \left(1 - \frac{P_i + \alpha_{ij} P_j}{k_i}\right) \frac{A}{A+S} - m P_i \frac{F}{P_i + F} - m_{Wi} P_i |\boldsymbol{u}| + D_i \Delta P_i \qquad \textbf{(3.1)}$$

Where $i = f$ and $j = b$ for the equation of the pattern-forming species, and vice versa for a non-pattern forming species. Here plant growth is described using the logistic growth equation, where r_i is the intrinsic growth rate of the plants and k_i is the plant carrying capacity. Competitive interactions between P_f and P_b are accounted for using the competitive Lotka-Volterra equations, with the term $\boldsymbol{\alpha}_{ij}$ representing the effect P_j has on P_i, and $\boldsymbol{\alpha}_{ji}$ representing the effect P_i has on P_j. Plant growth rate r_i is reduced when sediment accumulation within the plants reaches a maximum value A; this represents a negative feedback on plant growth due to sediment accumulation and organic matter content becoming high enough to be toxic for the plants (Barko and Smart (1983); Sofia Licci, personal communication). Plant mortality m is assumed to decrease with increasing plant density because of a reduction of flow stress in dense vegetation. This is represented by the term $F/(P_i + F)$, where F is an intraspecific facilitation term. Plant mortality caused by water flow stress is modelled as the product of the mortality constant m_{Wi} and net water speed $|\boldsymbol{u}| = \sqrt{(u^2 + v^2)}$ due to plant breakage or uprooting at higher velocities. Field sampling on clonal dispersal traits for the aquatic plant species *Berula erecta* and *Groenlandia densa* revealed that plant lateral expansion through vegetative reproduction could be described by a random walk (see Appendix 3.A: Figure 3.7). Therefore, we apply a diffusion approximation and use these data to parameterize different diffusion constants D_i for the beneficiary species (Holmes et al. 1994). Clonal dispersal traits for the hypothesized facilitator species *Callitriche platycarpa* could not be estimated based on field sampling, due to the complex morphology of this species.

Changes in sediment level are described as:

$$\frac{\partial S}{\partial t} = S_{in} - E_{max}\frac{K_S}{K_S + P_i}S|\boldsymbol{u}| - |\boldsymbol{u}|\nabla S + D_S\Delta S \tag{3.2}$$

where S_{in} is the sediment deposition rate (m t^{-1}), E_{max} is the maximal erosion rate of sediment (t^{-1}) and K_S represent the effects of plants in promoting sediment deposition. The term $|\boldsymbol{u}|\nabla S$ represents the advective flux of sediment over the bottom (i.e., as fluid mud) in any horizontal dimension, and D_S represents the horizontal dispersion rate of sediment, for instance due to bioturbation processes, which is modelled with a diffusion approximation.

Water flow is modelled using depth-averaged shallow water equations in non-conservative form (Vreugdenhil 1989), to determine water depth and its speed in both x and y directions. The effects of bed and vegetative roughness on flow velocity are represented by determining hydrodynamic roughness characteristics for each cover type separately using the Chézy coefficient, following the approach of Straatsma and Baptist (2008) and Verschoren et al. (2016).

Within the unvegetated cells of the simulated grid, C_d is calculated using Manning's roughness coefficient through the following relation:

$$C_d = \frac{1}{n}h^{1/6} \tag{3.3}$$

where n is Manning's roughness coefficient for an unvegetated gravel bed channel (s/[$m^{1/3}$]) and h is water depth (m).

For each grid cell occupied by submerged vegetation, C_d is calculated using of the equation of Baptist et al. (2007) and slightly modified by Verschoren et al. (2016) to account for reconfiguration of flexible submerged macrophytes, to express vegetation resistance as:

$$C_d = \sqrt{\frac{1}{C_b^{-2} + (2g)^{-1} D_c A_w}} + \frac{\sqrt{g}}{k_v} \ln \frac{h}{H_v} \quad \textbf{(3.4)}$$

where C_b is the Chézy roughness of the bed (same as C_d in Eq. 3.3), g is acceleration due to gravity (9.81 m s^{-2}), D_c is a species-dependent drag coefficient, A_w is the specific plant surface area (total wetted vertical surface area of the vegetation per unit horizontal surface area of the river (Sand-Jensen 2003; Verschoren et al. 2016)), directly related to plant biomass P_i, k_v is the Von Kármàn constant (0.41), and H_v is the deflected vegetation height (m). Deflected vegetation height varies as a function of incoming flow velocity, due to the high flexibility of submerged aquatic vegetation and reconfiguration at higher stream velocities (Sand-Jensen 2003; Schoelynck et al. 2013). Following the approach of Verschoren et al. (2016), H_v is calculated within each vegetated grid cell as the product of shoot length L (m) and the sine of the bending angle α, using an empirical relationship between bending angle and incoming current velocity based on flume experiments performed on single shoots of flexible aquatic macrophytes ($\alpha = 15.5 * |\boldsymbol{u}|^{-0.38}$) (Bal et al. 2011b). Table 3.1 provides an overview of the parameter values used, their interpretations, units and sources.

Table 3.1. Symbols, interpretations, values, units and sources used in the model simulations.

Symbol	Interpretation	Value			Unit	Source
		P_f	P_{b1}	P_{b2}		
r_i	Intrinsic growth rate species *i*	1	1	0.5	t^{-1}	Estimated
k_i	Carrying capacity of species *i*	200	200	200	g m^{-2} dry biomass	Sand-Jensen and Mebus (1996)
m_{Wi}	Plant mortality constant due to hydrodynamic stress	9	8	3	Dimensionless	Estimated
D_i	Diffusion constant of species *i*	0.00045	0.00025	0.00015	m^2 t^{-1}	Estimated
m_i	Mortality of species *i*	0.02	0.02	0.02	Dimensionless	Estimated
α_{fb}	Interaction coeff. of P_b on P_f		2	0.5	Dimensionless	Estimated
α_{bf}	Interaction coeff. of P_f on P_b		4	0.1	Dimensionless	Estimated
n	Manning's roughness coefficient for unvegetated gravel bed		0.035		$s/[m^{1/3}]$	Arcement and Schneider (1989)
D_c	Drag coefficient	0.5	0.5	0.5	Dimensionless	Naden et al. (2004)
L	Shoot length	0.5	0.5	0.5	m	Bal et al. (2011b)
S_{in}	Sediment deposition rate		0.0012		m t^{-1}	Estimated
E_{max}	Maximal sediment erosion		200		t^1	Estimated
Ki	Sediment deposition due to vegetation	0.0005	0.008	0.008		Estimated
D_S	Diffusion constant of sediment		0.01		m^2 t^{-1}	Estimated
A_i	Toxicity feedback of sediment accumulation on plant growth	0.02	0.005	0.008		Estimated

Model analysis: simulation of species coexistence patterns

To investigate whether spatial pattern formation could promote species coexistence through the creation of spatial heterogeneity in hydrodynamic conditions, we modelled the interaction between the pattern-forming species (P_f; facilitator) and two non-pattern forming species (P_b, beneficiary species). In the first model, we considered the interaction between P_f and a beneficiary species P_{b1} characterized by low resistance to hydrodynamic stress (= high mortality constant m_{Wi}; Table 3.1). In the second model, we considered the interaction between P_f and a second beneficiary species P_{b2} characterized by higher resistance to hydrodynamic stress (= low mortality constant m_{Wi}), but lower growth rate and lower dispersal ability. We modelled the pairwise interactions between the facilitator and each beneficiary separately instead of with a full three-species model. This choice was made to focus on the mechanisms and patterns allowing the coexistence of single beneficiary species with the self-organizing species, instead of studying the coexistence patterns of a whole community. Hence, we focused on studying a self-organized landscape with spatial facilitation, rather than exploring all possible modes of coexistence. The models were analysed by simulating the spatial development of vegetation after random seeding (increasing biomass to 1 in randomly chosen cells) on a spatial grid of 300 x 60 cells, corresponding to a river stretch of 25 m x 5 m. Simulations were run for 500 time steps, in abstract units due to our non-dimensional description of plant growth.

To test the regularity of the predicted spatial patterns, we analysed the resulting distribution patterns of P_f through spatial autocorrelation. To test the spatial dependence between the beneficiary species P_b and P_f, we used spatial cross-correlation. Both auto- and cross-correlation analyses were performed by calculating Moran's *I* in the 'ncf' package in R (Bjornstad, 2015). To test for self-organization and spatial association among species in the field, we then compared the auto- and cross-correlation functions from the predicted species distribution patterns of coexistence with field observations on the spatial distribution of *Groenlandia* and *Berula* around *Callitriche* (see following section '*Field observation of species coexistence patterns through aerial photographs*').

To further explore the implications of self-organization for species coexistence, as opposed to homogeneous environments, we compared the spatial model described above to a simplified, homogeneous (non-spatial) version of the model based on Eq. 3.1:

$$\frac{dP_i}{dt} = r_i P_i \left(1 - \frac{P_i + \alpha_{ij} P_j}{k_i}\right) - m_{Wi} P_i |\boldsymbol{u}| \tag{3.5}$$

Where $i = f$ and $j = b$ for the equation of the facilitator species, and vice versa for a beneficiary species. We used the model to explore the realized niche of each species along the hydrological gradient, under homogeneous (non-spatial) conditions (that is, without self-organization). This simplified version of the model does not account for spatial effects of sedimentation and intraspecific facilitation. For each incoming flow velocity U_{in} ($|\boldsymbol{u}|$ in Eq. 3.5), we explored the conditions under which the model predicted either stable coexistence, unstable coexistence or competitive exclusion between the facilitator and beneficiary species (based on the species isoclines of zero growth), as a result of their stress resistance and competitive abilities. Moreover, to show the hydrodynamic heterogeneity generated by the self-organization process and the species hydrological niches predicted in the spatial model, we investigated the frequency distribution of flow velocities within vegetated and unvegetated cells in the spatial model. The comparison between the two models provided insight and understanding of the mechanisms underlying species coexistence in space.

Field observation of species coexistence patterns through aerial photographs

To test for significant spatial association of species around self-organized patterns in the field, we examined the distribution of two potential beneficiary species (*Groenlandia* and *Berula*) around the hypothesized facilitator species (*Callitriche*). Submerged macrophytes often grow as well-defined stands composed of a single species or a mixture of species (Figure 3.1A); the patches tend to merge into a more homogeneous cover where streams have low flow velocities sustained over time (Figure 3.1B), while distinct streamlined patches are usually found in streams with sustained periods of moderate to high flow velocities (Figure 3.1C). Vegetation distribution was mapped in two reaches of 100 m in length, through low-altitude aerial photographs. The channels are located along the Rhône River

(France), near Serrières-de-Briord (45.815311 ° N, 5.427477 ° E) and Flévieu (45.766738 ° N, 5.479622 ° E) (see Appendix 3.B: Figure 3.8 for the location of the study sites). The first reach was mainly colonized by *Callitriche* and *Groenlandia*, with few patches of other macrophyte species, while the second reach was colonized only by *Callitriche* and *Berula.* Aerial pictures of the streambed were taken with a digital camera mounted on a pole at about 2 m height that was moved in the upstream direction along the stretch. Pictures were collected with a slight overlap and afterwards mosaicked using image processing software (Adobe Photoshop CC 2015). Patches of different species were identified and delineated as shown in Figure 3.1A; afterwards, pixels where the species was absent were given a value of 0 and pixels where the species was present were given the value of its blue channel in the RGB image, since the intensity of this channel was the one most closely related to differences in plant biomass (evaluated by visual inspection). This allowed us to obtain different raster maps of macrophyte distribution, one for each of the species considered in the study (non-target species were not included in the analysis). The resulting macrophyte maps were analysed through spatial autocorrelation (to test the distribution of the potential facilitator species) and cross-correlation (to test the spatial dependence between the facilitator and each of the potential beneficiary species), by calculating Moran's *I*.

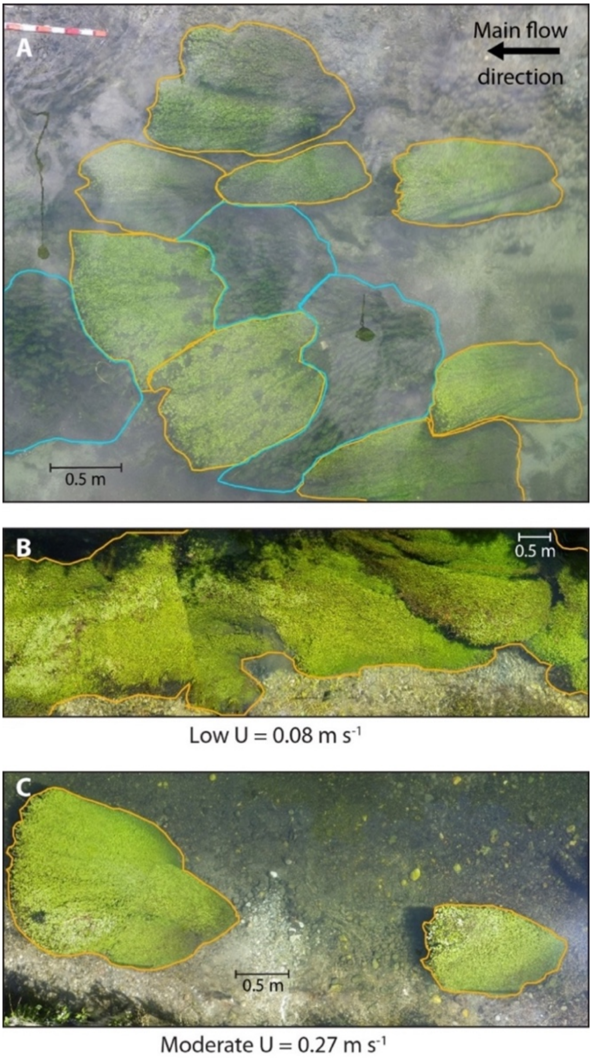

Figure 3.1: (A) Aerial picture showing the patchy distribution of the macrophyte species *Callitriche platycarpa* (light green patches, outlined in yellow), in the drainage channel of Serrières-de-Briord (France). Other aquatic macrophytes, such as *Groenlandia densa* (dark green vegetation, outlined in light blue), are often found in close proximity to, or within *Callitriche* patches, forming 'mixed' vegetation stands. (B) and (C) Aerial photographs of vegetation patterns observed in streams with two different values of incoming flow velocity (U, m s^{-1}). In streams with sustained periods of low flow velocities, vegetation patches tend to merge into a more homogeneous cover. In streams with moderate flow velocities, regular and well-defined vegetation patches are found, streamlined in the main current direction. Water flow is from right to left in the pictures.

Testing for positive interactions through a field transplantation experiment

To test for the presence of positive interactions between the hypothesized facilitator *C. platycarpa* and the two hypothesized beneficiary species living in its surroundings, we performed a field transplantation experiment in a naturally vegetated channel located along the Upper Rhône River (France), near Serrières-de-Briord (45.810657 ° N, 5.447169 ° E). The channel is 4.26 km long, uniform in terms of width and water depth, with relatively straight banks. The average width is 8.0 m and the average depth is 0.8 m, rarely exceeding 1.3 m. The channel has a substrate of fine sand ($d_{50} = 230.87$ µm). Flow velocities are on average 0.25 m s^{-1}, with a mean discharge of 1.48 ± 0.022 m^3 s^{-1} in August 2014.

Individuals of the two beneficiary species were collected within the same channel on 11th August 2014 and transplanted in five locations around the facilitator patches (upstream, middle and downstream of the patch; left and right sides of the patch). As a control, an additional treatment was located on bare sediment areas, as far as possible from the influence of existing patches. Since patch effects can be observed for a distance equal to its length (Sand-Jensen and Mebus 1996; Schoelynck et al. 2012), these transplants were located at a distance of at least twice the length of the nearest patch. All treatments were repeated ten times for each beneficiary species, around different *C. platycarpa* patches of average length (~ 1.2 m) and in areas outside the influence of other vegetation. Transplants were single plants attached to a stolon without internodes (shoot height of 22.17 ± 1.98 cm for *B. erecta*, 21.48 ± 1.98 cm for *G. densa*). Transplant survival was monitored two days, four days, and at weekly intervals after transplantation to test for facilitative effects on plant survival. All transplanted individuals were harvested at the end of the experiment (49 days after transplantation, on 29th September 2014). Growth rates were calculated in terms of shoot height as $GR_H = (H_2 – H_1)/H_1$, with H_1 and H_2 being the shoot height (cm) on day 1 and day 49 of the experiment. Here, the initial transplanted individuals were referred to as “mother ramets”. New ramets produced by mother ramets through vegetative reproduction were referred to as “daughter ramets”, and stolons and daughter ramets together were defined as “juveniles”. Shoot height, number of stolons, total stolon length, spacer length, and number of daughter ramets were measured on the transplants. Afterwards, biomass was separated into mother ramet and juveniles, dried in the oven at 60° for 48 h and weighed to obtain the dry mass of the transplants and the biomass investment in vegetative reproduction.

To characterize the flow velocity encountered by transplants for each treatment, both in the surroundings of *C. platycarpa* patches and on bare sediment, we measured flow velocities in the proximity of each transplant. Flow was measured for 100 s at 1 Hz using an Acoustic Doppler Velocimeter (ADV; FlowTracker, SonTek) at a water depth of 60% from the water surface, to obtain an estimate of average flow velocity over the water column. These measurements were used to define flow velocity encountered by plants during the experiment, and were performed on one occasion over the study period. This was representative of the flow conditions over the whole study period. The flow velocities encountered by each transplant were subsequently correlated to their growth rates, survival and traits of vegetative reproduction at the end of the experiment.

One-way ANOVA was applied to test for significant differences in dry biomass of transplants between positions around existing patches. Post-hoc comparisons were performed using a Tukey HSD test. Survival of transplants between treatments was analysed using Kaplan-Meier survival analyses and Mantel-Cox log rank tests with Bonferroni correction. The relationships between flow velocity and height increase, spacer length, daughter ramet dry mass, and between mother and daughter ramet height, were tested with a linear regression model. All statistical analyses were performed in R 3.1.2.

Results

Model simulation of species coexistence patterns

Model simulations showing self-organized pattern formation demonstrated that scale-dependent feedbacks between macrophytes, sedimentation, and hydrodynamics could generate the patchy vegetation distribution observed in the field (Figure 3.2A). Regular patterns of vegetation, consisting of well-defined high biomass patches alternating with bare sediment with little vegetation, develop at intermediate flow velocities. The patches are streamlined and oriented in the main direction of the flow. Due to a scale-dependent interaction of vegetation with water flow, increased flow resistance locally reduces flow velocities within the vegetation, while water flow is diverted and accelerated between the vegetation patches (arrows in Figure 3.2A). Sedimentation is promoted within the patches, up to a point where high sediment accumulation on the downstream side of the patches limits their further length growth in the streamwise direction. Our model highlights that self-organization processes between vegetation growth and hydrodynamics are a potential explanation for the patchy characteristics of many streams, especially at intermediate flow velocities.

When the pattern forming facilitator species P_f is allowed to interact with the non-pattern forming beneficiary species P_b, coexistence is promoted. A beneficiary species P_{b1} with low resistance to hydrodynamic stress is able to colonize the sheltered, low-flow areas in the wake region downstream of the P_f patches, but is outcompeted within the patches themselves (Figure 3.2B). A beneficiary species P_{b2} with lower growth rate r and higher resistance to hydrodynamic stress can coexist inside and locally around the margins of P_f patches, near the high-flow areas created on the sides (Figure 3.2C). Hence, our model shows that, in hydrodynamically stressful habitats, species with different resistance to flow stress can coexist through different spatial patterns, either in the wake of the patterned facilitator species P_f, or locally inside and along the margins of the dominant patterns. These new niches are created by the hydrodynamic heterogeneity resulting from the self-organization process.

Our model analyses also highlight that the presence and strength of the interactions between facilitator and beneficiary species depend strongly on hydrodynamic conditions. The realized biomass of each species under homogeneous conditions (Eq. 3.5) shows that changes in incoming flow velocity determine the shift from dominance of one species, to stable coexistence, to dominance of another species (realized biomass distributions in *light green*, *dark green* and *orange*; Figure 3.2D). At low incoming flow velocity (U_{in}), P_{b1} is the most successful competitor (Figure 3.2D); as flow velocity increases, P_{b1} and P_f can coexist within the range $0.07 \leq U_{in} \leq 0.09$. As incoming flow increases further, P_f

becomes the dominant species, until a range where it coexists with P_{b2}. At the highest flow velocities, P_{b2} is the most successful competitor due to its higher resistance to flow stress. Based on the species realized niches along the flow velocity gradient, our model analysis also shows that if P_f were uniformly distributed in space, it would attenuate incoming flow velocity U_{in} to a single realized velocity U_e that would be more favourable for its growth. This flow velocity falls in the range where P_f is predicted to be the only dominant species (Figure 3.2D). Instead, for the same flow velocity, a self-organizing P_f would separate the incoming flow into a low velocity U_e (inside the patches and in their wake) and a high velocity U_e (next to the patches), thus promoting coexistence and diversity by creating a much wider range of hydrodynamic conditions that provide the niches where each species can be dominant (Figure 3.2D-E).

Testing for hydrodynamic heterogeneity under self-organization highlights the very wide range of hydrological niches created by this process in the spatial model (Figure 3.2E). The frequency distribution of flow velocities over the simulated domain shows that self-organization creates a much wider range of hydrodynamic conditions, compared to homogeneous environments. Self-organized patterning leads to a bimodal distribution of flow velocities, with a low-flow peak in vegetated areas, and a high-flow peak in unvegetated areas between plant patches (frequency distributions in *dark green* and *blue*; Figure 3.2E). The self-organizing species therefore provides a spatial flow velocity gradient: low stress areas where less resistant species are more successful, and higher stress areas where more resistant species are dominant. Such hydrodynamic heterogeneity promotes coexistence by allowing all outcomes of species interactions to occur in space. Our model highlights that, under self-organization, beneficiary species can persist in environments they would not normally inhabit based on average flow conditions. Therefore, facilitation expands the niches of the beneficiary species and allows them to withstand stronger hydrodynamic stress levels.

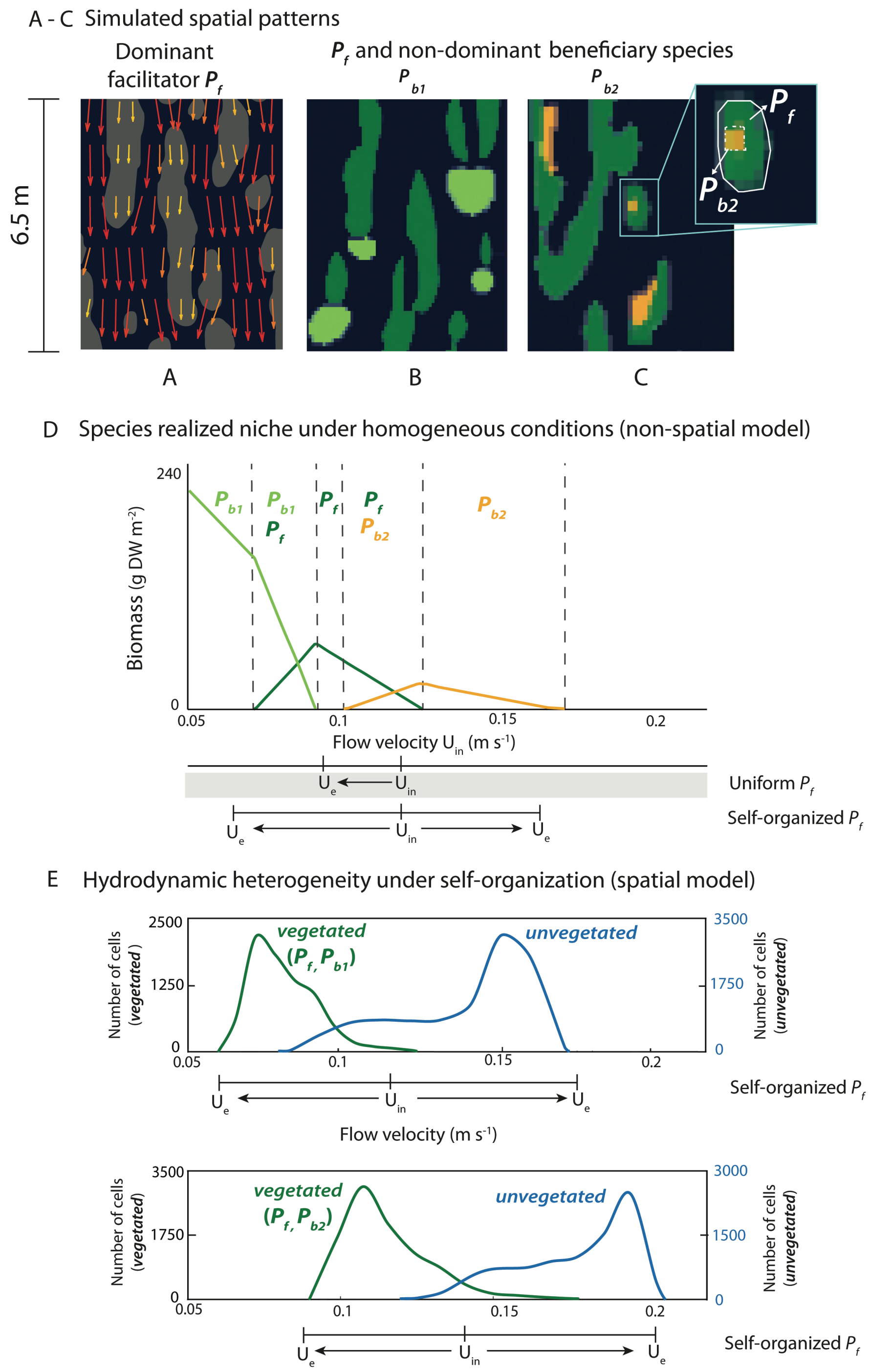

Figure 3.2: (Continued on the following page.)

Figure 3.2: (A) Spatial patterns of macrophyte distribution in the simulated stream reach. Small spatial heterogeneities lead to the development of regular patterns in the distribution of the facilitator P_f, where dense vegetation patches (*in grey*) alternate with almost bare sediment and low vegetation biomass. Due to a scale-dependent interaction with water flow, flow velocities are locally reduced within the vegetation and accelerated outside (indicated by arrow size and color, from yellow to red). (B) Beneficiary species characterized by low resistance to hydrodynamic stress (*light green*) colonize the sheltered, low-flow areas in the wake of the P_f patches (*dark green*), while being outcompeted within the patches themselves. (C) Beneficiary species with lower growth rate and higher resistance to hydrodynamic stress (*orange*) can coexist inside and locally around the P_f patches (*dark green*), near the high-flow channels created next to them. (D) Realized niches of P_f, P_{b1} and P_{b2} along the hydrodynamic stress gradient in the homogeneous model. Dashed lines indicate the limits between the flow velocity ranges where either one species is dominant, or two species coexist. Note the different effects of P_f on incoming flow velocity when P_f is uniformly distributed in space (U_{in} is reduced to a realized flow velocity U_e, in a region where P_f is still the dominant species) compared to the self-organized case (both low-flow and high-flow velocity zones are created, where P_{b1} or P_{b2} dominate). Parameters used are $r_f = 1.19$, $\alpha_{fb1} = 0.6$, $\alpha_{b1f} = 1.42$, $k_{b1} = 390$, $r_{b1} = 0.94$, $\alpha_{b2f} = 0.83$, $k_{b2} = 100$. Other parameters as in Table 1. (E) Hydrodynamic heterogeneity generated by self-organization in the spatial model: frequency distribution of depth-averaged flow velocities within vegetated (*dark green*) and unvegetated cells (*blue*) of the simulated domain.

Comparison between simulated and observed species coexistence patterns

Spatial autocorrelation analysis to test for self-organization in the field shows that the spatial patterns of P_f predicted by our numerical model display significant positive autocorrelation up to 1.5 – 2 m distance, followed by significant negative autocorrelation at a distance up to 3 – 3.5 m (Figure 3.3A and Figure 3.4A; *black lines* in Figure 3.3C and Figure 3.4C), reflecting a spatial pattern of vegetated patches alternating with open spaces with a wavelength of about 5 meters. High positive autocorrelation corresponds to more similar plant biomass over 1.5 – 2 m distance (plant aggregation into patches), while the significant negative autocorrelation indicates dissimilarity (plants are not present there due to the negative feedback on their growth).

The spatial correlation function from the field patterns of *C. platycarpa* is in close agreement with the results of the autocorrelation analysis on the predicted patterns. Autocorrelation analysis of *C. platycarpa* patches from our aerial pictures either showed significant positive autocorrelation up to 2 m distance, followed by significant negative autocorrelation from 3 to 5 m (Figure 3.4B; *black line* in Figure 3.4D), or it showed a directional effect of significant positive autocorrelation up to 6 m distance, but without negative correlation at any distance due to merging of neighbouring patches (Figure 3.3B; *black line* in Figure 3.3D). Hence, in the first case (Figure 3.4D) we found regular vegetation patches oriented parallel to the main flow direction, at a distance of roughly 8 m from each other; in the second case (Figure 3.3D), we found streamlined bands of vegetation distributed in the direction parallel to the main flow direction, with no clear gap between the patches due to their merging.

When a second species P_b is included in our model, the predicted outcome of species interaction is that P_b can coexist in the low-flow areas created in the wake of the patches of the pattern-forming species P_f (Figure 3.3A). Spatial cross-correlation analysis of P_f with P_b indeed shows a significant positive association of the beneficiary species in the wake of existing patches of the facilitator, as shown by the positive peak in the cross-correlation coefficient at around 1.0 m distance from them (*blue line* in Figure 3.3C). This spatial cross-correlation function closely matches the species coexistence patterns found in the field, where *Berula erecta* showed a significant positive association in the wake of *C. platycarpa* patches (Figure 3.3D), also with a positive peak at 1.55 m distance from existing patches.

When P_b is used to model a species with higher resistance to flow stress, a different pattern of coexistence is observed: the beneficiary species grows both within the patches and in the open interspaces around the pattern-forming species (Figure 3.4A; *blue line* in Figure 3.4C). This predicted pattern of coexistence is in strong agreement with field observations on coexistence patterns of *Groenlandia densa* and *Callitriche platycarpa*, where *Groenlandia* tended to coexist within and along the margins of *Callitriche* patches (Figure 3.4B; *blue line* in Figure 3.4D). In both cases, the two species are positively associated up to 2 m distance (i.e., where the patches of the patterned species are located), but negatively or non-significantly correlated from 2 to 5 m distance (i.e., where the patterned species is absent due to the negative feedback on its growth).

The directionality of the relationship between *Callitriche* and *Berula* in the field is proven by the mostly non-significant cross-correlation when repeating the analysis in the direction perpendicular to the flow on the field observations (*blue line* in Figure 3.3F). However, this pattern is not found in the model results, where the two species are positively cross-correlated up to 1.5 m distance and negatively cross-correlated up to 3.5 m distance (Figure 3.3E). The relationship between *Callitriche* and *Groenlandia* in the direction perpendicular to the flow in the field still shows a pattern of coexistence (Figure 3.4F), as confirmed by the analysis of the model predictions (Figure 3.4E), while also highlighting a shift in the lateral distribution of the two species as *Groenlandia* tends to grow along the margins of *Callitriche* patches.

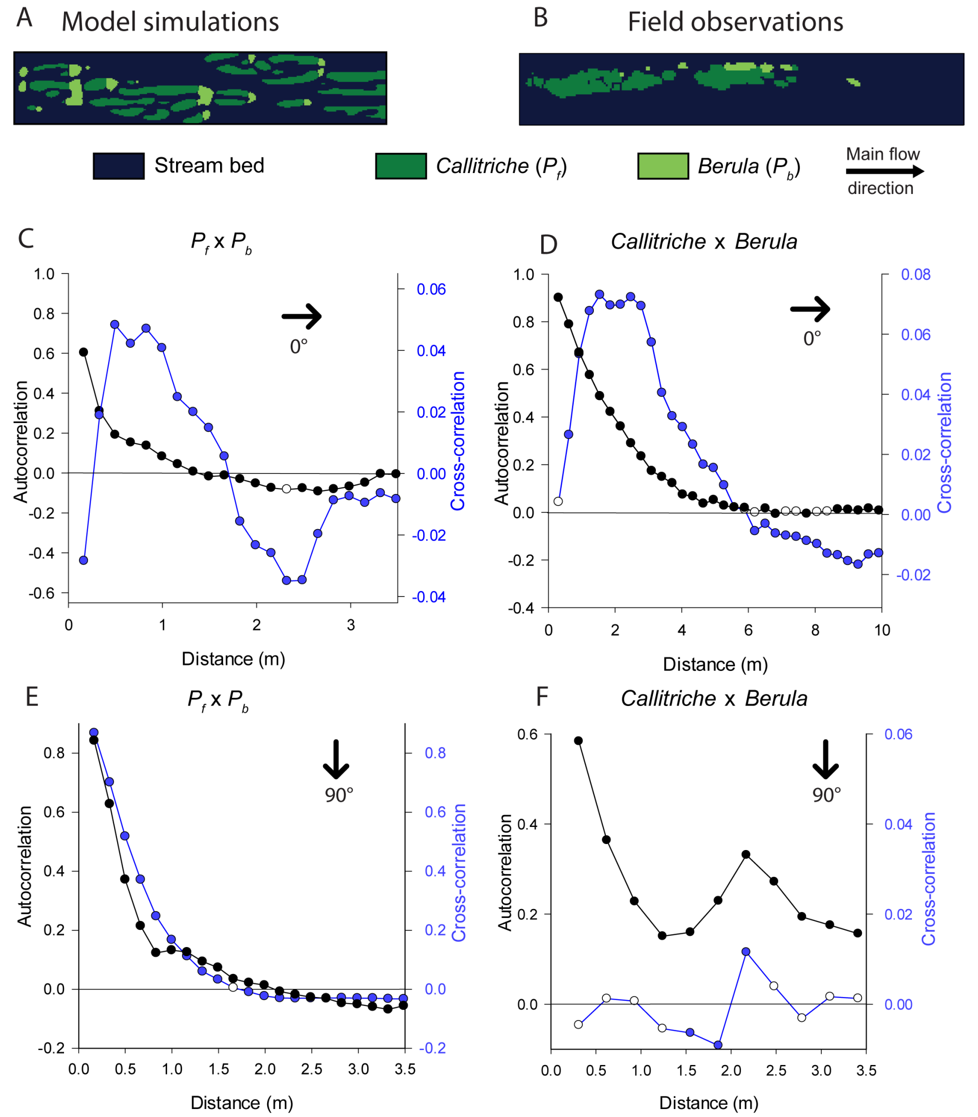

Figure 3.3: (A) Model simulations of aquatic vegetation development on a 150 x 30 grid for P_f (facilitator) and P_b (beneficiary). (B) Field observations of *Callitriche* and *Berula* distribution in a river stretch of 100 m, obtained from aerial pictures. Auto- and cross-correlation functions of species distribution patterns from model simulations (C) and field observations (D) in the direction parallel to the main water flow. Auto- and cross-correlation functions of species distribution patterns from model simulations (E) and field observations (F) in the direction perpendicular to the main water flow. In C and E, *black lines* are the autocorrelation functions for the simulated spatial patterns of P_f; *blue lines* are the cross-correlation functions between P_f and P_b. In D and F, *black lines* are the autocorrelation functions for *Callitriche platycarpa*; *blue lines* are the cross-correlation functions between *Callitriche* and *Berula*. Closed dots represent significant values.

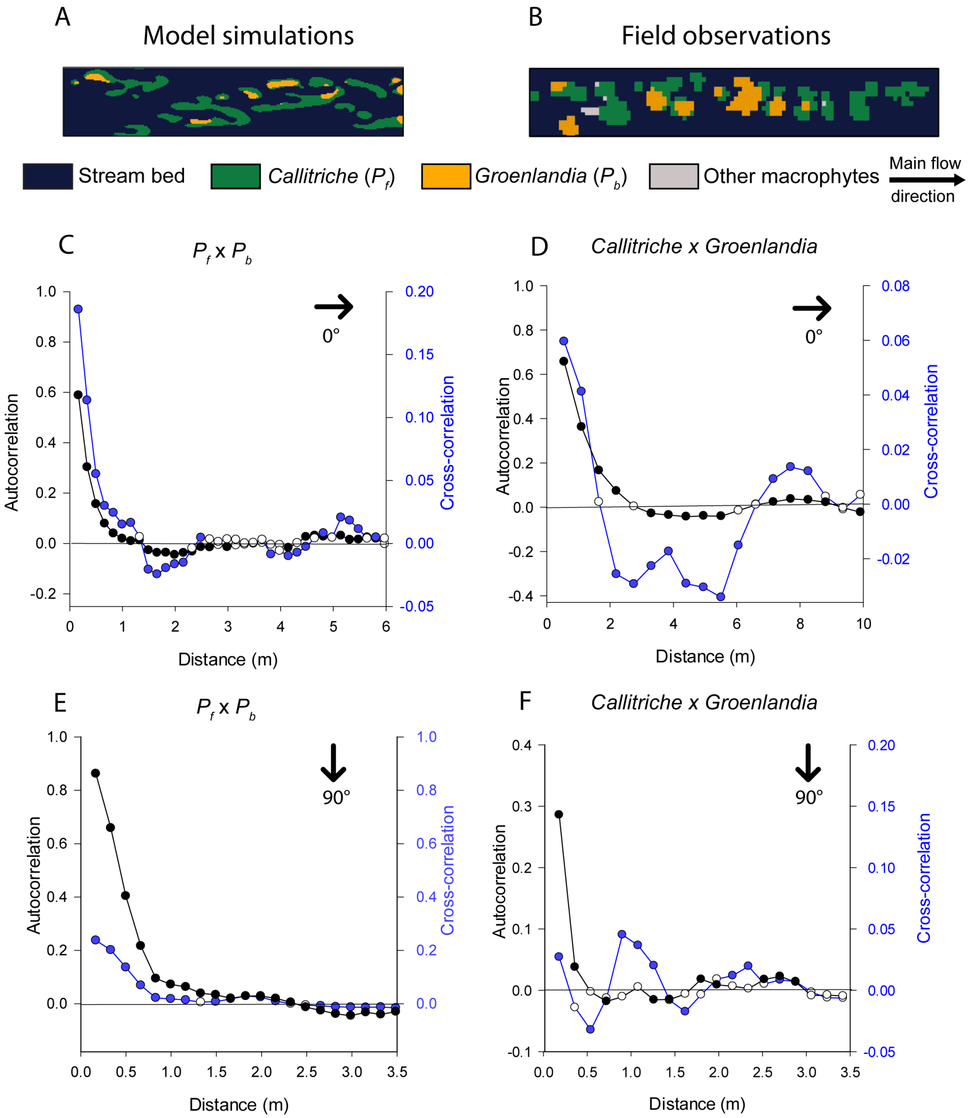

Figure 3.4: (A) Model simulations of aquatic vegetation development on a 150 x 30 grid for P_f (facilitator) and P_b (beneficiary). (B) Field observations of *Callitriche* and *Groenlandia* distribution in a river stretch of 100 m, obtained from aerial pictures. Auto- and cross-correlation functions of species distribution patterns from model simulations (C) and field observations (D) in the direction parallel to the main water flow. Auto- and cross-correlation functions of species distribution patterns from model simulations (E) and field observations (F) in the direction perpendicular to the main water flow. In C and E, *black lines* are the autocorrelation functions for the simulated spatial patterns of P_f; *blue lines* are the cross-correlation functions between P_f and P_b. In D and F, *black lines* are the autocorrelation functions for *Callitriche platycarpa*; *blue lines* are the cross-correlation functions between *Callitriche* and *Groenlandia*. Closed dots represent significant values.

Field transplantation: effects on growth, vegetative reproduction and survival

Growth rates

Our experiments testing for the presence of facilitative interactions showed a positive effect on the growth of both beneficiary species *Berula erecta* and *Groenlandia densa* when located in the wake of *Callitriche platycarpa* patches, compared to bare areas without vegetation. Transplants in locations sheltered by the patches ('Downstream' treatment) showed a significantly higher increase in shoot height compared with transplants on the 'Bare sediment' treatment (t-test, t = 4.3, df = 4.387, p = 0.02 for *Berula*; t = 5.5, df = 1.839, p = 0.04 for *Groenlandia*). The intensity of this effect was correlated with the reduction in flow velocity created by the facilitator species (r^2 = 0.96, p = 0.0004 for *Berula*, r^2 = 0.82, p = 0.03 for *Groenlandia*; Figure 3.5).

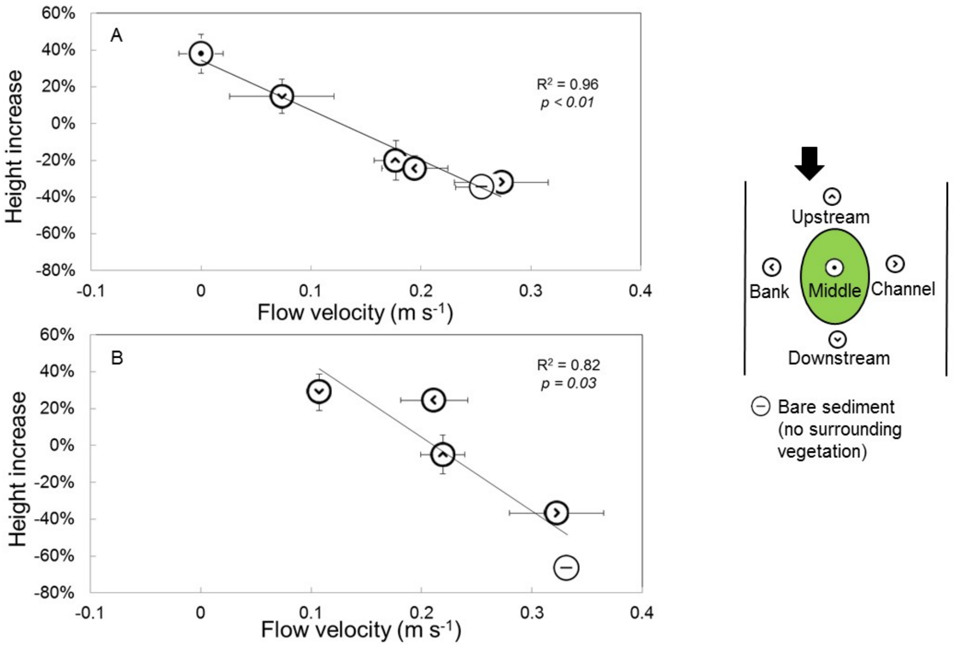

Figure 3.5: Relationship between flow velocity within and around *C. platycarpa* patches, and size increase of transplanted individuals of (A) *B. erecta* and (B) *G. densa* during the experimental period (t = 49 days).

Vegetative reproduction

No difference in dry mass invested in vegetative reproduction was found for either species between transplant positions (Figure 3.6C, F). Dry mass investment was not correlated with incoming flow velocity for *B. erecta* ($r^2 = 0.0168$, $p > 0.05$) or for *G. densa* ($r^2 = 0.48$, $p = 0.19$). A significant negative correlation was found between the average spacer length in the transplants and incoming flow velocity for *B. erecta* ($r^2 = 0.84$, $p = 0.01$; Figure 3.6A). The correlation was not significant for *G. densa* ($r^2 = 0.64$, $p = 0.19$; Figure 3.6D). A significant positive correlation was found between the height of the mother ramet transplant and their average daughter ramet height for both *B. erecta* ($r^2 = 0.65$, $p = 0.05$) and *G. densa* ($r^2 = 0.85$, $p = 0.02$) (Figure 3.6B, E).

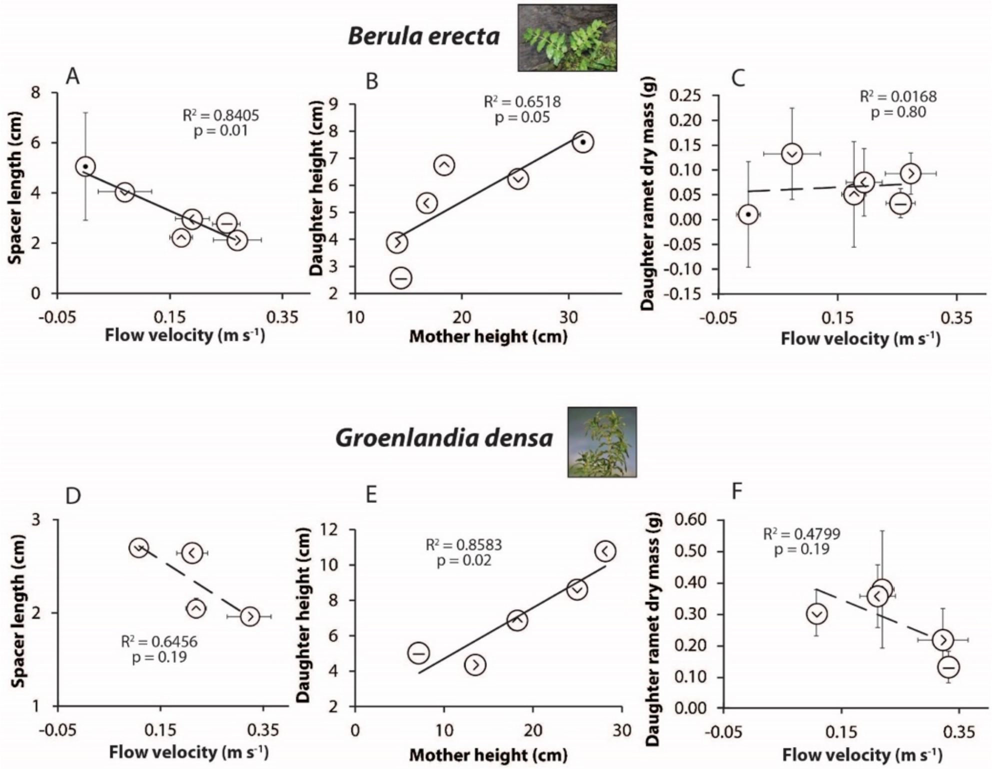

Figure 3.6: Relationships between flow velocity within and around *C. platycarpa* patches, and traits of vegetative reproduction for *Berula erecta* (A-C) and *Groenlandia densa* (D-F) at the end of the experiment (t = 49 days).

Transplant survival

Survival of transplanted individuals showed no significant relationship with local flow velocity up to 0.3 m s^{-1} ($r^2 = 0.20$, $p = 0.37$ for *B. erecta*; $r^2 = 0.44$, $p = 0.15$ for *G. densa*). However, survival curve analysis revealed significant differences in survival between treatments (Kaplan-Meier Mantel Cox, *Berula erecta*: $\chi^2 = 16.1$, $p = 0.00648$; *Groenlandia densa*: $\chi^2 = 11.9$, $p = 0.036$). Pairwise comparisons between treatments revealed that survival in the middle of the patch was significantly lower than on bare sediment for *B. erecta*, but not for *G. densa* ($p = 0.033$ and $p = 0.4205$ respectively, adjusted after Bonferroni correction; Table 3.2).

Table 3.2: Results of Kaplan–Meier Mantel–Cox log-rank test on transplant survival during the field experiment. Differences between treatments (transplant position around *C. platycarpa* patches) were tested against the 'bare sediment' treatment. P-values are adjusted using Bonferroni correction.

Species	Treatment	Log-rank of survival			
		χ^2	d.f.	p-value	adjusted p-value
Berula erecta	Middle	7.4	1	0.0066	0.0330
	Channel	5.1	1	0.0244	0.1220
	Downstream	2.3	1	0.1280	0.6400
	Upstream	1.2	1	0.2760	1.0000
	Bank	0.2	1	0.6860	1.0000
Groenlandia densa	Middle	3	1	0.0841	0.4205
	Channel	0.2	1	0.6590	1.0000
	Downstream	0.1	1	0.7470	1.0000
	Upstream	2.4	1	0.1180	0.5900
	Bank	0	1	0.8650	1.0000

Discussion

In a combined mathematical and empirical study, we reveal that bio-physical feedbacks between in-stream submerged plants and streamflow can generate spatial heterogeneity in hydrodynamic conditions that create a multitude of new niches, promoting species coexistence in streams. Central to this landscape of facilitation is spatial self-organization of submerged aquatic vegetation by means of deflection of water flow by the facilitator species, *Callitriche platycarpa*, which generates a patterned landscape of *Callitriche* patches. Our mathematical model shows that (1) the hydrodynamic heterogeneity results from the self-organization process and (2) it promotes coexistence by creating new niches for species that are adapted to a wider variety of environmental conditions. Species distribution patterns from our numerical model were in strong agreement with the spatial aggregation of different macrophyte species around *Callitriche platycarpa* patches observed in the field at the reach scale. A field transplantation experiment revealed that species coexistence results from a positive interaction due to stress amelioration, as the growth of these beneficiary species was facilitated by the hydrodynamic stress reduction mediated by *Callitriche* patches. Moreover, the effects of self-organized pattern formation on species interactions go beyond the spatial structure of the vegetation community. By affecting clonal growth traits, *Callitriche* patches also affect the density of the patches of other species, and therefore the spatial organization and appearance of vegetation patterns for the beneficiary species. Our study highlights that species coexistence in streams is, in part, explained by a biophysical feedback process that creates a heterogeneous landscape offering a multitude of facilitative effects.

Landscapes of facilitation through self-organized patchiness

Current theory largely ignores the spatial dimension when considering facilitative effects between species (Callaway (2007); Smit et al. (2007); Cavieres et al. (2014); but see van de Koppel et al. (2006); van de Koppel et al. (2015) for a review). Facilitative interactions are for the most part considered within the tussocks or patches of the facilitator species, and to date experiments have focused on this local scale, as beneficiary species are mainly considered to be living inside the facilitator patches (e.g. nurse plants in drylands; Callaway and Walker (1997); Badano and Cavieres (2006); but see Pescador et al. (2014)). Through this approach, many studies have shown the importance of facilitation but few have looked at its spatial variability. Here, we reveal that in self-organized ecosystems, facilitative interactions are far from being homogeneous in space, and display strong spatial heterogeneity due to the balance between positive and negative feedbacks. The self-organizing process leads to spatial separation of competition and facilitation, with opposite effects balancing throughout the landscape. Similar long-distance effects through modification of physical forcing by ecosystem engineers have also been observed in other systems, such as mussel beds on tidal flats (Donadi et al. 2013) or between adjacent tropical ecosystems at the landscape scale (Gillis et al. 2014a). The heterogeneity of facilitation and its spatial effects are important processes that have been identified in previous studies (Bruno and Kennedy 2000; van de Koppel et al. 2006), although not in the context of self-organized ecosystems. Hence, we show that self-organization acts as a strong structuring force of community composition and distribution by creating spatial variability in environmental conditions, leading to facilitative interactions at different spatial scales.

Our results emphasize that by triggering a self-organized pattern, a single engineering species may create a 'landscape of facilitation', where multiple mechanisms of coexistence co-occur due to the conditions created by the self-organized process. The conditions include: low stress – high competition inside the patch; low stress – low competition downstream of the patch; and high stress – low competition next to the patch. As the facilitative effects described here extend over longer distances, species with higher resistance to stress can locally colonize the open interspaces around the patches, exploiting the new niches created by the negative feedback without being exposed to high competition; less tolerant species can grow at a certain distance from the patch, where the positive feedback of stress reduction is still present, but there is no negative effect of competition. Although our model depicts a simplification of the complex hydrodynamic-vegetation interactions, the comparison between the predicted and observed spatial patterns suggests that the spatial distribution of *Berula erecta* is similar to that of a beneficiary species with lower resistance to hydrodynamic stress, while *Groenlandia densa* exhibits greater behavioural similarity to species with higher resistance to stress.

The differences in stress resistance between the two species are also supported by our transplantation experiments, where for *Groenlandia densa* we found a steeper inverse response of growth rate to hydrodynamic stress, compared to *Berula erecta*. Survival results for *Berula erecta* showed significantly higher mortality within the patch than in the other treatments, suggesting that short-range competition for light prevails in that location. Competition effects are also reflected in the displacement of *Berula erecta* at 2 m distance downstream of the *Callitriche* canopy, at an optimal spot between minimizing competition and maximizing hydrodynamic shelter. However, while we found a facilitative effect in terms of growth rates, we found no effect on the vegetative reproduction of beneficiary species. This observation is consistent with the ability of *B. erecta* to maintain its investment in vegetative growth and produce a more compact clonal growth form, despite the increased flow stress (Puijalon et al. 2005; Puijalon and Bornette 2006). Therefore, self-organization processes allow the coexistence of species with a wide range of growth strategies and sensitivity to stress.

Effects of self-organization on species coexistence

The process of pattern formation allows species to coexist, even if the number of resources on which they grow would predict competitive exclusion (Gause 1932). Our findings are relevant to furthering our understanding of species coexistence in a wide range of ecosystems with low underlying abiotic heterogeneity. The results from our study on submerged macrophytes in streams are also in accordance with previous theoretical studies of pattern formation and species coexistence in arid savannas (Gilad et al. 2004; Baudena and Rietkerk 2013; Nathan et al. 2013). These studies found coexistence of two species within the same spatial pattern (i.e. overlapping patches), and therefore confirmed that positive interactions occur within the limits of the facilitator species. Our study provides both theoretical and empirical evidence to show how one self-organizing species can have a profound effect on the distribution of different species and create multiple patterns of coexistence. Moreover, our research shows that such effects act both locally and at distance beyond the limits of the facilitator canopy (in the order of a few meters of the river reach in our study). This emphasizes the importance of self-organization in providing a potential explanation for the high biodiversity observed in many natural communities, despite theoretical predictions of low species coexistence.

The process we highlight, about the role of self-organization for species interactions, expands on the effects of ecosystem engineering and local facilitation between species, as self-organized patterns lead to the creation of heterogeneity from homogeneous abiotic conditions. While ecosystem engineering creates a local positive feedback, self-organized patchiness also results from a strong negative feedback. This negative feedback has a two-fold role. First, it prevents the facilitating species from dominating the entire habitat. Second, it changes environmental conditions within the inter-patch spaces, allowing for the coexistence of a wide range of species as compared to the original, more homogeneous habitat. Moreover, in hydrodynamically forced environments, self-organization creates a wider range of directional effects both inside and around the patterns, which adds to ecosystem engineering and local facilitation effects. The type of environmental stress will likely change the directionality of these effects. Relatively homogeneous environmental stressors (e.g. drought, light and nutrient availability) could lead to the same effect in all directions around an existing canopy, leading to isotropic patterns in the community structure. In contrast, if the environmental stress has a strong directional component (e.g. currents or waves), we can expect different effects in the zones adjacent to the patch, and therefore observe anisotropic patterns of species coexistence. Therefore, depending also on environmental conditions, the emergence of self-organized patterns determines distinct signatures in community spatial patterns that might be discerned from local facilitation effects.

The creation of new niches and the effects on biodiversity are not only limited to other plants, as animals can also strongly benefit from self-organized heterogeneity. For instance, fish can use both the shelter provided by plants as protection from predation, and the high-flow areas around patches as spawning and feeding grounds (Kozarek et al. 2010; Marjoribanks et al. 2016); and suspension-feeding invertebrates (e.g. blackfly larvae) can grow on the edge of submerged macrophyte patches, such as *Ranunculus* sp. where higher current velocities increase the flux of resources (Wharton et al. 2006). Thus, self-organization affects a multitude of species within stream communities at different trophic levels.

Relevance beyond stream ecosystems

The importance of pattern formation in promoting species coexistence, by creating a landscape of facilitation, is likely to be relevant for a wide range of self-organized ecosystems where feedback interactions occur between organisms and physical stress, without strong pre-existing environmental gradients or heterogeneity. Many of these systems are characterized by the presence of at least one habitat-forming species that provides structure for an entire community. For instance, similar effects of self-organization on facilitation may occur in arid or semi-arid systems, where periodic vegetation patterns can create different levels of edaphic and climatic stress for other species (Couteron 2001; Rietkerk et al. 2002). Other examples of ecosystems where self-organized patterns may create a landscape of facilitation are coastal environments. Mussel beds on relatively homogeneous intertidal flats reduce wave stress and increase habitat structural complexity and species richness (Gutiérrez et al. 2003; van de Koppel et al. 2005; van de Koppel et al. 2008; Donadi et al. 2013; Christianen et al. 2016). Banded patterns formed by seagrass patches in marine and estuarine environments interact with hydrodynamics and sedimentation (Van der Heide et al. 2010), increasing both habitable living spaces and areas protected from predation for fish and invertebrates (Heck and Orth 1980). Self-organized spatial patterns also emerge in intertidal salt marshes (van de Koppel et al. 2004), where critical facilitator plant species create different patterns in sediment deposition, salinity and redox conditions (Howes et al. 1981; Callaway 1994; Hacker and Bertness 1999). As the emergence of self-organized patterns is a widespread phenomenon, landscapes of facilitation may occur in many ecosystems. Thus, this process seems to be of general ecological importance to enhance species coexistence and biodiversity.

In ecosystems with limited underlying heterogeneity in abiotic conditions, the process of self-organized pattern formation leads to a landscape where different facilitative effects occur in different locations. While the importance of self-organization for ecosystem functioning has been increasingly recognized, we emphasize that self-organization is also a powerful structuring force of community composition and distribution. The findings of our study can be used to guide ecological restoration projects, to maximize biodiversity by showing the significance of the preservation or re-introduction of self-organized species. Exploring the implications of species coexistence promoted by self-organization on food web structure is also an interesting topic for future studies. Understanding of the intricate way in which competition and facilitation interact in many ecosystems is key to successful management of their biodiversity.

Appendix 3.A

Quantifying dispersal capabilities in relation to flow stress through clonal growth traits

For the two beneficiary species *Berula erecta* and *Groenlandia densa*, we measured clonal growth traits by sampling individuals growing aggregated into patches over a range of incoming flow velocities in the field, in order to *i)* test whether their dispersal through vegetative propagation could be described by the diffusion approximation, and *ii)* as input to parameterize the diffusion constants D_{Pi} in the model.

Different patches were selected for sampling, based on differences in local incoming flow velocity (n = 4 for *B. erecta*, n = 5 for *G. densa*). For five different positions inside the patch (upstream, downstream, and halfway in the length of the patch on the left side, middle and right side), we collected 5 clones (hereby defined as a set of physically interconnected individuals, or ramets). Plants were kept for no more than 48 hours before measurements were made. For each clone, spacer length (cm) was measured as the distance between consecutive individuals. Cumulative frequency distributions of spacer lengths were calculated for clones located in the upstream part of the patch, in order to test whether they could be described by Brownian motion (Figure 3.7). The average spacer length was calculated as the mean over the five replicated clones, in order to analyze the relationship between step length and incoming flow velocity (Figure 3.7).

Spreading strategies of *B. erecta* and *G. densa* revealed that *B. erecta* presents a more diffusive behavior, with larger distance between individuals at low flow velocity and individuals growing closely together at high flow velocity (Figure 3.7A, C). On the other hand, *G. densa* has a less diffusive behavior, with small spacers irrespective of flow velocity (Figure 3.7B, D). Average spacer lengths in the clones are negatively correlated with incoming flow velocities for *B. erecta* ($r^2 = 0.65$, $p < 0.05$). No significant correlation was found between average spacer lengths and incoming flow velocity in *G. densa* ($r^2 = 0.0014$, $p = 0.83$).

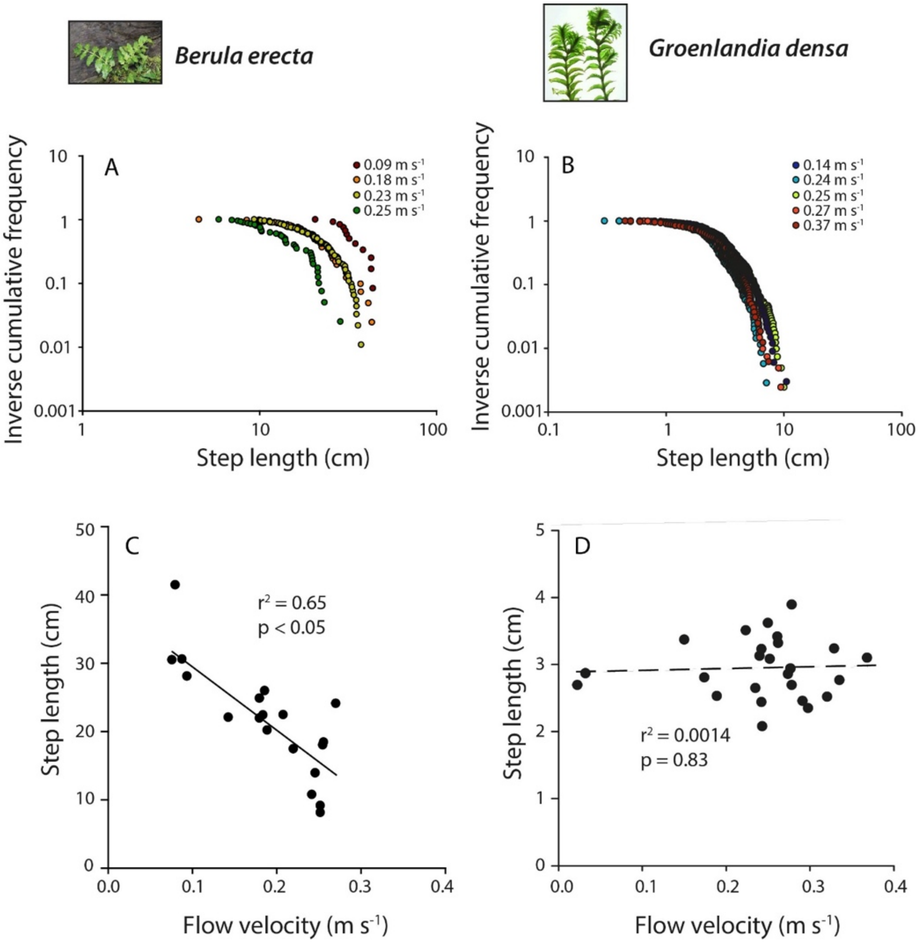

Figure 3.7: Cumulative distributions of step length (distance between individual plants in a clone) in patches sampled at different incoming flow velocities, and correlation between step length and incoming flow velocity for (A) *Berula erecta*, and (B) *Groenlandia densa*.

Appendix 3.B

Location of the study sites for spatial pattern analyses and field transplantations

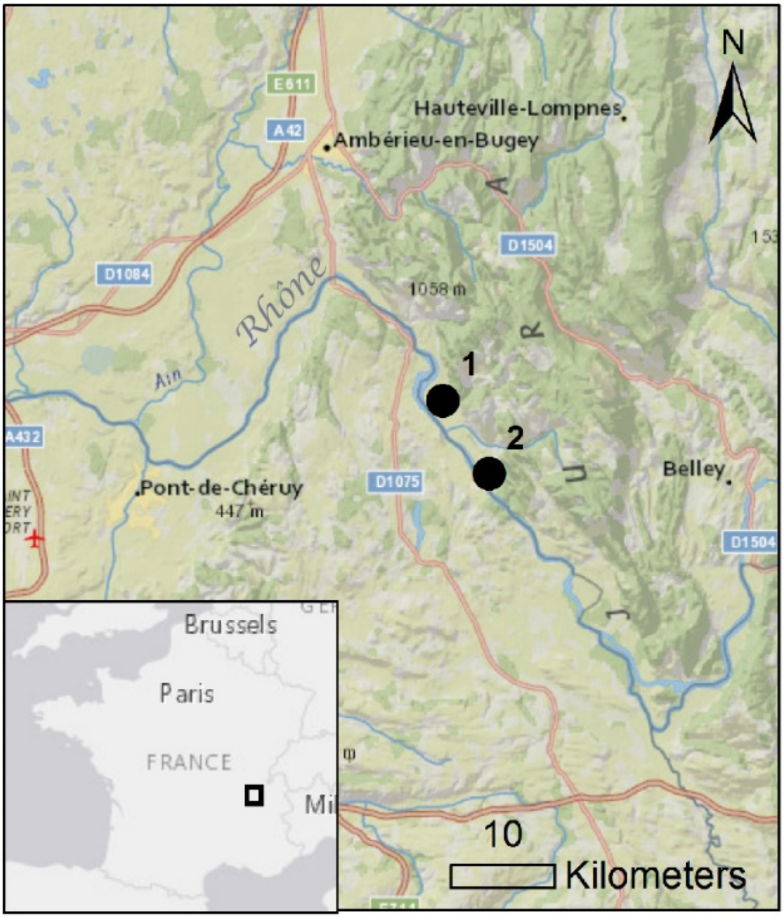

Figure 3.8: Location of the two study sites along the Rhône river, France (1: Serrières-de-Briord; 2: Flévieu). In both sites, aerial photographs were taken for the analysis of species coexistence patterns. Site 1 was also the location of the field transplantation experiment. *Sources: National Geographic, Esri, DeLorme, HERE, UNEP-WCMC, USGS, NASA, ESA, METI, NRCAN, GEBCO, NOAA, iPC* (main map)*; Esri, DeLorme, HERE, MapmyIndia* (inset map).

Chapter 4

Flow-divergence feedbacks underlie propagule retention by in-stream vegetation: the importance of spatial patterns for facilitation

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Submitted

Abstract

Facilitation has been increasingly recognized as an important driver of biodiversity. However, despite the patchy distribution of many facilitator species, it is still unknown if facilitation during dispersal and colonization depends on the mechanisms underlying self-organized spatial pattern formation. Using freshwater streams as a model system, we investigated if water flow divergence mechanisms affected the ability of submerged macrophyte patches to trap the vegetative propagules of other plant species and potentially benefit their colonization. We specifically focused on i) propagule traits, ii) hydrodynamic forcing, and iii) patch spatial configuration. We found that propagule buoyancy was negatively correlated with trapping chance, while propagule size did not influence trapping. Species-specific differences in buoyancy were maintained for weeks after fragmentation. Trapping of fragments was interactive and conditional upon incoming flow velocity and spatial patterning of the vegetation. At high flow velocities, the patch canopy was pushed over by the flow till below the water surface, which strongly decreased trapping of surface-drifting fragments. At low flow velocities, trapping depended on spatial vegetation patterns: at patchy intermediate cover in the cross-section, macrophytes diverted the flow towards unvegetated areas, thereby creating low-velocity areas were their canopy remained upright and propagules were retained. At peak cover with near-homogeneous vegetation, the flow divergence mechanism was prevented and trapping was reduced, as water mainly passed on top of the patches, pushing the canopies below the water surface. Overall, present results on the interplay of water movement and patch reconfiguration suggest that environmental heterogeneity generated by organisms themselves can enhance propagule retention and might potentially benefit colonization by sessile organisms. This process is however conditional upon spatial patchiness and environmental stress. Our study suggests that the self-organizing mechanisms underlying spatial patterns are crucial for species interactions. Hence, understanding the spatial component of species interactions is essential for restoration and conservation of biodiversity.

Introduction

Understanding the drivers of biodiversity is a key research topic in ecology. Facilitation, or positive interactions between species, has strong effects on the diversity and species composition of communities and is therefore a key process to understand biodiversity (Bertness and Callaway 1994; Callaway 1994; Bruno et al. 2003; Brooker et al. 2008; McIntire and Fajardo 2014). Positive interactions are often performed by foundation species (Dayton 1972) or ecosystem engineers (Jones et al. 1994), which create stable conditions for other species and provide much of the structure of a community. Facilitation can increase diversity through well-studied underlying mechanisms, such as enhanced resource availability, provision of refuges against physical stress and protection from predation or competition (Bertness et al. 1999; Borthagaray and Carranza 2007; Callaway 2007). The spatial component of facilitation is usually studied at the local scale of an individual patch, in locations under the protective influence of the facilitator (e.g. "nurse plant syndrome"; Niering et al. (1963); Padilla and Pugnaire (2006)), or along gradients of physical stress (Bertness and Callaway 1994; Bertness and Leonard 1997). However, many foundation species and ecosystem engineers generate striking spatial patterning at the landscape scale by self-organization processes, even in the absence of underlying abiotic gradients (Rietkerk and Van de Koppel 2008). Understanding the role of patchiness at the landscape scale for inter-specific facilitation is critical to maintain biodiversity.

Many self-organized spatial patterns in ecosystems emerge from scale-dependent feedbacks, whereby the interaction between the organisms and the environment leads to a positive feedback on a local scale, but a negative one inhibits their growth on larger scales (Rietkerk and Van de Koppel 2008). These feedbacks arise through different mechanisms, such as concentration of limiting resources (e.g. nutrients in peatlands; Eppinga et al. (2009)) or divergence of physical stress (e.g. water flow or snow; Hiemstra et al. (2002); Larsen et al. (2007); Weerman et al. (2010)). Here, the positive feedback of resource concentration or flow reduction within the patches is coupled with a negative feedback of resource depletion or increased flow stress outside the patches. Yet, it is unknown how the presence or absence of these underlying mechanisms affects facilitation. In such patchy systems, facilitative effects at the within-patch scale cannot be easily scaled up to facilitation at the larger, between-patch scale for the following two reasons. Firstly, the landscape configuration or total cover of the patches may affect the environmental conditions in the gaps between them, by changing their feedback interaction with the stress factor (Fonseca et al. 1983; Granata et al. 2001; Larsen and Harvey 2010; Kondziolka and Nepf 2014). Secondly, the balance between competition and facilitation can be strongly scale-dependent (van de Koppel et al. 2006), as abiotic conditions are mitigated in the patches, but competition with the facilitator might be very high. Hence, it is important to consider how facilitation is affected by self-organized spatial patchiness and its underlying feedback mechanisms.

While self-organization can be due to a number of mechanisms, we focus here on the divergence of water flow. This is a common principle underlying the patchy distribution of foundation species in many aquatic ecosystems, such as rivers (Schoelynck et al. 2012), salt marshes (Temmerman et al. 2007; Bouma et al. 2009a; Vandenbruwaene et al. 2011) and seagrass beds (Van der Heide et al. 2010). In such physically stressed environments, the arrival of dispersal units in favourable microsites within the patches of a facilitator species can be crucial (Aguiar and Sala 1997), especially for non-mobile organisms that require entrapment or stranding to establish (Rabinowitz 1978; Turner 1983; Nilsson et al. 2010). Here, any organism that enhances the arrival or retention of propagules can have a potential facilitative effect (Callaway 1995) and affect colonization rates (Bruno et al. 2003; McKee et al. 2007). In many of these systems, the environmental stress may also be the dispersal vector (e.g. wind, water). Previous studies on transport and retention through vegetated environments often assumed homogeneous distribution or a single cover value of the facilitator (Chang et al. 2008; Peterson and Bell 2012; Gillis et al. 2014b; Van der Stocken et al. 2015), despite its spatial patchiness. Considering only a single cover of the facilitator, overlooking its spatial structure in relation to environmental stressors, can tell us very little about the realized facilitative effects in a patchy landscape. Hence, we aim to test whether facilitation during dispersal and colonization depends on the flow divergence mechanism underlying spatial patchiness of the facilitator.

In lotic ecosystems, aquatic macrophytes are important foundation species (Carpenter and Lodge 1986). Submerged plants in rivers grow in a patchy pattern due to local flow reduction within the vegetation and divergence of water flow around it (Sand-Jensen and Mebus 1996; Sand-Jensen 1998; Cotton et al. 2006; Wharton et al. 2006; Schoelynck et al. 2012). Water flow is both the stress factor that leads to vegetation patchiness and one of the main dispersal vectors of plant propagules (e.g. seeds, vegetative fragments, stolons, turions; Goodson et al. 2001; 2003; Bornette & Puijalon 2011; Nilsson et al. 2010). Among vegetative propagules, fragments are of clear importance for the colonization of stream reaches (Barrat-Segretain et al. 1998), and can account for up to 90% of new plant establishment in streams (Sand-Jensen et al. 1999; Riis 2008). Retention of vegetative fragments in streams is a necessary step before primary colonization and a bottleneck to vegetation establishment (Figure 4.1), which relies on the availability of structures to entrap propagules (Riis and Sand-Jensen 2006; Riis 2008). Existing macrophyte canopies are one of the main potential retention agents for plant fragments: in the absence of vegetation, only 1% of dispersed shoots is retained in the sediment by contact with the stream bed (Riis 2008). However, interactions between vegetation and hydrodynamic stress may affect propagule retention: patches of flexible vegetation can reconfigure by bending down closer to the substrate, if hydrodynamic stress increases (Sand-Jensen and Pedersen 2008; Schoelynck et al. 2013), creating less of an obstruction in the water column. Propagule traits like buoyancy and size may also play a role in the dispersal process. For instance, buoyancy determines the propagule's position within the water column and thereby most likely the capability to travel for long distances vs. the chance of impacting with the vegetation structure (Riis and Sand-Jensen 2006). Hence, streams with self-organized patchy aquatic macrophytes provide a unique opportunity to test how flow divergence mechanisms affect propagule retention, and how this depends on the landscape-scale setting of these vegetation patches.

In this study, we aimed to test the effects of water flow divergence on propagule retention by existing macrophyte patches in streams. Specifically, we tested the effects of the patchy submerged macrophyte *Callitriche platycarpa* Kütz on the dispersal and retention of vegetative propagules of other sessile aquatic plant species that may co-occur in the field. As propagule retention is a necessary step before primary colonization (Riis (2008); Figure 4.1), we regard it as proxy for facilitation during dispersal and colonization. First, we tested the role of water flow divergence around vegetation patches on propagule retention. That is, we compared vegetation distributions where the flow divergence mechanism was in place (i.e., patchy vegetation, with unvegetated flow areas next to vegetated areas), to near-homogeneous vegetation distributions that prevented flow divergence (i.e., almost fully vegetated cross-sections, with no areas for lateral flow diversion). Second, for each vegetation configuration, we tested the effects of propagule traits (i.e., buoyancy and size) and hydrodynamic forcing (i.e., current velocity affecting the bending of the canopy) on the retention of propagules. For this study, we used a combination of mesocosm, flume and field experiments. In the discussion, we extrapolate our findings on propagule retention towards the implications of bio-physical feedbacks and self-organization for species interactions.

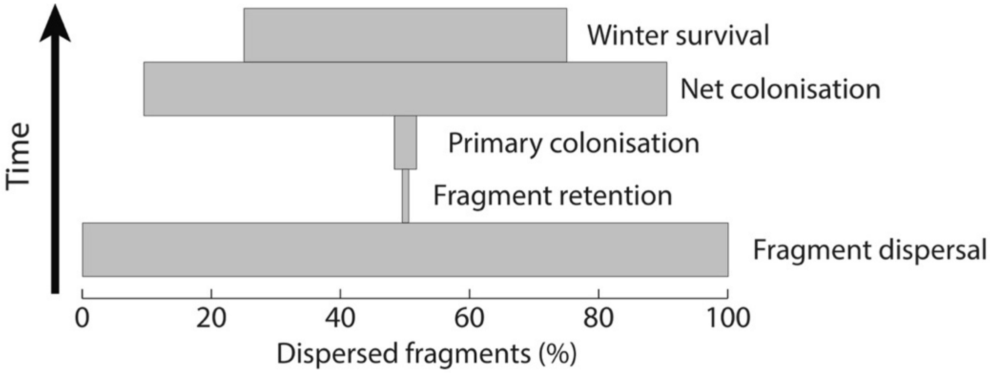

Figure 4.1: Consecutive processes involved in macrophyte colonization of lowland streams. Bars indicate the success rates based on the previous process (% of fragments). Modified from Riis (2008).

Materials and Methods

Studied species

The propagules of three freshwater macrophyte species, *Berula erecta* (Huds.) Coville, *Groenlandia densa* (L.) Fourr. and *Elodea nuttallii* (Planch.) St. John, were considered for this study (Figure 4.2). Here, we focused on the dispersal of vegetative fragments, as the processes of interaction with vegetation patterns may be different for vegetative and sexual propagules, particularly due to differences in size or buoyancy (Cellot et al. 1998; Merritt and Wohl 2002; Chang et al. 2008; Carthey et al. 2016). Vegetative fragments are important for macrophyte species recruitment in streams: they can be viable for more than 10 weeks (Barrat-Segretain et al. 1998), and can regrow into viable plants (i.e. regenerate) and develop new propagules (Barrat-Segretain et al. 1999). The vegetative propagules used in the experiments consisted of whole plants, comprising both aboveground and belowground parts. *B. erecta* has a rosette of petiolated-dissected leaves, *G. densa* is a caulescent species with opposite leaves, and *E. nuttallii* presents relatively rigid stems with short, densely packed leaves. This species selection allowed us to compare propagules with different floating traits: as previously observed for a species (*E. canadensis*) morphologically similar to *E. nuttallii* (Riis and Sand-Jensen 2006), propagules of this species have lower buoyancy and tend to drift slightly below the water surface, rather than on the water surface as is the case for *B. erecta* and *G. densa.*

Figure 4.2: Propagules of freshwater species used in the experiment: (A) *Berula erecta*, (B) *Groenlandia densa*, (C) *Elodea nuttallii.*

Sample collection

Individuals of the three freshwater species *B. erecta*, *G. densa* and *E. nuttallii* were collected by hand on 12 September 2014 in an artificial drainage channel located along the Rhône River near Serrières de Briord (France, 45.813551° N, 5.447440° E). Sample collection was performed at the end of the growing season to limit plant growth during storage or experiments. To investigate the effect of fragment size on their retention, propagules were selected in two contrasting sizes for each species to represent their normal range in propagule size (21.9 ± 2.6 cm and 48.4

± 2.2 cm for *B. erecta*; 17.8 ± 1.3 cm and 41.4 ± 3.4 cm for *G. densa*; 12.8 ± 2.5 cm and 40.8 ± 4.2 cm for *E. nuttallii*). Plants were stored in plastic bags and transported to the flume laboratory in NIOZ Yerseke (The Netherlands) within 24 h from collection, where they were kept outside in tanks with aerated tap water, with a water level of 20 cm and at natural light for one week before the experiments started.

Quantifying floating traits by a mesocosm experiment

In order to study how the traits of the dispersing propagules affected retention within submerged vegetation, and test whether the time spent in water after detachment could influence plant floating capacity, propagule buoyancy was monitored in a mesocosm experiment prior to the release in the flume. Propagule buoyancy was measured using a force transducer developed by the former WL Delft Hydraulics (now Deltares, Delft, The Netherlands). The transducer consisted of a solid platform, carried by two steel cantilever beams, with four temperature-corrected strain gauges mounted in pairs on opposite sides of each of the two steel cantilevers (for details see Bouma et al. (2005)). The voltage output for the force transducer was linear with forces up to 10 N. We measured the buoyancy of 12 fragments for each of the two size classes per species, for a total of 72 fragments. Buoyancy was monitored weekly up to a month after the start of the experiment. During the measurements, each individual plant was mounted on top of the transducer, and voltage readings were collected on a data logger at a frequency of 100 Hz and expressed as the mean value for 1 min.

Quantifying the dispersal and retention of plant propagules by a flume experiment

The ability of submerged aquatic vegetation to trap propagules of other species was assessed by mimicking the patch morphology of the aquatic macrophyte *Callitriche platycarpa* in a flume setup. Although *Callitriche* patches are often monospecific (Sand-Jensen et al. 1999; Demars and Gornall 2003), 'mixed' patches with individuals of different species have been observed frequently at our field sites (L. Cornacchia, personal observation). The experiments were conducted in the racetrack flume (17.5 m long, 0.6 m wide and 0.3 m of water depth) at the

Royal Netherlands Institute for Sea Research (NIOZ), using a smooth flume bottom. Patches of *C. platycarpa* (1.2 m in length) were mimicked using commercial fishing rope, which was mounted on boards and cut to recreate the typical patch morphology of this submerged macrophyte: plants are rooted at the upstream end and form a trailing canopy just beneath the water surface. In addition, *C. platycarpa* has gradually increasing canopy height from upstream to downstream (Licci et al. 2016). For an average sized *C. platycarpa* patch, plants located further downstream gradually increment their biomass and increase patch height, being able to reach the water surface and form floating leaf rosettes.

To test the role of water flow divergence around vegetation on propagule retention, we released the fragments in the flume with mimic submerged vegetation patches at the end of the four-week monitoring in the mesocosm (six fragments per species and size in each run). Ten replicates were completed for each combination of parameters for a total of 48 treatments: 4 vegetation configurations, 3 species differing in buoyancy (*B. erecta*, *G. densa*, *E. nuttallii*), 2 propagule sizes (small and large individuals), and 2 flow velocities (0.1 and 0.3 m s^{-1}). The four vegetation configurations consisted of two single-patch configurations (‘W’: wide patch, 0.4 m wide, corresponding to 66% of the flume width; ‘N’: narrow patch, 0.2 m wide, corresponding to 33% of the flume width) and two multiple-patch configurations (‘W--N’: W patch upstream of N patch, 0.75 m distance between their leading edges; ‘W----N’: W patch upstream of N patch, 1.90 m distance between their leading edges; Figure 4.3A). In the two single-patch configurations and the ‘W----N’ multiple-patch configuration, the flow divergence mechanism was maintained by keeping a channelled flow area next to the vegetation. Instead, flow divergence was prevented in the ‘W--N’ configuration by placing the patches close together to create an almost fully vegetated cross-section, with no areas for lateral flow redistribution. These configurations were selected to mimic the spatial arrangements observed at the field sites and on other freshwater streams, with patches both growing isolated or close to neighbouring patches (Cotton et al. 2006; Sand-Jensen and Pedersen 2008; Cornacchia et al. 2016). Within each configuration, the vertical structure of the vegetation was quantified by measuring the canopy height and water height of each patch in three points along its central axis, using a reinforced meter rule. The difference between water depth and canopy height was calculated for each measurement point; the free-flowing space within each configuration was then expressed as the minimum difference observed over all points across the patches in the section.

Individual propagules were released onto the water surface upstream of the patch mimics. We measured the time for propagules to move through the vegetated section, and recorded the total time they were stopped due to entanglement in the patch canopy. If this time exceeded 2 min, we considered the propagules to be trapped indefinitely in submerged vegetation, as longer-term preliminary tests showed no fragment release once the stopping time exceeded 2 min. Hence, the trapping capacity inside each patch configuration was determined as the percentage of propagules retained within a patch for more than 2 min. For the two multiple-patch configurations ('W--N' and 'W----N'), the sum of the fragments trapped within each patch was the value used in the analyses.

Quantifying the role of vegetation cover and structure on propagule retention in the field

Field experiments on the role of vegetation cover and vertical structure on propagule retention were conducted in two naturally vegetated channels located along the Rhône River (France), near Serrières-de-Briord (45.815 ° N, 5.427 ° E) and Flévieu (45.767 ° N, 5.480 ° E). The channels are uniform in terms of width and water depth, with relatively straight banks. The two channels present similar length (3.19 and 4.26 km for Flévieu and Serrières-de-Briord channels, respectively), width (5.8 – 8.0 m), depth (0.75 – 1.00 m) and substrate characteristics (fine to coarse gravel bed). Flow velocities are on average 0.18 and 0.25 m s^{-1}, respectively, with a discharge of 0.73 and 1.30 m^3 s^{-1} in July. The field release experiments were used to assess the impact of the natural macrophyte structure in the water column (presence of floating vegetation vs. fully submerged vegetation) on propagule retention, as well as the effects of increasing vegetation cover on propagule retention in natural conditions. Here, we selected different sections along the channels to represent different percentage cover of either fully submerged or both submerged and floating-leaved *Callitriche platycarpa* stands. Within each section, the vertical structure of *C. platycarpa* patches was quantified by measuring the canopy height and water height of each vegetation patch in three points along its central axis, using a reinforced meter rule. The difference between water depth and canopy height was calculated for each measurement point; the free-flowing space within each section was then expressed as the minimum difference observed over all points across the macrophyte beds in the section. Five fragments of each species (23.5 ± 1.0 cm for *B. erecta*; 20.9 ± 0.5 cm for *G. densa*; 20.4 ± 0.9 cm for *E. nuttallii*) were collected from neighboring patches and released at the beginning of each section. Ten replicate releases were completed for each fragment. We measured the time for fragments to move through the section and recorded whether the propagules were retained in submerged vegetation for more than 2 min. Hence, the percentage of trapped fragments was calculated as the percentage of propagules retained inside the *C. platycarpa* patches for more than 2 min.

Statistical analyses

All statistical analyses were performed in R 3.1.2 (R Core Team 2015). We used repeated-measures ANOVA to analyse changes in propagule buoyancy over time. A one-way ANOVA was used to test for differences in buoyant force between species. The effects of propagule size on trapping capacity could not be tested for *E. nuttallii*, as the larger propagules of this species fragmented during the mesocosm monitoring. Therefore, we used a generalized linear model (GLM) with a logit link function and binomial error distribution to test the effects of two propagule species (*G. densa* and *B. erecta*) and their propagule size, spatial configuration, flow velocity and their interactions on trapping capacity in the flume study. As the effect of propagule size was not significant, we used a GLM to test the effects of all three propagule species, spatial configuration, flow velocity and their interactions on trapping capacity. For the field study, a GLM was constructed to test the effects of propagule species, vegetation type (submerged/emerged), vegetation cover and their interactive effects on trapping capacity. Significance of predictors was determined using likelihood ratio tests to compare the full model with reduced models using the ‘anova’ function. Tukey’s contrasts for multiple comparisons were performed using the ‘glht’ function in the package ‘multcomp’. Linear regression was used to test for the relationship between buoyant force and trapping capacity in the flume experiment, and between free-flow space over the canopy and trapping capacity in the field study.

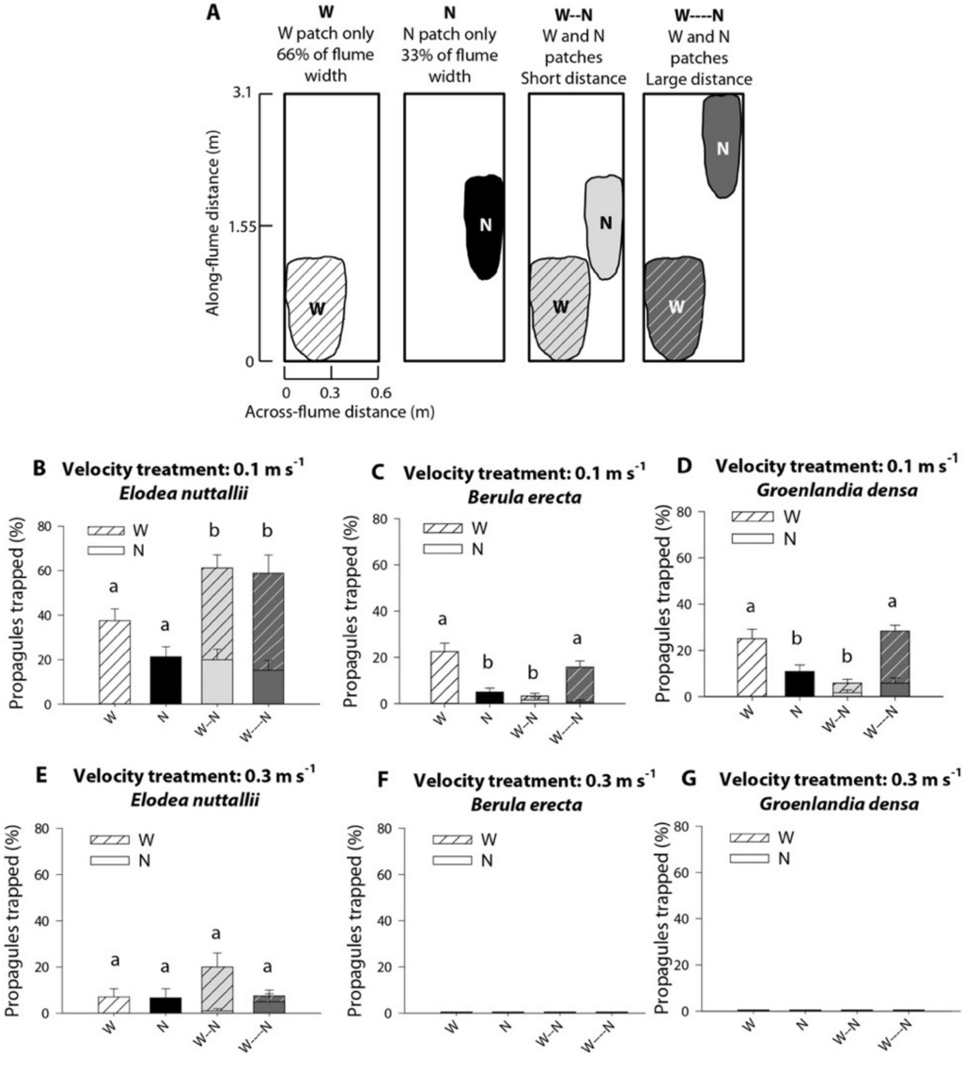

Figure 4.3: (A) Schematic top view of the four single- and multiple-patch spatial configurations of *Callitriche platycarpa* mimics in the racetrack flume tank. 'W' indicates the wide patch, corresponding to 66% of the flume width; 'N' is the narrow patch, corresponding to 33% of the flume width. Water flow direction is from bottom to top of the figure. (B) Percentage of vegetative propagules trapped within single or multiple patch configurations at the 0.1 m s^{-1} velocity treatment, for *E. nuttallii*, (C) *B. erecta* and (D) *G. densa*. (E) Percentage of vegetative propagules trapped within single or multiple patch configurations at the 0.3 m s^{-1} velocity treatment, for *E. nuttallii*, (F) *B. erecta* and (G) *G. densa*. Propagules trapped (%) are means (+1 SE) of 12 propagules for n = 10 runs. Hashed bars indicate the propagules trapped in patch 'W', and solid bars indicate the propagules trapped in patch 'N'. The sum of the propagules trapped in both patches was used in the analyses. Letters denote significant differences (Tukey's contrasts, $p < 0.05$).

Results

Effects of propagule traits on propagule trapping

Changes in propagule buoyancy since dislodgement – mesocosm measurements

Propagule buoyancy for the three species did not change significantly over time during the four-week time spent in the water column after fragmentation (repeated-measures ANOVA, $F_{2,66} = 0.879$, $p = 0.42$ for *E. nuttallii*, $F_{2,66} = 1.327$, $p = 0.27$ for *B. erecta*, $F_{2,63} = 2.405$, $p = 0.098$ for *G. densa*; Figure 4.4). Hence, the time spent in the water column after detachment could be regarded as a marginal factor in terms of dispersal and trapping for such a time scale. However, the buoyant force differed significantly between species (one-way ANOVA, $F_{2,221} = 57.7$, $p < 0.001$). *E. nuttallii* showed significantly lower buoyant force than *B. erecta* and *G. densa* (Tukey's HSD $p < 0.001$ for both pairwise comparison). Buoyancy values also differed between the two surface floating species, with significantly higher values for *B. erecta* than *G. densa* (Tukey's HSD $p < 0.001$).

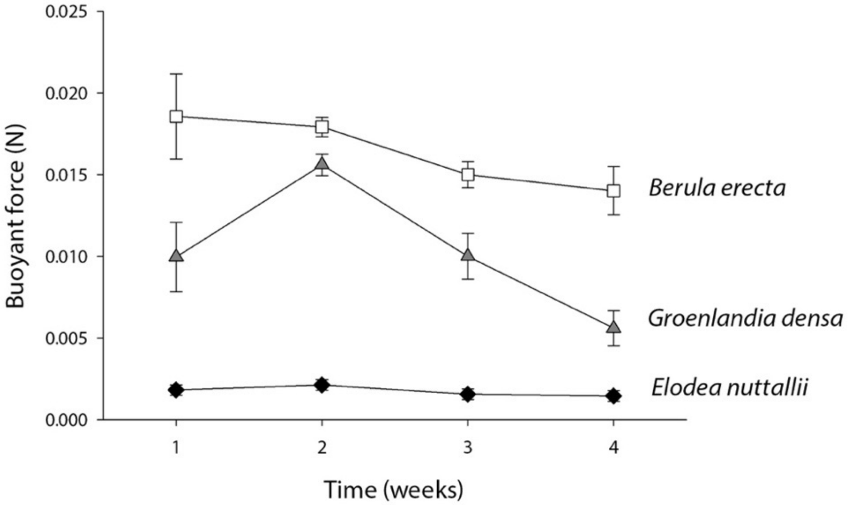

Figure 4.4: Mean (+SE) values of buoyant force (N) of the aquatic plant species (n = 24) *Elodea nuttallii* (*diamonds*), *Groenlandia densa* (*triangles*) and *Berula erecta* (*squares*) during the experimental period.

The influence of propagule size and buoyancy on propagule trapping – flume experiments

Results showed that propagule buoyancy, but not propagule length, affected the chance of being trapped by submerged vegetation. Testing with a GLM revealed that there were no significant interactions between propagule size, species, flow velocity and patch spatial configuration on trapping of *G. densa* and *B. erecta* fragments (Table 4.1, p = 1.00). No difference in trapping was found between small and large fragments of the two species (likelihood ratio test, $\chi^2 = 1.983$, d.f. = 1, p = 0.16), thus rejecting our hypothesis that large fragments have a greater chance of being trapped. However, buoyancy (as measured at the end of the monitoring period in the mesocosm experiment) was negatively correlated with the percentage of propagules trapped in the flume experiments at the 0.1 m s^{-1} velocity treatment ($r^2 = 0.56$, $p < 0.05$; Figure 4.5).

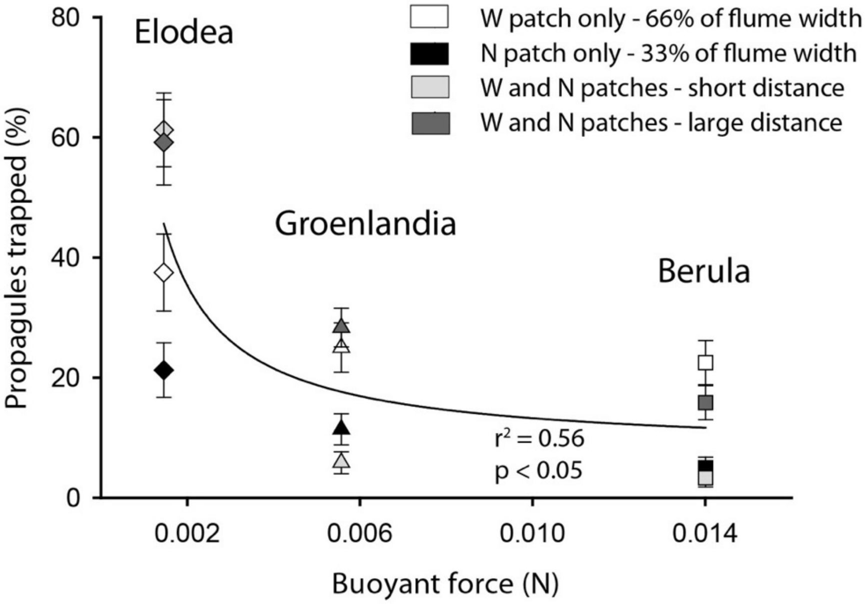

Figure 4.5: Percentage of retained propagules of *Elodea nuttallii* (*diamonds*), *Groenlandia densa* (*triangles*) and *Berula erecta* (*squares*) for two single-patch configurations (66% and 33% of vegetation in the cross-section) and two multiple patch configurations (short and large spacing between the patches) at the 0.1 m s^{-1} velocity treatment, in relation with their buoyant force (N) measured at the end of the 4-week monitoring in the mesocosm experiment.

Table 4.1: Analysis of deviance table of the generalized linear model for the effects of propagule species (*G. densa* and *B. erecta*), propagule size, vegetation spatial configuration and flow velocity on propagule trapping in the flume experiments.

	df	Deviance	Residual df	Residual Dev.	p (> Chi)
Species	1	6.078	318	410.52	**0.013**
Propagule size	1	1.983	317	408.54	0.159
Spatial configuration	3	54.807	314	353.73	**< 0.01**
Flow velocity	1	210.431	313	143.30	**< 0.01**
Species × Propagule size	1	0.058	312	143.24	0.809
Species × Spatial configuration	3	2.464	309	140.78	0.481
Propagule size × Spatial configuration	3	2.300	306	138.48	0.512
Species × Flow velocity	1	0.000	305	138.48	0.999
Propagule size × Flow velocity	1	0.000	304	138.48	0.999
Spatial configuration × Flow velocity	3	0.000	301	138.48	1.000
Species × Propagule size × Spatial configuration	3	0.738	298	137.74	0.864
Species × Propagule size × Flow velocity	1	0.000	297	137.74	0.999
Species × Spatial configuration × Flow velocity	3	0.000	294	137.74	0.999
Propagule size × Spatial configuration × Flow velocity	3	0.000	291	137.74	0.999
Species × Propagule size × Spatial configuration × Flow velocity	3	0.000	288	137.74	0.999

Effects of spatial vegetation patterns & vegetation cover on propagule trapping

Patch size and spatial configuration – flume experiments

Our flume studies showed that propagule trapping was strongly affected both by changes in vegetation patch size (in terms of width in the cross-section) and their spatial distribution (in terms of distance between vegetation patches) ($\chi^2 = 39.677$, d.f. = 3, $p < 0.001$; Table 4.2). The net-effect was, however, strongly conditional upon flow velocity and the propagule species ($\chi^2 = 28.083$, d.f. = 2, $p < 0.001$). For that reason, we discuss the results per species and velocity treatment in the subsequent two paragraphs.

Table 4.2: Analysis of deviance table of the generalized linear model for the effects of all propagule species (*G. densa*, *B. erecta* and *E. nuttallii*), vegetation spatial configuration and flow velocity on propagule trapping in the flume experiments.

	df	Deviance	Residual df	Residual Dev.	p (> Chi)
Species	2	162.374	397	610.81	**< 0.001**
Spatial configuration	3	39.677	394	571.13	**< 0.001**
Flow velocity	1	259.398	393	311.73	**< 0.001**
Species × Spatial configuration	6	53.546	387	258.18	**< 0.001**
Species × Flow velocity	2	28.083	385	230.10	**< 0.001**
Spatial configuration × Flow velocity	3	3.592	382	226.51	0.309
Species × Spatial configuration × Flow velocity	6	0.000	376	226.51	1.00

Within the 0.1 m s^{-1} velocity treatment, there was a statistically significant two-way interaction between the effects of species and configuration on propagule trapping ($\chi^2 = 46.021$, d.f. = 6, $p < 0.001$). When submerged vegetation cover in the cross section was halved, by decreasing patch width from 66% to 33% of the flume width, the chance of propagules getting trapped decreased more than twofold for the two surface-floating species *G. densa* and *B. erecta* (Tukey's contrasts, $z = 2.792$, $p = 0.025$ and $z = 3.614$, $p = 0.001$, respectively; Figure 4.3C and D, W and N). When two patches were positioned a short distance apart (0.75 m between their leading edges) and therefore partially next to each other, leading to a cross section with 100% vegetation cover, trapping chance significantly dropped compared to the W configuration (Tukey's contrasts, $p < 0.001$ for both species), as the flow was confined to a narrow channel in between the two patches (Figure 4.3C and D, W--N). As the distance between the patches increased to a gap of 70 cm (Figure 4.3C and D, W----N), trapping ability was significantly higher than when patches were closely aligned (Tukey's contrasts, $z = 4.222$, $p < 0.001$ for *G. densa*, $z = 2.994$, $p = 0.01$ for *B. erecta*), but not significantly different from the W treatment ($z = 0.584$, $p = 0.93$ for *G. densa*, $z = -1.306$, $p = 0.54$ for *B. erecta*). Patch configuration significantly affected propagule trapping also for the neutrally buoyant species, *E. nuttallii* ($\chi^2 = 34.844$, d.f. = 3, $p < 0.001$). No significant difference in propagule trapping of *E. nuttallii* was found between the two single-patch configurations (Tukey's contrasts, $z = 2.233$, $p = 0.11$), or between the two multiple-patch configurations ($z = -0.146$, $p = 0.99$; Figure 4.3B, W--N); however, the two multiple-patch configurations retained a significantly higher percentage of propagules than the single-patch configurations ($p \leq 0.05$; Figure 4.3B, W----N).

Within the 0.3 m s^{-1} velocity treatment, trapping significantly decreased as the patch canopy reconfigured as it was compressed to the substrate forming the bed of the flume, thus leading to very low trapping compared to the 0.1 m s^{-1} treatment ($\chi^2 = 124.52$, d.f. = 1, $p < 0.001$ for *G. densa,* $\chi^2 = 81.104$, d.f. = 1, $p < 0.001$ for *B. erecta*, $\chi^2 = 75.805$, d.f. = 1, $p < 0.001$ for *E. nuttallii*; Figure 4.3F and G, Table 4.3). Only sinking propagules of *E. nuttallii* were trapped in this treatment, and no significant difference in trapping was found between the different configurations ($\chi^2 = 6.2693$, d.f. = 3, $p = 0.09$; Figure 4.3E).

Vertical structure of macrophyte vegetation – flume and field experiments

Flume and field release experiments on the effects of the presence of floating vegetation versus fully submerged vegetation showed that macrophyte vegetation structure in the water column affected fragment trapping. That is, in both flume and field experiments, there was a significant negative relationship between the number of trapped fragments (averaged over all three species) in each section, and the minimum amount of free-flowing space measured between the water surface and canopy height over all patches in the section ($R^2 = 0.50$, $p = 0.014$, $R^2 = 0.67$, $p = 0.01$; Figure 4.6A). This indicates that a critical canopy height in the water column is needed for patches to be able to act as trapping agents for propagules. As some flume configurations created a fully constrained situation for neutrally buoyant propagules to drift, which was never found in the field, they were considered outliers and excluded from the comparison between flume and field results (*red diamonds* in Figure 4.6A).

Percentage cover of macrophyte vegetation – field and flume experiments

Field releases within river stretches of different percentage cover of macrophytes showed that, within each of the sections, the number of fragments passing through the section was significantly affected by vegetation cover, propagule species, and the presence of either fully submerged or mixed (submerged and floating-leaved) vegetation patches (GLM, Table 4.4, Figure 4.7). Propagule species had a significant interactive effect with both vegetation type ($\chi^2 = 7.406$, d.f. = 2, $p = 0.02$) and total macrophyte cover ($\chi^2 = 22.664$, d.f. = 8, $p = 0.003$). No significant interactive effects were found between vegetation type and total macrophyte cover ($\chi^2 = 7.777$, d.f. = 4, $p = 0.10$).

In the fully submerged vegetation case, changes in vegetation cover did not significantly influence fragment retention ($\chi^2 = 7.69$, d.f. = 6, $p = 0.26$; Figure 4.7B), with no significant differences in trapping between species ($\chi^2 = 4.34$, d.f. = 2, $p = 0.11$). However, both vegetation cover, propagule species and their interaction were significant in the mixed vegetation case, where part of the vegetation was emergent, and part of the vegetation was submerged ($\chi^2 = 22.619$, d.f. = 8, $p = 0.003$; Figure 4.7B and C). Highest trapping occurred at intermediate macrophyte cover in the stream (45 – 70%). At higher vegetation cover (86%), vegetation patches started to reconfigure as they were compressed to the river bed, thereby transforming their floating canopy into a submerged canopy, leading to changes in the ratio of floating to submerged vegetation cover (locations M1 to M4 in Figure 4.7B and C). Significant differences in trapping between species were found with 45% and 70% vegetation cover in the mixed vegetation case, while no significant differences were found with no vegetation (0% cover), sparse vegetation (25% cover) and full reconfiguration of the vegetation (86% cover), where very few propagules were retained for all three species. In the 45% cover release, fragment retention for *E. nuttallii* (36 ± 4%) and *G. densa* (22 ± 3.6%) was significantly higher than for *B. erecta* (2 ± 2%) (Tukey's contrasts, z = 3.316, p = 0.0041 and z = 2.626, p = 0.03). In the 70% cover release, *G. densa* fragment retention (66 ± 7.3%) was significantly higher than both *E. nuttallii* (32% ± 8%) and *B. erecta* (38% ± 6.3%) (z = 3.330, p = 0.002 and z = 2.764, p = 0.01), while no significant differences were found between the latter two species. Comparison between the field and flume results showed a similar relationship between propagule trapping and vegetation cover, with highest trapping at intermediate cover (40%) and declining at higher cover (> 60%) (Figure 4.7D). As observed in the field, the decline of propagule trapping at highest vegetation cover in the flume was due to canopies being pushed over by the flow towards the river bed (Figure 4.6B; Figure 4.7E).

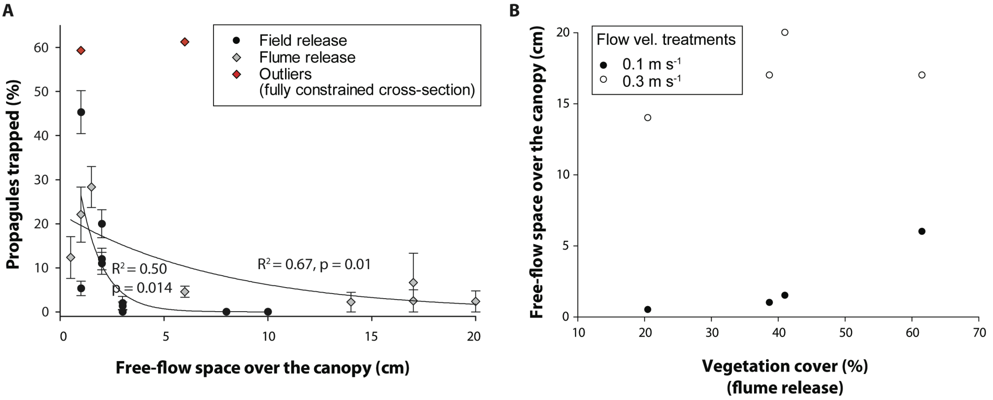

Figure 4.6: (A) The number of propagules trapped (%) averaged over the three aquatic plant species, for different amounts of free-flow space over the canopy (i.e., the difference between the canopy height and the height of the water surface; cm). *Black circles* are field releases and show the minimum amount of free-flowing space measured over all vegetation patches in the section, for each of the submerged and mixed vegetation sites where field releases were carried out (same locations as in Figure 4.7). *Grey diamonds* are flume releases and show the minimum amount of free-flowing space over the canopy during the flume releases. *Red diamonds* are outliers in the flume release of neutrally buoyant fragments, where the patch configuration created a fully constrained situation that was not found in the field. Outliers were not included in the averaged measurements. For both field and flume releases, the number of fragments trapped within the canopy is inversely correlated with the distance between the patch canopy and the water surface ($R^2 = 0.50$, p = 0.014; $R^2 = 0.67$, p = 0.01). (B) Changes in free-flow space over the canopy with increasing vegetation cover in the flume releases, for low (0.1 m s^{-1}) and high (0.3 m s^{-1}) flow velocity treatments.

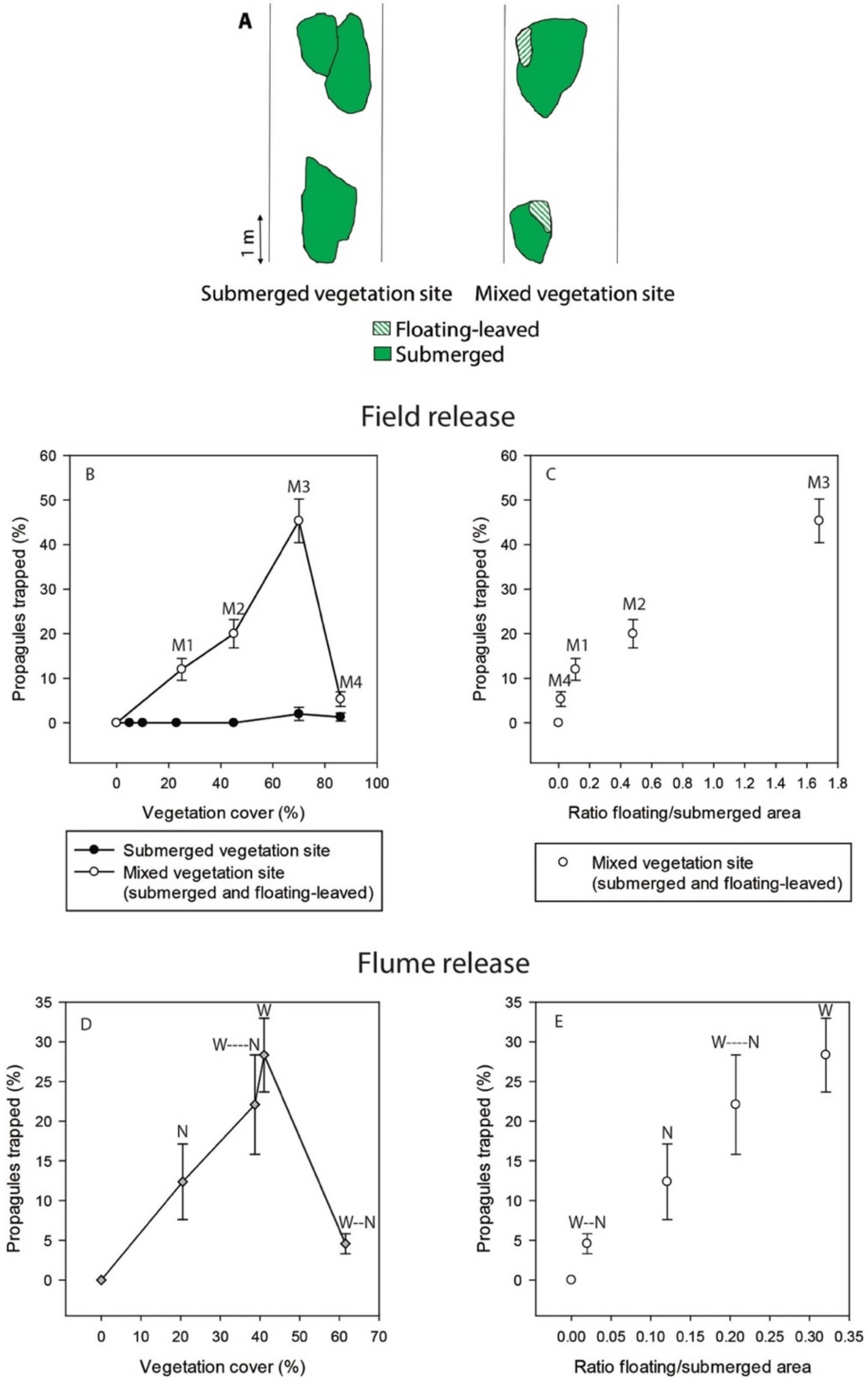

Figure 4.7: (Continued on the following page.)

Figure 4.7: (A) Schematic planform representation of two example sections of a submerged vegetation site (*left*) and a mixed vegetation site (*right*), which were selected as locations for the field releases. These two types of locations show contrasting vegetation types: in the submerged vegetation site, the whole canopy is submerged and does not float on the water surface; in the mixed vegetation site, a certain portion of the canopy is composed of floating leaves reaching the water surface. For each location selected for the field releases, vegetation cover (%) was calculated as the cover over the whole section. (B) Relationship between fully submerged and mixed (floating and submerged) *C. platycarpa* vegetation cover (%) in the section and propagules trapped (%) in the field releases. Each point denotes a different site along the channels where field releases were conducted; labels M1 to M4 indicate mixed vegetation sites. (C) Relationship between the ratios of floating/submerged *C. platycarpa* cover in the section for the mixed vegetation sites (M1 to M4), and number of fragments trapped in each site in the field releases. (D) Relationship between vegetation cover (%) and propagules trapped (%) in the flume releases. Labels (N, W, W--N, W----N) indicate flume configurations. (E) Relationship between the ratios of floating/submerged vegetation cover and number of fragments trapped in each flume configuration.

Discussion

Facilitation has been increasingly recognized as an important driver of biodiversity (McIntire and Fajardo 2014). Despite the patchy distribution of many facilitator species at the landscape scale, it is largely unknown how facilitation is affected by self-organized spatial patchiness and its underlying feedback mechanisms in such landscape setting. Using aquatic macrophytes as a model system, we showed that the feedback between vegetation and water flow diversion, leading to self-organization, is crucial for retention of propagules of other species. By diverting the incoming flow towards unvegetated areas, macrophytes locally create low-flow areas of reduced velocity where their canopy stands upright and can reach the water surface. This in turn can potentially benefit other plant species during the dispersal and colonization phase, as most propagules are retained in low-velocity areas where the plant canopies are upright. In contrast, when the flow divergence mechanism is prevented by having full vegetation cover, there is no propagule trapping. Since the flow cannot be diverted laterally, water preferentially flows on top of the canopies, flattening them down. As this causes propagules to also float over the submerged vegetation, there is no facilitation in that the plants are unable to overcome an important bottleneck in colonization. Our results highlight that self-organization and its underlying feedback processes are essential to enhance propagule retention, potentially leading to consequences for species colonization and diversity.

Is propagule retention a good proxy for facilitation during plant dispersal and colonization?

It is largely acknowledged that facilitation can improve survival or growth of organisms once they have reached a location under the protective influence of the facilitator (e.g. nurse plant syndrome; Niering et al. (1963); Callaway (1995)). For this reason, studies of facilitation generally focus on the number of seedlings that establish within a patch versus the bare interspaces between patches (Padilla and Pugnaire 2006). Far less attention is given to whether facilitation may enhance the arrival of organisms in such suitable sites. In our study, we reveal that existing vegetation enhances the arrival and retention of propagules of other species. Retention of propagules represents a suitable proxy for facilitation during plant dispersal and colonization, for a variety of reasons. Once trapped in submerged vegetation patches, the fragments are prevented from being lost at sea or in the river system and are retained in a favourable slow-flow site, indicating a facilitative effect (Callaway 1995). Plants located in the downstream part of a patch might re-root in the underlying mound of deposited sediment, when high flow velocities push the canopy towards the streambed (Minckley 1963), or could be released again during high flows, suggesting a stepwise manner of reaching and colonizing new sites (Engström et al. 2009). As colonization times for macrophyte shoots usually range between 1 to 10 days (Barrat-Segretain et al. 1998; Barrat-Segretain et al. 1999), establishment might be successful if timing between high flow events is long enough to allow re-rooting of fragments (Riis and Biggs 2003; Riis 2008). Hence, as primary colonization appears to be the main constraint for vegetation establishment, with less than 5% of retained shoots being able to colonize the stream (Riis (2008); Figure 4.1), propagule retention is a good proxy for facilitation, as it plays a large role in ensuring that enough individuals can successfully colonize.

Our findings may also provide a new perspective on biological dispersal. Dispersal is often treated as a stochastic, random process (Hubbell 2001; Lowe and McPeek 2014), where colonization is considered to be limited by propagule availability rather than by thresholds to establishment. Our results instead show that dispersal depends on both propagule traits and on the existing cover of foundation species, in a habitat that is modified by the foundation species itself. Hence, the conditionality of this process suggests that propagule retention in suitable sites may require a 'Window of Opportunity' (Balke et al. 2011), which appears to be created by a combination of fragment traits, hydrodynamic stress and pre-existing vegetation cover determining the available habitat space for colonization (Figure 4.8). Hence, our findings suggest that the interaction between biological and physical factors can influence the windows of opportunity for establishment.

Bio-physical stress divergence and implications for abiotic dispersal vectors

Our study reveals that vegetation patchiness due to flow divergence feedbacks creates the optimal conditions for retention of dispersal units. As such, it reinforces the importance of foundation species in creating heterogeneity and habitats for many other species (Dayton 1972; Jones et al. 1994). As water is a very common dispersal vector for plants (seeds and other propagules; Nilsson et al. (2010)) and animals (e.g. passive drift of motile invertebrate fauna or sessile organisms during mobile larval stage; Malmqvist (2002)) in both marine and freshwater environments, the effects of self-organized patterning on dispersal and retention might affect a large number of species at different trophic levels within a community.

Beyond aquatic ecosystems, similar processes may be generalized to a wide range self-organized environments where species are patchily distributed. In terrestrial environments, such as grasslands, prairies or arid ecosystems, patchy vegetation creates a mosaic of suitable and unsuitable sites for establishment (Aerts et al. 2006; Pueyo et al. 2008). Although the stress divergence feedback may involve other dispersal vectors (e.g. wind), facilitative interactions occurring in this stage are in a similar way crucial for colonization. Therefore, we highlight the need to further include bio-physical interactions and the spatial component of facilitation in future studies.

Towards an understanding of the link between self-organization and facilitation

Pattern formation is a widespread phenomenon in ecological communities (Rietkerk and Van de Koppel 2008), with important implications for ecosystem structure and functioning (Temmerman et al. 2007; Weerman et al. 2010). Our findings suggest that self-organized spatial patterns also have emergent properties for interspecific facilitation at the landscape-scale. Under self-organization, macrophytes themselves generate hydrodynamic heterogeneity, thereby creating both low-flow and high-flow velocity areas through flow redistribution around the patches (Chapter 2 & 3). Consequently, the process of flow regulation by macrophytes can potentially facilitate their colonization: in both our flume and field experiments, we found that propagules are retained in the low-flow areas where plant canopies are upright. Therefore, the self-organizing mechanisms underlying spatial patterns are crucial for facilitation. While our study reveals that self-organization is essential for facilitation during dispersal and primary colonization, facilitation also occurs in later life stages where it improves growth or reproductive success. Self-organized patterns create a balance between competition and facilitation in space due to scale-dependent feedbacks (van de Koppel et al. 2006; Donadi et al. 2013; van de Koppel et al. 2015). Yet, as facilitation is often studied at the local, within-patch scale, future studies should explore how local facilitation effects in other life stages translate to facilitation at the between-patch, landscape scale. The link between self-organization and facilitation is therefore an important topic for future research.

Conclusions

Overall, our study extends on the body of literature on both self-organized pattern formation as well as facilitation in natural communities, by linking these processes at the landscape scale. Whereas previous studies have focused on the positive effects of ecosystem engineers on other species through local amelioration of physical conditions, we show that the stress divergence mechanisms underlying spatial pattern formation cause facilitation patterns. That is, when facilitation is mediated by a pattern-forming species, the self-organizing feedbacks underlying these patterns are also crucial to maintain the facilitative effects. If the spatial pattern is absent, the facilitation effect also gets lost. Hence, bio-physical feedback processes underlying spatial pattern formation must be considered when using them as restoration tools and for optimal management of biodiversity.

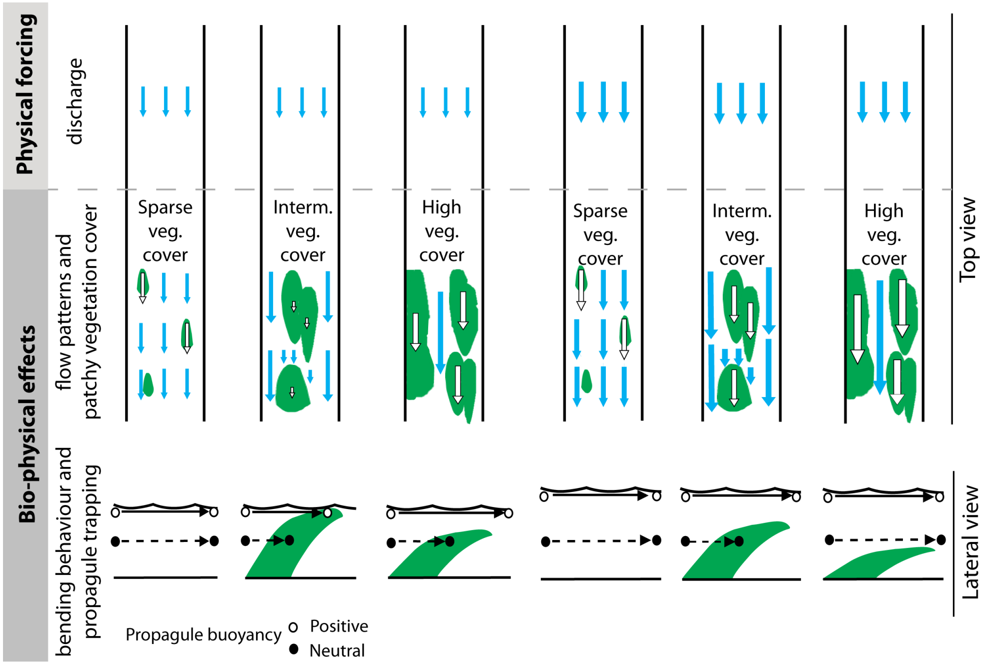

Figure 4.8: Conceptual framework showing the main factors affecting canopy emergence of the flexible submerged macrophyte *Callitriche platycarpa*, and the resulting outcome for trapping chance of aquatic plant vegetative propagules. Conditions leading to floating or bending of the canopy include both direct and indirect effects on flow velocity (e.g. increase in channel flow velocity due to higher discharge vs. changes in flow patterns due to bio-physical interactions). In the planform representations of the stream, green shapes represent aquatic macrophyte patches, blue arrows are flow patterns between the canopy, and white arrows are flow patterns on top of the canopy (arrow length and width proportional to flow velocity). Bottom graphs are longitudinal sections through a *Callitriche* patch and show changes in bending behaviour of the canopy, and the consequences for propagule trapping. The buoyancy characteristics of the dispersal units also influence the final outcome in terms of trapping chance, with stronger effects for buoyant propagules.

Table 4.3: Percentage of propagules trapped in the flume experiments for each aquatic plant species and for different propagule sizes, in the four patch configurations and two velocity treatments (0.1 and 0.3 m s^{-1}).

Species		***Elodea nuttallii***	***Groenlandia densa***		***Berula erecta***	
Propagule size		One size	Small	Large	Small	Large
Patch configuration	**Water velocity ($m\ s^{-1}$)**	**% of propagules retained**				
W patch only – 66% of flume width	0.1	37.50	23.33	26.66	21.67	23.33
	0.3	7.14	0	0	0	0
N patch only – 33% of flume width	0.1	21.25	11.67	10.00	3.33	6.67
	0.3	6.66	0	0	0	0
W and N patches – short distance	0.1	61.25	6.67	5.0	3.33	3.30
	0.3	20.00	0	0	0	0
W and N patches – large distance	0.1	59.33	21.67	35.00	11.67	20.00
	0.3	7.50	0	0	0	0

Table 4.4: Analysis of deviance table of the generalized linear model for the effects of vegetation type (submerged and mixed), vegetation cover and propagule species on propagule trapping in the field experiments.

	df	Deviance	Residual df	Residual Dev.	p (> Chi)
Vegetation type	1	148.332	298	315.05	**< 0.001**
Vegetation cover	4	143.053	294	171.99	**< 0.001**
Species	2	13.543	292	158.45	**0.001**
Vegetation type × Vegetation cover	4	7.777	288	150.67	0.10
Vegetation type × Species	2	7.406	286	143.27	**0.02**
Vegetation cover × Species	8	22.664	278	120.60	**0.003**
Vegetation type × Vegetation cover × Species	8	2.230	270	118.37	0.97

Chapter 5

Plants face the flow in V-formation: a study of plant patch alignment in streams

L. Cornacchia, A. Folkard, G. Davies, R.C. Grabowski, J. van de Koppel, D. van der Wal, G. Wharton, S. Puijalon, T.J. Bouma

Abstract

Interactions between biological and physical processes, so-called bio-physical feedbacks, are important for landscape evolution. While these feedbacks have been quantified for isolated patches of vegetation in both freshwater and marine ecosystems, we still lack knowledge of how the location of one patch affects the occurrence of others. To investigate the spatial distribution of vegetation patches, we measured the most common distances observed between patches of the aquatic macrophyte *Callitriche platycarpa* in natural streams using aerial images. To understand the hydrodynamic consequences of different spatial configurations, we arranged two *C. platycarpa* patches into 10 different combinations of longitudinal and transversal separation distances in a field manipulation experiment. We then measured flow velocity patterns around the patch pair, as well as drag force patterns around an existing patch. Our results suggest that vegetation patches in streams organize themselves in V shapes to minimize drag forces, creating an optimal configuration that reduces hydrodynamic stress and may therefore encourage patch growth. We observed that the leading edge of the downstream patch is most frequently at about 1/3 of the length of the upstream patch (in the longitudinal distance, L). In the transversal distance (T), the downstream patch is most frequently at 80% of the width of the upstream patch, hence growing partially sheltered by its overhanging canopy. Drag forces acting on plants were positively correlated with the flow velocities created by a vegetation patch in its surroundings. Locations around a single patch with the lowest drag forces corresponded to the most common separation distances observed in natural pairs of patches, and temporal growth dynamics indicated a preferential angle of new patch occurrence at 0 to 60° from existing patches, where 0°/180° is the across-stream direction and 90° is downstream. Our results highlight that when arranged in V-configurations, neighboring patches tend to grow in a slightly angled line that resembles V-formation in migratory birds. This knowledge can increase our understanding of how bio-physical interactions shape the positioning of organisms in a variety of landscapes.

Introduction

Biogeomorphic landscapes, such as rivers, mangroves and salt marshes, are characterized by strong interactions between biological and physical processes. These reciprocal interactions, also referred to as bio-physical feedbacks, are fundamental for landscape formation and evolution (Corenblit et al. 2007; Murray et al. 2008). Such environments are characterized by the presence of ecosystem engineers (Jones et al. 1994), organisms that are able to modify their habitat through their action or their own physical structure. To understand these biogeomorphic systems, many studies have focused on interactions between vegetation, hydrodynamics and sedimentation processes (Leonard and Luther 1995; Madsen et al. 2001; Schulz et al. 2003; Bouma et al. 2007). Although these landscapes are often characterised by patchy vegetation, at least during the establishment phase, we still have a limited understanding of how such patchiness may affect the processes and mechanisms controlling vegetation establishment and the hydrodynamics of these systems, despite many plants being the keystone species in these systems.

Across different ecosystems, flow-vegetation interactions have been quantified in homogenous fields of vegetation (Kouwen and Unny 1973; Nepf 1999; Nepf and Vivoni 2000; Järvelä 2005; Chen et al. 2013) as well as in isolated patches of vegetation (Sand-Jensen and Vindbœk Madsen 1992; Bouma et al. 2009b; Chen et al. 2012; Zong and Nepf 2012). However, patches in a landscape rarely grow in isolation but rather in mosaics, which may consist of more than one species (Cotton et al. 2006; Wharton et al. 2006; Temmerman et al. 2007; Van der Wal et al. 2008; Adhitya et al. 2014). In addition, feedback processes between vegetation patches and flow are location and scale-dependent (Rietkerk and Van de Koppel 2008; van Wesenbeeck et al. 2008; Bouma et al. 2009b; Schoelynck et al. 2012), with reduced stress within the vegetation and increased stress outside the vegetation, so that different patches potentially interact at larger scales. As patterns of current velocity affect spatial patchiness (Fonseca and Bell 1998), and turbulence levels increase in the wake downstream of a submerged vegetation canopy, the size of the gap between vegetation patches is also relevant for both physical and ecological processes (Folkard 2005; Folkard 2011). Recent attention has been focused on the interaction between established neighboring patches in terms of flow patterns (Folkard 2005; Vandenbruwaene et al. 2011; Adhitya et al. 2014) and sediment deposition (Meire et al. 2014), and their implications for landscape evolution (Kondziolka and Nepf 2014; De Lima et al. 2015). However, knowledge is still lacking on how the location of one patch may affect the occurrence of another patch, potentially leading to optimal spatial configurations due to hydrodynamic stress reduction.

Several studies have revealed the importance of facilitation, i.e. positive interactions between species, for establishment by mediation of physical stress (Bruno et al. 2003; Callaway 2007). Thus, positive feedbacks for one patch may extend to a certain distance after it (Bruno and Kennedy 2000), leading to a facilitative effect on the establishment or growth of other species. However, studies of facilitation mostly focus on interspecific interactions – that is, between individuals of different species. Consequently, we know relatively little about intraspecific facilitation mediated by existing vegetation patches and its effects on distribution patterns in the landscape. Intraspecific facilitation may be expected to be a key process in flow-dominated systems, as currents and drag forces may impose a stress that limits growth and seedling establishment (Vogel 1994; Schutten et al. 2005; Puijalon et al. 2008; Balke et al. 2011; Silinski et al. 2015). It is known that vegetation patches may increase flow velocity in some adjacent areas, while reducing it directly downstream of the patch (Bouma et al. 2007; Chen et al. 2012; Schoelynck et al. 2012; Meire et al. 2014). As a consequence, optimal spatial configurations of vegetation patches might be expected to emerge due to patterns of hydrodynamic stress reduction, specifically in terms of drag force reduction. To address this issue, we studied plant-flow interactions in streams, as they offer an ideal model system given their unidirectional flows.

Plant-flow interactions have been studied intensively in vegetated streams. That is, many studies have been carried out on individual patches of submerged aquatic macrophytes (for example, Sand-Jensen and Mebus 1996; Sand-Jensen 1998; Sukhodolov and Sukhodolova 2009). Macrophyte patches, however, do not typically grow in isolation: on the scale of a stream reach, the stands grow in a pseudo-braided distribution due to their interaction with water flow (Dawson 1989; Sand-Jensen and Vindbœk Madsen 1992; Cotton et al. 2006). As a result, far less is known about whether existing vegetation patchiness might affect further patch occurrence and stream landscape development. Interactions between vegetation patches are likely to be relevant for plant establishment in lotic environments, where primary colonization is challenging due to forces that act to dislodge seedlings and fragments (Riis 2008; Balke et al. 2014). Despite its relevance, it is unknown how the location of established macrophyte patches influences where new patches can occur, thus creating optimal configurations with reduced hydrodynamic stress.

In this study, we investigated the spatial distribution of vegetation patches and the implications of this for longer term stream landscape development. To study whether patches occur at locations where hydrodynamic stress is reduced due to the presence of other patches, we analyzed the patch separation distances observed in naturally-vegetated streams using aerial images. We measured the effects of varying patch separation distance on flow velocity, turbulence and drag on plants, through a field manipulation. We considered drag reduction as a proxy for the benefits associated with occurring at a certain location around a vegetation patch. To test whether the locations with the lowest drag forces corresponded to the most frequent patch distributions, we related patterns of drag reduction to the observed probability of patch occurrence at different distances around a single patch. Finally, we tested whether such preferential patch distributions were supported by long-term field observations of temporal patch dynamics in a lowland chalk stream.

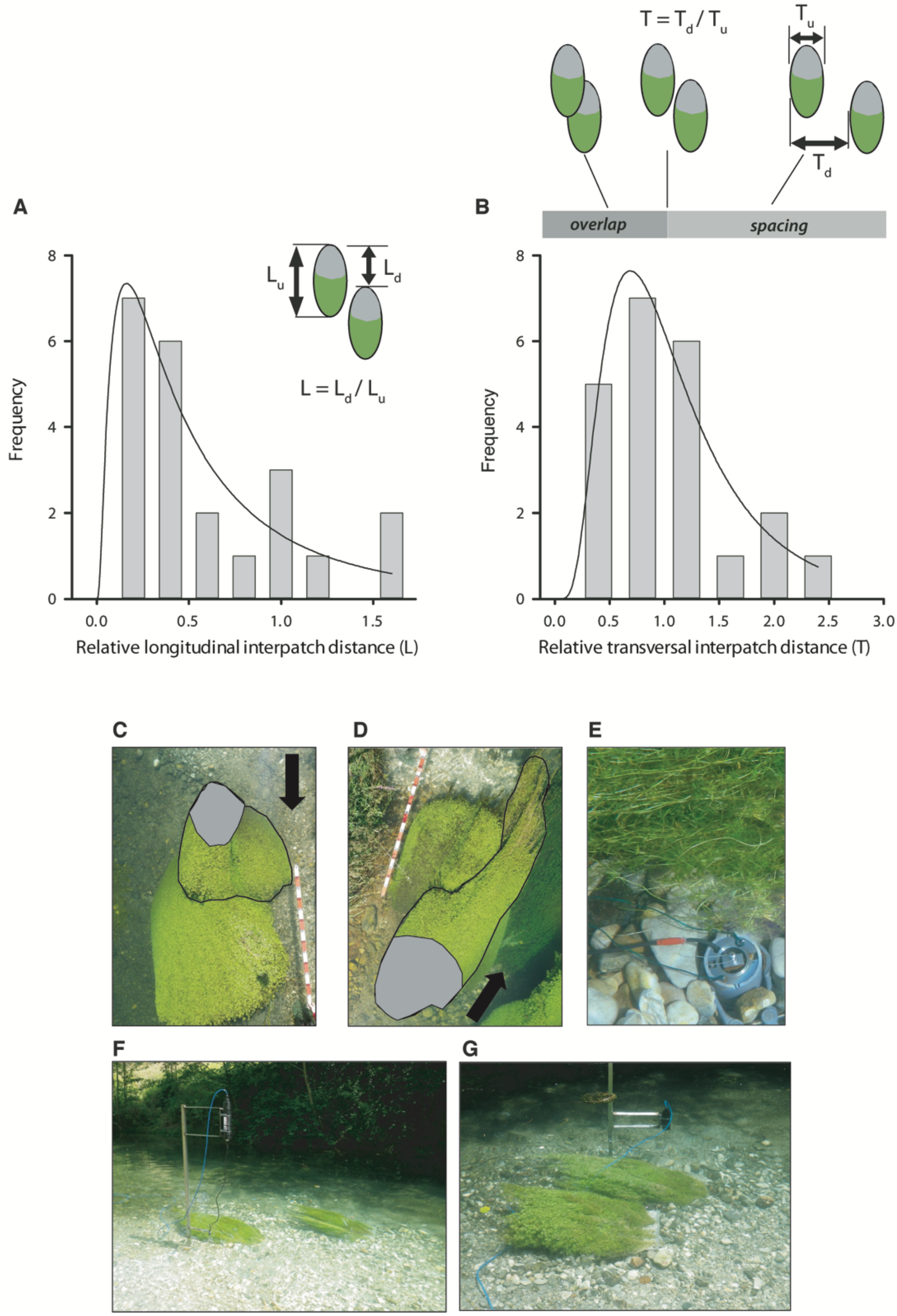

Figure 5.1: (Continued on the following page.)

Figure 5.1: Frequency distribution of (A) observed relative longitudinal interpatch distance (distance between upstream edges divided by upstream patch length) and (B) relative transversal interpatch distance (transversal gap between lateral edges divided by upstream patch width) of neighbouring patches of *Callitriche platycarpa*. The aerial pictures show macrophyte patch pairs (C, D) growing in a staggered distribution, with overlapping canopies. The canopy of the upstream patch is outlined in black. Grey areas indicate the extent of the rooted area. Arrows indicate main river flow direction. E shows the force transducer employed in the field for drag measurements on macrophytes. F and G illustrate the experimental setup in the field with the transplanted vegetation patches and ADV for flow velocity measurements.

Materials and methods

Measuring patch inter-distance by aerial pictures of natural streams

To investigate the existence of preferential distributions of plant patches, we collected aerial images of a naturally-vegetated drainage channel located along the Rhône River (France), near Serrières-de-Briord (45.815311 ° N, 5.427477 ° E). The channel is uniform in terms of width and water depth, with relatively straight banks. The average channel width is 8.0 m and the average depth is 0.8 m, rarely exceeding 1.3 m. Aerial images of the streambed were taken with a digital camera mounted on a pole at about 2 m height. We identified pairs of neighboring patches for the dominant aquatic macrophyte species *Callitriche platycarpa*. The pairs could clearly be distinguished as separate patches, through the presence of an unvegetated area between their rooting parts. In selecting neighboring patches, we assumed that the influence of an upstream patch would be maximum within 1.5 m distance from it, and would only decay beyond it. We measured the absolute longitudinal inter-patch distance (distance between their upstream edges in the streamwise direction, L_d in m) and transversal inter-patch distance (distance between their lateral edges in the spanwise direction, T_d in m) between the pairs (Figure 5.1). To account for differences in absolute distances due to the variability in patch sizes, we converted them into relative distances. To obtain relative longitudinal distances (L), we divided the absolute distance L_d by the length of the upstream patch L_u. To obtain relative transversal distances (T), we divided the absolute distance T_d by the width of the upstream patch T_u (Figure 5.1). The frequency distributions of relative longitudinal and transversal distances were first converted into probability distributions. Then, the probability distributions in the two directions were multiplied by each other to obtain the probability of naturally-observed occurrence of vegetation patches for each combination of L and T distances. This point grid was imported into GIS software and interpolated to obtain a two-dimensional probability map of naturally-observed patch occurrence (%) at different distances from an existing patch, using kriging interpolation.

Quantifying the effects of the distance between patches on flow velocity and drag by a field manipulation experiment

Flow velocity measurements

To assess the effects of different patch configurations on flow reduction and acceleration, we measured the changes in flow velocity with varying patch separation distance through a field manipulation. Plants were detached from existing patches, transplanted on perforated metal plates and fixed through cable ties at the roots, to recreate two *C. platycarpa* patches (1.2 m in length, 0.6 m in width) that could be moved and arranged at different distances in the river bed. The two patches were arranged into 10 different configurations, representing a combination of longitudinal and transversal distances (Figure 5.2). The patch located upstream ("patch U") was kept fixed, while the other one ("patch D") was moved downstream and/or laterally to create the configurations. The patch characteristics (width, length and density) were maintained constant between the fixed and mobile patches.

Vertical flow velocity profiles were measured with a 3D acoustic Doppler velocimeter (ADV, Nortek) over 2 min at 10 Hz. Hydrodynamic profiles were measured at five vertical locations at 5, 10, 20, 40 and 90% of the water surface elevation above the river bed. Around the pair of vegetation patches, vertical profiles were located at 0.2 m and 0.1 m distance from the upstream edges, and 0.2 m on both sides of each patch (at 0.35 m along their length), i.e. in the gap between the patches. For each point measurement in the profile, the averages of velocity components u, v and w were calculated (corresponding to velocities in the x, y and z directions; m s^{-1}). Depth-averaged flow velocities u (in the streamwise direction) are expressed relative to incoming flow velocity, which was a fixed measurement point located 0.5 m upstream of patch U.

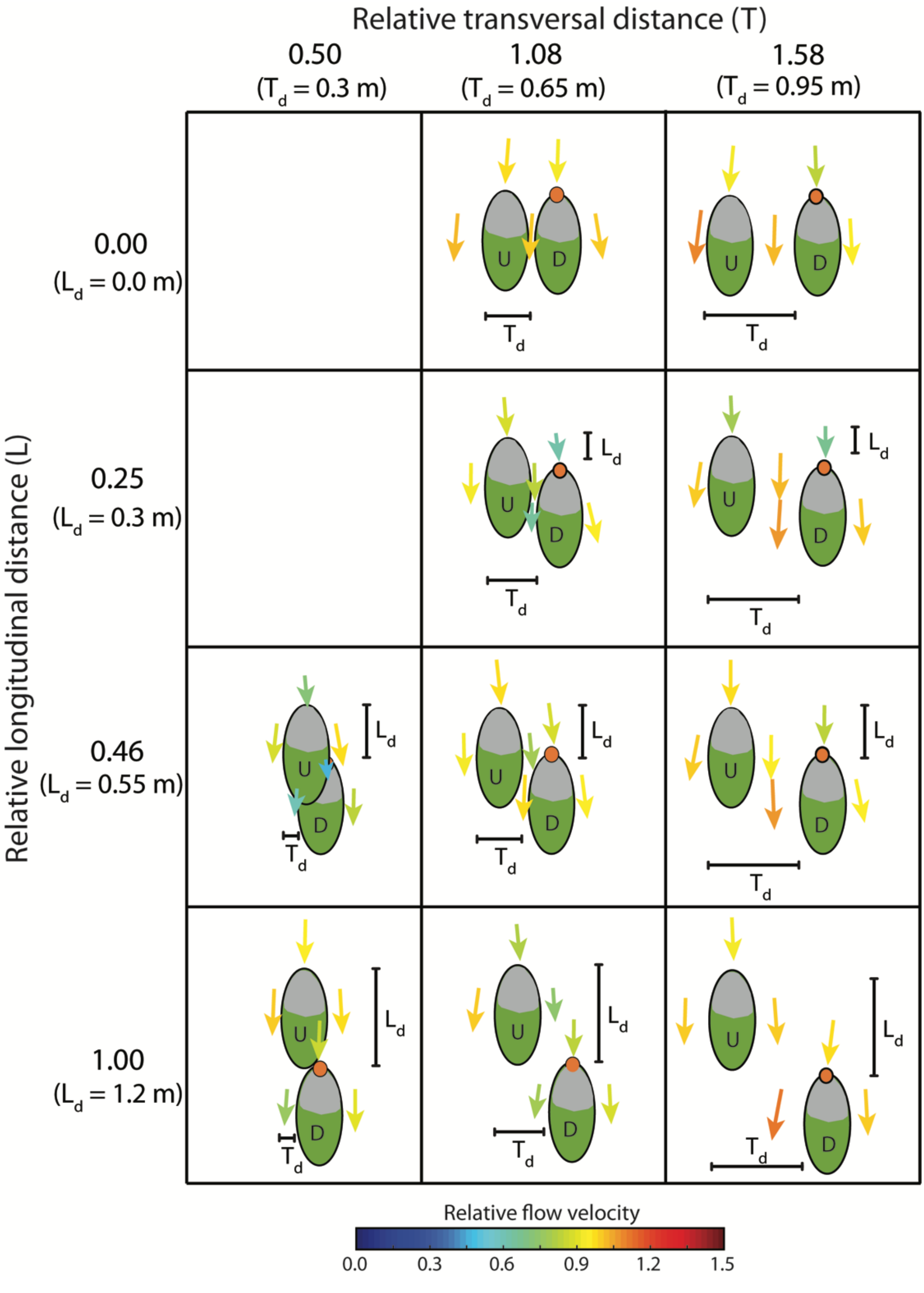

Figure 5.2: (Continued on the following page.)

Figure 5.2: Overview of the ten patch configurations used in the field experiments, with indication of inter-patch distance in the longitudinal and transversal directions. L and T are relative distances; T_d and L_d are absolute distances (in m). Patch "U" was kept fixed, while patch "D" was moved downstream and/or laterally. Arrows indicate flow direction, and arrow size and color indicate velocity magnitude relative to a measurement point located 0.5 m upstream of patch U. Grey areas indicate the extent of the rooted area. Orange dots are locations of drag measurements.

Turbulent kinetic energy

To determine the effects of different patch configurations on turbulence, we measured the changes in turbulent kinetic energy (TKE, $m^2\ s^{-2}$) with different patch separation distances. TKE is a hydrodynamic parameter that can negatively affect plants through direct effects on their growth (Jaffe and Forbes 1993). Also, by governing processes of sediment trapping and resuspension (Hendriks et al. 2008), it can potentially affect plant establishment by reducing sediment stability. TKE was therefore calculated for the profile located at 0.1 m from the upstream edge of patch D, to investigate its potential implications for establishment. We first calculated $u'(t) = u(t) - \bar{u}$ where $u(t)$ is the time series of flow measurements and $\bar{u}$ is the time-averaged velocity ($m\ s^{-1}$) in the streamwise direction at each vertical position. The corresponding spanwise and vertical turbulent velocity components v' and w' were calculated in the same way. For each point measurement in the profile, turbulent kinetic energy (per unit mass) was then calculated as $TKE = \frac{1}{2}\left(\overline{u'^2} + \overline{v'^2} + \overline{w'^2}\right)$.

Drag force measurements

To investigate the benefits of different patch configurations in terms of drag reduction, we measured the effects of varying patch separation distance on drag forces. Drag forces were measured using a force transducer developed by the former WL Delft Hydraulics (now Deltares, Delft, The Netherlands). The transducer consisted of a solid platform, carried by two steel cantilever beams, with four temperature-corrected strain gauges mounted in pairs on opposite sides of each of the two steel cantilevers (for details see Bouma et al. (2005)). The voltage output for the force transducer was linearly correlated with forces up to 10 N ($r^2 = 0.99$, $p < 0.001$). During the measurements, a *C. platycarpa* plant was mounted on top of the transducer and placed into the river bed at the upstream edge of patch D. For the measurements, we selected isolated plants of 55 cm in height on average and with 4 to 9 ramifications. Plants were attached to the transducer by their stem, and positioned in a natural growth position to closely represent the natural conditions. Voltage readings were collected on a data logger at a frequency of 100 Hz and expressed as the mean value for 1 min. As bending and leaning of the plant on the vegetation patch interferes with measuring the actual drag on the individual, drag measurements were also performed by removing patch D and repeating the measurement on the single plant. For comparison between individuals, drag was expressed as a function of total plant surface area.

Effects of patch interactions on longer term landscape development: evidence from temporal field surveys

To test whether occurrence at certain distances and directions from initial vegetation patches was more common than others, we analyzed monthly field surveys of vegetation development that had been conducted on a chalk stream reach within the Frome-Piddle catchment (Dorset, UK) over two years (July 2008 to July 2009, and bimonthly thereafter until July 2010). The study reach was a straight section of 30 m long by 7-9 m wide. The dominant in-channel aquatic macrophyte was water crowfoot (*Ranunculus penicillatus* subsp. *pseudofluitans*) which has highly similar flexibility and structural traits to *Callitriche platycarpa*: very flexible stems, with an overhanging canopy rooted only at the upstream edge. Although these data refer to a different species than the one used in the manipulative experiments, we believe their patch establishment dynamics to be comparable: the main factors affecting initial establishment are closely related to mechanical stresses (e.g. drag, flow velocity) imposing a constraint on the plants and likely affecting plant morphological types in a similar way, rather than being referred to species-specific properties of growth rates.

The data set from the Frome-Piddle catchment afforded a unique opportunity to assess the occurrence of new vegetation and changes in vegetation cover and distribution over time. During each survey, macrophyte distribution was mapped along transects that were located at 1-m distance intervals along the 30-m long study reach. Along each transect, measurement points were located at 0.5 m intervals to record macrophyte presence and species. Reach survey data were analyzed using GIS software. The total station coordinates of the transect markers were used to georeference a digitized version of the reach within a GIS. The output resulted in an array of points that were spatially arranged along transect lines. Vegetation cover observed at points in the reach data set were interpolated using an Inverse Distance Weighted (IDW) interpolation method. If the predicted surface outputs from IDW differed from the substrate cover observed at any extra observation point not used in the IDW, the substrate cover observed at that point prevailed above the IDW interpolation. Separate vegetation patches were derived using the minimum bounding geometry enclosing each of the polygon outputs from IDW.

We tested the hypothesis that directions of growth of new patches compared to existing patches during the survey period show preferential directions for plant growth, instead of being uniformly distributed in all directions. Therefore, three different survey periods were selected over the two years (December 2008 – April 2009, September 2009 – January 2010, January 2010 – July 2010). These periods were chosen because there was a net increase in *Ranunculus* cover within each of them, so that the phase of new macrophyte patch colonization could be captured. The distance and direction (angle) between each new vegetation patch and the closest existing patch at the beginning of the survey period were calculated using the ‘Near’ tool in ArcMap 10.4.

Statistical analyses

A chi-squared test was used to test for significant differences in the frequency of observed longitudinal and transversal distances between vegetation patches. Regression analysis was used to test the effects of varying longitudinal and transversal distances on flow velocities in four different positions (between the patches, at the upstream edge of patch D, next to patch U, next to patch D), and on turbulent kinetic energy at the upstream edge of patch D. We tested whether relative flow velocities would increase linearly with increasing inter-patch distances, or follow a quadratic relationship which might be expected if relative flow velocities first increase until a maximum at intermediate distances, and then decrease to 1 as they become equal to incoming flow velocity. In that case, patches become far enough apart so that they do not interact anymore. Hence, we fitted both linear and quadratic models using single (L or T distances) and multiple (L and T distances) predictor variables. We then used Akaike's information criterion to compare the adequacy of the candidate models, and selected the model with the lowest AIC score (Akaike 1998). Regression analysis was used to test for the relationship between flow velocities and drag forces on *C. platycarpa* in the field flume experiment. Ordinary Least Square (OLS) regression was used for spatial regression between the experimental drag measured around a vegetation patch, and the probability of naturally-observed patch occurrence. The latter was first log-transformed (natural log of original value + 0.5) due to its skewed distribution. A chi-squared test was used to test for significant differences in angle of growth compared to a uniform distribution in all directions. A paired t-test was used to compare drag forces measured on single plants to drag on plants located at the upstream edge of a vegetation patch.

Results

Observed distances between pairs of macrophyte patches in natural streams

We tested for the presence of preferential distributions of plant patches, and results suggested that some distances between neighboring patches occurred most frequently (Figure 5.1). We observed that the downstream patch was most frequently located between 1/3 to halfway down the length of the upstream patch (i.e., L = 0.3 – 0.5) ($\chi^2_8 = 20.54$, $p = 0.008$). This longitudinal separation distance was relatively constant, regardless of the size and shape of the patches we analyzed (width/length ratios ranged from 0.25 to 0.83). In the transversal direction, the downstream patch was most frequently located at 80% of the width of the upstream patch (i.e. T = 0.8), hence partially overlapping with, and sheltered by, the overhanging canopy of the patch ahead ($\chi^2_6 = 14.90$, $p = 0.021$).

Table 5.1: Regression results of linear and quadratic models including single (T, L) or multiple (T and L) predictor variables. Final selected models (in bold) are based on Akaike Information Criterion (AIC) values.

		Linear model			*Quadratic model*		
		Predictor variables					
		T * L	**T**	**L**	**T * L**	**T**	**L**
Relative $\overline{U}$ between patches	R^2	0.82	0.79	0.00	0.87	0.81	0.06
	p-value	0.01	0.0005	0.84	0.058	0.002	0.79
	AIC	-17.64	**-19.96**	-4.06	-16.99	-19.08	-2.67
Relative $\overline{U}$ upstream of patch "D"	R^2	0.40	0.24	0.05	0.71	0.33	0.28
	p-value	0.33	0.15	0.49	0.26	0.24	0.31
	AIC	-6.22	-7.71	-5.59	-9.37	-7.05	-6.28
Relative $\overline{U}$ next to patch "U"	R^2	0.41	0.22	0.00	0.90	0.25	0.69
	p-value	0.329	0.16	0.99	0.033	0.36	0.016
	AIC	-25.53	-26.77	-24.19	**-40.09**	-25.10	-33.95
Relative $\overline{U}$ next to patch "D"	R^2	0.33	0.31	0.00	0.38	0.31	0.085
	p-value	0.45	0.09	0.95	0.76	0.26	0.73
	AIC	-22.32	-26.05	-22.29	-19.15	-24.05	-21.18
TKE upstream of patch "D"	R^2	0.31	0.00	0.27	0.76	0.07	0.62
	p-value	0.48	0.99	0.11	0.18	0.77	0.03
	AIC	-80.09	-80.31	-83.53	-86.83	-79.04	**-87.99**

Effects of the distance between patches on flow velocity and turbulence patterns

Measurements of the hydrodynamic effects of different patch configurations showed that flow velocity and turbulence patterns were strongly affected by the distance between patches. In between the patches, mean flow velocity was strongly reduced when the patches were partly overlapping, but it increased as they became further apart. That is, we found a significant linear relationship between flow velocities in between the patches and the relative transversal (T, spanwise) distance between the patches ($F_{1,8} = 31.45$, $r^2 = 0.79$, $p < 0.001$; Figure 5.3A – C; Table 5.1). When the patches were close together, with only a 5-cm gap or less between them ($T \leq 1.08$), flow velocities between them were reduced and the pair tended to behave more like a single patch. However, flow velocity accelerated when the gap between the patches, and therefore T, increased.

We found that turbulence stress was minimized at intermediate distances along the length of an upstream patch, while it increased both when the patches were next to each other and when one was immediately downstream of the other. Turbulent kinetic energy upstream of the patch was significantly related to relative longitudinal distance L through a quadratic relationship ($F_{2,7} = 5.719$, $r^2 = 0.62$, $p = 0.03$), the highest TKE occurring when patches are located next to each other (for $L = 0$; Figure 5.3D – F). From $L=0$, TKE decreases with increasing relative longitudinal distance until a minimum at $L = 0.66$, after which it increases again for $L > 0.66$ as it enters the high TKE region in the wake of the upstream patch. This minimum TKE at $L = 0.66$ seems to be the point at which there is an optimal combination of sheltering from the oncoming flow by the upstream patch (which increases with L), and avoidance of the high TKE region in the wake of the upstream patch (which decreases with L). For the mean flow velocities upstream of patch D, results of single and multiple regression showed no significant relationship with T and L distances (Table 5.1).

We found areas of weakest flow deflection (i.e. reduced hydrodynamic stress) around the upstream patch at intermediate longitudinal distances, and in particular when the two patches were partly overlapping. However, flow deflection increased both when the patches were next to each other and when one was immediately downstream of the other. That is, a significant non-linear (quadratic) relationship was found between flow velocities next to patch U and both relative transversal (T) and relative longitudinal (L) distances ($F_{5,4} = 7.931$, $r^2 = 0.90$, $p = 0.03$; Figure 5.3G – I; Table 5.1). As L increases, flow velocity first decreases for intermediate distances (between 0.16 and 0.58), due to weaker flow redirection around the patch. Then, it increases again to become equal to incoming flow velocity, following a quadratic relationship. As T increases, and therefore the gap between the patches increases, the flow velocity increases until it becomes equal to incoming flow velocity for $T \geq 1.5$. However, flow velocities next to patch

D showed no significant relationship with relative transversal (T) and longitudinal (L) distances (Table 5.1).

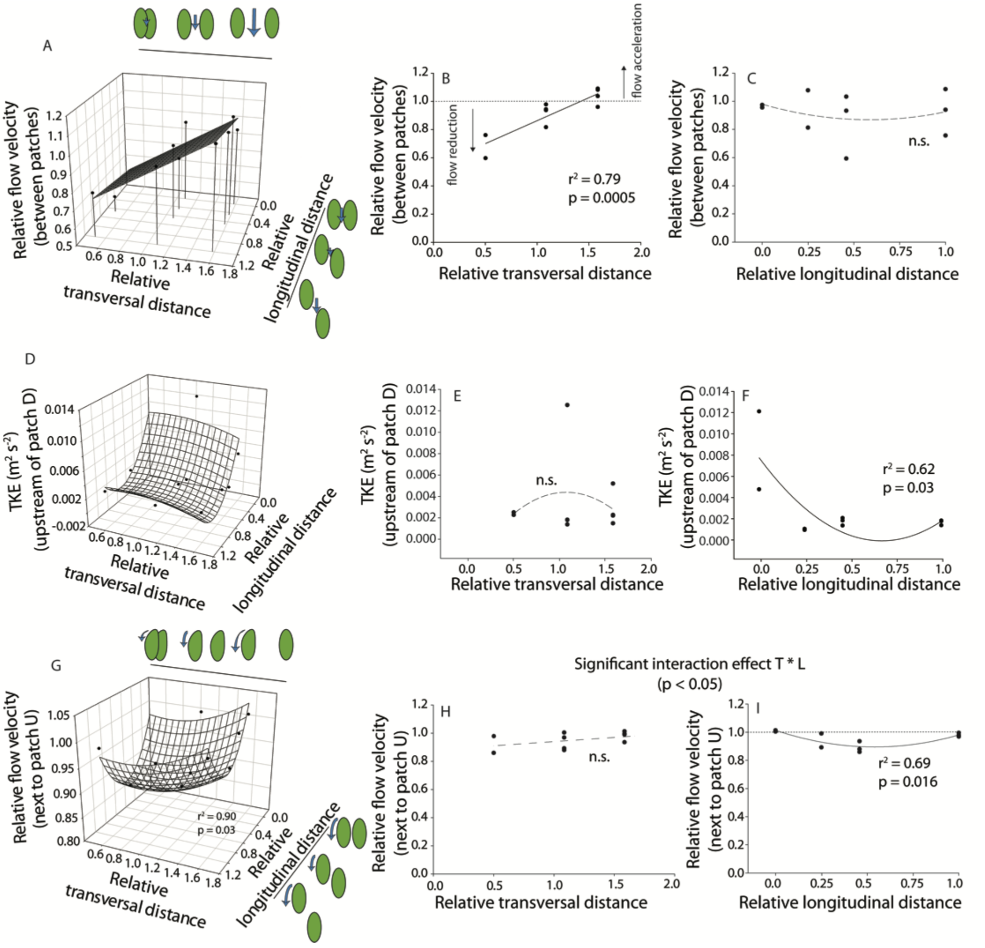

Figure 5.3: Relative flow velocity measurements (m s^{-1}) in between the patches (A – C) and on the side of patch U (G – I) for the ten configurations, showing the effects of increasing relative longitudinal and transversal distances. (D – F) Relationship between relative longitudinal and transversal distances and turbulent kinetic energy (TKE, m^2 s^{-2}) at the upstream edge of patch D.

Effects of patch separation distances on drag forces

We found that existing vegetation patches create sheltered areas where drag is minimized, and that new patches are more likely to occur in these locations. Measurements of drag forces in locations around a vegetation patch revealed a significant relationship between flow velocity and drag force per unit surface area on *C. platycarpa* individuals ($r^2 = 0.92$, $p = 0.0001$; Figure 5.4A). As our field drag force measurements were in the same order of magnitude as measurements performed on the same species in a laboratory flume (Puijalon et al. 2011), we conclude that the field set-up worked well. Plotting the drag in an interpolated spatial grid around a patch shows that positions with lowest drag forces correspond to the most frequent locations of neighboring patches based on our field observations (Figure 5.4B & D): the probability of observed patch occurrence in a certain position is inversely related to the observed drag force in that position (ordinary least squares spatial regression, $r^2 = 0.28$, $p < 0.0001$, Figure 5.4C). Drag forces ranged from 0.19 to 4.63 N m^{-2}, due to the flow modification by the vegetation patch, with lowest drag forces right along the lateral edge of the patch, at ≥ 0.55 m from the upstream edge. This distance along the length of the patch corresponded to the end of the rooted area and the start of the floating canopy.

Comparison of average drag force measurements on single plants, representing the conditions of initial establishment, compared to plants located at the upstream edge of a well-established patch (n = 10 configurations) showed that *C. platycarpa* individuals experience significantly higher drag when alone (Figure 5.5; paired t-test, $t = -2.28$, d.f. = 19, $p = 0.03$). This observation shows that drag forces on the upstream plants are mitigated by leaning onto other plants in a patch.

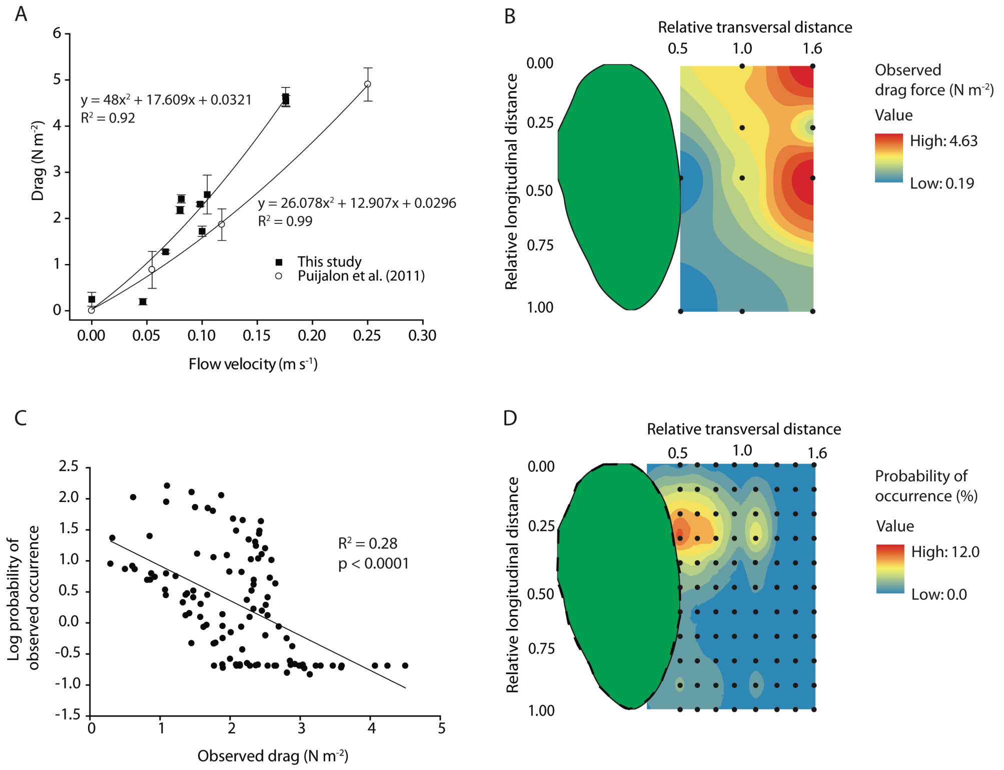

Figure 5.4: (A) Drag forces per unit surface area on single individuals of *C. platycarpa* around existing vegetation patches in the field flume (this study) and in a laboratory flume (Puijalon et al., 2011). Each point (black squares) relates to a position around the patch. (B) Map of drag forces acting on a single *Callitriche platycarpa* individual, at different distances from an existing vegetation patch (in green). Black dots indicate the locations of the drag measurements (same points as black squares in A). (C) Spatial regression between the experimental drag in a certain position around a vegetation patch, and the probability of occurrence of a patch in the same position. (D) Map of probability of occurrence (%) of a vegetation patch at different distances from an existing vegetation patch, based on the combination of the observed frequency distributions of relative longitudinal and transversal distances in Figure 5.1. Black dots indicate the grid of distance observations. Note that the vegetation patch (green shape with dashed line border) provides an indication of the average size of an existing patch; the actual size observed in natural neighboring patches may vary.

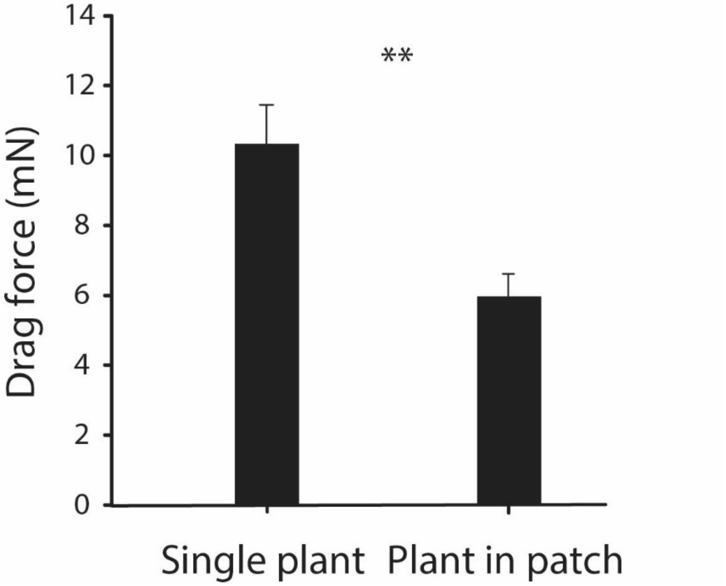

Figure 5.5: Drag forces on a single plant vs. a plant located in a vegetation patch, averaged over the ten vegetation configurations (paired t-test, t = -2.2813, d.f. = 19, p = 0.03). Error bars indicate standard error.

Effects of patch interactions on longer term landscape development: evidence from temporal field surveys

Temporal field surveys showed that new vegetation patches were found at specific directions from existing vegetation patches. Most of new patches were observed at angles between 0 – 60° from existing patches ($\chi^2_5 = 24.34$, $p < 0.001$ for all survey periods together; Table 5.2). Within each of the three time steps we analysed, the most common direction of growth was at angles between 0 and 60° from existing patches, in the direction downstream towards the right bank; and the second most common direction was at angles between 120 and 180°, in the direction downstream towards the left bank ($\chi^2_5 = 9.20$, $p = 0.1$ for Dec. 08 – Apr. 09; $\chi^2_5 = 12.80$, $p = 0.025$ for Sept. 09 – Jan. 10; $\chi^2_5 = 10.88$, $p = 0.053$ for Jan. 10 – July 10). Overall, these observations support that new patches occur in a slightly angled line with respect to existing patches, in agreement with areas of reduced drag forces around a well-established patch and observed distances between natural patch pairs.

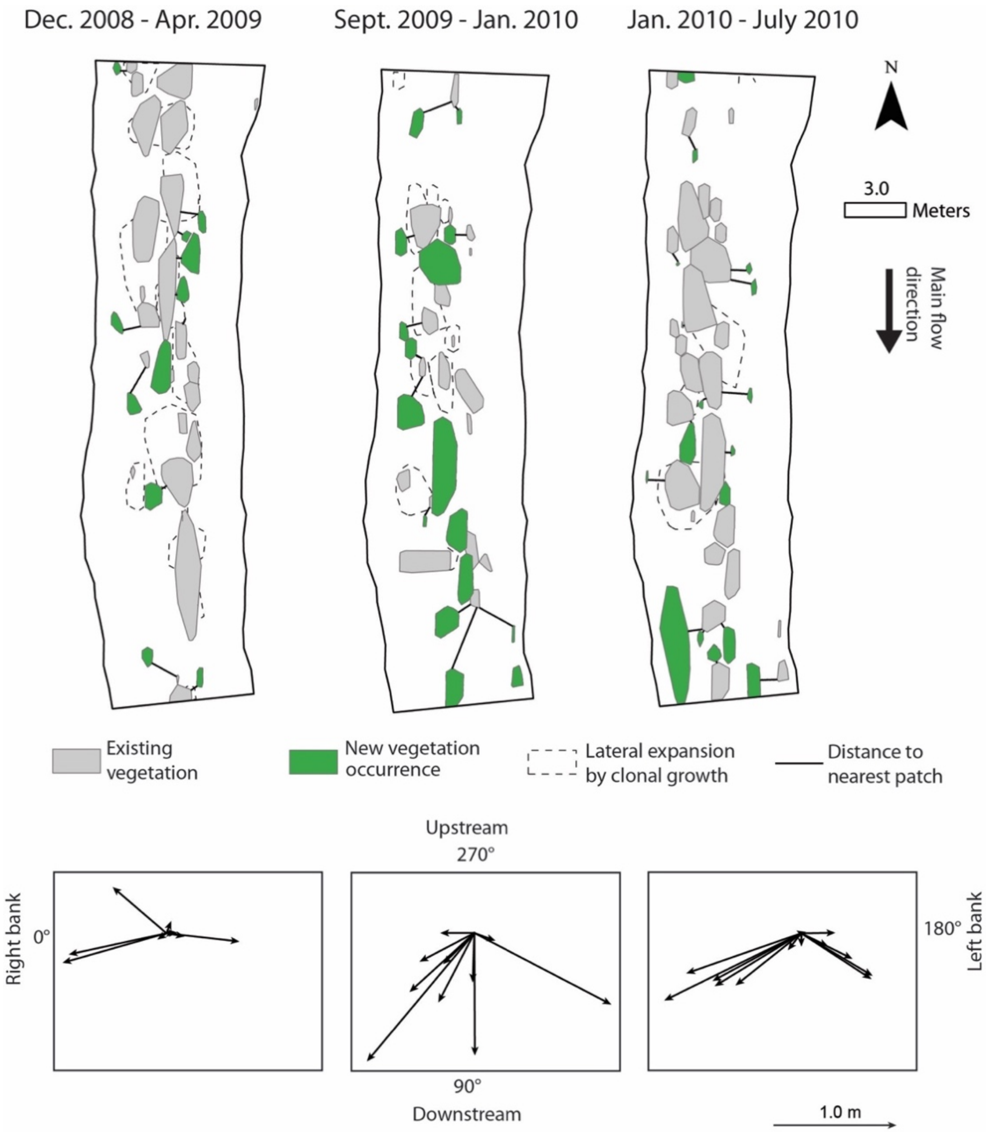

Figure 5.6: *Top*: Planform representation of the distribution of in-stream macrophyte patches of *Ranunculus penicillatus* subsp. *pseudofluitans*. In grey: existing vegetation patches at the start of the survey period; dotted lines: lateral expansion of initial vegetation patches through clonal growth; in green: new patches occurring at the end of the survey period. Black lines indicate distance and direction of growth of the newly occurring vegetation, with respect to the nearest existing patch. *Bottom*: distance and direction of growth (°) of new vegetation patches in each time period over the stream bed.

Table 5.2: Direction of growth of newly occurring vegetation patches with respect to the nearest existing vegetation patch (°), based on field observations performed in three different time periods over the annual growth cycle. Observations are on the species *Ranunculus penicillatus* subsp. *pseudofluitans*.

	Angle to nearest vegetation patch (°)	Dec. 08 – Apr. 09	Sept. 09 – Jan. 10	Jan. 10 – July 10	**Total**
Downstream	0 – 60	5	5	6	16
	60 – 120	0	3	1	4
	120 – 180	3	2	4	9
Upstream	180 – 240	1	0	5	6
	240 – 300	1	0	0	1
	300 – 360	1	0	1	2
Total		11	10	17	38
χ^2		9.20	12.80	10.88	24.34
d.f.		5	5	5	5
p- value		0.1	0.025	0.053	< 0.001

Discussion

While most studies of bio-geomorphic feedbacks to date have focused on isolated or already established patches, our study shows that vegetation patches in streams organize themselves in V-shapes to minimize hydrodynamic and drag forces. Field observations showed that patches are more likely to grow between 1/3 to halfway down the length of an upstream patch, and slightly off to its side (overlapping with part of their width). Measurements in the field revealed that these locations correspond to areas where drag is minimized, due to hydrodynamic sheltering by well-established vegetation patches. Field manipulations supported this hypothesis, showing that mean flow velocity is reduced by partially overlapping with upstream patches in the across-stream direction, and turbulent stress is minimized when growing halfway down the length of an upstream patch in the main flow direction. Flow deflection around the upstream patch is weakest when a partial V-shape is formed, pointing to locations where other patches can occur on the other side of the V. Temporal growth dynamics supported the occurrence of new patches in V-formations over longer time scales, resembling the flight formation adopted by migratory birds (Portugal et al. 2014). Our results highlight that bio-physical interactions shape the way organisms position themselves in landscapes, in both air- and water flow and across different spatial scales.

Facilitative interactions within the landscape of a self-organized species

The positive and negative feedbacks underlying the formation of self-organized patterns have been identified for a wide range of ecosystems (Rietkerk et al. 2002; van de Koppel et al. 2005; Larsen et al. 2007). At the scale of a single patch, it is well known that a positive feedback of reduced flow stress within patches is linked to a negative feedback limiting lateral growth (Bouma et al. 2009b; Schoelynck et al. 2012). However, while positive feedbacks are generally observed at a small scale within a patch (Rietkerk and Van de Koppel 2008), knowledge on the larger-scale facilitation by a self-organized species on itself is limited. Our study provides a first indication of colonization mechanisms operating at this larger, between-patch scale. We show how an existing vegetation patch modifies flow velocities and resulting drag forces in its surroundings, hence leading to positive or negative effects on the occurrence of other patches, operating at a distance. Facilitative interactions within the same self-organized species, and over larger scales, might therefore be an important but overlooked process determining the evolution of spatial patterns over time.

The spacing of the vegetation patches closely resembles the flight formation observed in many species of migratory birds to maximize the upward motion of air from the bird ahead and reduce drag due to air resistance (Lissaman and Shollenberger 1970; Weimerskirch et al. 2001; Portugal et al. 2014). Moreover, a similar flight pattern is also used by aircrafts flying in formation. The preferred angle for birds flying in a V flock is 45° from the bird ahead (Portugal et al. 2014), which is comparable to our temporal observations showing preferential patch occurrence at 0 to 60° from existing patches, with a peak around 30°. However, it is important to note that flight patterns of birds are due to behavioural differences, while vegetation patch configurations are related to colonization processes. A landscape resembling the patchy configuration observed in our study sites is also predicted by a model accounting for interactions between neighbouring patches of emergent vegetation (De Lima et al. 2015). While the position immediately in the wake of another patch could seem equally or even more beneficial in terms of drag reduction, the V position might be a hydrodynamic optimum to maximize drag reduction while still ensuring exposure to light and delivery of nutrients by water flow. Similarly, in mussel beds, aggregation at high densities provides the advantage of protection from physical stress, but also increases competition for food (van de Koppel et al. 2005; De Paoli 2017). Therefore, the balance between reducing stress and maintaining resource availability might be an important factor influencing patch distributions in different self-organized systems.

The consistency between the neighbouring patch distances observed for *Callitriche platycarpa* and the temporal vegetation dynamics of *Ranunculus penicillatus* suggest that such V-shaped settlement might be environment-specific. Thus, it might be a general process for submerged aquatic vegetation in running waters, at least for species with similar morphologies and experiencing comparable drag forces (Bal et al. 2011b). Further studies are necessary to test if a clear dominant species may be needed to achieve this configuration, and how the presence of other species might affect the patterns and spacing between patches.

Initial patterns control future pattern formation: implications for ecosystem resilience

Our results on the role of patchiness on vegetation distribution suggest that initial vegetation patterns determine where future patches occur. This creates patterns at multiple spatial scales: a patch-patch scale during initial establishment, which over time leads to a pseudo-braided pattern at the landscape scale, with vegetated bands separated by unvegetated channels. These patterns likely develop on two different time scales. On a short temporal scale, survival and establishment of plant individuals depend on successful root development (in the order of days; Barrat-Segretain et al. (1998); Barrat-Segretain et al. (1999)) against dislodgment due to currents and drag (as in our field manipulation). After colonization, single shoots develop into patches on a longer temporal scale (in the order of months, based on our monitoring data and literature studies, e.g. Cotton et al. (2006); Wharton et al. (2006)). Therefore, the complex self-organized patterning of stream macrophytes likely results from processes interacting at different spatial and temporal scales.

Pattern formation at multiple scales, both spatial and temporal, has been found to increase resilience in self-organized ecosystems, for example in mussel beds (Liu et al. 2014). Thus, the presence of a few initial patches can facilitate the establishment of new patches, it might promote faster recovery and create a self-reinforcing state that increases the resilience of lotic ecosystems against disturbance, induced for instance by flood events. The sheltering effect presumably becomes stronger as the number of patches increases, eventually developing into near-full vegetation cover (cf. Van der Wal et al. (2008) for *Spartina* tussocks growing into a fully vegetated salt marsh). In regularly disturbed ecosystems, where the hydrologic regime and flow variability are among the primary factors controlling macrophyte establishment and development (Riis and Biggs 2003), this process may be crucially important for vegetation recovery.

Organisms aligning to physical flows: generalities across landscapes and spatial scales

Many organisms move in organized groups or assemble in formations, of which the V-shaped flock of migratory birds is one of the most striking examples (Portugal et al. 2014). For instance, fish swimming in schools gain protection from predators and reduce energetic costs of locomotion (Krause and Ruxton 2002; Marras et al. 2015). Lobsters move in formation by queueing into a single line to reduce drag per individual during migration (Bill and Herrnkind 1976). At even smaller scales, bacteria have been found to organize into flocks or stream-like aggregates when feeding on prey or close to starvation (Thutupalli et al. 2015). Yet, these examples were so far thought to be limited to organisms exhibiting forms of collective behaviour. Our study shows that not only moving organisms, but also sessile ones such as aquatic plants, can organize in V-formation to minimize drag forces. In different types of fluids, organisms are exposed to different flow velocities but mechanical stresses still pose important constraints, as drag can be 25 times higher for aquatic plants under current flow velocity than for terrestrial plants at a comparable air flow velocity (Denny and Gaylord 2002). Therefore, our study suggests the general role of bio-physical interactions in shaping how organisms align themselves to aero- and hydrodynamic flows in different landscapes and across multiple spatial scales.

Chapter 6

Turbulence-mediated facilitation of resource uptake in patchy stream macrophytes

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Submitted

Abstract

Many landscapes are characterized by a patchy, rather than homogeneous, distribution of vegetation. Often this patchiness is composed of single-species patches with contrasting traits, interacting with each other. To date, it is unknown whether patches of different species affect each other's uptake of resources by altering hydrodynamics conditions, and how this depends on their spatial patch configuration. Patches of two contrasting aquatic macrophyte species (i.e., dense canopy-forming *Callitriche* and sparse canopy-forming *Groenlandia*) were grown together in a racetrack flume and placed in different patch configurations. We measured $^{15}NH_4^+$ uptake rates and hydrodynamic properties along the centerline and the lateral edge of both patches. When the species with a taller, denser canopy (*Callitriche*) was located upstream of the shorter, sparser species (*Groenlandia*), it generated turbulence in its wake that enhanced nutrient uptake for the sparser *Groenlandia*. At the same time, *Callitriche* benefitted from being located at a leading edge where it was exposed to higher mean velocity, as its canopy was too dense for turbulence to penetrate from upstream. Consistent with this, we found that ammonium uptake rates depended on turbulence level for the sparse *Groenlandia* and on mean flow velocity for the dense *Callitriche*, but Total Flow Kinetic Energy was the best descriptor of uptake rates for both species. By influencing turbulence, macrophyte species interact with each other through facilitation of resource uptake. Hence, heterogeneity due to multi-specific spatial patchiness has crucial implications for both species interactions and aquatic ecosystem functions and services of nutrient load reduction.

Introduction

In many ecosystems, vegetation shapes entire landscapes by interacting with physical processes (Dietrich and Perron 2006; Corenblit et al. 2011). Vegetation modifies habitats through its effects on hydrodynamics and sedimentation (Leonard and Luther 1995; Madsen et al. 2001; Schulz et al. 2003; Bouma et al. 2007), hence acting as an ecosystem engineer (Jones et al. 1994). In coastal and fluvial aquatic ecosystems, many studies first considered interactions between hydrodynamics and homogeneous vegetation (Kouwen and Unny 1973; Nepf 1999; Nepf and Vivoni 2000; Järvelä 2005; Chen et al. 2013), and later focused on isolated or pairs of patches (Sand-Jensen and Vindbœk Madsen 1992; Folkard 2005; Bouma et al. 2009b; Vandenbruwaene et al. 2011; Chen et al. 2012; Zong and Nepf 2012). Generally, vegetation patches locally reduce flow velocities, while increasing them in some adjacent areas (Bouma et al. 2007; Chen et al. 2012; Schoelynck et al. 2012; Meire et al. 2014).

In aquatic ecosystems, the interaction between vegetation and hydrodynamics regulates important ecological processes such as nutrient delivery and uptake by plants, as nutrients can be taken up from the water column through plant shoots (Madsen and Cedergreen 2002; Bal et al. 2013). These processes are crucial for community primary productivity (Thomas et al. 2000; Cornelisen and Thomas 2002; Cornelisen and Thomas 2004; Cornelisen and Thomas 2006; Morris et al. 2008). Previous studies on uptake rates in relation to hydrodynamic conditions mainly focused on seagrasses, using flume experiments with dissolved ^{15}N-labelled ammonium or nitrate (the main nitrogen sources in natural conditions; Haynes and Goh (1978)). These works identified the important effects of water velocity and flow alteration by seagrass canopies on resource uptake (Thomas et al. 2000; Cornelisen and Thomas 2006), and the dependence of uptake rates on the rate of mass transfer to the leaf surface under unidirectional flow (Cornelisen and Thomas 2004). Further, Morris et al. (2008) identified spatial patterns in ammonium uptake within seagrass patches, with higher uptake observed at the leading edge of the patch where the TKE and velocity within the patch were highest. In a study of nutrient uptake by river macrophytes, Bal et al. (2013) found that ammonium uptake increased with flow velocity. Because the diffusive boundary layer decreases with increasing velocity, the uptake rate also increases with increasing velocity (Thomas et al. 2000; Cornelisen and Thomas 2004; Morris et al. 2008; Bal et al. 2013).

However, most of the previous studies dealt with monospecific canopies or focused on a single species at a time, creating a monospecific community, while in reality natural landscapes are a diverse community made up of multiple species. Different patches of single species are heterogeneously distributed, and this patchiness is a common characteristic of aquatic habitats (Sand-Jensen and Vindbœk Madsen 1992). A few examples are patchy seagrass meadows (Fonseca et al. 1983), and streams characterized by a 'pseudo-braided' distribution of plant stands between areas of faster flow (Dawson and Robinson 1984; Cotton et al. 2006; Wharton et al. 2006). This additional level of complexity has just started to be integrated in studies of hydrodynamic-vegetation interactions. For instance, Weitzman et al. (2015) focused on hydrodynamic implications of multi-specific canopies, but considered canopy heterogeneity in the vertical dimension. Adhitya et al. (2014) focused on hydrodynamics and spatial configurations of seagrass patches with different densities, but did not test the consequences for resource uptake. Bal et al. (2013) focused on nutrient uptake rates within monospecific patches of two species next to each other, but they only tested a single spatial configuration and therefore did not investigate the effects of spatial patchiness. To date, it is still unknown how patches of different species interact with each other by altering hydrodynamics and uptake of resources, and how this depends on their landscape configuration.

Multispecies effects could be important for hydrodynamics and nutrient uptake because the density, flexibility and canopy structure of different species affect hydrodynamics differently (Peralta et al. 2008; Bouma et al. 2013). As we cannot easily predict the flow alteration by heterogeneous species distributions, our understanding of the implications for species interactions and nutrient load reduction in aquatic ecosystems is limited. Generally, the hydrodynamic controls on uptake rate are expected to be dependent on the macro-scale rate of delivery (mean flow velocity; e.g. Cornelisen and Thomas (2006)), or on the micro-scale processes that determine the concentration gradient at the leaf boundary layer (turbulence; e.g. Morris et al. (2008)). However, in a diverse community there might be cases where a single hydrodynamic parameter is not sufficient to describe uptake rates for multiple species with different traits and effects on hydrodynamic conditions. For instance, turbulence might not develop in very dense canopies. On the other hand, the mean flow speed can be relatively constant within sparse canopies, but turbulence might be locally variable. Therefore, understanding the interaction between multiple species in terms of nutrient uptake, mediated by their hydrodynamic effects, is essential to gain a more realistic understanding of species interactions and productivity in heterogeneous, multi-specific communities.

In this study, we use streams colonized by aquatic macrophytes as a model system. We investigate how patches of two different species with contrasting morphological traits interact with each other by influencing hydrodynamics, and thereby ammonium uptake. Moreover, we test how this depends on their spatial configuration (patchiness). Here, we define multi-specific patchiness as a community composed of patches of different species. Specifically, we study the interaction between two macrophyte species that co-occur under field conditions and have contrasting density and canopy structure. *Callitriche platycarpa* forms very dense patches that exhibit increasing canopy height with increasing patch length ('dense' species). *Groenlandia densa* has a more open canopy, and its canopy height is constant along the patch length ('sparse' species). In the field, the dense patches of *Callitriche* are distributed quite regularly at a distance of about 8 meters, and *Groenlandia* patches tend to aggregate around them (Chapter 3). Given the differences in shoot density and canopy architecture between the two species, we hypothesize that the effects of the dense *Callitriche* patches on hydrodynamics may facilitate the delivery and uptake of resources by the sparse *Groenlandia* patches. To test this hypothesis, patches of the two species were arranged in different configurations in a laboratory flume. To investigate the role of spatial configuration and reciprocal species effects on nutrient uptake, both the species upstream and the relative location of the species downstream were varied. We discuss the implications of multi-specific spatial patchiness on facilitation, aquatic ecosystem functioning and services of nutrient load reduction.

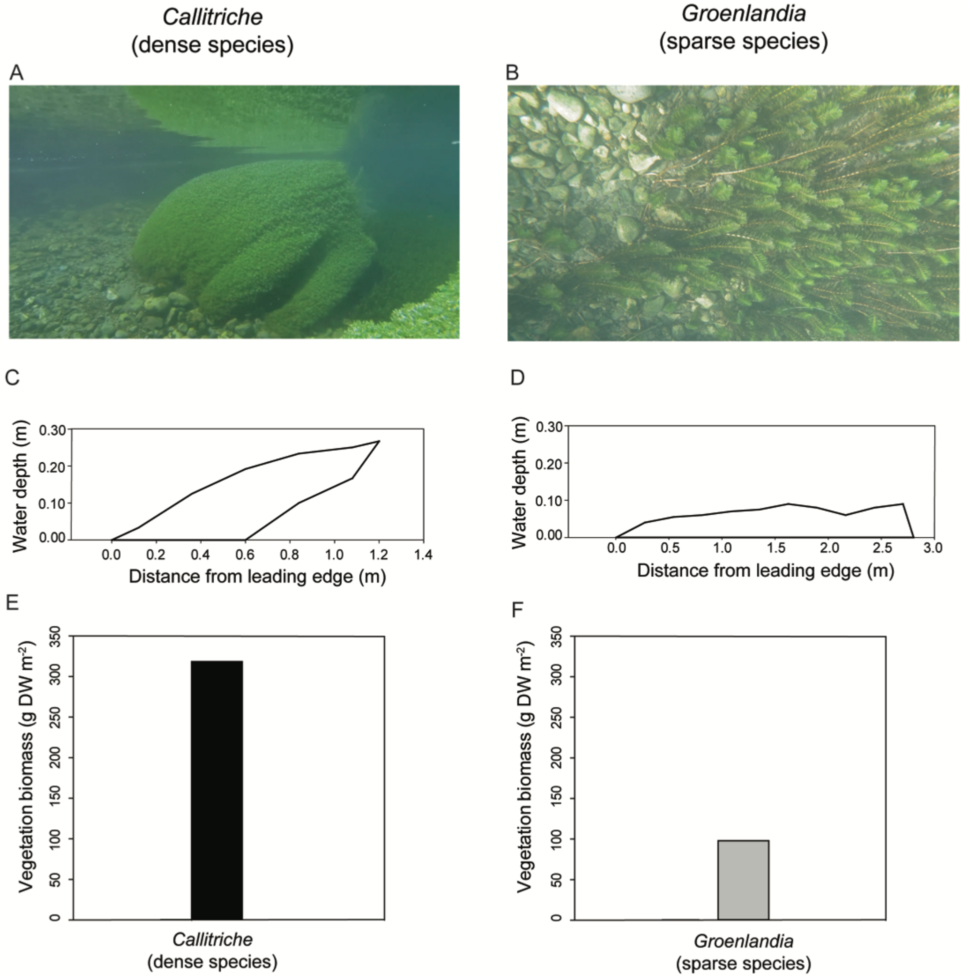


Figure 6.1: (A) Natural patches of Callitriche and (B) Groenlandia in the field. (C, D) Lateral view of the two patches, with the black outline indicating canopy height at increasing distance from the patch leading edge. (E, F) Mean vegetation biomass (g DW m^{-2}) used in the transplanted patches of Callitriche and Groenlandia.

Materials and methods

Plant material

We tested the effect of macrophyte patch species and configuration on ammonium uptake rates using two submerged macrophytes species, *Callitriche platycarpa* and *Groenlandia densa*. Both species were collected in February 2015 from a wetland on the Ain River (France). Plants were stored in plastic bags and transported to the laboratory in NIOZ Yerseke (The Netherlands) within 24 hours from collection. Until installation in the flume, the two macrophyte species were stored in a green house, in tanks with aerated tap water, and exposed to natural light. The macrophytes were allowed to recover for two days in the green house before starting the experiments. In order to be used for the experimental setup, individual plants were transplanted in stainless steel trays (30 × 29.5 × 5 cm). The trays were filled with a bottom layer of river sand (4.5 cm) and a top layer (0.5 cm) of fine gravel (0.2 cm grain size). A false bottom in the flume allowed the trays to be inserted with the soil surface at the same level as the flume bed. Based on the naturally occurring densities of the two species in the field, we constructed patches of 97 g DW m^{-2} for *Groenlandia* ('sparse' species) and 318 g DW m^{-2} for *Callitriche* ('dense' species) (Figure 6.1). We used a different patch length for each species to resemble the typical lengths observed in the field, i.e. 2.7 m and 1.2 m on average for *Groenlandia* and *Callitriche* respectively (L. Cornacchia, personal observation). We used a total of 9 trays for *Groenlandia*, for a total patch coverage of 2.7 × 0.3 m^2. For *Callitriche*, plants were rooted in two trays (0.6 × 0.3 m^2). When *Callitriche* was placed upstream, three trays (filled with the same soil as the plant trays) were placed between the two patches, to account for the presence of the typical overhanging canopy for this species. That is, when the flume was running, a total coverage of 1.20 × 0.3 m^2 was observed due to shoots bending; this region was considered as part of the *Callitriche* patch (see schematic diagram in Figure 6.2). A distance of one tray (0.3 m) between the two patches was used for the configurations in which *Groenlandia* was in the upstream position. The flume section next to each patch was left open (without plants, but filled with the same soil substrate used in the plant trays) in all configurations. The canopies of both species were fully submerged during the experiments.

Flume setup and experimental configurations

All experiments were performed within a unidirectional racetrack flume using a water depth of 0.35 m and with a cross-sectionally-averaged velocity of 0.24 m s^{-1}. For a more detailed description of the flume, see Bouma et al. (2005). To test for the effects of patch spatial configuration on ammonium uptake rates, the two patches were arranged one downstream of the other, either on the same side of the flume ('aligned' configurations), or on opposite sides ('staggered' configurations) (Figure 6.2). These different spatial configurations are both commonly observed in natural streams, where patches grow downstream of other patches, or in a staggered arrangement (L. Cornacchia, personal observation). Moreover, patches of different species can be found co-occurring at very short distances from each other, at the scale of 0.5 m (Chapter 3; Figure 3.4). To test for interactions between the two species, in terms of reciprocal effects on ammonium uptake rates, we also switched the species located upstream for each of these configurations ('Sparse-Dense' or 'Dense-Sparse' configurations).

Measuring spatial patterns in $^{15}N\text{-}NH_4^+$ uptake rates and canopy hydrodynamics

To determine spatial patterns of ammonium uptake rates by the macrophyte species, we measured uptake rates at selected locations within the patches (Figure 6.2). Nutrient uptake rates were determined inside the two patches at 10%, 50% and 90% of the patch length (0.27, 1.45 and 2.43 m from the leading edge in *Groenlandia*; 0.12, 0.6 and 1 m from the leading edge in *Callitriche*) and, for each location along the patch length, at 0.15 and 0.25 m of the patch width. For each incubation experiment, macrophyte individuals were randomly selected from the tanks where they were kept with freshwater and were transplanted into plastic pots (5 shoots per pot). Before transplantation in the flume, plant roots were removed to prevent ammonium uptake by that means from the labelled water that penetrated into the sand. Each plastic pot was then placed in one of the patch locations described above, and inserted in the trays so that their upper part was in line with the sediment level to avoid scouring effects. The pots were replaced after each incubation experiment and new plants were transplanted.

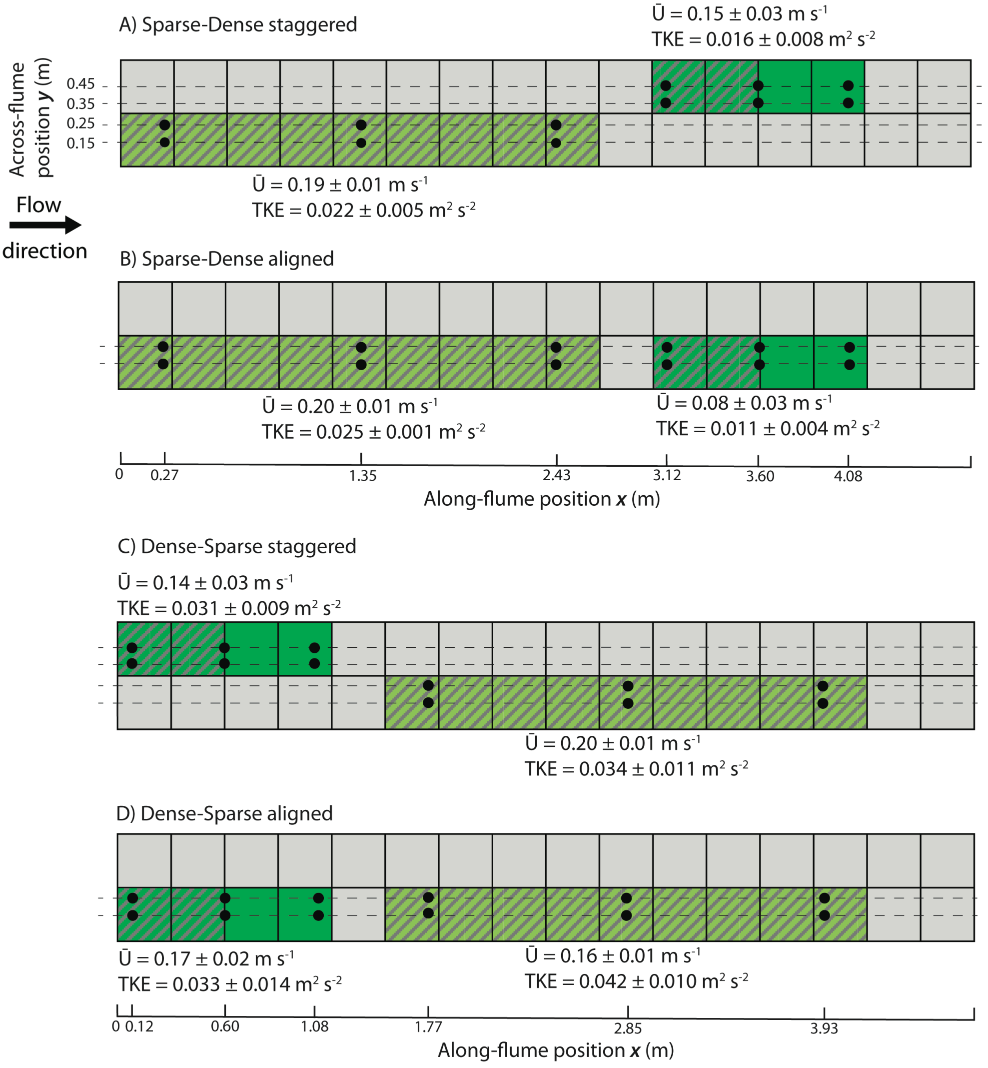


Figure 6.2: Schematic diagram of the four spatial configurations of aquatic macrophytes in the test section of the flume. Light green indicates patches of *Groenlandia* (sparse canopy), and dark green indicates patches of *Callitriche* (dense canopy). Diagonal lines indicate the boxes in which plants were rooted. Black circles are locations of plant specimens removed after the incubations experiments for assessment of $^{15}NH_4^+$ uptake rates, and of Acoustic Doppler Velocimeter (ADV) profile measurements. Numbers indicate mean (± SE) water velocity ($\bar{U}$, m s^{-1}) and turbulent kinetic energy (TKE, m^2 s^{-2}) within each species patch.

In the incubation experiments, ^{15}N-NH$_4^+$ was added to the water creating a 20 to 30 µM solution, with 30% of the N as ^{15}N abundance, following Bal et al. (2013). At the start and end of the experiment, three replicate water samples were taken to measure NH$_4^+$ concentration in the water. The same labelled water was used to perform four experiments, before replacing it with freshwater and a new label for the next runs (based on Bal et al. (2013)). Given the large volume of the flume water, there was a negligible decrease in NH$_4^+$ and ^{15}N-NH$_4^+$ concentrations over this time span (data not shown). Incubations were performed under artificial light conditions. The stable isotope was added near the paddles that drive the flow in the flume to ensure mixing. Each incubation experiment lasted for 6 hours, and two replicate runs were performed for each configuration. At the end of the 6 hours, macrophytes were collected from the test positions, rinsed with tap water to remove excess isotope from the plant surface, and folded into aluminum foil. In addition to the samples collected (n = 30 for each species), five specimens per species were randomly selected during the experiments from our species stock, to determine the background ^{15}N signal. The plants were dried in the oven for 48 hours at 60° C, and individual biomass was weighed. Dried macrophytes were ground to a fine powder using a ball mill (MM 2000, Retsch, Haan, Germany). A subsample of about 3 mg of powder per plant was sent to the laboratory for mass spectrometry analysis of the isotope ratio. The samples were analysed for total N content and ^{15}N-atomic percentage (as (^{15}N/total N) × 100) with an Elemental Analyser (Thermo Electron FlashEA 1112) and subsequent isotope ratio mass spectrometry (Thermo Delta V - IRMS).

To calculate the ^{15}NH$_4^+$ uptake rate (V in µmol g^{-1} (DM) h^{-1}) of each sample, we followed the equation in Bal et al. (2013):

$$V = \frac{N_{pl}}{\Delta t} \cdot \left(A_{\%f} - A_{\%backgr}\right) \qquad \textbf{(6.1)}$$

where $A_{\%f}$ is the ^{15}N abundance in the biomass of the sample after incubation (%) calculated as the measured ^{15}N-atomic percentage; $A_{\%backgr}$ is the background ^{15}N abundance in the biomass (%) calculated as the mean of the ^{15}N-atomic percentage measured on five background specimens for each species; Δt (h) is the incubation time (6 h) and N_{pl} is the N content of the dry biomass (µmol g^{-1} (dry mass (DM)) of each sample.

Hydrodynamic measurements

To test the relationship between hydrodynamic parameters and nutrient uptake, vertical profiles of velocity were measured with a 3D acoustic Doppler velocimeter (ADV, Nortek) over 2 min at 10 Hz. Within each profile, velocity was measured at seven vertical locations at 2, 5, 10, 12, 15, 17 and 27 cm above the channel bed. The profiles were measured in the same streamwise and lateral locations as the plant samples collected for nutrient uptake estimation, i.e. at 10%, 50% and 90% of the length of each patch in the streamwise (x) direction, and at 0.15 and 0.25 m of the patch width in the spanwise (y) direction (Figure 6.2). The height of the vegetation canopy in each location was measured with a ruler in cm.

Depth-averaged velocity (<Ū>, m s^{-1}) at each profile position was calculated as a vertical average over the entire flow depth. To calculate Turbulent Kinetic Energy (TKE, $m^2 s^{-2}$) within the canopy, we first calculated $u'(t) = u(t) - \overline{U}$, in which $u(t)$ is the time series of flow measurements in the streamwise direction and $\overline{U}$ is the time-averaged velocity at each vertical position. The corresponding spanwise and vertical turbulent velocity components v' and w' were calculated in the same way. For each point measurement within the canopy in the profile, turbulent kinetic energy (per unit mass) was then calculated as:

$$TKE = \frac{1}{2}\left(\overline{u'^2} + \overline{v'^2} + \overline{w'^2}\right) \qquad \textbf{(6.2)}$$

Reynolds stress (τ_{xz}, Pa) at the top of the canopy at each location was calculated as:

$$\tau_{xz} = -\overline{\rho u'(t) w'(t)} \qquad \textbf{(6.3)}$$

in which ρ =1000 kg m^{-3} is the density of the flume water.

Volumetric flow rate of water through the patches (Q_c, $m^3\ s^{-1}$) was calculated as:

$$Q_c = \sum_{0}^{Z_c} Q_i \quad \text{and} \quad Q_i = y(z_i - z_{i-1})\bar{u}_{z_i} \qquad \textbf{(6.4)}$$

in which Z_c is the canopy height, Q_i the volumetric flow rate of water through the layer $(z_i - z_{i-1})$, y is the patch width (0.3 m) and $\bar{u}_{z_i}$the double-averaged *u* component (i.e., averaged in time and spatially averaged in the two lateral positions) of the velocity at depth z_i.

Total Flow Kinetic Energy ($m^2\ s^{-2}$) within the canopy is a sum of mean-flow and turbulence contributions. This parameter is more representative of the instantaneous velocity, which is more relevant to the boundary layer dynamics, especially in cases with low velocity and higher TKE. Specifically, previous studies have suggested that strong instantaneous velocity and/or plant motion can periodically strip away the diffusive sub-layer, which, if frequent enough, will enhance flux to the plant surface (Koch 1994; Stevens and Hurd 1997; Huang et al. 2011). Total Flow Kinetic Energy was calculated as follows:

$$Total\ Flow\ Kinetic\ Energy = TKE + {}^{1}\!/_{2}\,(U^2 + V^2 + W^2) \qquad \textbf{(6.5)}$$

in which *U*, *V* and *W* are the time-average velocities in the streamwise, spanwise and vertical directions. This corresponds to calculating the mean of the instantaneous total kinetic energy at each time step in the ADV measurements.

Measuring channel-scale patterns of ammonium uptake

To investigate how the relationship between hydrodynamic parameters and ammonium uptake develops at the scale of a whole channel, we tested the correlation between the total in-patch $^{15}NH_4^+$ uptake rates and in-patch average hydrodynamic parameters (mean flow velocity, TKE and Total Flow Kinetic

Energy). This allowed us to test whether spatial patch configurations that generated higher mean flow velocity, Total Flow Kinetic Energy or TKE levels within the canopies promoted higher uptake at the channel scale. The total in-patch $^{15}NH_4^+$ uptake rates for each configuration was calculated as the sum of the uptake rates estimated in all sampling points ($n = 6$ per species; Figure 6.2). This total uptake was used as an estimate of channel-scale uptake, but is not necessarily a measure of total ammonium uptake rates per biomass or aerial cover.

Statistical analyses

To test for statistical differences in $^{15}NH_4^+$ uptake rates of each species under four flume spatial configurations, one-way ANOVA was used. Pearson's correlation coefficient was used to test for significant correlation between $^{15}NH_4^+$ uptake rates (μmol g^{-1} (DM) h^{-1}) and hydrodynamic parameters (depth-averaged velocity $<\bar{U}>$ (m s^{-1}); Reynolds stress t_{xz} (Pa); turbulent kinetic energy TKE (m^2 s^{-2}); Total Flow Kinetic Energy (m^2 s^{-2}); and volumetric flow rate, Q_c (m^3 s^{-1}), and between channel total $^{15}NH_4^+$ uptake rates and average hydrodynamic parameters within both species patches (mean flow velocity, TKE and Total Flow Kinetic Energy). Alpha values of less than or equal to 0.05 were considered to be significant. All statistical analyses were performed in R 3.1.2 (R Core Team 2015).

Results

Relationship between canopy hydrodynamic parameters and nutrient uptake

We found that the two macrophyte species affected each other's ammonium uptake rates by altering mean flow velocity and turbulence. Ammonium uptake rates depended on either mean flow velocity (*Callitriche*) or turbulence (*Groenlandia*), but Total Flow Kinetic Energy was the single best descriptor of uptake rates for both species (Figure 6.3; Table 6.1). Specifically, $^{15}NH_4^+$ uptake rates for the sparse *Groenlandia* were significantly correlated with TKE ($r = 0.66$, $p < 0.001$), but not with mean flow velocity ($r = -0.17$, $p = 0.41$) (Figure 6.3; Table 6.1). The opposite was true for the dense *Callitriche*: uptake rates were significantly correlated with mean flow velocity ($r = 0.40$ $p = 0.05$), but not with

TKE ($r = 0.33$, $p = 0.1$) (Figure 6.3; Table 6.1). However, Total Flow Kinetic Energy, which is more representative of the instantaneous velocity, described uptake for both species ($r = 0.79$, $p < 0.0001$ for *Groenlandia*; $r = 0.45$, $p = 0.02$ for *Callitriche;* $r = 0.54$, $p < 0.0001$ for both species together) (Figure 6.3A; Table 6.1). No significant relationship was found between ammonium uptake rates and either Reynolds stress or Q_c (Table 6.1).

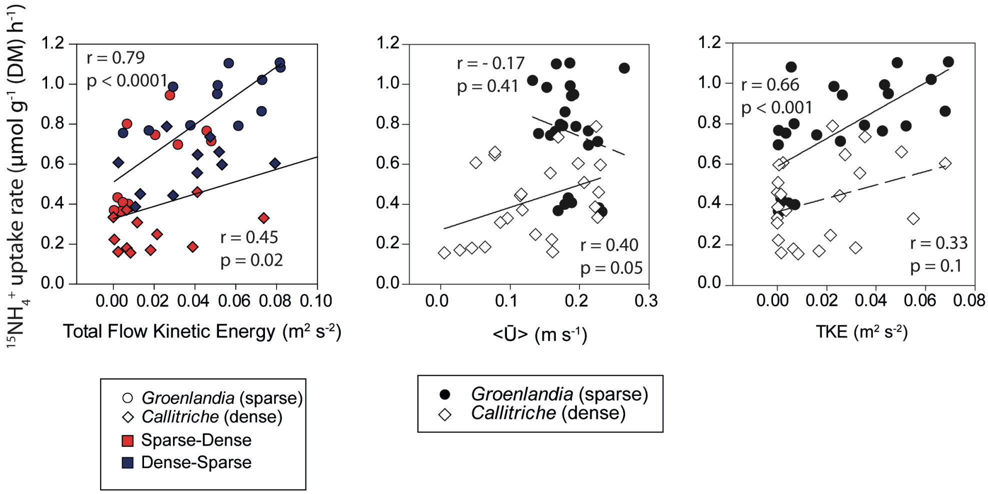


Figure 6.3: Scatter plots of $^{15}NH_4^+$ uptake rates (µmol g^{-1} (DM) h^{-1}) against Total Flow Kinetic Energy (m^2 s^{-2}), depth-averaged velocity <Ū> (m s^{-1}) and turbulent kinetic energy TKE (m^2 s^{-2}) for the sparse *Groenlandia* (circles) and the dense *Callitriche* (diamonds). 'Sparse-Dense' configurations are in red, 'Dense-Sparse' configurations are in blue. Black lines are linear regression lines for the *Groenlandia* and *Callitriche* data separately. Solid lines represent significant relationships ($p \leq 0.05$), dashed lines indicate non-significant relationships.

Table 6.1: Pearson's correlation of canopy height (cm) and hydrodynamic parameters (depth-averaged velocity $<\bar{U}>$ [m s^{-1}]; Reynolds stress τ_{xz} [Pa]; turbulent kinetic energy TKE [m^2 s^{-2}]; total flow kinetic energy [m^2 s^{-2}] and canopy water flow Q_c [m^3 s^{-1}]) with NH_4^+ uptake rates (µmol g^{-1} (DM) h^{-1}) of *Groenlandia*, *Callitriche* and both species considered together. Correlations in bold are significant at $p \leq 0.05$.

	Groenlandia (n = 24)	*Callitriche* (n = 24)	All (n = 48)
Height	0.13	-0.19	**-0.30**
$<\bar{U}>$	-0.17	**0.40**	**0.39**
τ_{xz}	0.02	-0.17	0.03
TKE	**0.66**	0.33	**0.52**
Total Flow Kinetic Energy	**0.79**	**0.45**	**0.54**
Q_c	-0.08	0.19	-0.09

Effects of patch spatial configurations on nutrient uptake

When located upstream, the dense *Callitriche* patch increased turbulence and thereby enhanced the uptake of resources by the sparse *Groenlandia* patch located downstream. The ammonium uptake rates were influenced by both macrophyte species and spatial patch configuration (order and alignment). Importantly, the Dense-Sparse (D-S) configurations led to higher uptake rates for both species. Testing for the effects of macrophyte species and patch spatial configuration on ammonium uptake revealed a significant two-way interaction between the two (two-way ANOVA, $F_{3,447} = 6.521$, $p = 0.0002$). Ammonium uptake rates were significantly higher for the sparse *Groenlandia* than for the dense *Callitriche* (one-way ANOVA, $F_{1,453} = 133.3$, $p < 0.001$). Average uptake rates for the sparse *Groenlandia* were 0.76 µmol g^{-1} (DM) h^{-1} ± 0.38, almost double than for the dense *Callitriche* (0.41 µmol g^{-1} (DM) h^{-1} ± 0.22).

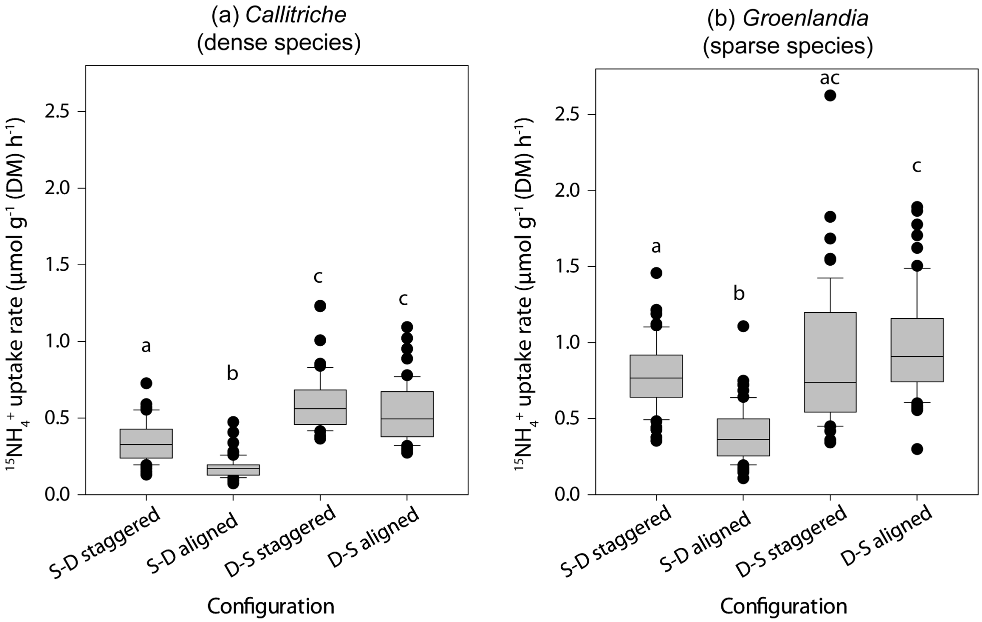


Figure 6.4: Boxplots of the distribution of $^{15}NH_4^+$ uptake rates (µmol g^{-1} (DM) h^{-1}) within patches of the dense *Callitriche* (a) and the sparse *Groenlandia* (b) in each spatial configuration (S indicating sparse vegetation, D indicating dense vegetation, see Figure 6.2). Letters denote significant differences (Tukey's HSD, $p < 0.05$).

The upstream-downstream order and spatial patch alignment of the species significantly affected uptake rates for both the sparse *Groenlandia* (one-way ANOVA, $F_{3,222} = 37.41$, $p < 0.001$; Figure 6.4) and the dense *Callitriche* (one-way ANOVA, $F_{3,225} = 88.95$, $p < 0.001$; Figure 6.4). We generally found that when the denser species (*Callitriche*) was located upstream of the sparser one (*Groenlandia*), ammonium uptake rates for both species increased significantly, compared to patch configurations in the Sparse-Dense order (Figure 6.4). This significant increase in uptake rates was related to the hydrodynamic effects of different configurations, and particularly the traits of *Callitriche* (i.e. density and canopy height, which blocks a larger fraction of flow depth). When the dense patch of *Callitriche* was upstream, it generated higher TKE that influenced the downstream patch of *Groenlandia* (Figure 6.2), enhancing its uptake rates (Figure 6.3). Also, when the dense *Callitriche* was upstream, its leading edge was exposed to higher mean velocity compared to when it was trailing behind the sparse patch (Figure 6.2), thereby increasing its uptake rates (Figure 6.3). Specifically, for the dense *Callitriche*, uptake rates within the Sparse-Dense order were higher in the staggered than in the aligned configuration (Tukey's HSD, $p < 0.05$). However, uptake rates were significantly higher in the two Dense-Sparse configurations than in both the S-D configurations (Tukey's HSD, $p < 0.05$), irrespective of the staggered or aligned arrangement. For the sparse *Groenlandia*, uptake rates within the Sparse-Dense order were significantly lower in the aligned than in the staggered arrangement (Tukey's HSD, $p < 0.05$). In the Dense-Sparse configurations, no significant difference in uptake rates was found between the staggered or aligned arrangement (Tukey's HSD, $p > 0.05$). Uptake rates in the D-S aligned configuration were significantly higher than in the S-D staggered configuration, but were not significantly different from the D-S staggered case (Tukey's HSD, $p > 0.05$). Instead, the D-S staggered configuration was not significantly different from the S-D staggered and the D-S aligned configurations (Tukey's HSD, $p > 0.05$).

We found that the vegetation distributions that generated higher Total Flow Kinetic Energy levels within the patches generally promoted higher total uptake at the channel scale (Figure 6.5). Testing for the hydrodynamic parameter-uptake relationships at the channel scale revealed a significant positive relationship between the in-patch Total Flow Kinetic Energy (average of both patches in each configuration) and the channel total ammonium uptake ($r = 0.99$, $p = 0.009$; Figure 6.5). Channel total ammonium uptake was also significantly related to in-patch TKE ($r = 0.97$, $p = 0.02$), but not to mean flow velocity ($r = 0.91$, $p = 0.08$).

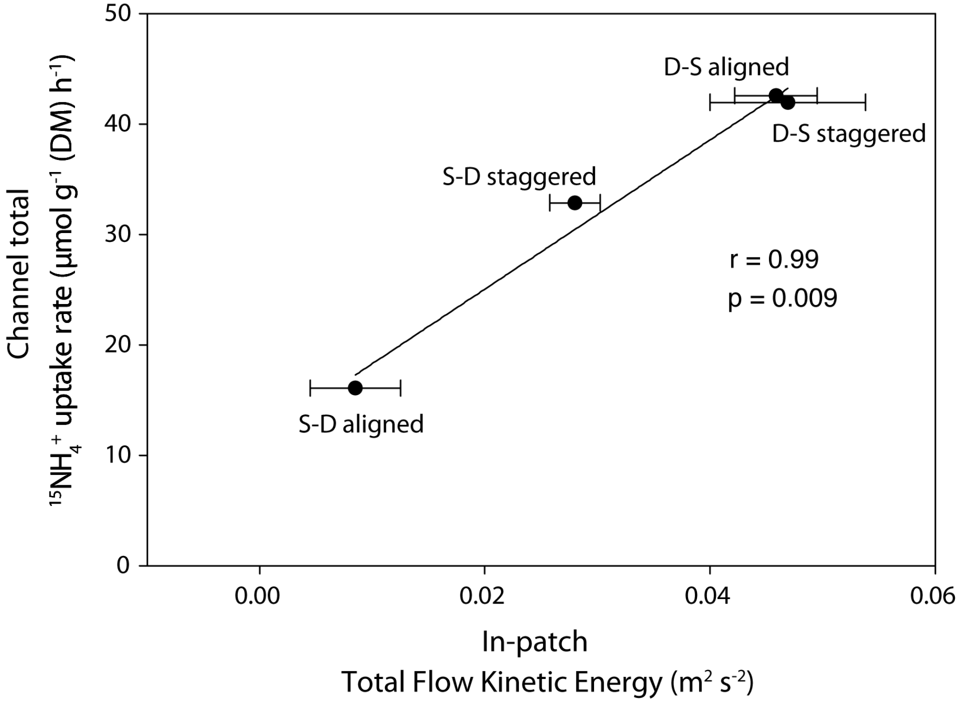


Figure 6.5: Scatter plots of channel total $^{15}NH_4^+$ uptake rates (µmol g^{-1} (DM) h^{-1}) in each spatial configuration against Total Flow Kinetic Energy (m^2 s^{-2}) averaged within patches of *Callitriche* and *Groenlandia* in each spatial configuration (S indicating sparse vegetation, D indicating dense vegetation, see Figure 6.2). Error bars represent standard error of the mean.

Discussion

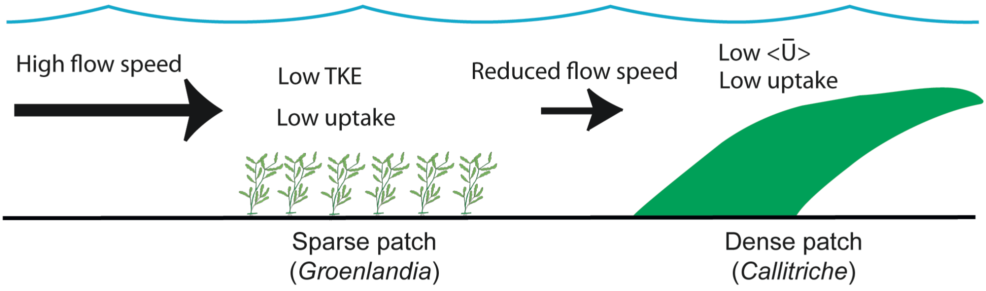
In aquatic ecosystems, the interaction between vegetation and hydrodynamics regulates important ecological processes such as nutrient delivery and uptake by plants, which are crucial for community primary productivity (Thomas et al. 2000; Cornelisen and Thomas 2006; Morris et al. 2008). In the present study, we found that, by generating turbulence, dense macrophyte patches facilitate resource uptake by neighboring sparse patches. Flume measurements showed that the dense *Callitriche* acted as a strong ecosystem engineer, creating high-turbulence regions in its wake that facilitated nutrient uptake of a weaker ecosystem engineer (i.e., the sparse *Groenlandia*). While the sparse vegetation benefitted from the high turbulence generated in the wake of a dense patch, the dense vegetation benefitted from being located at a leading edge, where it was exposed to higher mean velocity, compared to when it was located downstream of another patch (Figure 6.2; Figure 6.6). We identified Total Flow Kinetic Energy as the best descriptor of the nutrient removal capacity of streams, especially in heterogeneous multi-species communities. Overall, spatial configurations that lead to higher Total Flow Kinetic Energy within the patches were the ones that led to higher total ammonium uptake. Hence, our results highlight the importance of turbulence as an agent of interaction between different species. Moreover, this study suggests that accounting for interactions between heterogeneous, multi-specific patchy vegetation is crucial to understand aquatic ecosystem functioning and services of nutrient load reduction.

Implications of resource uptake in mono- and multi-species communities

Previous studies on seagrasses and freshwater aquatic macrophytes generally found that nutrient uptake rates increased with turbulent mixing (Morris et al. 2008) or mean flow velocity (Cornelisen and Thomas 2006; Bal et al. 2013). Yet, in our study, neither of these traditional hydrodynamic parameters could accurately describe uptake rates for both species. Moreover, contrary to previous studies (Morris et al. 2008; Bal et al. 2013), we did not find a significant relationship between ammonium uptake rates and volumetric flow rate, likely because the two species have different flexibility and density traits that affect patch compression. We identified Total Flow Kinetic Energy as the best descriptor of uptake rates for both species. To our knowledge, this parameter has not been related before to nutrient uptake rates by aquatic vegetation. Previous studies have suggested that TKE may influence nutrient uptake (Anderson and Charters 1982; Koch 1994), and the total energy parameter captures this influence. Specifically, when TKE is weak, flux is controlled by the time-mean diffusive sub-layer thickness, which is a function of the mean velocity (e.g. Hansen et al. (2011); Rominger and Nepf (2014); Lei and Nepf (2016)). However, when the TKE is high, periodic disturbances of the diffusive sub-layer by the turbulence can create instantaneously higher concentration gradients at the surface and, thus, higher flux (e.g. Stevens and Hurd (1997); Huang et al. (2011); Rominger and Nepf (2014)). By reflecting both the mean current and TKE magnitudes, the total flow energy captures both regimes of flux. The Total Flow Energy is particularly suitable in heterogeneous systems where upstream TKE generation (e.g. by larger, denser patches) can influence flux downstream, i.e. the TKE is not locally generated and thus uncorrelated with the local velocity. In the dense *Callitriche* patches, the canopy is often too dense for turbulence to form within the patch or to penetrate from the free stream. Under these low TKE conditions, the flux is correlated by the local mean velocity, which sets the scale of the diffusive sub-layer. For the sparse *Groenlandia*, mean flow velocity is relatively constant in the canopy and we found no correlation with uptake rates. However, the TKE is elevated both by local stem generation and the penetration of turbulence generated upstream. Under these high TKE conditions, the uptake rates have a high correlation with the TKE intensity. In landscapes made up of patches of different species, regions with flux controlled by mean velocity and regions controlled by TKE are heterogeneously distributed, so that neither mean velocity nor TKE can capture the channel-scale nutrient uptake. Because it can describe both regions of low TKE (uptake controlled by mean velocity) and high TKE (uptake controlled by TKE intensity), we propose Total Flow Energy as a new descriptor of nutrient uptake capacity of rivers, which could be used to estimate ecosystem services of nutrient load reduction.

Our results reveal the important role of patch spatial configuration in influencing the interaction between the two species. While we found clear effects of the upstream-downstream patch arrangement on ammonium uptake rates, we only observed a significant effect of patch arrangement (staggered vs. aligned) in the Sparse-Dense configurations. In addition to the role of spatial configuration, the distance between the patches might affect the intensity of the interaction between them. The stronger interactions between patches likely occur when the distance between them is less than the wake length of the upstream patch (Folkard 2005). It might be expected that the wake length is in turn related to patch density, because density determines at what distances the patch effects will dissipate (Zong and Nepf 2012). Further studies should be undertaken to investigate the detailed hydrodynamic consequences of different spatial patch configurations, testing for the effects of a wider range of distances and its interactive effect with patch density.

(a) Sparse-Dense species configurations



(b) Dense-Sparse species configurations

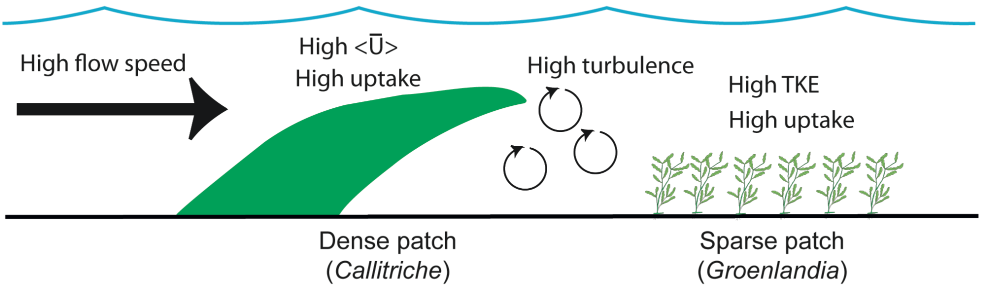


Figure 6.6: Schematized drawing of the effects of multispecific spatial patchiness on hydrodynamics and nutrient uptake rates. In Sparse-Dense configurations (a), the sparser vegetation is exposed to high mean flow but low turbulence, and does not benefit from being located at the leading edge. Similarly, the denser vegetation is exposed to low mean flow speed due to sheltering by the patch upstream, and hence has lower uptake rates. Instead, in Dense-Sparse configurations (b), uptake rates of both species are higher: the denser vegetation benefits from being at the leading edge and exposed to high mean flow speed (which increases uptake rates); at the same time, the sparser vegetation benefits from the high turbulence created in the wake of the denser patch.

Turbulence-mediated species interactions: implications for species distributions and nutrient load reduction

The study of turbulence-mediated interactions between macrophyte species suggests a possible mechanism behind the co-occurrence of *Groenlandia* patches around *Callitriche* in the field. Recently, it has been shown that *Groenlandia* shoots grow better around *Callitriche* patches than on bare, unvegetated sediment (Chapter 3, Figure 3.5). The wake of the *Callitriche* patches is both a high-turbulence and low-velocity region (Sand-Jensen 1998). Thus, a combination of enhanced resource uptake by turbulence, and reduced biomass losses by flow velocity, might be the conditions behind the improved growth rates of *Groenlandia* plants around *Callitriche* patches. As the sparse *Groenlandia* tends to surround the dense *Callitriche* patches in regularly spaced aggregations every 8 m (Chapter 3, Figure 3.4), the interaction between the two species might enhance the overall nutrient removal capacity of the river. However, care must be taken when upscaling the relationship between hydrodynamics and resource uptake at the channel scale. In our incubations, we focused only on uptake rates of a single nutrient (ammonium), which is energetically less costly, but some species might invest in nitrate uptake. This is an interesting aspect that should be explored in future studies of channel-scale nitrogen uptake by vegetation. As a future perspective, we might be able to use the knowledge on these types of species interactions as tools to enhance restoration success of degraded (eutrophic) sites.

Overall, our study highlights the importance of turbulence for species interactions and facilitation. To investigate species interactions, previous studies mainly focused on flow velocity or wave stress reduction by ecosystem engineers (e.g. Bruno (2000); Donadi et al. (2013)), but largely overlooked the effects on other flow characteristics. Therefore, our study reveals the need for a better understanding of turbulence as an agent of interaction between species.

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).

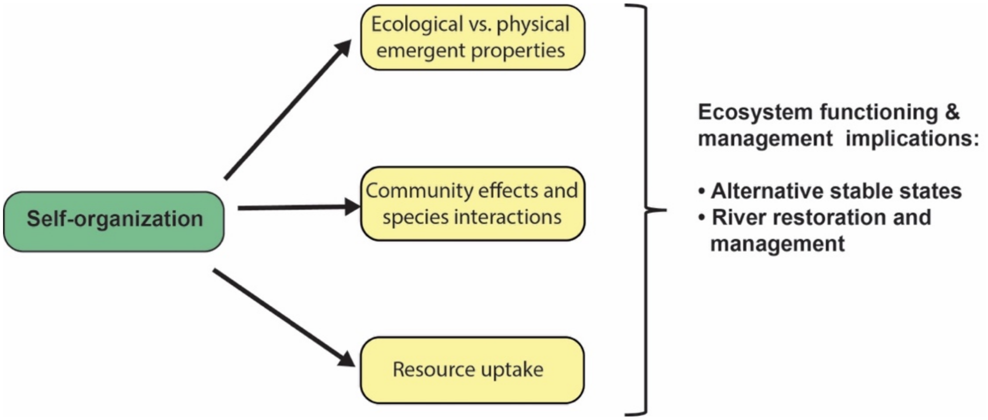


Figure 7.1: Overview of the main themes and implications related to the findings of this thesis, in terms of advancing self-organization theory from both a fundamental and an applied perspective.

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 (Baattrup-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.

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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.

Samenvatting

Zelforganisatie wordt in toenemende mate erkend als een belangrijk regulerend proces in ecosystemen. Veel studies naar zelforganisatie in de biologie hebben zich gericht op de emergente, d.w.z. spontaan verschijnende, effecten van zelfgeorganiseerde ruimtelijke patronen op biologische eigenschappen, zoals verhoogde productiviteit of veerkracht tegen verstoringen. Ondanks het veelvuldig voorkomen in biologische theorieën is zelforganisatie nog niet uitgebreid onderzocht in geofysische studies. De meeste studies slagen er niet in de wisselwerking tussen biologische en fysische processen volledig in het onderzoek mee te nemen. Hierdoor is onbekend of het zelforganisatieproces dat voortkomt uit deze terugkoppelingen ook emergente effecten heeft op zowel fysische als biologische eigenschappen. In dit proefschrift bestudeer ik, uitgaand van onderwaterplanten in beken als modelsysteem, de emergente effecten van zelforganisatie – ten gevolge van de tweezijdige interactie tussen plantengroei en herverdeling van waterstroming – op zowel hydrologische als ecologische processen. In het bijzonder onderzoek ik de rol van zelforganisatie van zulke waterplanten in termen van regulatie van de waterstroming (stroomsnelheid en diepte), biologische interacties (groei, verspreiding en ruimtelijke patroonvorming) en opname van nutriënten. Mijn onderzoek combineert veldexperimenten en veldobservaties, stroomgootexperimenten in het laboratorium en wiskundige modellen.

In Hoofdstuk 2 onderzoek ik of zelforganisatie, ten gevolge van de tweezijdige interactie tussen plantengroei en herverdeling van waterstroming, emergente gevolgen heeft voor de hydrodynamiek op de schaal van de beek. In een gecombineerde wiskundige model- en empirische studie laat ik zien dat het zelforganisatieproces heterogeniteit creëert in plantenbiomassa en waterstroming. Dit stabiliseert zowel stroomsnelheid als waterhoogte onder variabele rivierafvoer, met gunstige effecten op voor het ecosysteem. Mijn resultaten leggen daarom een belangrijke link bloot tussen plantgedreven zelforganisatieprocessen in beekecosystemen en de ecosysteemdiensten die deze beken leveren in termen van waterstroomregulering en habitatdiversiteit.

De in Hoofdstuk 2 bestudeerde regulering van de waterstroming door onderwaterplanten wijst op belangrijke implicaties van plantgedreven hydrodynamische heterogeniteit voor soorteninteracties en biodiversiteit. In Hoofdstuk 3 onderzoek ik daarom de relatie tussen zelforganisatie en facilitatie. Modelvoorspellingen suggereren dat zelfgeorganiseerde patroonvorming de co-existentie bevordert van plantensoorten in leefgemeenschappen in stromend water door een “landschap van facilitatie” te creëren. Hierin ontstaan meerdere nieuwe niches voor soorten die zijn aangepast aan een breed scala aan hydrodynamische condities. Modelvoorspellingen worden bevestigd door veldwaarnemingen van samen voorkomende soorten en transplantatie-experimenten die de hypothese van facilitatie ondersteunen. Deze studie benadrukt dan ook dat begrip van de wijze waarop competitie en facilitatie in veel ecosystemen met elkaar wisselwerken cruciaal is voor een succesvol beheer van biodiversiteit.

Het zelforganisatieproces zoals beschreven in Hoofdstuk 2 en 3 is gebaseerd op het omleiden van waterstroming rond vegetatie. Omleiding van fysische krachten is een algemeen mechanisme dat in veel ecosystemen ten grondslag ligt aan patroonvorming door soorten. Tot op heden is echter onbekend of de onderliggende mechanismen voor zelfgeorganiseerde ruimtelijke patroonvorming van belang zijn voor het faciliteren van soortenvestiging. Het invangen van plantpropagulen door reeds aanwezige vegetatie is een belangrijk knelpunt voor de vestiging van waterplanten in beken. De waterstroming is zowel het transportmechanisme van plantpropagulen als de stressfactor die leidt tot ruimtelijke vegetatiepatronen. In Hoofdstuk 4 onderzoek ik de gevolgen van dit stromingsomleidingsmechanisme voor de facilitatie door het invangen van propagulen in reeds aanwezige plekken met vegetatie, gebruikmakend van mesocosmos-, stroomgoot- en veldstudies. Mijn onderzoek suggereert dat terugkoppeling tussen de herverdeling van vegetatie en de waterbeweging, wat tot zelforganisatie leidt, de vestiging van waterplantensoorten kan vergemakkelijken tijdens hun verspreiding en eerste kolonisatie.

In Hoofdstuk 5 test ik of het patroon van ruimtelijk verspreide patches van waterplanten, ten gevolge van de tweezijdige wisselwerking tussen vegetatie en hydrodynamiek, invloed heeft op de vegetatievestiging door facilitatie *binnen* eenzelfde soort. Manipulatie-experimenten in het veld demonstreren dat vegetatie in beken zichzelf in V-vormen schikken om hydrodynamische krachten en weerstand te minimaliseren, vergelijkbaar met de vluchtformatie van trekvogels. Mijn bevindingen onderstrepen dat biofysische interacties vormgeven hoe organismen zichzelf positioneren in landschappen blootgesteld aan fysische stromingen.

In Hoofdstuk 6 verken ik ten slotte de emergente effecten van zelfgeorganiseerde ruimtelijke patronen, ontstaan door verschillende soorten, op de grondstofopname. Veel studies aan plant-hydrodynamische terugkoppelingen gaan uit van één plantensoort. Natuurlijke landschappen zijn echter diverse leefgemeenschappen bestaand uit plekken van verschillende soorten met tegengestelde eigenschappen. Deze plekken beïnvloeden elkaar mogelijk door hun hydrodynamische effecten, bijvoorbeeld door beïnvloeding van de grondstofopname, die cruciaal is voor de productiviteit. Mijn bevindingen suggereren dat plukken macroscopisch grote waterplantsoorten met elkaar wisselwerken door de grondstofopname te vergemakkelijken door de turbulentie te veranderen. Dit test ik aan de hand van experimenten in een rondlopende stroomgoot waarbij hydrodynamische metingen gecombineerd worden met ^{15}N gelabelde ammonium-incubaties. Mijn onderzoek toont het belang aan van turbulentie als interactiemiddel tussen verschillende soorten. De bevindingen suggereren bovendien dat interacties tussen heterogeen verdeelde meersoortige plukkerige vegetatie cruciaal zijn om het functioneren van het aquatische ecosysteem en de verdiensten van nutriëntenladingsvermindering te kunnen begrijpen.

Concluderend belicht mijn onderzoek de cruciale emergente effecten van zelforganisatie op een breed scala aan fysische en biologische eigenschappen in ecosystemen. Deze studie legt een tot nog toe onontdekt verband bloot tussen zelfgeorganiseerde biologische patronen en ecosysteemdiensten zoals stromingsregulering, habitat- en soortendiversiteit. Begrip van de regulerende rol van ruimtelijke zelforganisatie is essentieel voor het behoud van de waardevolle ecosysteemdiensten die ze ondersteunt. In veel ecosystemen worden biofysische interacties nog altijd behandeld vanuit een statische benadering die de dynamische terugkoppelingen niet volledig omvat. Toekomstige empirische- en modelstudies naar andere biogeomorfologische landschappen zouden moeten trachten deze wederzijdse terugkoppelingen verder mee te nemen. Dit zal bijdragen aan ons begrip van het volledige scala aan emergente eigenschappen van ruimtelijke patroonvorming in ecosystemen en bredere toepasbaarheid van de hier gepresenteerde conclusies. De bevindingen in dit proefschrift suggereren ook hoe biofysische interacties benut kunnen worden om beheer en herstel van aquatische ecosystemen te sturen. Zo kunnen onze fundamentele onderzoeksvragen over zelforganisatie direct gekoppeld worden aan toegepast onderzoek. Dergelijke koppelingen zijn waardevol om beheer en behoud van ecosystemen in goede banen te leiden.

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Loreta

Curriculum vitae

Loreta Cornacchia was born in Bari (Italy), on March 22, 1988. She graduated from high school in Gravina in Puglia in 2007, and then moved to Bologna (Italy), where she earned a Bachelor's degree in Natural Science (2010). She later moved to Rome, where she completed a Master's degree in Ecobiology (2012). During her Master thesis, she did an internship at ISPRA (Istituto Superiore per la Protezione e la Ricerca Ambientale) in Rome, where she worked on remote sensing applications to study vegetation evolution in coastal areas. During this internship, she discovered her passion for scientific research, and particularly for the interactions between vegetation and hydrodynamic forces. Between August 2013 and October 2017, she carried out her PhD in the framework of the project HYTECH (Marie Curie ITN) in the Department of Estuarine and Delta Systems in NIOZ – Yerseke. During the HYTECH project, she spent 9 months at Université Claude Bernard Lyon 1, three months at Queen Mary University of London and one month at IGB – Leibniz-Institute of Freshwater Ecology and Inland Fisheries (Berlin, Germany). During her PhD research, she supervised several Bachelor and Master students in fieldwork and laboratory experiments.

List of publications

Cornacchia, L., Licci, S., van de Koppel, J., van der Wal, D., Wharton, G., Puijalon, S., Bouma, T. J. (2016). Flow Velocity and Morphology of a Submerged Patch of the Aquatic Species *Veronica anagallis-aquatica* L. In Hydrodynamic and Mass Transport at Freshwater Aquatic Interfaces (pp. 141-152). Springer International Publishing

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