# SPATIOTEMPORAL HETEROGENEITY IN LOWLAND STREAMS

## A BENTHIC MACROINVERTEBRATE PERSPECTIVE

JAN DE BROUWER

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This thesis was prepared through the department of Freshwater and Marine Ecology (FAME), at the Institute for Biodiversity and Ecosystem Dynamics (IBED) at the University of Amsterdam (UvA) in the Netherlands.

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# Spatiotemporal Heterogeneity in Lowland Streams
## a benthic macroinvertebrate perspective

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# CONTENT

# 1

# CHAPTER 1

# GENERAL INTRODUCTION AND OUTLINE OF THE THESIS

## INTRODUCTION TO SPATIOTEMPORAL HETEROGENEITY IN LOWLAND STREAMS

## INTRODUCTION TO SPATIOTEMPORAL HETEROGENEITY IN LOWLAND STREAMS

The structure and functioning of lowland streams is governed by multiple factors and processes related to hydrology, morphology, chemistry and biology, which interact over different scales ranging from ecoregion to catchment, stream and (micro)habitat. Ecoregions are considered as assemblages of ecosystems and are therefore a representation of spatially interconnected ecological processes representing a nesting of ecosystems, each with its own biodiversity (Loveland & Merchant 2004). From an ecological point of view, ecoregions are not only separated based on species composition, but also on conditional factors. These conditional factors act on geological timescales and refer to major differences in climate, geology, geohydrology, geomorphology, geochemistry and geobiology (Hynes 1970). These conditional factors determine system processes, including the precipitation cycle, the temperature regime, the planform of the stream network, the location of streams and their potential hydrologic regime, on the highest hierarchical level of space and time, composing selective forces that potentially drive evolution. The genepools that evolved from the palette of gradients within an ecoregion are determined by the total set of (historical) conditions of its ecosystems (Vannote et al. 1980). The ecoregion of concern in the present thesis is the North-Western European plain, where conditional factors clearly separate lowland stream ecosystems from those at mid or high altitudes in highlands and mountainous areas, as well as from the other plains around the world.

The low gradient, nearly flat to moderately sloped landscapes of the North-Western European plain comprise catchments of lowland stream networks. The catchment is the platform on which the operational factors related to hydrology, morphology, chemistry and biology interact. Nowadays, lowland streams originate from springs and rainwater fed trenches from which water is transported downstream along the path of least resistance. In the past, extensive, slightly eluded marshes, fens and bogs formed the source of many low gradient streams, but most of these have been reclaimed and intensively drained to enable agricultural and urban development. Along the course, the water is replenished by confluence streams, groundwater seepage, wastewater effluent and precipitation, simultaneously influencing water volume, stream shape and water quality (Allan & Castello 2007). The flowing water initiates erosion and deposition processes that shape the longitudinal and transversal streambed profile. As the volume of water increases, so do its transversal dimensions. In turn, the shape of the bed influences the flow patterns. Generally, relatively high flow velocities are observed in the headwaters in comparison to those in middle courses, depending on slope and secondary inflow (Gordon et al. 2015). In addition, currents in meandering streams diverge across the wet profile as the flow velocities of the outer bends exceed those of the inner bends.

As the water flows over the streambed, friction sets sediment, organic particles and debris into motion. The erosion, transport and sedimentation processes induced by the flow define the streambed properties. Depending on exogenous inputs and local hydraulic conditions, substrate particles either accumulate, decay or redistribute. Interactions between the streamflow and the environment further shape the dynamic benthic stream bottom and differentiate the stream bed. Transport and (re)distribution of instream elements drive the formation of habitats and hence, build the platform of biological processes and food webs in which each habitat has its own set of chemical, morphological, hydraulic and biological conditions.

On the various scales discussed above, each meso- or microhabitat is part of the stream continuum (Vannote et al. 1980). Aquatic species respond to the abiotic conditional and operational factors, which interact at different scales. None of these abiotic factors acts solely, as there are always mutual interactions. Morphology, for example, can respond to the action of stream hydrology, but can also reduce discharge fluctuations. Alternatively, species can be adapted to stream hydrology (Statzner et al. 2001) and many species, ranging from trees to small invertebrates, can directly influence stream hydrology and morphology (Statzner 2012). Despite a dominant hierarchical effect, feedback mechanisms are always present (Verdonschot et al. 1998). Thus, factors interact on different hierarchical scales and with a different intensity. Some of the most important operational factors that directly determine the occurrence of benthic macroinvertebrates in streams are termed key ecological factors. Organisms, for example, directly depend on oxygen availability and temperature as driver of biological processes, flow that provides both oxygen and food, and substrate heterogeneity that offers food and shelter. Habitat heterogeneity and flow, two of the key ecological factors for in-stream organisms, strongly interact, but these interactions are poorly studied from an ecological point of view. Hence, the interactions between habitat heterogeneity and flow need urgent clarification.

### Spatial heterogeneity

Abiotic conditional and operational factors act on different scales in space and time. The spatial diversity of conditions in lowland streams that match the various requirements for aquatic life is termed spatial or habitat heterogeneity (Southwood 1977). Spatial heterogeneity is variable within and between lowland streams. On the different scales, it is generated by environmental gradients in four directions; longitudinal, transversal, vertical and temporal (Frissell et al. 1986, Ward et al. 1989), extending beyond the channel, beyond the valley to the catchment boundaries (Ward et al. 1998).

Habitats can be distinguished based on their composition, including amongst others, the type of material, the hydraulic conditions and the oxygen regime. Sand is the dominant bed material in lowland streams. Water is the driving force that shapes the texture and composition of the streambed (Bunn & Arthington 2002, Palmer et al. 2010) and organic matter presence and composition strongly determines the metabolism and oxygen regime. Large woody debris and vegetation provide additional bed variability. In stream stretches shaded by riparian trees, woody debris dominates, whereas macrophytes dominate in the non-shaded stretches (Pedersen et al 2006). Besides shading, riparian trees provide exogenous organic matter inputs, such as logs, branches, leaves and seeds (Allan 1995).

Large instream morphological structures influence the streambed substrate pattern through the trapping of fine sediments and particulate organic matter (Wolfert 2001, Lorenz et al. 2009). Particulate organic matter accumulates in wakes where flow velocities are low. Oxygen concentrations in these accumulations might drop as a result of decomposition processes. In zones with high flow velocities scour, abrasion and transport of bed material takes place, redistributing sediment and organic particles within the stretch. Coarse particulate organic matter is gradually decomposed into smaller fragments and further distributed over the streambed by the current. In this way, the fragments of falling leaves and other forms of particulate organic matter form a patchy mosaic on the sandy streambed. This mosaic is composed of a variety of (micro)habitats, offering a diversity of niches for typical lowland stream inhabiting species (Tolkamp 1980, Verdonschot 1995).

The patches or habitats in lowland streams are spatial units, each with unique conditions within the range of meso- to micro-scale. The patches differ in composition, size, configuration, distribution and other characteristics within the stream landscape (Pringle et al. 1988), in a random pattern. In lowland streams, the set of habitats can form a mosaic of which the combination of diversity, patchiness and distribution define its spatial heterogeneity.

### Temporal heterogeneity

Spatial heterogeneity merely represents a snapshot of environmental conditions in time. The gradual or abrupt changes in habitat composition much depend on changes in flow (Palmer 2005). Streams are continuously subjected to changes and are thus never in a true state of equilibrium. Therefore, it is not surprising that communities are adapted to changes in these dynamic ecosystems (Wiens1984; DeAngelis & Waterhouse 1987; Pickett et al. 1992). Change in habitat composition or disturbance by flow is part of the natural stream functioning (Resh et al. 1988) and includes flow extremes in both directions, as spates as well as low flows and even droughts might occur. The level of flow disturbance depends on the magnitude, duration, frequency, timing and rate of change (Poff et al. 1997). According to the intermediate disturbance theory, biodiversity is highest at intermediate disturbance levels and lowest at extremely low or high disturbance levels (Connell 1978, Shiel & Burslem 2003).

Dynamic streams are characterized by a high resistance and resilience, defined as the level of disturbance that the system can withstand or absorb without shifting to completely different ecological conditions (Holling 1973, Gunderson & Lance 2001). Exceeding certain thresholds of these conditions will consequently result in the loss of diversity. In lowland streams, disturbance by spates can initiate erosion of the sediment, leading to the loss of resources due to the abrasion of organic matter patches and to homogenization of the substrate causing only the mineral sediment to remain and even to incision of the bed profile. Disturbance by low flows comprises sedimentation of fine material (silt) during flow cessation, covering resources and triggering anoxic conditions. Nonetheless, there may be highly resistant areas within a stream stretch where organic patches remain during spates and during a period of low discharge not all organic substrates turn into anoxic mud. These remaining patches are used by macroinvertebrates as refugia, acting as a source of colonists when conditions improve. At the same time disturbance provides opportunities, as new habitat patches can be formed, while the remaining ones are replenished. In other words, the damage of a disturbance event is lowered by the resistance and resilience of the macroinvertebrates and their habitat, depending on environmental properties, traits of biota and ecological interactions. Spatial heterogeneity can therefore diminish disturbance and its effects over time, which is referred to as the patch dynamics concept (Townsend 1989).

## The response of the macroinvertebrate community: heterogeneity as driver of stream biodiversity

Hydrological and morphological processes in space and time lead to a variety of habitat structures and sediment patterns in streams. These habitat patches are potentially colonized by organisms that, in turn, can cause modifications to this meso- and micro-scale environment (Statzner 2008). For benthic macroinvertebrates, substrate patches provide resources, such as shelter and food. Many insects with partially aquatic life cycles move as adults along the stream in up- and downstream direction to find suitable egg deposition sites. After hatching, larvae move in and between habitat patches during their development. Hence, this is the scale directly experienced by organisms and to which they respond during their life cycle, i.e. the meso- and microhabitat.

Each specific habitat patch provides conditions in which some species can live, while others move elsewhere, because the specific patch does not meet their specific requirements. As such, local habitat conditions serve as filters, which can be hydrological, morphological, chemical and biological (Southwood 1977, 1988). These filters act under natural conditions but can, due to human activities, also put additional pressures on the organisms. Examples of chemical pressures include pesticides, heavy metals and low oxygen concentrations. Hydrological pressures comprise of spates and low flows. The biological filters include species interactions such as competition, predation and food availability. However, one of the most distinctive filters in lotic ecosystems is the interplay between hydraulic and morphologic processes, which influence all other filters that together determine the composition, diversity, and distribution of benthic macroinvertebrates (Statzner et al. 1988, Quinn & Hickey 1994, Beisel et al., 2000, Beauger et al. 2006, Timm et al. 2011). The physical habitat conditions are thus the main drivers of benthic macroinvertebrate occurrence and abundance, as long as physicochemical factors, such as temperature regime and chemical loads, do not exceed the species thresholds (Allan & Castillo 2007).

## Linking spatiotemporal heterogeneity and biodiversity

Streams are a continuum, in which longitudinal and lateral fluxes of energy and nutrients occur (Webster 1975, Webster & Patten 1979, Vannote et al. 1980, Ensign & Doyle 2006). In shaded lowland streams exogeneous sources provide these heterotrophic ecosystems with energy that is stored in organic material which is distributed in patches on the streambed. These patches form the physical habitat for benthic macroinvertebrates and also provide food. These macroinvertebrates consume and shred the organic material accumulated in the patches into smaller fragments, filter dislodged particles from the water, incorporate material in their system and transfer particles between patches. The patch dynamics theory underpins the value of these patches, their spatial configuration and mutual interactions within the dynamic stream continuum (Pringle et al.1988, Townsend 1989). This theory and the intermediate disturbance theory (Connell 1978, Shiel & Burslem 2003), jointly formed the basis of a conceptual model that links biodiversity to spatial and temporal heterogeneity (Fig. 1, derived from Arrington & Winemiller 2004).

## Stream restoration - Reverse anthropogenic disturbances

Stream degradation has been recognized for decades (Hynes 1960). The severe deterioration of stream ecosystems in Europe has led to the development of the Water Framework Directive to warrant improvement of both the abiotic and biotic status of surface waters (WFD; 2000/60/EC), to stop aquatic ecosystem degradation and to increase ecological quality (EEA 2007). The main pressures that resulted in stream degradation and species losses are channelization and flow regulation (Feld 2011). Most channelized and regulated lowland streams are spatially

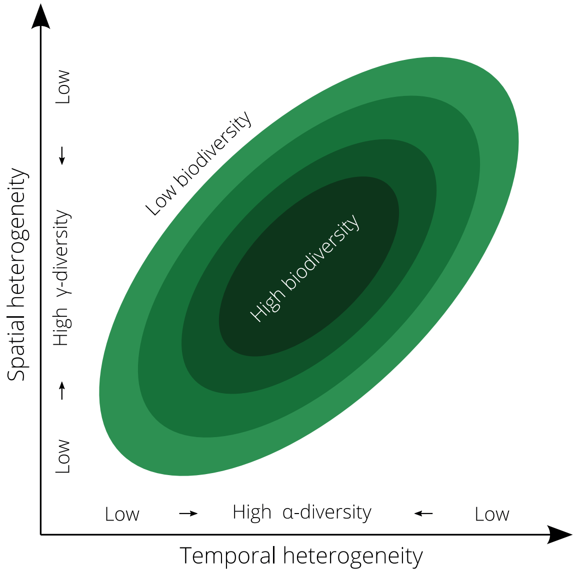

**FIGURE 1** Conceptual model depicting the joint effects of spatial heterogeneity and temporal heterogeneity in on biodiversity. This model is derived from Arrington & Winemiller (2004) and combines the “intermediate disturbance hypothesis” (Connell 1978, Shiel & Burslem 2003) and the “patch dynamics concept” (Townsend 1989)

homogeneous in terms of habitats, characterized by highly dynamic discharge patterns, which currently sustain only a fraction of their potential biodiversity (Verdonschot 1995), as postulated in the conceptual model depicted in figure 1. In the last decades, conservation and restoration has become common practice (Ormerod 2003, Palmer et al. 2004, Bernhardt et al. 2005, Dudgeon et al. 2006), in order to reverse stream degradation (Wohl 2015). Most restoration projects are based on the assumption that creating 'the appropriate environmental conditions' will automatically lead to biological improvement (Palmer 1997). Therefore, most restoration projects aimed to increase spatial heterogeneity and to reduce temporal heterogeneity in order to restore ecological processes and increase biodiversity (Holling 1973, Gunderson 2000, Miller et al. 2010, Palmer et al. 2010, Feld 2011, Wohl 2015, Rubin et al. 2017). Addition of large woody debris and channel reconfiguration are two of the most frequently applied restoration methods (Palmer 2014).

### Stream restoration - The environmental-ecological opposition

The effects of stream restoration are measured using environmental and ecological indicators (Wortley et al. 2013). So far, success rates based on ecological indicators fall behind the improvements of environmental indicators (Jähnig et al. 2010, Leps et al. 2016). Generally, the increased spatial heterogeneity as observed post restoration has limited or no positive effects on benthic macroinvertebrate indicators (Friberg et al. 1998, Muotka et al. 2002, Lepori et al. 2005), although some studies presented positive results (Jungwirth, Moog & Muhar 1993; Gerhard & Reich 2000). From an ecological perspective, it can thus be concluded that the international targets to stop degradation and increase biological standards (EEA, 2007) were not met, despite expensive restoration efforts (Feld et al. 2011).

Apparently, the increased environmental heterogeneity did not improve the conditions for macroinvertebrates and thus, may be ineffective in terms of ecological recovery (Palmer 2010, Haase et al. 2013). Yet, the question why ecological success is limited despite the observed increase in physical heterogeneity remains unanswered. This could be due various constraints, such as the fragmented and small scale implementation of restoration measures (Bond & Lake 2003, Bernhardt et al. 2005, Palmer et al., 2007, 2010), dispersal constraints of the target indicator species (Sundermann et al. 2011, Westveer 2018), the presence of confounding factors that interact in a multi-stressed environment (Townsend et al. 2008, Ormerod 2010, Leps et al. 2015) or a too short recovery time post restoration (Jones & Schmitz 2009, Leps et al. 2016). Finally, the ecological indicators chosen might be inadequate to detect changes (Rubin 2017).

The methods and results of previous restoration efforts should help to distinguish effective measures and monitoring strategies from failed efforts (Palmer et al 2010, Suding 2011, Feld 2011). However, despite decades of experience with implementing restoration practices, it is still challenging to effectively restore streams and to define effective ways of monitoring (Lepori et al. 2005), primarily because monitoring of restoration projects is generally lacking or poorly executed (Bash & Ryan 2002, Bernhardt et al. 2005). The time consuming and costly nature of monitoring tends to reduce the level of detail to the macroscale, which may be inadequate to measure recovery from a species perspective at smaller scales (Bond & Lake 2003). Therefore, incorporating community ecological theory in restoration practices is essential to improve degraded systems (Palmer et al. 1997) and the relevant interactions between organisms and their physical habitat should be better understood in order to make proper choices in stream restoration (Verdonschot et al. 1998). Currently, it is questionable to what extent hydrological and morphological assessments are based on human perspectives rather than on the needs of benthic macroinvertebrates (Verdonschot 2013). In stream restoration, the focus on macroscale factors and processes such as sediment transport and discharge levels may not improve ecologically relevant factors, including better quality resources for benthic macroinvertebrates. Therefore, we argue that a focus on microhabitat factors at the species level, such as critical thresholds for near bed flow and the significance of structural complexity and temporal stability of habitat conditions, instead of the commonly used discharge averaged flow metric, may help to resolve the environmental-ecological opposition.

**TABLE 1** Schematic overview of linkages between spatial and temporal heterogeneity, flow and habitat. All spatiotemporal components are linked and change habitat filters for benthic macroinvertebrates continuously

| | Flow | | Habitat |
|---|---|---|---|
| Spatial heterogeneity | Configuration of flow conditions | ↔ | Structural complexity |
| | ↕ | ⤡ ⤢ | ↕ |
| Temporal heterogeneity | Flow dynamics | ↔ | Patch dynamics |

## Aim

In lowland streams, spatiotemporal heterogeneity of habitat structures and flow together shape the physical environment that affects biota on different scales (tab. 1). However, it is still unclear on which scale these key factors have the strongest effect on benthic macroinvertebrates. At the same time there is an urgent need to improve the ecological quality of lowland streams in terms of biodiversity.

Therefore, this thesis aimed at identifying the relevant scales of spatiotemporal heterogeneity for benthic macroinvertebrates in lowland streams. To this purpose, species specific ranges of conditions, thresholds and requirements were studied to test the hypothesis that moderate spatial and temporal heterogeneity at the meso- and micro-scale carries the highest macroinvertebrate diversity in lowland streams and to determine the optimal conditions for characteristic running water species to improve future restoration efforts.

## Thesis outline

The outline of this thesis, the main topics and their position within the instream habitat at the meso- and microscale are shown in figure 2, based on the hierarchical order of major stream ecosystem components and the key ecological factors that drive the stream ecosystem.

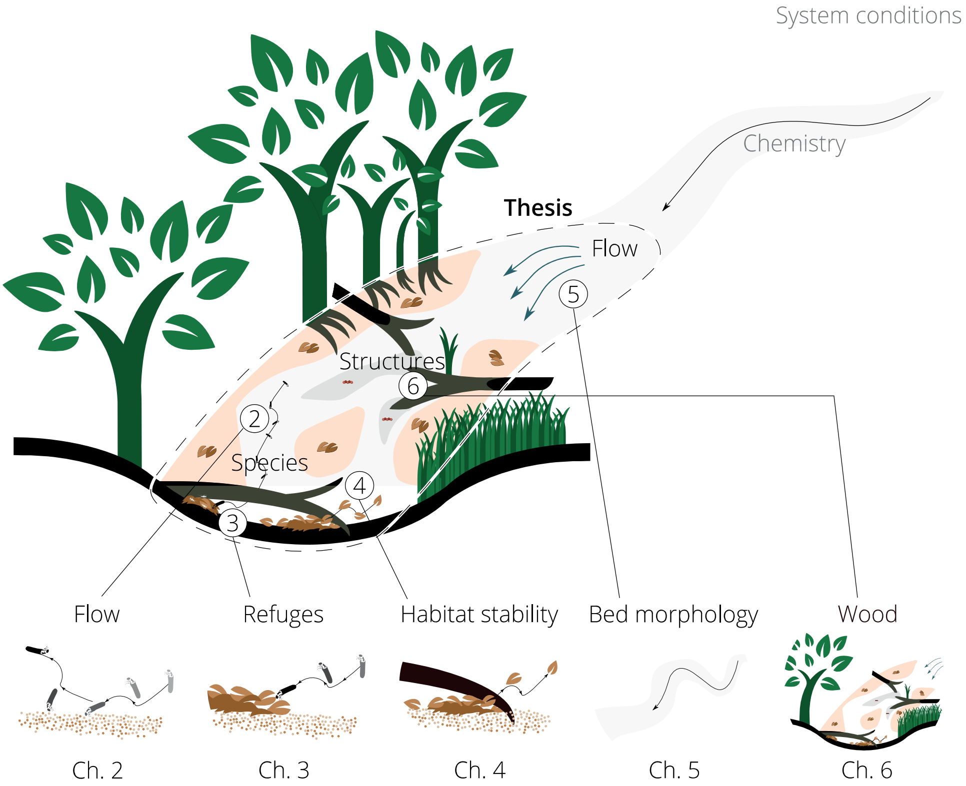

**FIGURE 2** Coherence of the chapters in this thesis, including key ecological factors and processes in sand-bed lowland streams according to Verdonschot (1998)

The species-specific responses of benthic macroinvertebrates to flow dynamics are poorly understood. Therefore, in **chapter two**, the tolerance ranges for flow velocity of six caddisfly-species of the family Limnephilidae were quantified based on the process of returning to a homogeneous stream bottom from drift after being dislodged. This behavior of escaping from drift is crucial for the resilience of species when individuals become dislodged during a spate. The resilience of species to flow also depends on their ability to find refuges. **Chapter three** shows how refuges influenced the process of returning to the bottom from drift for caddisfly larvae. An organic matter patch is only a safe refuge if it persists during spates. Therefore, resistance to flow is the decisive factor for habitat patches to become stable over time. As primary source of exogeneous organic material in lowland streams, leaves are an important food resource, fuel the biochemical cycle of streams, offer morphological habitat structures and thus, are an important habitat for macroinvertebrates. A major question though, is under which flow conditions leaf patches remain stable over time. Therefore, **chapter four** unravels the hydraulic conditions around leaf packs in an experiment that was designed to define optimal and critical flow conditions for leaves to persist at a specific spot. The presence and perseverance of areas that reflect the measured conditions would enable leaf patches to become resistant and thus, stable over time. However, wood removal, channelization and regulation practices changed the natural spatiotemporal heterogeneity in many streams on the Western European plain in the past decades (Nijboer et al. 2002), which disturbed the natural mechanism of organic matter retention. **Chapter five** therefore evaluated the effects of profile reconstruction on morphology and, at the mesoscale, substrate patterns in field situations. Channelized streams with deep, wide and straightened profiles were changed into more shallow, narrow and meandering channels intending to increase base flows, decrease temporal discharge dynamics, retain organic matter patches and increase habitat heterogeneity. Manual (re-) introduction of large wood patches may effectively retain organic matter. In **chapter six**, the effects of introducing large wood on the spatiotemporal heterogeneity of flow, structures and the wood-patch-inhabiting macroinvertebrate assemblages were studied. Potentially, both profile reconstruction and large wood addition can stimulate the development towards a diverse macroinvertebrate assemblage.

Finally, chapter seven provides a synthesis that describes the key ecological processes that link the physical environment to the benthic community structure of sandbed lowland streams. Furthermore, possible prospects and limitations of abiotic monitoring for determining stream ecological quality are discussed.

## REFERENCES

Allan JD. 1995. Stream Ecology: Structure and Function of Running Waters. Dordrecht, Netherlands: Kluwer. 388 pp.

Allen JD, Castillo MM. 2007. Stream Ecology: Structure and Function of Running Waters, Second Edition. Springer.

Arrington DA, Winemiller KO. 2004. Organization and maintenance of fish diversity in shallow waters of tropical floodplain rivers. In Proceedings of the Second International Symposium on the Management of Large Rivers for Fisheries (LARS2). Wellcomme R, Petr T (eds) RAP Publication 2004/16: pp.25–36. Bangkok: FAO Regional Office for Asia and the Pacific.

Bash JS, Ryan CM. 2002. Stream restoration and enhancement projects: is anyone monitoring? Environmental management 29: 877-885.

Beauger A, Lair N, Reyes-Marchant P, Peiry JL. 2006. The distribution of macro-invertebrate assemblages in a reach of the River Allier France, in relation to riverbed characteristics. Hydrobiologia 571: 63–76.

Beisel JN, Usseglio-Polatera P, Thomas S, Moreteau JC. 2000. The spatial heterogeneity of a river bottom: a key factor determining macroinvertebrate communities. Hydrobiologia 442-423: 163–171.

Bernhardt ES, Palmer MA, Allan JD, Alexander G, Barnas K, Brooks S, Carr J, Clayton S, Dahm C, Follstad-Shah J, Galat D, Gloss S, Goodwin P, Hart D, Hassett B , Jenkinson R, Katz S, Kondolf GM, Lake PS, Lave R, Meyer JL, O'Donnell TK, Pagano L, Powell B, Sudduth E. 2005. Synthesizing U.S. river restoration efforts. Science 308: 636–637.

Bond NR, Lake PS. 2003. Local habitat restoration in streams: constraints on the effectiveness of restoration for stream biota. Ecological Management and Restoration 4:193–198.

Bunn SE, Arthington AH. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. Environmental management 30(4): 492–507.

Connell JH. 1978. Diversity in tropical rain forests and coral reefs. Science 199: 1302–1310.

Council of the European Communities (2000) Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 establishing a framework for Community action in the field of water policy, Official Journal of the European Communities L327: 1–73.

Deangelis D, Waterhouse CJ. (1987). Equilibrium and Nonequilibrium Concepts in Ecological Models. Ecological Monographs 57: 1–21.

Dudgeon D, Arthington AH, Gessner MO, Kawabata ZI, Knowler DJ, Lévêque C, Naiman RJ, Prieur-Richard AH, Soto D, Stiassny ML, Sullivan CA. 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. Biological Reviews 81: 163–182.

EEA (European Environment Agency). 2007. Halting the loss of biodiversity by 2010: Proposal for a first set of indicators to monitor progress in Europe. EEA technical report 11/2007, Luxembourg, 38 pp.

Ensign SH, Doyle MW. 2006. Nutrient spiralling in streams and river networks. Journal of Geophysical Research 111: 1-13.

Feld CK, Birk S, Bradley DC, Hering D, Kail J, Marzin A, Melcher A, Nemitz D, Pedersen ML, Pletterbauer F, Pont D, Verdonschot PFM, Friberg N. 2011. From natural to degraded rivers and back again: a test of restoration ecology theory and practice. Advances in Ecological Research 44: 119–209.

Friberg N, Hansen HO, Kronvang B, Svendsen LM. 1998. Long-term, habitat-specific response of a macroinvertebrate community to river restoration. Aquatic Conservation: Marine and Freshwater Ecosystems 8: 87–99.

Frissell CA, Liss WJ, Warren CE, Hurley MD. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. Environmental Management 10: 199–214.

Gerhard M, Reich M. 2000. Restoration of streams with large wood: Effects of accumulated and built-in wood on channel morphology, habitat diversity and aquatic fauna. International Review of Hydrobiology 85: 123–137.

Gordon RP, Lautz LK, McKenzie JM, Mark BG, Chavez D, Baraer M. 2015. Sources and pathways of stream generation in tropical proglacial valleys of the Cordillera Blanca, Peru. Journal of Hydrology 522: 628–644.

Gunderson LH, Allen CR, Holling CS. (2010). Foundations of ecological resilience. Washington, DC: Island Press. 496 pp.

Gunderson LH. 2000. Ecological resilience – In theory and application. Annual Review of Ecology and Systematics 31: 425-439.

Haase P, Hering D, Jähnig SC, Lorenz AW, Sundermann A. 2013. The impact of hydromorphological restoration on river ecological status: a comparison of fish, benthic invertebrates, and macrophytes. Hydrobiologia 704: 475–488.

Holling CS. 1973. Resilience and stability of ecological systems. Annual Review of Ecology and Systematics 4: 1–23.

Hynes HBN. 1960. The Biology of Polluted Waters. Liverpool University Press, Liverpool, England, 202 pp.

Hynes HBN. 1970. Ecology of Stream Insects. Annual review of Entomology 15: 25–42.

Jähnig SC, Brabec K, Buagni A, Erba S, Lorenz AW, Ofenböck T, Verdonschot PFM, Hering D. 2010. A comparative analysis of restoration measures and their effects on hydromorphology and benthic invertebrates in 26 central and southern european rivers. Journal of Applied Ecology 47: 671–680.

Jones HP, Schmitz OJ. 2009. Rapid recovery of damaged ecosystems. PLoS One 4(5): 1–6, e5653.

Jungwirth M, Moog O, Muhar S. 1993. Effects of river bed restructuring on fish and benthos of a fifth order stream, River Research and Applications 8: 195–204.

And/or Lake PS. 2000. Disturbance, patchiness, and diversity in streams. Journal of the North American Benthological Society 19: 573–592.

Leeuwen van CG. 1981. From ecosystem to ecodevice. In: Tjallingii S, Veer D (eds), Perspectives in Landscape Ecology: pp. 29–36. Pudoc, Wageningen.

Lepori F, Palm D, Malmqvist B. 2005. Effects of stream restoration on ecosystem functioning: detritus retentiveness and decomposition. Journal of Applied Ecology 42: 228–238.

Leps M, Sundermann A, Tonkin JD, Lorenz AW, Haase P. 2016. Time is no healer: increasing restoration age does not lead to improved benthic invertebrate communities in restored river reaches. Science of The Total Environment 557–558: 722–732.

Leps M, Tonkin JD, Dahm V, Haase P, Sundermann A. 2015. Disentangling environmental drivers of benthic invertebrate assemblages: the role of spatial scale and riverscape heterogeneity in a multiple stressor environment. Science of the Total Environment 536: 546–556.

Lorenz AW, Jähnig SC, Hering D. 2009. Re-meandering German lowland streams: Qualitative and quantitative effects of restoration measures on hydromorphology and macroinvertebrates. Environ Management 44: 745–754.

Loveland TR, Merchant JM. 2004. Ecoregions and ecoregionalization: geographical and ecological perspectives. Environmental management 34(1): S1.

Miller SW, Budy P, Schmidt J. 2010. Quantifying macroinvertebrate responses to in-stream habitat restoration: applications of meta-analysis to river restoration. Restoration Ecology 18: 8–19.

Muotka T, Laasonen P. 2002. Ecosystem recovery in restored headwater streams: the role of enhanced leaf retention. Journal of Applied Ecology 39:145–156.

Naiman RJ, Decamps H. 1997. The ecology of interfaces: riparian zones. Annual review of Ecology and Systematics 28: 621–658.

Ormerod SJ, Dobson M, Hildrew AG, Townsend CR. 2010. Multiple stressors in freshwater ecosystems. Freshwater Biology 55: 1–4.

Ormerod SJ. 2003. Restoration in applied ecology: editor's introduction. Journal of Applied Ecology 40: 44–50.

Palmer M, Allan JD, Meyer J, Bernhardt ES. 2007. River restoration in the twenty-first century: Data and experiential knowledge to inform future efforts. Restoration Ecology 15: 472–481.

Palmer MA, Ambrose RF, Poff NL. 1997. Ecological theory and community. Restoration Ecology 5(4): 291–300.

Palmer MA, Bernhardt ES, Allan JD, Lake PS, Alexander G, Brooks S, Carr J, Clayton S, Dahm CN, Follstad Shah J, et al. 2005. Standards for ecologically successful river restoration. Journal of applied ecology 42(2): 208–217.

Palmer MA, Hondula KL, Koch BJ. 2014. Ecological restoration of streams and rivers: Shifting strategies and shifting goals. Annual Review of Ecology, Evolution, and Systematics 45: 247–269.

Palmer MA, Menninger HL, Bernhardt E. 2010. River restoration, habitat heterogeneity and biodiversity: a failure of theory or practice? Freshwater biology 55(s1): 205–222.

Pedersen TCM, Baattrup-Pedersen A, Madsen TV. 2006. Effects of stream restoration and management on plant communities in lowland streams. Freshwater Biology 51: 161–179.

Perring MP, Standish RJ, Price JN, Craig MD, Erickson TE, Ruthrof KX, Whiteley AS, Valentine LE, Hobbs RJ. 2015. Advances in restoration ecology: rising to the challenges of the coming decades. Ecosphere 6(8): 1–15.

Pickett STA, Parker V, Fiedler P. 1992. The New Paradigm in Ecology: Implications for Conservation Biology Above the Species Level. In: Fiedler PL, Jain SK (eds) Conservation Biology. Springer, Boston, MA.

Poff NL, Allan JD, Bain MB, Karr JR, Prestegaard KL, Richter BD, Sparks RE, Stromberg JC. 1997. The natural flow regime. Bioscience 47: 769–784.

Pringle CM, Naiman RJ, Bretschko G, Karr JR, Oswood MW, Webster JR, Welcomme RL, Winterbourne MJ. 1988. Patch dynamics in lotic systems: The stream as a mosaic. Journal of the North American Benthological Society 7: 503–524.

Quinn JM, Hickey CW. 1994. Hydraulic parameters and benthic invertebrate distributions in two gravel-bed New Zealand rivers. Freshwater biology 32: 489-500.

Resh VH, Brown AV, Covich AP, Gurtz ME, Li HW, Minshall GW, Reice SR, Sheldon AL, Wallace JB, Wissmar R. 1988. The role of disturbance in stream ecology. Journal of the North American Benthological Society 7: 433–455.

Rubin Z, Kondolf GM, Rios-Touma B. 2017. Evaluating stream restoration projects: what do we learn from monitoring? Water 9(3): 174, 1–16.

Sheil D, Burslem DFRP. 2003. Disturbing hypotheses in tropical forests. Trends in Ecology and Evolution 18: 18–26.

Southwood TRE. 1977. Habitat, the templet for ecological strategies? Journal of Animal Ecology 46: 337–365.

Southwood TRE. 1988. Tactics, strategies and templets. Oikos 52: 3-18.

Suding KN. 2011. Toward an era of restoration in ecology: successes, failures, and opportunities ahead. Annual Review of Ecology, Evolution, and Systematics 42: 465–487.

Statzner B, Gore JA, Resh VH. 1988. Hydraulic stream ecology: observed patterns and potential applications. Journal of the North American Benthological Society 7: 307–360.

Statzner B. 2008. How Views about Flow Adaptations of Benthic Stream Invertebrates Changed over the Last Century. International Review of Hydrobiology 93: 593–605.

Statzner, Bernhard & A Gore, James & H Resh, Vincent. 1988. Hydraulic Stream Ecology: Observed Patterns and Potential Applications Author(s). Journal of the North American Benthological Society 7(4): 307-360.

Sundermann A, Antons C, Cron N, Lorenz AW, Hering D, Haase P. 2011. Hydromorphological restoration of running waters: effects on benthic invertebrate assemblages. Freshwater Biology 56(8): 1689–1702.

Timm et al. 2011, onvindbaar à alternative Statzner B, Higler B. 1986. Stream hydraulics as a major determinant of benthic invertebrate zonation patterns. Freshwater Biology 16:127–139.

Tolkamp H.H. (1980) Organism-substrate relationships in lowland streams. PhD Thesis, Wageningen University.

Townsend CR, Uhlmann SS, Matthaei CD. 2008. Individual and combined responses of stream ecosystems to multiple stressors. Journal of Applied Ecology 45: 1810–1819.

Townsend CR. 1989. The patch dynamics concept of stream community ecology. Journal of the North American Benthological Society 8: 36–50.

Vannote RL, Minshall GW, Cummins KW, Sedell JR, Cushing CE. 1980. The river continuum concept. Canadian journal of fisheries and aquatic sciences 37(1): 130–137.

Verdonschot PFM, Spears BM, Feld CK, Brucet S, Keizer-Vlek H, Borja A, et al. 2013. A comparative review of recovery processes in rivers, lakes, estuarine and coastal waters. Hydrobiologia 704: 453–474.

Verdonschot PFM, Driessen JMC, Mosterdijk HG, Schot JA. 1998. The 5-S-Model, an integrated approach for stream rehabilitation. In: Hansen HO, Madsen BL (eds), River Restoration ’96, Session lectures proceedings. National Environmental Research Institute: pp. 36–44. International Conference arranged by the European Centre for River Restoration, Denmark.

Verdonschot PFM, Nijboer RC. 2002. Towards a decision support system for stream restoration in the

Netherlands: an overview of restoration projects and future needs. Hydrobiologia 478: 131–148.

Verdonschot PFM. 1995. Typology of Macrofaunal Assemblages - a Tool for the Management of Running Waters in the Netherlands. Hydrobiologia 297: 99–122.

Vinson MR, Hawkins CP. 1998. Biodiversity of stream insects: variation at local, basin, and regional scales. Annual Review of Entomology 43: 271–293.

Ward JV, Bretschko G, Brunke M, Danielopol D, Gibert J, Gonser T, Hildrew AG. 1998. The boundaries of river systems: the metazoan perspective. Freshwater Biology 40(3): 531–569.

Ward JV.1989. The four dimensional nature of lotic ecosystems. Journal of the North American Benthological Society 8: 2–8.

Webster JR, Patten BC. 1979. Effects of watershed perturbation on stream potassium and calcium dynamics. Ecological Monographs 49: 51–72.

Webster JR. 1975. Analysis of potassium and cal- cium dynamics in stream ecosystem on three southern Appalachian watersheds of contrasting vegetation. PhD Thesis. University of Georgia, Athens. And/or

Webster JR. 2007. Spiraling down the river continuum: stream ecology and the U-shaped curve. Journal of the North American Benthological Society 26: 375–389.

Westveer JJ. 2018. Go with the flow: unravelling the ecological mechanisms of dispersal and colonization by aquatic macroinvertebrates in restored lowland streams. PhD Thesis, University of Amsterdam.

Wiens JA. 1984. On understanding a non-equilibrium world: myth and reality in community patterns and processes. In: Strong Jr. DR, Simberloff D, Abele LG, Thistle AB (eds) Ecological Communities: Conceptual Issues and the Evidence. pp. 439-457. Princeton University Press, Princeton, N.J.

Wohl E, Bledsoe BP, Jacobson RB, Poff NL, Rathburn SL, Walters DM, Wilcox AC. 2015. The natural sediment regime in rivers: Broadening the foundation for ecosystem management. Bioscience 65: 358–371.

Wolfert HP. 2001. Geomorphological change and river rehabilitation: case studies on lowland fluvial systems in The Netherlands, Ph.D. thesis, Alterra Scientific Contributions 6: 200 pp.

Wortley L, Hero JM, Howes M. 2013. Evaluating ecological restoration success: a review of the literature. Restoration Ecology 21: 537–543.

Zonneveld IS. 1989. The land unit - a fundamental concept in landscape ecology and its applications. Landscape ecology 3(2): 67–86.

# 2

## CHAPTER 2

# FLOW VELOCITY TOLERANCE OF LOWLAND STREAM CADDISFLY LARVAE (TRICHOPTERA)

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De Brouwer JHF, Besse-Lototskaya AA, ter Braak CJF, Kraak MHS,
Verdonschot PFM

## ABSTRACT

The process of macroinvertebrate drift in streams is characterized by dislodgement, drift distance and subsequent return to the bottom. While dislodgement is well studied, the fate of drifting organisms is poorly understood, especially concerning Trichoptera. Therefore, the aim of the present study was to determine the ability of six case-building Trichoptera species to return to the stream bottom under different flow velocity conditions in a laboratory flume. The selected species occur in North-West European sandy lowland streams along a gradient from lentic to lotic environments. We determined species specific probability curves for both living and dead (control) specimens to return to the bottom from drift at different flow velocities and established species specific return rates. Species on the lotic end of the gradient had highest return rates at high flow velocity and used active behaviour most efficiently to return to the bottom from drift. The observed gradient of flow velocity tolerance and species specific abilities to settle from drift indicate that, in addition to dislodgement, the process of returning to the bottom is of equal importance in determining flow velocity tolerance of Trichoptera species.

*Keywords:* Trichoptera, Drift, Return rates, Flow velocity, Lowland streams

## INTRODUCTION

Benthic invertebrates in streams are either sessile, move around actively, or are passively being moved around by the current. Weak stream flows may move invertebrates that live on or in the upper layer of the substratum to a limited extent, while strong flows can actually dislodge them and initiate drift (Vogel 1994). Drift is regarded as the dominant form of invertebrate movement in streams (Waters 1972; Brittain & Eikeland 1988), travelling short to long distances before returning to the stream bottom (McLay 1970, Neves 1979).

Previous studies revealed that drift densities of most species increase with increasing flow velocity (e.g. Corkum et al. 1977, Fonseca and Hart 1996, Gibbins et al. 2005, 2010). Yet, dislodgement occurs at both high and low flow velocity and can be initiated by multiple causes (e.g. reviewed in Waters 1972, Brittain & Eikeland 1988, Hart & Finelli 1999). Regardless of the cause of dislodgement, drifting invertebrates will eventually need to descend from the water column to prevent being washed out of the system. Hence, the process of drift is characterized by dislodgement, drift distance and subsequent return to the bottom (Lancaster 2008). Yet, the fate of most dislodged organisms is poorly understood (Palmer et al. 1996, Downes & Keough 1998, Lancaster 2008) and abilities of invertebrates to use behavioural moves to end drifting are scarcely documented (but see Lancaster et al. 2009, Oldmeadow et al. 2010), despite the importance of movements to colonize unexploited habitats (Rice et al. 2010). Thus for most species it remains unknown whether they passively return to the bottom from drift or use active behavioural moves (Poff & Ward 1991, Oldmeadow et al. 2010).

Especially for caddisfly larvae, escape from drift has been poorly documented. Therefore, the aim of this study was to quantify flow velocity thresholds at which selected case building Limnephilidae (Trichoptera), ranging from lotic to lentic species, are able to return to the stream bottom. We hypothesized that all species, being benthic invertebrates, use active behavioural moves to do so, but that drifting specimens of species from lotic environments can return to the stream bottom at higher flow velocities than species from lentic environments. To test this hypothesis, we performed experiments in a controlled laboratory environment, in which flow velocity was manipulated.

## MATERIALS AND METHODS

### Test species

The Limnephilidae are a relatively large family comprising many species with large differences in ecology and distribution, despite a high morphological similarity. Six species of Limnephilidae were selected for this experiment: *Limnephilus* *lunatus* (Curtis, 1834), *Limnephilus rhombicus* (Linnaeus 1758), *Anabolia nervosa* (Curtis 1834), *Halesus radiatus* (Curtis 1834), *Chaetopteryx villosa* (Fabricius 1798) and *Micropterna sequax* (McLachlan 1875). The selected species occur in North-West European sandy lowland streams along a gradient from lentic to lotic environments in the order listed above (Graf et al. 2006, Graf et al. 2008, Graf and Schmidt-Kloiber 2011). For a detailed description of their distribution see Verdonschot et al. (2014).

Fifth instar larvae were manually picked from sites where large populations of the respective species occur. Specimens were collected from the Warnsbornse beek, Coldenhovense beek, Seelbeek and drainage ditches (the Netherlands). Specimens were kept in an artificial rearingstream in separate compartments containing 200–300 conspecifics and a surplus of organic material (detritus, leaves, twigs and plants) on a bottom of fine gravel and sand. Food levels were kept high by adding extra leaves, detritus and wheat fragments weekly. Environmental conditions in the laboratory rearing-stream were kept constant with a water temperature of 10 °C, a flow velocity range of 0.05–0.10 m/s and a day:night light regime of 16:8 h.

### Experimental setup

The experiments were conducted in a channel, which is part of a fully controlled recirculating laboratory flume system with adjustable flow velocity. Water is stored in a reservoir from which it is pumped through flow-homogenizing lamellae to flow through the channel before returning to the reservoir. The stream bed is comprised of sand grains glued to acrylic plates whilst the sides of the channel are smooth. All tests were conducted under controlled treatment-specific flow velocities, constant water temperature and light regime. The flow velocity treatments ranged from 0.10 to 0.85 m/s in steps of 0.05 m/s. The mean column

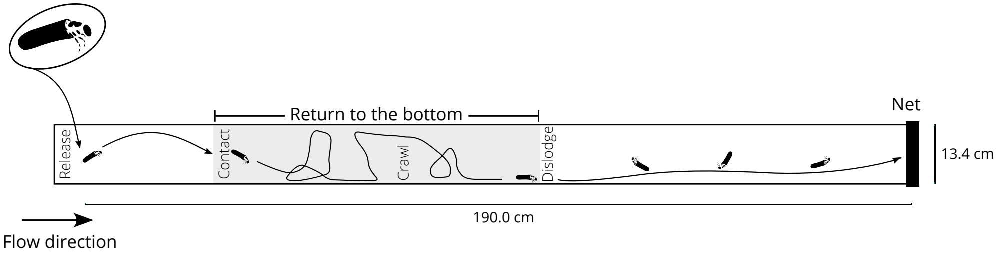

**FIGURE 1** Schematic overview of the experimental setup with the laboratory flume viewed from above. Specimens were released in drift at the upstream end (left in the figure). They can return to the bottom and settle out on the bed (first arrow point), crawl over the bottom (grey area) or may be dislodged again (second arrow in the right)

velocity (i.e. 0.6 x flow depth) of the flow classes was continuously monitored at the centre of the channel using an electromagnetic flow meter (SENSA RC2 ADS, model V6d).

Per test run, one specimen was released in the water column at the entrance of the test section and monitored while the flow velocity was kept constant. Control experiments were performed with dead specimens. Test specimens were free to move upstream and downstream after release in the test section for a maximum of 6 min in each test-run (Fig. 1). Preliminary tests showed that 6 min was sufficient to ensure that specimens attached firmly and to rule out secondary dislodgements. We tested 20 different specimens (replicates) per species per flow velocity treatment. Experiments were stopped if specimens reached the lower end of the test section within the 6 min, which were then classified as 'lost by drift'.

### Data analysis

Return rate (R) is defined by the number of specimens that returned to the bottom from drift and remained on the bottom of the test section during the 6 min. We set the flow velocity intolerance threshold, the flow speed at which specimens cannot return to the bottom, at R = 0.15. Below R = 0.15, no more tests were performed at higher flow velocities for that respective species. After each run, the test specimen was killed in ethanol and the measurement repeated with the dead specimen in order to perform the control measurement.

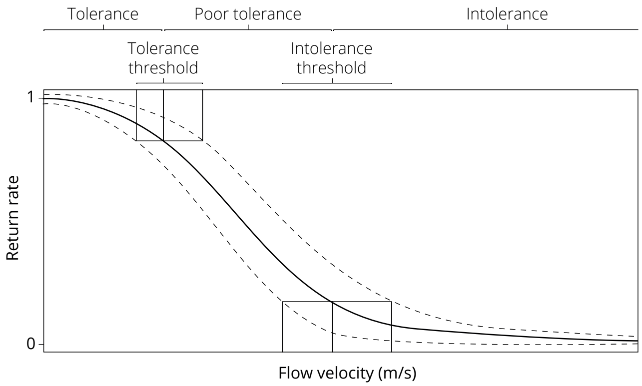

**FIGURE 2** Hypothetical example of a probability curve (P-spline) that shows the decreasing ability of a species to return to the bottom from drift. In the probability curve, the tolerance range ($R > 0.85$),the tolerance threshold ($R = 0.85$), poor tolerance ($0.85 > R > 0.15$), the intolerance threshold ($R = 0.15$) and the intolerance range ($R < 0.15$) are indicated

Bayesian P-splines (see Supplementary appendix) and credible intervals were derived from the return rates (n = 20) at each of the tested flow velocity treatments per species for both living and dead (control) animals. The Bayesian P-splines are S-shaped probability curves calculated by a regression through the observations and illustrate species-specific tolerance for flow velocity.

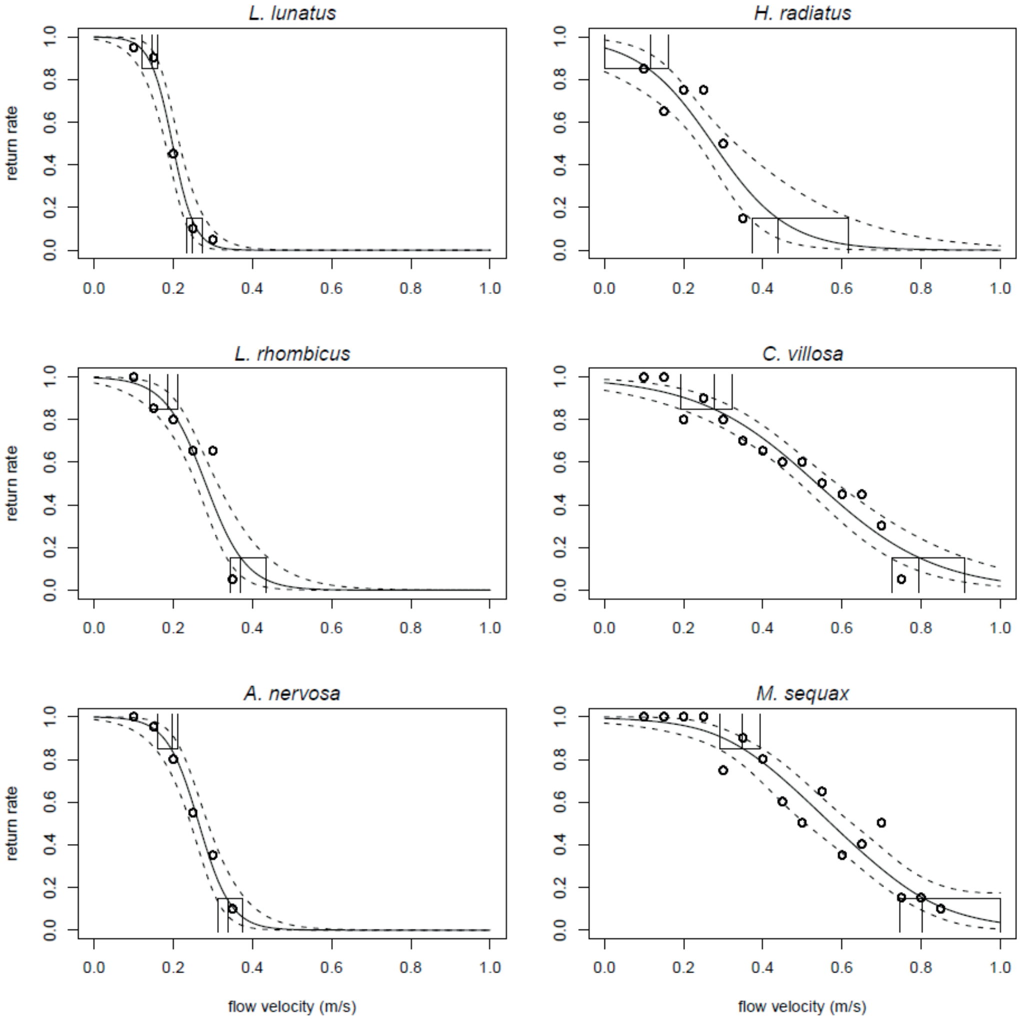

**FIGURE 3** Probability curves (P-splines) of living Trichoptera larvae to return to the stream bottom from drift at different flow velocities. Each figure shows the species specific mean tolerance threshold and intolerance threshold (in m/s) including credible intervals of active specimens

The probability curves consist of five phases: the flow velocity tolerance range (R: 1.00–0.85), the tolerance threshold (R = 0.85), the exponential phase of decreasing return to the bottom (poor tolerance, R: 0.85–0.15), the intolerance threshold (R = 0.15) and the intolerance range (R: 0.15–0.00) (Fig. 2).

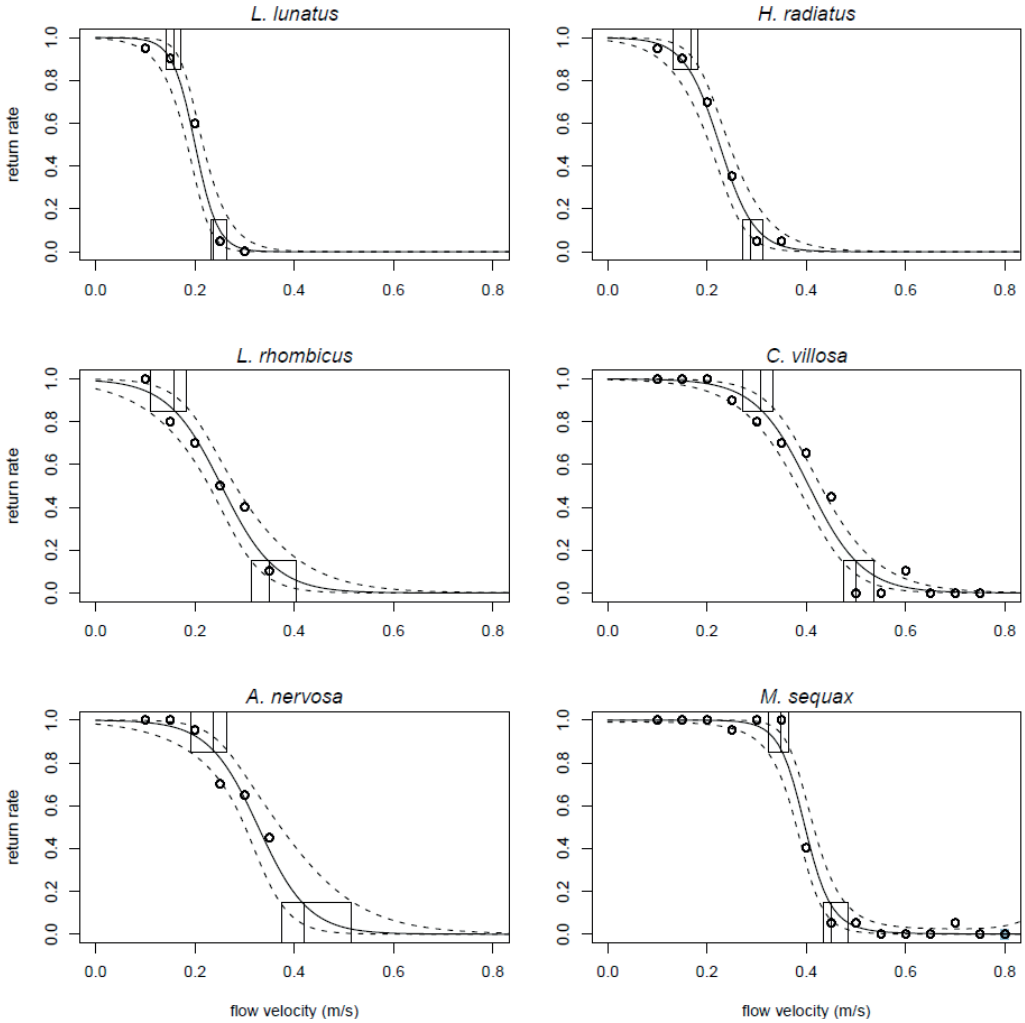

**FIGURE 4** Probability curves (P-splines) of dead (control) Trichoptera larvae to return to the stream bottom from drift at different flow velocities. Each figure shows the species-specific mean tolerance threshold and intolerance threshold (in m/s) including credible intervals of specimens

## RESULTS

The probability curves showed that each species has a specific tolerance for flow velocity (Fig. 3). The species can be ordered along a range based on their tolerance threshold (R>0.85) for flow velocity from low to high tolerance: *H. radiatus*, *L. lunatus*, *A. nervosa*, *L. rhombicus*, *C. villosa*, *M. sequax*. Based on the slope of the range of poor tolerance, species can be ordered differently: *L. lunatus*, *A. nervosa*, *L. rhombicus*, *H. radiatus*, *C. villosa*, *M. sequax*. Further, the species were ranked in this order (Fig. 3) based on their intolerance threshold (R>0.15).

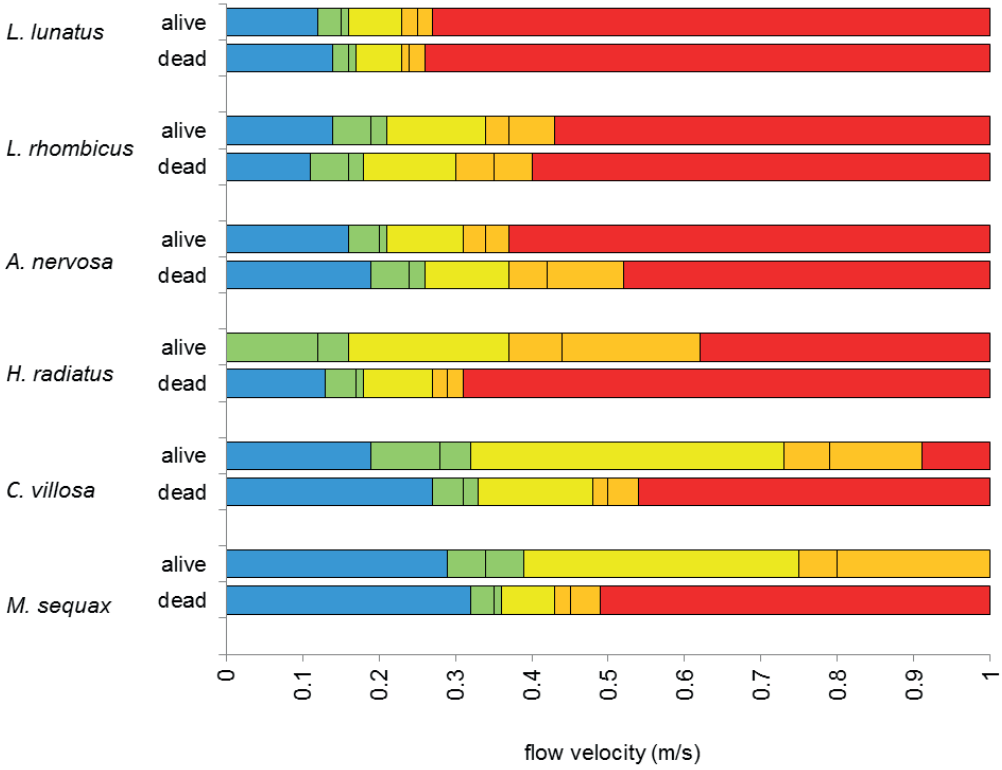

**FIGURE 5** Species-specific flow velocity tolerance: range of tolerance (R: 1.00–0.85, blue square), tolerance threshold including credible interval (R = 0.85, green square), exponential phase of decreasing return to the bottom (poor tolerance, R: 0.85–0.15, yellow square), intolerance threshold including credible interval (R=0.15, yellow square) and range of intolerance (R: 0.15–0.00, red square) shown for living and dead (control) specimens

The return rate (R)>0.85 was similar for live and dead specimens (Fig. 4). For *L. lunatus* and *L. rhombicus*, there was no difference between the intolerance thresholds (R = 0.15) of live and dead specimens. The intolerance threshold of dead *A. nervosa* was even higher than that of live specimens. The other three species had higher living intolerance threshold than the dead ones.

Comparison of the species specific ranges of tolerance of living and dead individuals in one figure (Fig. 5) clearly shows that behavioural movements of *H. radiatus*, *C. villosa* and *M. sequax* were efficient, strongly enlarging the flow velocity tolerance of these species.

## DISCUSSION

Lowland streams are multi-stressed environments in which each stressor can be limiting for a species to survive (Corkum 1992, Allan & Johnson 1997, Brosse et al. 2003, Weigel 2003, Ormerod et al. 2010). Hydromorphology, nevertheless, is considered a main stressor to determine macroinvertebrate community composition in European lowland streams (Hering et al. 2006, Feld & Hering 2007). It is challenging, though, to separate effects of flow velocities from other disturbances, especially sediment transport and altered habitat structure, since both factors interact (Hynes 1970).

Trichoptera have a high diversity of traits and strategies, they occur in all European ecoregions and in all types of water bodies (Conti et al. 2014). More specifically, within the family of Limnephilidae, the different species occur along a wide range of flow velocities (Mérigoux & Dolédec 2004, Dolédec et al. 2007, Sagnes et al. 2008, Mérigoux et al. 2009). This difference is also reflected by their drift numbers under different flow conditions (Gibbins et al. 2005, Gibbins et al. 2010). Similar to other species groups (Ephemeroptera: Ciborowski et al. 1977, Gibbins et al. 2005, Gibbins et al. 2010; Simuliidae: Fonseca & Hart 1996), the numbers of drifting trichopterans increase with increasing flow velocity (Verdonschot et al. 2012). But besides dislodgement, the process of drift is also characterized by drift distance and subsequent return to the bottom. Therefore in the present study, we tested whether increasing flow velocity also affected the ability of species to return to the stream bottom.

We selected five out of six species that Verdonschot et al. (2012) tested and showed that the number of specimens able to return to the stream bottom from drift decreases with increasing flow velocity, and that only the three truly lotic species showed successful active ‘returning’ behaviour, such as by crawling and attaching. The presently documented flow velocity tolerances also are consistent with the test species' classifications based on current preference and longitudinal zonation (Verdonschot et al. 2014). Even though all species occur in slow flowing streams (0.2–0.3 m/s), only *H. radiatus*, *C. villosa* and *M. sequax* are restricted to (slow) running waters, while *L. lunatus*, *L. rhombicus* and *A. nervosa* also frequently populate littoral habitats, in pools, lakes and bogs, and are considered more limnophilous (Graf et al. 2006, Graf et al. 2008, Graf and Schmidt-Kloiber 2011, Waringer & Graf 2011). The latter authors also indicate that *M. sequax* and *C. villosa* are often found in springs and spring brooks and have more affinity with flow than *H. radiatus*.

The tolerance threshold of 0.16–0.21 m/s we determined for drifting specimens to return to the bottom overlaps the flow velocity range that Schnauder et al. (2010) reported to dislodge *A. nervosa* (0.125–0.193 m/s). The authors further noted the species struggling to keep the case in position at high flow velocity while remaining on the stream bed. Likewise, our results showed that live specimens of *A. nervosa* could not actively influence the return rate and did not benefit from active behaviour.

The role of active movements in return rates from drift is poorly documented as opposed to active resistance to dislodgement. Some studies showed that Limnephilidae species offered active resistance to dislodgement (Otto 1976, Waringer 1989), while studies that included many species have observed a wide range of critical flow velocities for dislodgement (Statzner et al. 1988, Schnauder et al. 2010). In the current study, we showed that flow velocity dependent return rates of Trichoptera were species specific, both for live and dead specimens. The latter observation indicates that case properties influence return rates. The underlying cause and mechanism for the observed differences of flow tolerance between species requires further study, including case properties and/or behavioural tactics. The importance of active behaviour is indicated by the present observation that only three species exhibiting high flow velocity tolerance showed additional active behaviour to return to the bottom, such as trough crawling and attaching.

Most studies that focussed on escaping drift tested species of the order Ephemeroptera. Poff and Ward (1991), for example, showed that some species could not control drift as numbers fluctuated directly with flow velocity (e.g. *Paraleptophlebia heteronea* and *Ephemerella infrequens*), whilst other Ephemeroptera species could (e.g. *Epeorus longimanus* and *Baetis sp*). In laboratory experiments, the number of drifting *Baetis vagans* increased with increasing flow velocity, opposite to *Paraleptophlebia molli* (Corkum et al. 1977) and both *Baetis rhodani* and *Ecdyonurus torrentis* were able to reduce drift distance by using active behaviour, with species-specific responses depending on hydrological conditions (Oldmeadow et al. 2010). The three studies mentioned above observed that Ephemeroptera that occur in lotic environments are more effective in their ability to return to the bed than species that occur in lentic environments, as observed for the Trichoptera in the current study. In contrast to Ephemeroptera larvae (Corkum et al. 1977, Poff & Ward 1991, Oldmeadow et al. 2010), the Trichoptera tested in this study showed no distinct swimming movements, but active behavioural movements like crawling and attaching were most beneficial for *H. radiatus*, *C. villosa* and *M. sequax*.

Average flow velocities in Dutch lowland streams are 0.2–0.3 m/s (Tolkamp 1980, Verdonschot 1995). We experimentally verified that *M. sequax* and *C. villosa* show return rate tolerances within this range, whereas the other four species showed lower tolerance limits. Especially, *L. lunatus* cannot return to the bottom from drift at 0.3 m/s and will therefore need low flow areas.The role of low flow areas as refuges for drifting specimens to return to the bottom requires further research. Other studies have shown that refuges can reduce dislodgement probabilities of specimens and enable them to resist dislodgement despite relatively high shear stress (Lancaster & Hildrew 1993, Lancaster 1996, Gabel et al. 2008, Gabel et al. 2012). The current observations show that flow velocities of 0.6 m/s, which are often reached during peak discharges in these lowland streams, are critical for all species. This means that once dislodged, the specimens cannot actively return to the bottom. Again, the role of refugia can be important as they can passively "catch" drifting specimens. Only *M. sequax* and *C. villosa* can tolerate velocities of 0.6 m/s, so management of lowland streams should try to prevent peak flows that exceed 0.6 m/s.

## CONCLUSIONS

In this study we aimed to determine flow velocity thresholds for Limnephilidae to escape from drift and return to the bottom. We showed that the ability to return to the bottom from drift and the effect of behaviour on this process are species specific. Species on the lotic end of the gradient had higher return rates at high flow velocity treatments and used active behaviour more efficiently to return to the bottom from drift than those on the lentic end of the species gradient. We conclude that, in addition to dislodging resistance, the ability to settle from drift is of equal importance in determining flow velocity tolerance in lowland stream Trichoptera species.

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## REFERENCES

Allan JD, Johnson LB. 1997. Catchment-scale analysis of aquatic ecosystems. Freshwater Biology 37: 107–111.

Brittain JE, Eikeland TJ. 1988. Invertebrate Drift - a Review. Hydrobiologia 166(1): 77–93.

Brosse S, Arbuckle CJ, Townsend CR. 2003. Habitat scale and biodiversity: influence of catchment, stream reach and bedform scales on local invertebrate diversity. Biodiversity and Conservation 12: 2057–2075.

Ciborowski JJH, Pointing PJ, Corkum LD. 1977. Effect of Current Velocity and Sediment on Drift of Mayfly Ephemerella-Subvaria Mcdunnough. Freshwater Biology 7: 567–572.

Conti L, Schmidt-Kloiber A, Grenouillet G, Graf W. 2014. A trait-based approach to assess the vulnerability of European aquatic insects to climate change. Hydrobiologia 721: 297–315.

Corkum LD. 1992. Spatial Distributional Patterns of Macroinvertebrates Along Rivers within and among Biomes. Hydrobiologia 239(2): 101–114.

Corkum LD, Pointing PJ, Ciborowski JJH. 1977. Influence of Current Velocity and Substrate on Distribution and Drift of 2 Species of Mayflies (Ephemeroptera). Canadian Journal of Zoology-Revue Canadienne De Zoologie 55: 1970–1977.

Dolédec S, Lamouroux N, Fuchs U, Merigoux S. 2007. Modelling the hydraulic preferences of benthic macroinvertebrates in small European streams. Freshwater Biology 52: 145–164.

Downes B J, Keough MJ. 1998. Scaling of colonization processes in streams: Parallels and lessons from marine hard substrata. Australian Journal of Ecology 23: 8–26.

Feld CK, Hering D. 2007. Community structure or function: Effects of environmental stress on benthic macroinvertebrates at different spatial scales. Freshwater Biology 52: 1380–1399.

Fonseca DM, Hart DD. 1996. Density-dependent dispersal of black fly neonates is mediated by flow. Oikos 75: 49–58.

Gabel F, Garcia XF, Brauns M, Sukhodolov A, Leszinski M, Pusch MT. 2008. Resistance to ship-induced waves of benthic invertebrates in various littoral habitats. Freshwater Biology 53: 1567–1578.

Gabel F, Garcia XF, Schnauder I, Pusch MT. 2012. Effects of ship-induced waves on litttoral benthic invertebrates. Freshwater Biology 57: 2425–2435.

Gibbins CN, Scott E, Soulsby C, McEwan I. 2005. The relationship between sediment mobilisation and the entry of Baetis mayflies into the water column in a laboratory flume. Hydrobiologia 533: 115–122.

Gibbins CN, Vericat D, Batalla RJ. 2010. Relations between invertebrate drift and flow velocity in sand-bed and riffle habitats and the limits imposed by substrate stability and benthic density. Journal of the North American Benthological Society 29: 945–958.

Graf W, Schmidt-Kloiber A. 2011. Additions to and update of the Trichoptera Indicator Database. www.freshwaterecology.info, version 5.0.

Graf W, Murphy J, Dahl J, Zamora-Muñoz C, López-Rodríguez MJ. 2008. Distribution and Ecological Preferences of European Freshwater Organisms. In: Schmidt-Kloiber A, Hering D (eds) Trichoptera, pp. 388. Trichoptera Vol. 1. Pensoft Publishers, Sofia-Moscow.

Graf W, Murphy J, Dahl J, Zamora-Muñoz C, López-Rodríguez MJ & Schmidt-Kloiber A. 2006. Trichoptera Indicator Database. Euro-limpacs project, Workpackage 7 - Indicators of ecosystem health, Task 4, www.freshwaterecology.info, version 5.0.

Hart DD, Finelli CM. 1999. Physical-biological coupling in streams: The pervasive effects of flow on benthic organisms. Annual Review of Ecology and Systematics 30: 363–395.

Hering D, Johnson RK, Kramm S, Schmutz S, Szoszkiewicz K, Verdonschot PFM. 2006. Assessment of European streams with diatoms, macrophytes, macroinvertebrates and fish: a comparative metric-based analysis of organism response to stress. Freshwater Biology 51: 1757–1785.

Hynes HBN. 1970. Ecology of Stream Insects. Annual Review of Entomology 15: 25–42.

Lancaster J. 1990. Predation and Drift of Lotic Macroinvertebrates during Colonization. Oecologia 85: 48–56.

Lancaster J. 1996. Scaling the effects of predation and disturbance in a patchy environment. Oecologia 107: 321–331.

Lancaster J, Downes BJ, Glaister A. 2009. Interacting environmental gradients, trade-offs and reversals in the abundance-environment relationships of stream insects: when flow is unimportant. Marine and Freshwater Research 60: 259–270.

Lancaster J, Hildrew AG. 1993. Flow Refugia and the Microdistribution of Lotic Macroinvertebrates. Journal of the North American Benthological Society 12: 385–393.

McLay C. 1970. A theory concerning the distance travelled by animals entering the drift of a stream. Journal of the Fisheries Research Board of Canada. 27: 359–370 .

Merigoux S, Dolédec S. 2004. Hydraulic requirements of stream communities: a case study on invertebrates. Freshwater Biology 49: 600–613.

Merigoux S, Lamouroux N, Olivier JM, Dolédec S. 2009. Invertebrate hydraulic preferences and predicted impacts of changes in discharge in a large river. Freshwater Biology 54: 1343–1356.

Neves RJ. 1979. Movements of larval and adult Pycnopsyche guttifer (Walker) (Trichoptera: Limnephilidae) along Factory Brook, Massachusetts. American Midland Naturalist 102: 51–58.

Oldmeadow DF, Lancaster J, Rice SP. 2010. Drift and settlement of stream insects in a complex hydraulic environment. Freshwater Biology 55: 1020–1035.

Ormerod SJ, Dobson M, Hildrew AG, Townsend CR. 2010. Multiple stressors in freshwater ecosystems. Freshwater Biology 55: 1–4.

Otto C. 1976 Factors Affecting Drift of Potamophylax-Cingulatus (Trichoptera) Larvae. Oikos 27: 93–100.

Palmer MA, Arensburger P, Martin AP, Denman DW. 1996. Disturbance and patch specific responses: The interactive effects of woody debris and floods on lotic invertebrates. Oecologia 105: 247–257.

Poff NL, Ward JV. 1991. Drift Responses of Benthic Invertebrates to Experimental Streamflow Variation in a Hydrologically Stable Stream. Canadian Journal of Fisheries and Aquatic Sciences 48: 1926–1936.

Rice SP, Lancaster J, Kemp P. 2010. Experimentation at the interface of fluvial geomorphology, stream ecology and hydraulic engineering and the development of an effective, interdisciplinary river science. Earth Surface Processes and Landforms 35(1): 64–77.

Sagnes P, Merigoux S, Peru N. 2008. Hydraulic habitat use with respect to body size of aquatic insect larvae: Case of six species from a French Mediterranean type stream. Limnologica 38: 23–33.

Schnauder I, Rudnick S, Garcia XF, Aberle J. 2010. Incipient motion and drift of benthic invertebrates in boundary shear layers. In: Dittrich A, Koll K, Aberle J, Geisenhainer P (eds) River Flow 2010.

Proceedings of 5th International Conference on Fluvial Hydraulics, September 7–10, Braunschweig, Germany.

Statzner B, Gore JA, Resh VH. 1988. Hydraulic Stream Ecology - Observed Patterns and Potential Applications. Journal of the North American Benthological Society 7: 307–360.

Tolkamp HH. 1980. Organism-substrate relationships in lowland streams. PhD Thesis, Wageningen University, Wageningen: 211pp.

Verdonschot PFM. 1995. Typology of Macrofaunal Assemblages - a Tool for the Management of Running Waters in the Netherlands. Hydrobiologia 297: 99–122.

Verdonschot PFM, Besse-Lototskaya AA, Dekkers DBM, Verdonschot RCM. 2012. Mobility of lowland stream Trichoptera under experimental habitat and flow conditions. Limnologica 42: 227–234.

Vogel S. 1994. Life in moving fluids: the physical biology of flow. Princeton University Press, Princeton.

Waringer JA. 1989. Resistance of a cased caddis larva to accidental entry into the drift: the contribution of active and passive elements. Freshwater Biology 21: 411–420.

Waringer J, Graf W. 2011. Atlas of Central European Trichoptera Larvae. Erik Mauch Verlag, Dinkelscherben.

Waters TF. 1972 The drift of stream insects . Annual Review of Entomolgy 17: 253–272.

Weigel BM. 2003. Development of stream macroinvertebrate models that predict watershed and local stressors in Wisconsin. Journal of the North American Benthological Society 22: 123–142.

# SUPPLEMENTARY APPENDIX

## Statistical analysis

We did not want to assume from the start that the percentage resistant specimens followed a linear logistic response curve (Jongman et al. 1995) with respect to flow velocity. We allowed for more flexibility of the response curve by using a penalized spline (P-spline) approach (Eilers and Marx 1996, Marx and Eilers 1998). In this approach the flexibility is governed by the penalty parameter, with higher penalty giving curves that are smoother and closer to the linear logistic curve. We used a Bayesian method to estimate the penalty parameter and fitted a Bayesian P-spline (Lang and Brezger 2004) by integrated nested Laplace approximation (Rue et al. 2009) to the full Bayesian model as implemented in the INLA R package (Rue et al. 2014) and a dedicated R-function (available upon request). As in logistic regression, we used a logistic link function and a binomial distribution for the response. We used as prior for the penalty parameter a type 2 Gumbel distribution (with parameter $\lambda=3$), which gives more credit to the linear logistic curve than the usual Gamma distribution (Martins et al. 2014). Bayesian P-splines average over the posterior distribution of the penalty instead of fitting these once by mixed models/marginal maximum likelihood (MML) or empirical Bayes. This Bayesian procedure better acknowledges the uncertainty in the smoothing parameters than MML and the uncertainty bands (credible intervals) around the curves incorporate this uncertainty. We estimated 95% credible intervals for the expected response. For TEAM we use the identity link and a normal distribution, in which case high penalty results in a straight regression line.

## References

Jongman RHG, ter Braak CJF, van Tongeren OFR. 1995. Data analysis in community and landscape ecology. Cambridge University Press, Cambridge.

Eilers PHC, Marx BD. 1996. Flexible smoothing with B-splines and penalties. Statistical Science 1: 89-121.

Martins TG, Simpson DP, Riebler A, Rue H. 2014. Penalising model component complexity: A principled, practical approach to constructing priors. arXiv 1403.4630v2.

Marx BD, Eilers PHC. 1998. Direct generalized additive modeling with penalized likelihood. Computational Statistics & Data Analysis 28: 193-209

Lang S, Brezger A. 2004. Bayesian P-splines. Journal of Computational and Graphical Statistics 13: 183-212.

Rue H, Martino S, Chopin N, 2009. Approximate Bayesian inference for latent Gaussian models by using integrated nested Laplace approximations. Journal of the Royal Statistical Society: Series B (Statistical Methodology) 71: 319-392.

Rue H, Martino N, Lindgren F, Simpson D, Riebler A. 2014. INLA, functions which allow to perform full Bayesian analysis of latent Gaussian models using Integrated Nested Laplace Approximaxion. http://www.r-inla.org/:version 0.0-1396629476.

# 3

## CHAPTER 3

This chapter is based on the paper:

# THE SIGNIFICANCE OF REFUGE HETEROGENEITY FOR LOWLAND STREAM CADDISFLY LARVAE TO ESCAPE FROM DRIFT

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De Brouwer JHF, Kraak MHS, Besse-Lototskaya AA, Verdonschot PFM

## ABSTRACT

In lowland streams, macroinvertebrates that dislodge from the bed drift in downstream direction, but eventually need to return to the bottom to remain in the system. Refuges are important to all drift phases, since they may help larvae to avoid dislodgement and to escape from drift, even more so if the refuge structure is complex and heterogeneous. The aim of the present study was therefore to determine the influence of refuge heterogeneity on the ability of caddisfly larvae to return to the bottom from drift and to avoid secondary dislodgement. To this purpose a series of indoor flume experiments were undertaken, testing six Limnephilidae (Trichoptera) species, that occur on a gradient from lotic to lentic environments. Bed morphology (plain, refuges with or without leaf patches) and flow velocity (low (0.1 m/s), intermediate (0.3 m/s) and high (0.5 m/s) were manipulated. We showed that all species were favoured by refuges and that especially for species on the lentic end of the gradient (*L. lunatus*, *L. rhombicus* and *A. nervosa*), the ability to escape from drift and to avoid secondary dislodgement was increased. Moreover, we showed that all species spent more time in refuges than in open channel parts and more time in heterogeneous refuges (leaf patches) than in bare refuges, the latter being especially the case for larvae of the lotic species. For lentic species, not well adapted to high flow velocity, refuges are thus crucial to escape from drift, while for the lotic species, better adapted to high flow velocity, the structure of the refuge becomes increasingly important. It is concluded that refuges may play a crucial role in restoring and maintaining biodiversity in widened, channelized and flashy lowland streams.

# INTRODUCTION

In lowland streams, drift is an important process for macroinvertebrate dispersal (Waters 1972, Brittain & Eikeland 1988). Macroinvertebrates disperse over short and long distances, but in the end, drifting individuals need to return to the stream bottom to remain in the system (McLay 1970, Neves 1979). Previous studies showed that higher flow velocities result in higher drift densities (Corkum et al. 1977, Fonseca & Hart 1996, Gibbins et al. 2005, Gibbins et al. 2010). The processes of dislodgement and drift are intensively studied (Lancaster 2008), but the next step, either being washed out or return to the bottom is hardly studied (Palmer et al. 1996, Downes & Keough 1998, Lancaster 2008). However, some macroinvertebrates can use behavioural movement to end drift (Lancaster et al. 2009, Oldmeadow et al. 2010). De Brouwer et al. (2017) showed that the process of returning to the bottom is species specific and that abilities to escape from drift reflect the flow velocity tolerance gradient in which they occur in streams.

All phases of the drift process, dislodgement, drift distance and return to the bottom, may highly depend on the heterogeneity of the habitat, since structures and substrates can ameliorate negative effects of flow disturbance on benthic invertebrates (Lancaster & Hildrew 1993, Lancaster 1996, Hart & Finelli 1996, Rice et al. 2010). Heterogeneous environments, that include stable habitat patches like leaf packages, offer refuges in which organisms can find shelter. This may help individuals to avoid dislodgement, since movement to refuges prior to high flow is a commonly used avoidance strategy to prevent dislodgement (Borchardt & Statzner 1990, Borchardt 1993, Lancaster & Hildrew 1993). Refuges may also serve as focal points for individuals increasing return rates to the bottom from drift, but this beneficial role of refuges in ending drift has only been scarcely documented. Once returned to the bottom, resilience and resistance traits, like a streamlined, flattened small body and possessing means to cling to the substratum (Townsend & Hildrew 1994, Townsend et al. 1997), that enabled the different species to return (De Brouwer et al. 2017), may also help them to prevent secondary dislodgement, and even more so if the refuge structure is complex and heterogeneous. This, however, has never been studied. The aim of the present study was therefore to determine the influence of refuge heterogeneity on the ability of caddisfly larvae to return to the bottom from drift and to avoid secondary dislodgement. To this purpose a series of indoor flume experiments were undertaken, testing six Limnephilidae (Trichoptera) species, that occur on a gradient from lotic to lentic environments (Verdonschot et al. 2014, De Brouwer et al. 2017). Bed morphology and flow velocity were manipulated. We hypothesized that the presence of refuges in streams increases return rates to the bottom from drift, helps to avoid secondary dislodgement and that heterogeneous refuges (leaf patches) are used more effectively by caddisfly larvae than bare refuges.

## MATERIALS AND METHODS

### Test species

Six morphologically similar species of the large Limnephillidae family, with varying ecology and distribution, were selected for this experiment. The selected species were similar to those selected by de Brouwer et al. (2017): Limnephilus lunatus (Curtis, 1834), Limnephilus rhombicus (Linnaeus, 1758), Anabolia nervosa (Curtis, 1834), Halesus radiatus (Curtis, 1834), Chaetopteryx villosa (Fabricius, 1798) and Micropterna sequax (McLachlan, 1875). In this order, these six species are distributed along a lentic to lotic gradient (Graf et al. 2006, Graf et al. 2008, Graf et al. 2011). Within lowland streams, the first three species can be considered lentic and the latter three lotic (Verdonschot et al. 2014), responding clearly differently to flow velocity (De Brouwer et al. 2017).

Approximately 1500 fifth instar larvae per species were collected and all individuals were identified one by one. Specimens were collected from similar sites to those reported by de Brouwer et al. (2017), i.e. Warnsbornse beek, Coldenhovense beek, Seelbeek and drainage ditches (the Netherlands). Approximately 250 specimens were kept in separate compartments within an artificial rearing stream with a bottom consisting of fine gravel, sand and organic material, a water temperature of 10°C, a flow velocity range of 0.05-0.10 m/s and a day:night light regime of 16:8 h. Additional organic material and wheat fragments were provided to maintain sufficient food levels. The environmental conditions reflect a natural spring setting.

### Outline of the study

To determine the influence of refuges with or without leaf patches on the ability of caddisfly larvae to return to the bottom from drift and to avoid secondary dislodgement, a series of indoor flume experiments were undertaken with the six selected Limnephilidae species. The responses of the test species to three different flow velocities were tested in channels with plain beds (control) and with refuges with or without leaf packages (treatments).

### Experimental flumes

In the experiment, a fully controlled recirculating laboratory flume system was used (Verdonschot et al. 2012). These flumes enabled near homogeneous flow conditions and accurate control of flow velocity (Fig. 1).

### Bed morphology

The stream bed of the channel was comprised of sand grains (<250μm) glued to acrylic plates, mimicking a flat, sandy stream bottom. A control channel and a test channel were established (Fig. 1). The test channel consisted of three zones: Zone 3T, two-thirds of the width of the channel, represented a bare homogeneous bottom morphology. The zones 1T and 2T, one-third of the width of the channel, consisted of 12 alternating refuges, with or without leaf packages. The leaf packages consisted of Quercus rubor leaves attached to frames, which were fixed to the channel bed, such that macroinvertebrates could enter and leave these patches (Fig. 1b). The control channel consisted entirely of a bare homogeneous bottom, but to compare the control and the treatment channel, we referred to the same spatial zones as in the treatment channel (Zone 1C, Zone 2C and Zone 3C)(Fig. 1a).

### Flow velocity

All tests (6 species x 20 specimens x 3 flow velocities = 360 runs) were conducted under constant water temperature and light regime. Three flow velocities were

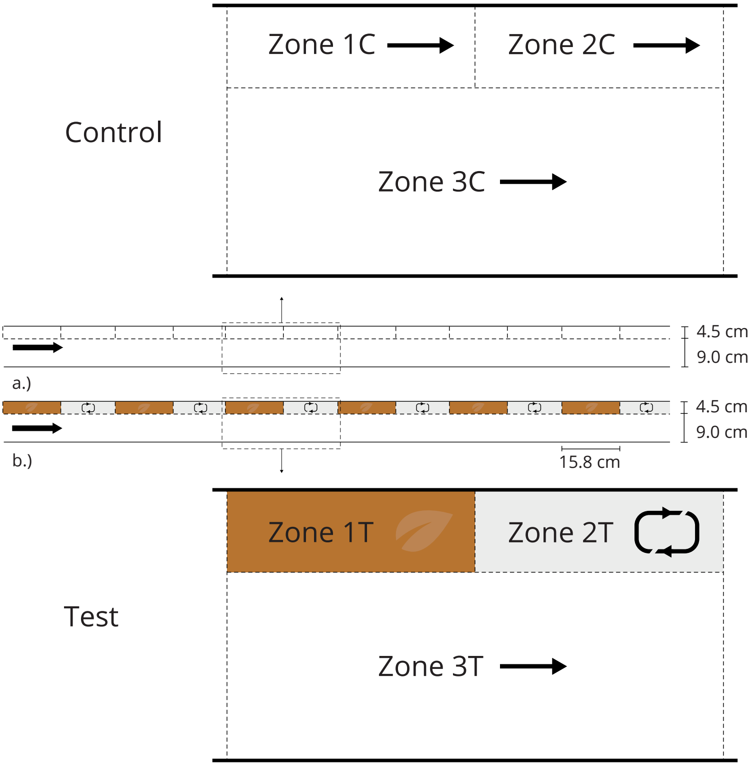

**FIGURE 1** Schematic overview of the control (**a.**) and the test (**b.**) channel. The control channel consisted of a planar bottom habitat in Zone 1C, Zone 2C and Zone 3C. The test channel included leaf patches (yellow area) in Zone 1T, bare refuges (white shaded area) in Zone 2T and a planar bottom habitat (white area) in zone 3T. Leaf patches and bare refuges occurred six times on the longitudinal axis of the channel

tested: low (0.1 m/s), intermediate (0.3 m/s) and high (0.5 m/s), reflecting the natural range of flow conditions in lowland streams. Near bed flow velocity was measured in the water column above all zones in all treatments, at the centre of the channel and in the refuges, using an electromagnetic flow meter (SENSA RC2 ADS, model V6d).

### Experimental runs

One specimen was used per test run and each test run had a constant flow velocity. Specimens were released just below the water level, in the most upstream part of the test section and behaviour and movement was monitored for six minutes, similar to de Brouwer et al. (2017). For each species, twenty specimens (replicates) were tested for each flow velocity over the six minutes or until specimens were washed out of the test section. In the latter case, specimens were classified as 'lost by drift'. The time individuals remained in the experiment was used as an indicator for: (1) the ability to return to the bottom from drift and (2) the resistance to

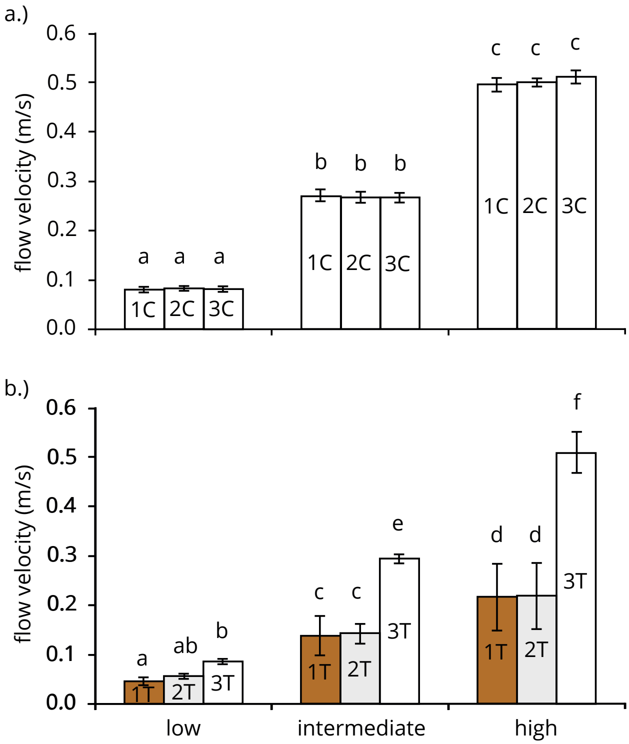

**FIGURE 2** Mean (±SD) flow velocity in the control (**a.**) and test (**b.**) channel per flow velocity (low (0.1m/s), intermediate (0.3m/s) and high (0.5m/s)). Leaf patches (yellow bars), bare refuges (white shaded bars) and planar bottom habitat (white bars) are distinguished. Central codes in the bars indicate the channel zone. Different letters above the bars indicate significant differences (Bonferroni test, P<0.05)

secondary dislodgement. For the animals that remained the entire 6 minutes test period in the channels, we continuously monitored the time individuals spent in the different spatial zones (Fig. 1), using visual observations. These visual observations were inputted into computer software, registering the time spent in the different habitat categories, bare stream sediment and refuges with or without leaf packages (Noldus, Observer®XT 10.5).

### Data analysis

To evaluate if the experimental design resulted in the desired differences in flow velocities between the bare homogeneous bottom and refuges with or without leaf packages, one way ANOVA applying a Bonferroni correction was used. Next, we assessed whether there were significant differences in residence time of caddisfly larvae between the entire control channel (Fig. 1a: 1C+2C+3C) and the test channel (Fig. 1b: 1T+2T+3T) using Mann-Whitney U tests. To quantify the attractiveness of refuges, we compared the time spent in Zone 1T+2T by individuals that returned to the bottom with the time spent in 1C+2C, using a Mann-Whitney U test. Subsequently, we assessed whether individuals merely seek refuges or specifically the physical structures offered by the heterogeneous refuges (leaf patches) by comparing the time individuals spent in Zone 1T (leaf patches) and in Zone 2T (bare refuges) using Wilcoxon Signed Rank tests.

In addition to subjecting the data to traditional statistics, we employed an intergrated modeling approach allowing to analyse all data simultaneously and, most importantly, to identify interactions between the experimental variables. To this purpose we selected a parsimonious model on the basis of having the lowest corrected Akaike Information Criterion (AICc) value using the dredge function in the R package MuMin version 1.15.630 and report the two best models and their main and interaction effects (Tab. suplemental 1-4). Statistical analysis was carried out in R (version 3.0).

## RESULTS

In the control channel, flow velocities were not significantly different between Zone 1C, Zone 2C and Zone 3C (Fig. 2). In the test channel, flow velocities in Zone 1T (leaf patches) and Zone 2T (bare refuges) were similar and approximately 50% of those in the open channel (Zone 3T). Moreover, flow velocities showed no significant differences between the control channel (Zone 3C) and the open part of the treatment channel (Zone 3T) and matched the targeted values.

The higher the flow velocity, the fewer individuals remained in the channels (Tab. 1) and the shorter the time they remained in the channels (Fig. 3). Yet, species and treatment specific differences were also observed. The number of individuals remaining in the channels and the residence time increased over the lentic-lotic species gradient, with *L. lunatus* being the most vulnerable to high flow velocity, in contrast to *C. villosa* and *M. sequax* (Tab. 1, Fig. 3). At intermediate and high flow velocity, in the test channel (1T+2T+3T) a significant (P<0.05) higher number of individuals returned to the bottom from drift and remained in the system than in the control channel (1C+2C+3C) (Tab 1). Moreover, all species remained longer in the test channel (1T+2T+3T) than in the control channel (1C+2C+3C) and in five cases this difference was significant (P<0.05), especially concerning the lentic species (four out of five cases; Fig. 3).

With only a single exception (*A. nervosa* at low flow velocity), all species spent more time in the refuges (with or without leaves; 1T+2T) than on the bare homogeneous bottom (1C+2C) (Fig. 4). In six cases this difference was significant (P<0.05), five cases concerning lotic species. In four other cases (three lentic and one lotic

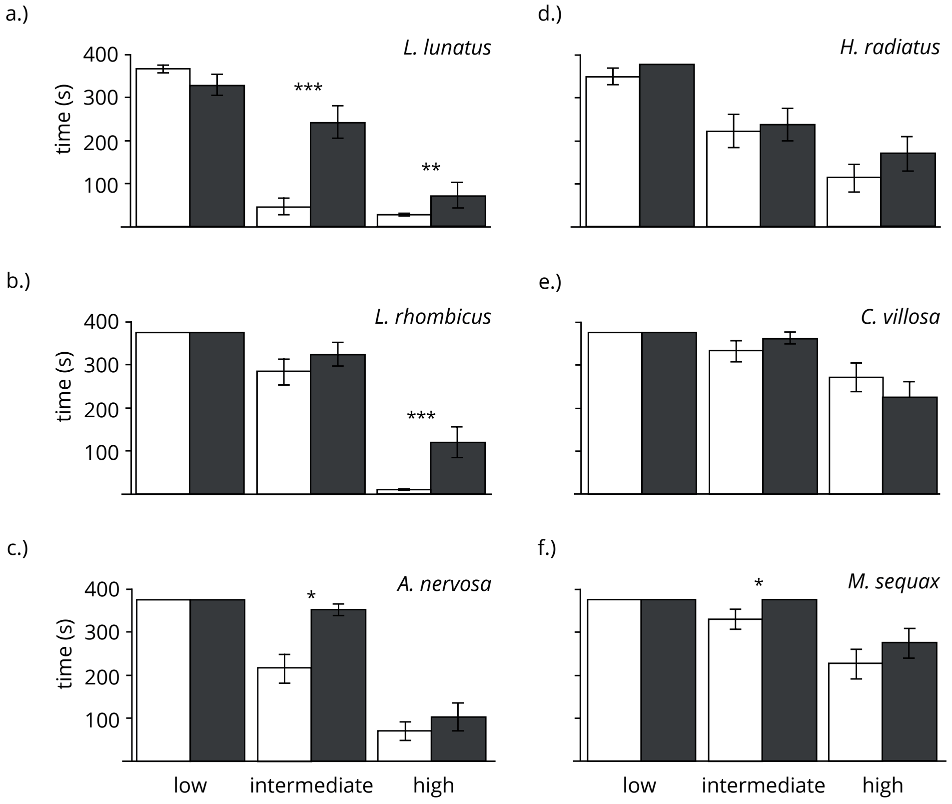

**FIGURE 3** Mean (±SD) time *L. lunatus* (**a.**), *L. rhombicus* (**b.**), *A. nervosa* (**c.**), *H. radiatus* (**d.**), *C. villosa* (**e.**) and *M. sequax* (**f.**) individuals spent in the control (white bars) and test channel (black bars) per flow velocity (low (0.1m/s), intermediate (0.3m/s) and high (0.5m/s)). Asterisks indicate significant differences between the control and the test channel (*P=0.05–0.01, **P=0.01–0.001, ***P=0.001–0.001). The maximal test duration was 360 seconds

species) no time at all was spent on the bare homogeneous bottom (1C+2C), while considerable time was spent in the refuges (with or without leaves; 1T+2T) (Fig. 4).

Irrespective of flow velocity, in fourteen out of seventeen cases the larvae spent more time in leaf patches (1T) than in the bare refuges (2T) (Fig. 5). In nine cases this difference was significant ($P<0.05$), especially concerning the lotic species (seven out of nine cases; Fig. 5).
The parsimonious logistic regression model (Supplemental Tab. 1 ) selected on the basis of AICc showed that the probability of escaping from drift was higher in

**TABLE 1** Number of individuals (out of 20) that escaped from drif and remained in the channels during the 360 seconds test period

| Species | Flow velocity category | Control (C) | Test (T) |
|---|---|---|---|
| *L. lunatus* | low | 19 | 17 |
| *L. lunatus* | intermediate | 1 | 12 |
| *L. lunatus* | high | 0 | 3 |
| *L. rhombicus* | low | 20 | 20 |
| *L. rhombicus* | intermediate | 13 | 17 |
| *L. rhombicus* | high | 0 | 5 |
| *A. nervosa* | low | 20 | 20 |
| *A. nervosa* | intermediate | 8 | 16 |
| *A. nervosa* | high | 1 | 4 |
| *H. radiatus* | low | 17 | 20 |
| *H. radiatus* | intermediate | 10 | 12 |
| *H. radiatus* | high | 3 | 8 |
| *C. villosa* | low | 20 | 20 |
| *C. villosa* | intermediate | 16 | 19 |
| *C. villosa* | high | 12 | 10 |
| *M. sequax* | low | 20 | 20 |
| *M. sequax* | intermediate | 15 | 20 |
| *M. sequax* | high | 10 | 14 |

the test channel than in the control channel, was higher for lotic species than for lentic species and decreased with increasing flow velocity. The model contained one interaction term (P<0.05), between type of species and flow velocity, showing that the difference in probability of escaping from drift between lotic species and lentic species increased with increasing flow rate.

## DISCUSSION

In freshwater lowland streams, dislodged macroinvertebrates need to return to the bottom to remain in the system (Lancaster et al. 2008). While dislodgement is well studied, the fate of drifting organisms is poorly understood. De Brouwer

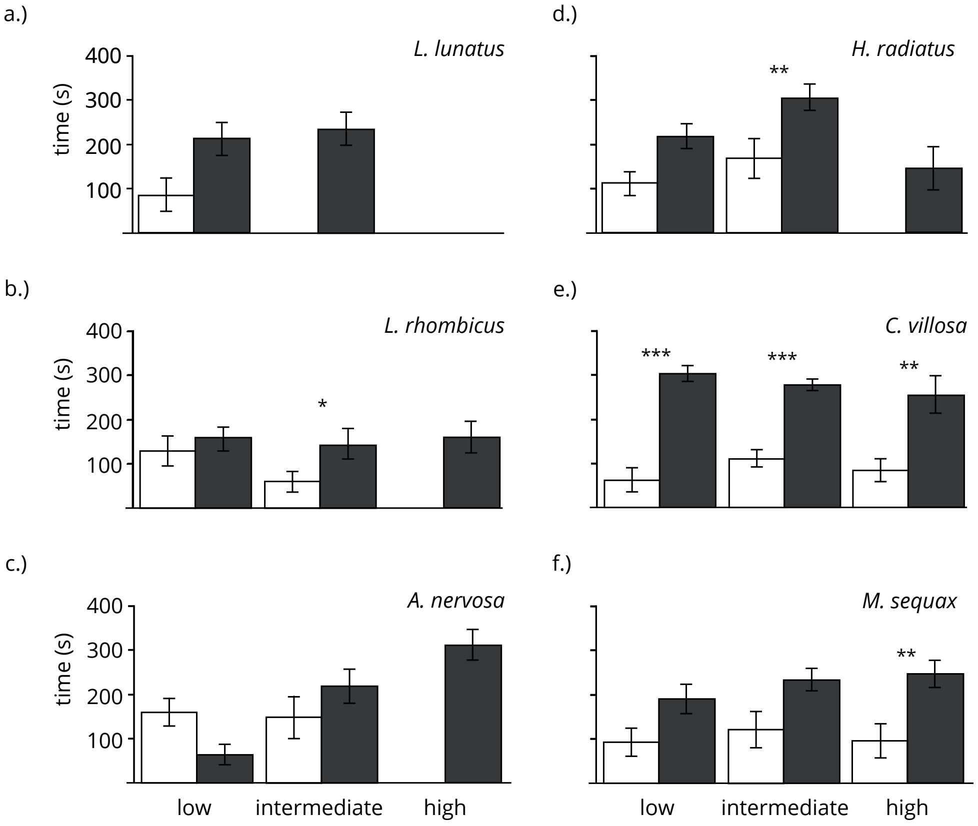

**FIGURE 4** Mean (±SD) time *L. lunatus* (**a.**), *L. rhombicus* (**b.**), *A. nervosa* (**c.**), *H. radiatus* (**d.**), *C. villosa* (**e.**) and *M. sequax* (**f.**) individuals spent in the control zones 1C+2C (white bars) and in the refuges 1T+2T (black bars) per flow velocity (low (0.1m/s), intermediate (0.3m/s) and high (0.5m/s)). Asterisks indicate significant differences between the control zones 1C+2C and the refuges 1T+2T (* : P=0.05-0.01, ** : P=0.01-0.001, *** : P=0.001-0.001). Only data for the individuals that remained in the experiment for the entire 360 seconds test period are included

et al. (2017) previously demonstrated that the Trichoptera species with the highest return rates at high flow velocity are distributed along the lotic end of the gradient. This group of species used active behaviour most efficiently to end drift. Subsequently, in the present study we aimed to elucidate the importance of refuge heterogeneity for the same six caddisfly species to escape from drift and to avoid secondary dislodgement. We showed that all species benefitted from refuges and that especially for species on the lentic end of the gradient (*L. lunatus*, *L. rhombicus* and *A. nervosa*), the ability to escape from drift and to avoid secondary dislodgement was increased. Moreover, all species spent more time in refuges than in open channel parts and more time in heterogeneous refuges

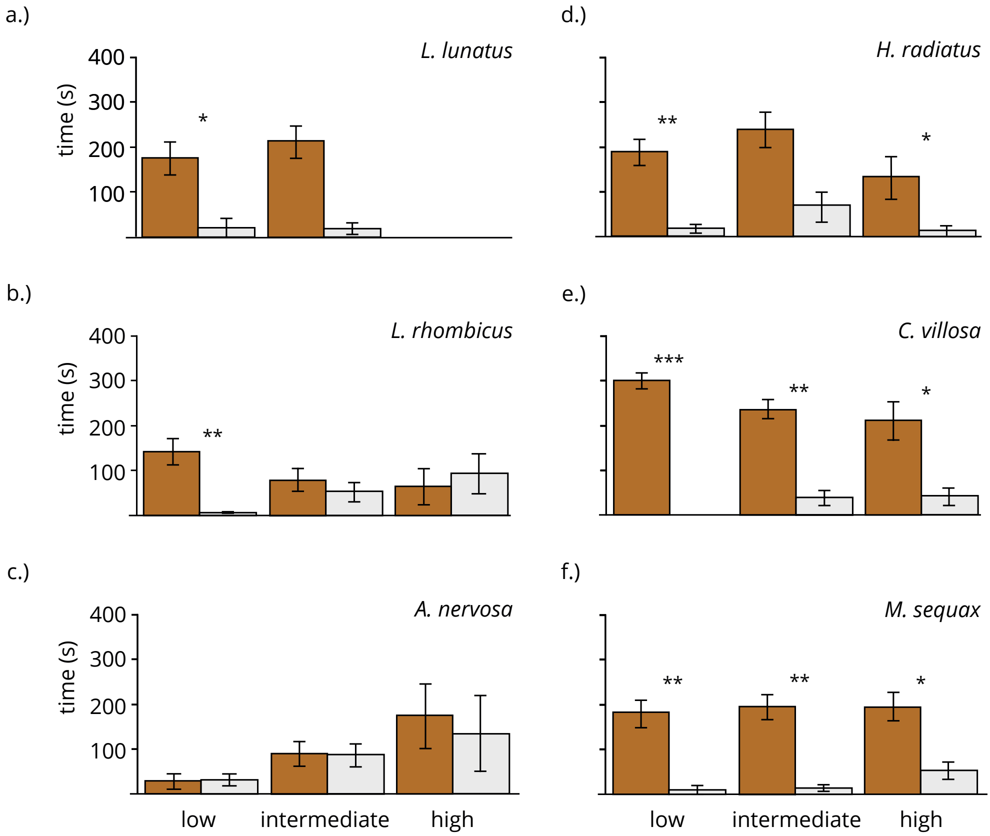

**FIGURE 5** Mean (±SD) time *L. lunatus* (**a.**), *L. rhombicus* (**b.**), *A. nervosa* (**c.**), *H. radiatus* (**d.**), *C. villosa* (**e.**) and *M. sequax* (**f.**) individuals spent in the leaf patches (yellow\ bars) and in the bare refuges (white shaded bars) per flow velocity (low (0.1 m/s), intermediate (0.3 m/s) and high (0.5 m/s)). Asterisks indicate significant differences between the leaf patches (1T) and the bare refuges (2T) (*: P = 0.05–0.01, **: P = 0.01–0.001, ***: P = 0.001–0.001). Only data for the individuals that remained in the experiment for the entire 360 seconds test period are included

(leaf patches) than in bare refuges, the latter being especially the case for larvae of the lotic species.

Our results thus suggest that the characteristics of the refuge are important. Except for *A. nervosa*, all species spent more time in heterogeneous refuges (leaf patches) than in bare refuges, indicating the higher importance of habitat structure over merely low flow, especially for the lotic species. Meanwhile, comparing the number of larvae that were able to escape from drift between the control and test channel revealed that, although beneficial to all species, the differences were largest for the lentic species. Hence it is concluded that for the lentic species, not well adapted to high flow velocity, refuges are crucial to escape from drift. The lentic species seek refuges to escape flow, more independent being it leaves or bare refuges. While for the lotic species, better adapted to high flow velocity, the structure of the refuge becomes increasingly important, as refuges also provide structure and food. Being able to cope with flow, their preference may be more food driven. In agreement, Verdonschot et al. (2012) reported that these species indeed show a strong preference for leaf habitats.

Several studies showed that local hydromorphological conditions influence settlement rates (Butman 1987, Palmer 1988, Butman et al. 1988, Gross et al. 1992). Some studies even reported larval movements to sites where hydraulic forcing is relatively low prior to extreme events to evade floods (Palmer 1996, Sedell et al. 1990, Lancaster 2000, Lytle & Poff 2004), which is especially effective if disturbance events are predictable (Dudgeon 1995, Lytle & Poff 2004). Also Oldmeadow et al. (2010) showed that two Ephemeroptera species actively swam towards low flow areas while in drift, but also that both species differed in their ability to reach those refuges.

The role of refuges in avoiding and overcoming the adverse effects of floods depends on the stability of the refuges. Hauer et al. (2007) considered habitat stability to be a morphodynamic necessity for aquatic organisms in their study on fish spawning, and for macroinvertebrates, substrate erosion can indeed induce catastrophic drift (Statzner 2008). This may imply that escaping from drift is more likely in streams where refuges are stable and abundant. Such streams may better sustain macroinvertebrate communities, because the recovery of a community from high drift loss depends on new colonists (Allen & Castillo 2007), originating from refuges. This becomes even more important in the nowadays often widened, channelized and flashy lowland streams where the studied species occur, and where flow velocities frequently exceed 0.3 m/s and even 0.5 m/s (Gardeniers 1985; Verdonschot 1995). Based on the results of the present study we therefore argue that especially the more lentic and littoral species, *L. lunatus*, *L. rhombicus* and *A. nervosa* (Graf et al. 2006, Graf et al. 2008), may only thrive in channelized lowland streams if refuges are abundantly present to limit population depletions during high flows.

This study highlighted the importance of refuges in freshwater lowland streams for caddisfly larvae to escape from drift and to avoid secondary dislodgement. Active movements in drift and the ability to move into refuges are key strategies to minimise drift and hence displacement distance. Flow regimes of many streams have, however, become more flashy and unpredictable (Poff et al. 1997, Bunn & Arthington 2002, Solomini et al. 2006) by increasing drainage infrastructure and maintenance activities to enhance run-off from urban and agricultural area's (Tolkamp 1980, Verdonschot 1995, Verdonschot & Nijboer 2002). Channelization and maintenance measures have reduced the number of refuges, such as leaf patches, organic debris and wood, while vegetation is often periodically removed Hering et al. 2000, Allan 2004, Pedersen & Friberg 2009). Hence, lowland streams have changed into multi-stress environments and communities in channelized sections of streams are less persistent than those in natural sections with refuges (Negishi et al. 2002) and refuges increase community persistence during high flows (Sueyoshi et al. 2014). Refuges may thus play a crucial role in restoring and maintaining biodiversity in widened, channelized and flashy lowland streams.

## ACKNOWLEDGEMENTS

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## REFERENCES

Allan JD. 2004. Landscapes and riverscapes: The influence of land use on stream ecosystems. Annual Review of Ecology Evolution and Systematics 35: 257–284.

Allen JD, Castillo MM. 2007. Stream ecology: structure and function of running waters. Dordrecht, Springer.

Bartón K. 2016. MuMIn: multi-model inference. R package. https://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf (accessed 11 October 2016).

Borchardt D, Statzner B. 1990. Ecolocical impact of urban stormwater runoff studied in experimental flumens-population loss by drift and availability of refuge space. Aquatic sciences 52: 299–314.

Borchardt D. 1993. Effects of Flow and Refugia on Drift Loss of Benthic Macroinvertebrates - Implications for Habitat Restoration in Lowland Streams. Freshwater Biology 29: 221–227.

Brittain JE, Eikeland TJ. 1988. Invertebrate Drift - a Review.  Hydrobiologia 166: 77–93.

Bunn SE, Arthington AH. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. Environmental Management 30: 492–507.

Butman CA. 1987. Larval Settlement of Soft-Sediment Invertebrates - the Spatial Scales of Pattern Explained by Active Habitat Selection and the Emerging Role of Hydrodynamical Processes. Oceanography and Marine Biology 25: 113–165.

Butman CA, Grasle JP, Webb CM. 1988. Substrate choices made by marine larvae settling in still water and in a flume flow. Nature 333: 771–773.

Corkum LD, Pointing PJ, Ciborowski JJH. 1977. Influence of current velocity and substrate on distribution and drift of two species of mayflies (Ephemeroptera). Canadian Journal of Zoology 55: 1970-1977.

De Brouwer JHF, Besse-Lototskaya AA, Ter Braak CJF, Kraak MHS, Verdonschot PFM. 2017. Flow velocity tolerance of lowland stream caddisfly larvae (Trichoptera). Aquatic Sciences 79: 419-425.

Downes BJ, Keough MJ. 1998. Scaling of colonization processes in streams: Parallels and lessons from marine hard substrata. Australian Journal of Ecology 23: 8-26.

Dudgeon D. 1995. Life history, secondary production and microdistribution of Hydrocyphon (Coleoptera: Scirtidae) in a tropical forest stream. Archiv fur Hydrobiologie 133: 261–271.

Feld CK. 2013. Response of three lotic assemblages to riparian and catchment-scale land use: implications for designing catchment monitoring programmes. Freshwater Biology 58: 715–729.

Fonseca DM, Hart DD. 1996. Density-dependent dispersal of black fly neonates is mediated by flow. Oikos 75: 49-58.

Gardeniers JJP, Tolkamp HH. 1985. The effect of stream regulation on the macroinvertebrate communities of Dutch lowland streams. Paper presented at the 3th International Symposium of Regulated Streams, Edmonton.

Gibbins CN, Scott E, Soulsby C, McEwan I. 2005. The relationship between sediment mobilisation and the entry of Baetis mayflies into the water column in a laboratory flume. Hydrobiologia 533: 115-122.

Gibbins CN, Vericat D, Batalla RJ. 2010. Relations between invertebrate drift and flow velocity in sand-bed and riffle habitats and the limits imposed by substrate stability and benthic density. Journal of the North American Benthological Society 29: 945–958.

Graf W, Schmidt-Kloiber A. 2011. Additions to and update of the Trichoptera Indicator Database. www.

freshwaterecology.info, version 5.0.

Graf W, Murphy J, Dahl J, Zamora-Muñoz C, López-Rodríguez MJ. 2008. Distribution and Ecological Preferences of European Freshwater Organisms. In: Schmidt-Kloiber A, Hering D (eds) Trichoptera, pp. 388. Trichoptera Vol. 1. Pensoft Publishers, Sofia-Moscow.

Graf W, Murphy J, Dahl J, Zamora-Muñoz C, López-Rodríguez MJ & Schmidt-Kloiber A. 2006. Trichoptera Indicator Database. Euro-limpacs project, Workpackage 7 - Indicators of ecosystem health, Task 4, www.freshwaterecology.info, version 5.0.

Gross TF, Werner FE and Eckman JE. 1992. Numerical Modeling of Larval Settlement in Turbulent Bottom Boundary-Layers. Journal of Marine Research 50: 611–642.

Hart DD, Finelli CM. 1999. Physical-biological coupling in streams: The pervasive effects of flow on benthic organisms. Annual Review of Ecology and Systematics 30: 363–395.

Hauer C, Unfer G, Schmutz S, Habersack H. 2007. The importance of morphodynamic processes at riffles used as spawning grounds during the incubation time of nase (Chondrostoma nasus). Hydrobiologia 579: 15–27.

Hering D, Kail J, Eckert S, Gerhard M, Meyer EI, Mutz M, Reich M, Weiss E. 2000. Coarse woody debris quantity and distribution in Central European streams. International Review of Hydrobiololgy 85: 5–23.

Holomuzki JR, Biggs BJF. 2000. Taxon-specific responses to high-flow disturbance in streams: Implications for population persistence. Journal of the North American Benthological Society 19: 670–679.

Lancaster J, Hildrew AG. 1993a. Characterizing in-Stream Flow Refugia. Canadian Journal of Fisheries and Aquatic Sciences 50: 1663–1675.

Lancaster J, Hildrew AG. 1993b. Flow Refugia and the Microdistribution of Lotic Macroinvertebrates. Journal of the North American Benthological Society 12: 385–393.

Lancaster J. 1996. Scaling the effects of predation and disturbance in a patchy environment. Oecologia. 107: 321-331.

Lancaster J. 2000. Geometric scaling of microhabitat patches and their efficacy as refugia during disturbance. Journal of Animal Ecology 69: 442–457.

Lancaster J. 2008. Movement and dispersion of insects in stream channels: what role does flow play? In: Lancaster J, Briers RA (eds) Aquatic Insects: Challenges to Populations. CAB International, Wallingford: 139–157.

Lancaster J, Downes BJ, Glaister A. 2009. Interacting environmental gradients, trade-offs and reversals in the abundance-environment relationships of stream insects: when flow is unimportant. Marine and Freshwater Research 60: 259-270.

Lytle DA, Poff NL. 2004. Adaptation to natural flow regimes. Trends in Ecology & Evolution 19: 94–100.

McLay C. 1970. A theory concerning the distance travelled by animals entering the drift of a stream. Journal of the Fisheries Research Board of Canada 27: 359-370.

Negishi JN, Inoue M, Nunokawa M. 2002. Effects of channelisation on stream habitat in relation to a spate and flow refugia for macroinvertebrates in northern Japan. Freshwater Biology 47: 1515–1529.

Neves RJ. 1979. Movements of larval and adult Pycnopsyche guttifer (Walker) (Trichoptera: Limnephilidae) along Factory Brook, Massachusetts. American Midland Naturalist 102: 51-58.

Oldmeadow DF, Lancaster J, Rice SP. 2010. Drift and settlement of stream insects in a complex hydraulic environment. Freshwater Biology 55: 1020–1035.

Palmer MA. 1988. Epibenthic Predators and Marine Meiofauna - Separating Predation, Disturbance, and Hydrodynamic Effects. Ecology 69: 1251–1259.

Palmer MA, Arensburger P, Martin AP, Denman DW. 1996. Disturbance and patch specific responses: The interactive effects of woody debris and floods on lotic invertebrates. Oecologia 105: 247–257.

Pedersen ML, Friberg N. 2009. Influence of disturbance on habitats and biological communities in lowland streams. Fundamental and Applied Limnology 174: 27–41.

Poff NL, Allan JD, Bain MB, Karr JR, Prestegaard KL, Richter BD, Sparks RE, Stromberg JC. 1997. The natural flow regime. Bioscience 47: 769–784.

Poff NL, Ward JV. 1989. Implications of Streamflow Variability and Predictability for Lotic Community Structure - a Regional-Analysis of Streamflow Patterns. Canadian Journal of Fisheries and Aquatic Sciences 46: 1805–1818.

Reid MA, Thoms MC. 2008. Surface flow types, near-bed hydraulics and the distribution of stream macroinvertebrates. Biogeosciences 5: 1043–1055.

Rice SP, Lancaster J, Kemp P (2010). Experimentation at the interface of fluvial geomorphology, stream ecology and hydraulic engineering and the development of an effective, interdisciplinary river science. Earth Surface Processes and Landforms 35: 64–77.

Sedell JR, Reeves GH, Hauer FR, Stanford JA, Hawkins CP. 1990. Role of Refugia in Recovery from Disturbances - Modern Fragmented and Disconnected River Systems. Environmental Management 14: 711–724.

Solimini AG, Cardoso AC, Heiskanen AS. 2006. Indicators and methods for the ecological status assessment under the Water Framework Directive. Linkages between chemical and biological quality of surface waters. Institute for Environment and Sustainability, Joint Research Center, European Communities: 262.

Statzner B. 2008. How Views about Flow Adaptations of Benthic Stream Invertebrates Changed over the Last Century. International Review of Hydrobiology 93: 593–605.

Sueyoshi M, Nakano D, Nakamura F. 2014. The relative contributions of refugium types to the persistence of benthic invertebrates in a seasonal snowmelt flood. Freshwater Biology 59: 257–271.

Tolkamp HH. 1980. Organism-substrate relationships in lowland streams. PhD Thesis, Wageningen University, Wageningen: 211 pp.

Townsend CR, Hildrew AG. 1994. Species traits in relation to a habitat templet for river systems. Freshwater Biology 31: 265-275.

Townsend CR, Dolédec S, Scarsbrook MR. 1997. Species traits in relation to temporal and spatial heterogeneity in streams: a test of habitat templet theory. Freshwater Biology 29: 221-227.

Verdonschot PFM. 1995. Typology of Macrofaunal Assemblages - a Tool for the Management of Running Waters in the Netherlands. Hydrobiologia 297: 99–122.

Verdonschot PFM, Nijboer RC. 2002. Towards a decision support system for stream restoration in the

Netherlands: an overview of restoration projects and future needs. Hydrobiologia 478: 131–148.

Verdonschot PFM, Nijboer RC. 2004. Testing the European stream typology of the Water Framework Directive for macroinvertebrates. Hydrobiologia 516(1-3): 35-54.

Verdonschot PFM, Besse-Lototskaya AA, Dekkers DBM, Verdonschot RCM. 2012. Mobility of lowland stream Trichoptera under experimental habitat and flow conditions. Limnologica 42: 227–234.

Verdonschot PFM, Besse-Lototskaya AA, Dekkers DBM, Verdonschot RCM. 2014. Directional movement in response to altered flow in six lowland stream Trichoptera. Hydrobiologia 740: 219–230.

Waters TF. 1972. Drift of Stream Insects. Annual Review of Entomology 17: 253–272.

# SUPPLEMENTARY APPENDIX

## Statistical results

The statiscical procedure is described in the main article. The results of the parsimonious logistic regression model are shown in this section.

For logistic regression in R see:

https://ww2.coastal.edu/kingw/statistics/R-tutorials/logistic.html

```
glm.out = glm(cbind(Menarche, Total-Menarche) ~ Age, family=binomial(logit), data=menarche)
```

For our data:

```
summary(glm(cbind(N_remain, N_float)~ChannelType,family= binomial, data = Data))
```

gives a positive coefficient for ChannelTypeTest, as number that remain in Test is higher than in Control (257 vs 205 with fixed total).

**TABLE 1** Model selection table ranked by AICc. The models included a selection of factors: channel type test (ChT), flow velocity category (Flw), species group (SpG) and interactions. Channel types include test (T) conditions. Flow velocity categories include low, intermediate and high flow velocity. Species groups include species on the lentic end of the gradient (*L. lunatus, L. rhombicus* and *A. nervosa)* and species on the lotic end of the gradient (*H. radiatus, C. villosa* and *M. sequax)*

| Model | (Int) | ChT | Flw | SpG | ChT: Flw | ChT: SpG | Flw: SpG | ChT: Flw: SpG | df | Loglik | AICc | delta | weight |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 40 | 2.956 | + | + | + |  |  | + |  | 7 | -80.588 | 179.2 | 0 | 0.348 |
| 56 | 2.855 | + | + | + |  | + | + |  | 8 | -78.926 | 179.2 | 0.01 | 0.346 |
| 8 | 2.609 | + | + | + |  |  |  |  | 5 | -84.563 | 181.1 | 1.95 | 0.131 |
| 24 | 2.528 | + | + | + |  | + |  |  | 6 | -83.909 | 182.7 | 3.54 | 0.059 |
| 48 | 3.229 | + | + | + | + |  | + |  | 9 | -79.49 | 183.9 | 4.73 | 0.033 |
| 16 | 2.874 | + | + | + | + |  |  |  | 7 | -83.063 | 184.1 | 4.95 | 0.029 |
| 128 | 4.078 | + | + | + | + | + | + | + | 12 | -73.362 | 184.3 | 5.11 | 0.027 |
| 64 | 3.1 | + | + | + | + | + | + |  | 10 | -78.174 | 185.1 | 5.97 | 0.018 |
| 32 | 2.835 | + | + | + | + | + |  |  | 8 | -82.587 | 186.5 | 7.33 | 0.009 |
| 39 | 3.367 |  | + | + |  |  | + |  | 6 | -94.453 | 203.8 | 24.63 | 0 |
| 7 | 3.033 |  | + | + |  |  |  |  | 4 | -98.213 | 205.7 | 26.54 | 0 |
| 4 | 3.126 | + | + |  |  |  |  |  | 4 | -108.635 | 226.6 | 47.38 | 0 |
| 12 | 3.367 | + | + |  | + |  |  |  | 6 | -107.365 | 229.6 | 50.45 | 0 |
| 3 | 3.505 |  | + |  |  |  |  |  | 3 | -121.106 | 249.0 | 69.78 | 0 |
| 6 | -0.1483 | + | + |  |  |  |  |  | 3 | -237.404 | 481.6 | 302.38 | 0 |
| 22 | -0.1782 | + | + |  | + |  |  |  | 4 | -237.309 | 483.9 | 304.73 | 0 |
| 5 | 0.1782 |  | + |  |  |  |  |  | 2 | -245.972 | 496.3 | 317.13 | 0 |
| 2 | 0.2796 | + |  |  |  |  |  |  | 2 | -252.703 | 509.8 | 330.59 | 0 |
| 1 | 0.5826 |  |  |  |  |  |  |  | 1 | -260.912 | 523.9 | 344.76 | 0 |

**TABLE 2** Analysis of deviance table. Likelihood Ratio Test of fixed effects between model 40 and model 56

| Resid. | Df Resid. | Dev | Df | Deviance | Pr(>Chi) |
|---|---|---|---|---|---|
| 1 | 29 | 89.434 | | | |
| 2 | 28 | 86.110 | 1 | 3.3241 | 0.06827 . |

Table 1 shows that model 40 and model 56 models rank highest on the AICc mode. Table 2 shows an indication of deviation between both models. Table 3 and table 4 show evidence that the number of specimens that remain (on the logistic scale) are lower at intermediate and high flow velocity than for low flow velocity (Flowintermediate, Flowhigh) and higher in the test channel than in the control channel (ChannelTypeTest).

The bottom line of table 3 provides evidence that difference in number that remain (on the logistic scale) between low and high flow is higher for lotic species than for lentic species (Flowhigh:SpGrlotic). The number that remain (on the logistic scale) = estimated probability of remaining in channel. The bottom line of table 4 shows an indication that the difference in number that remain (on the logistic scale) that remain between Control and Test is lower for lotic species than for lentic species.

**TABLE 3** Summary statistics of model 40 including channeltype (ChT), flow velocity category (Flw), species group (SpG) and interaction between flow velocity category and species group (Flw:SpG)

| Estimate | Std. | Error | z | value | Pr(>\|z\|) |
|---|---|---|---|---|---|
| (Intercept) | 2.9564 | 0.5137 | 5.755 | 8.65 e-09 | *** |
| ChannelTypeTest | 1.0873 | 0.2125 | 5.116 | 3.11e-07 | *** |
| Flowintermediate | -3.248 | 0.5467 | -5.941 | 2.83e-09 | *** |
| Flowhigh | -5.7213 | 0.5982 | -9.563 | < 2e-16 | *** |
| SpGrlotic | 0.2984 | 0.7776 | 0.384 | 0.7012 | |
| Flowintermediate:SpGrlotic | 0.7182 | 0.8309 | 0.864 | 0.3874 | |
| Flowhigh:SpGrlotic | 1.8152 | 0.8548 | 2.124 | 0.0337 | * |

**TABLE 4** Summary statistics of model 56 including channeltype (ChT), flow velocity category (Flw), species group (SpG), the interaction between flow velocity category and species group (Flw:SpG) and the interaction between flow velocity category and species group (ChT:SpG)

| Estimate | Std. | Error | z | value | Pr(>\|z\|) |
|---|---|---|---|---|---|
| (Intercept) | 2.8546 | 0.516 | 5.532 | 3.17e-08 | *** |
| ChannelTypeTest | 1.5376 | 0.3358 | 4.579 | 4.66e-06 | *** |
| Flowintermediate | -3.3529 | 0.5557 | -6.033 | 1.61e-09 | *** |
| Flowhigh | -5.9532 | 0.6255 | -9.518 | < 2e-16 | *** |
| SpGrlotic | 0.4997 | 0.7859 | 0.636 | 0.5249 | |
| Flowintermediate:SpGrlotic | 0.851 | 0.8366 | 1.017 | 0.309 | |
| Flowhigh:SpGrlotic | 2.1206 | 0.8782 | 2.415 | 0.0158 | * |
| ChannelTypeTest:SpGrlotic | -0.7884 | 0.4362 | -1.807 | 0.0707 | . |

# 4

## CHAPTER 4

# FLOW THRESHOLDS FOR LEAF RETENTION IN HYDRODYNAMIC WAKES DOWNSTREAM OF OBSTACLES

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De Brouwer JHF, Eekhout JPC, Besse–Lototskaya AA, Hoitink AJF, Ter Braak CJF, Verdonschot PFM

## ABSTRACT

Leaves are the major component of terrestrial litter input into aquatic systems. Leaves are distributed by the flow, accumulate in low flow areas, and form patches. In natural streams, stable leaf patches form around complex structures, such as large woody debris. Until now, little is known about flow conditions under which leaf patches persist. This study aims to quantify flow conditions for stable leaf patches and entrainment of leaf patches. We hypothesize that entraining flow processes, such as turbulence, Reynolds stress, or lift forcing (vertical flow velocity), best explain local leaf retention. This study was performed in an unscaled flume experiment, which conditions coincide with conditions found in low–energetic lowland streams. We positioned a wooden obstacle perpendicular to the flow on the bed of the flume. A leaf patch was positioned downstream from the wooden obstacle. The experiment was performed under 5 flow conditions. We monitored leaf patch cover and near–bed flow conditions in the area downstream of the wooden obstacle. We showed that near–bed flow velocities explain leaf retention better than more complex flow velocity derivatives such as turbulence, Reynolds stress, and vertical flow velocity. The entrainment near–bed flow velocity for leaves ranges from 0.037 to 0.050 m/s. Flow velocities frequently exceed those values, even in low–energetic lowland streams. Therefore, complex structures, such as woody debris, create flow conditions to support stable leaf patches. Thus, adding instead of removing obstacles may be a key strategy in restoring biodiversity in deteriorated streams.

*Keywords:* Current velocity, Flow velocity, Leaves entrainment, Leaves transport, Lowland streams, Wake

## INTRODUCTION

Leaves are the major component of terrestrial litter input into aquatic ecosystems (Abelho 2001). Leaves are periodically deposited in very large quantities (Richardson et al. 2005, Webster et al. 1999, Webster & Meyer 1997) and are biologically processed and transported by the flow (Hoover et al. 2006, Webster et al. 1999). In stretches where flow velocity is lowered, for example, due to the presence of woody debris, leaves may form stable patches. Leaf patches are often densely colonized biodiversity hotspots in streams (Kobayashi & Kagaya 2004, Kobayashi & Kagaya 2005), that is, refuges that offer shelter and food (Lancaster 2008, Lancaster & Belyea 1997, Lancaster & Hildrew 1993, Richardson 1992). A substantial decrease of leaf patches may therefore lead to a decline in species abundance and diversity (Richardson et al. 2010, Rowe & Richardson 2001) potentially affecting ecosystem functioning (Bunn & Arthington 2002, Hart & Finelli 1999, Poff et al. 1997, Poff et al. 2007).

Many lowland streams are low–energetic. Although single–thread streams in lowland areas often appear to be highly sinuous, they remain virtually fixed in time. Active morphological processes such as the development of alternate bars and chute cut–off may occur as a response to human measures (Eekhout & Hoitink 2015, Eekhout et al. 2013), but after an initial period of adjustment, the streams tend to maintain stable (Eekhout et al. 2014). Eekhout et al. (2015) showed that typical deteriorated lowland streams have cross–sectional–averaged flow velocities of 0.08–0.13 m/s and homogeneous bed substrate. In contrast, natural stream bottoms consist of a combination of mineral (50%) and organic microhabitats (50%: Verdonschot et al. 1995), respectively ranging from silt, sand, and gravel, to fine and coarse particulate organic matter (e.g. fallen leaves), mosses, local stands of vascular hydrophytes, and course woody debris (logs and debris dams). As the organic material plays a dominant role, these stream types are often indicated as organic streams. Leaves are particularly important in these lowland stream ecosystems, where they serve as one of the major food sources for macroinvertebrates (Verdonschot et al. 1995). The ecological importance of leaf input, processing, and transport has been recognized for decades (e.g. Hynes 1970) and linked to organic matter budgets, ecosystem metabolism, and decomposition (reviewed in Tank et al. 2010). However, leaf retention is still poorly understood (Hoover et al. 2006, Statzner 2008).

Bed load transport of sediment depends on the physical particle characteristics and the degree of exposure to flow, that is, particles are distributed according to shape, size, and specific weight (Hynes 1970). Due to their relatively high surface–weight ratio, the transport of leaves obviously behaves differently from

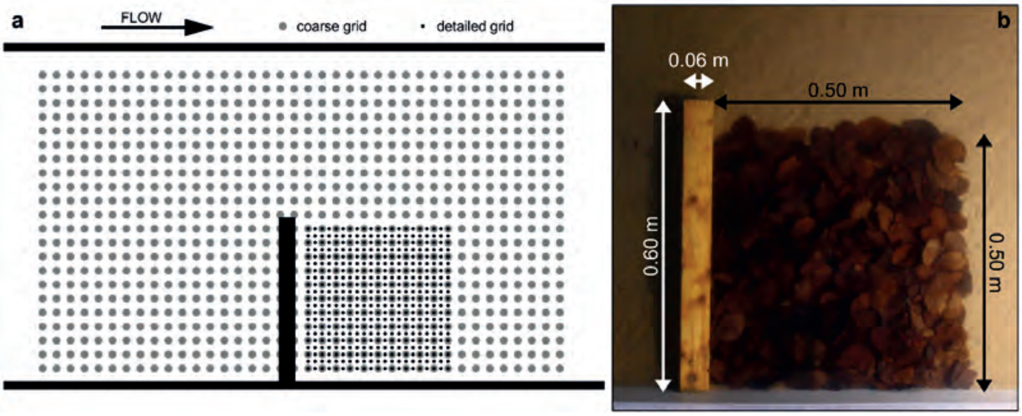

**FIGURE 1** (a) Positions of near-bed flow velocity measurements in and around the test section. The black bar represents the wooden obstacle upstream of the test section. (b) Picture of the test section at the start of an experimental run

the transport of sediment (Young et al. 1978). Previous studies showed that leaf patch stability relates to discharge in the field (e.g. Gorecki et al. 2006, Hoover et al. 2006, Larrañaga et al. 2003, Li & Dudgeon 2011, Young et al. 1978) and to cross–sectional–averaged flow velocity in flumes (Koljonen et al. 2012, Trodden 2012). Discharge and cross sectional–averaged flow velocity are bulk parameters though, which are not interchangeable from one stream to another due to site specific dimensions and environmental heterogeneity (e.g. Trodden 2012).

Previous research showed that local structural heterogeneity increases the leaf retention capacity of streams (e.g. Canhoto & Graça 1998, Cordova et al. 2008, Ehrman & Lambert 1992, James & Henderson 2005, Koljonen et al. 2012, Speaker et al.1984, Trodden 2012, Young et al. 1978). Stable leaf patches are scarce in fast flowing zones without obstacles but are often present in still water zones such as backwaters, margins, and eddies or in riffle areas with obstacles (Abelho, 2001, Nakajima et al. 2006). The general view is that flow velocities should be near zero for stable leaf patches to persist (e.g. Kemp et al. 2000, Trodden 2012), although leaves entrain at sites with high flow velocities. Stream structures and obstacles deflect the flow and create wakes where flow velocities are reduced or become negative relative to the normal flow (Daniels & Rhoads 2004, Manga & Kirchner 2000, Manners et al. 2007), thus creating conditions for leaf patch formation. Leaves stick to these obstacles (Ehrman & Lambert 1992, Cordova et al. 2008) or deposit in still water zones (Hoover et al. 2010). The number of leaves retained from drift increases with the number of structures, unless high densities of structures evoke strong interferential currents and fail to effectively retain leaves (Trodden 2012).

Although the mechanism of leaf retention by stream structures is clearly linked to flow reductions, until now, no direct relationship has been reported between flow conditions and leaf retention. Hence, little is known about the flow conditions under which leaf patches form and stabilize and entrain in streams. Therefore, the aim of this study was to quantify the flow conditions for leaf patch stability and leaf entrainment. To this purpose, we tested leaf patch stability and quantified near–bed flow conditions in a wake behind a wooden obstacle in an unscaled flume experiment, which conditions coincide with conditions found in lowland streams (Eekhout et al. 2015). We hypothesize that leaf patch size and shape are determined by the incipient motion of leaves and that leaf patch stability is best explained by hydraulic properties including turbulence, Reynolds stress, and lift forcing (vertical flow velocity), analogously to sediment transport theory.

## MATERIALS AND METHODS

### Experimental set–up

The experiments were performed in a straight, tilting laboratory flume in the Kraijenhoff van de Leur Laboratory for Water and Sediment Dynamics at Wagenigen University. The flume has an internal width of 1.2 m, an internal height of 0.5 m, and a total length of 14.4 m. The flume bottom was covered with a moveable 0.1–m–thick sand bed layer (median grain size: 390 μm). A rectangular wood piece was fixed to the bottom of the flume and to one side of the flume wall. The wooden obstacle deflected the homogeneous flow and created a variable flow pattern in the test section. The submerged wooden obstacle emerged 0.06 m from the sand bed and covered half the width of the flume. The test section was located 5 m from the beginning of the flume (Fig. 1). Each experimental run lasted for a period of 75 min. The experimental runs were repeated 15 times for each flow condition.

**TABLE 1** Flow conditions tested in the experiments and the corresponding bulk discharge, Froude number, and cross-sectional-averaged flow velocities

| Class | Q ($dm^3$/s) | Fr | $U_{av}$ (m/s) |
|---|---|---|---|
| Very low | 7.2 | 0.033 | 0.04 |
| Low | 10.8 | 0.050 | 0.06 |
| Intermediate | 14.4 | 0.066 | 0.08 |
| High | 18.0 | 0.082 | 0.10 |
| Very high | 21.6 | 0.099 | 0.12 |

Five flow conditions were tested in the experiments (Tab. 1). Test runs showed that leaves did not entrain at cross–sectional–averaged flow conditions of 0.04 m/s and that the majority of leaves were entrained at 0.12 m/s. Therefore, we set these two conditions as the minimum (I) and maximum (V), respectively, and added three additional conditions with 0.02–m/s increments. These test conditions are further referred to as I, II, II, IV, and V (Tab. 1). The water depth was kept constant throughout the experiment at 0.15 m. To achieve this, discharge was kept constant and the flume was tilted such that a water depth of 0.15 m could be maintained throughout the experiment. All the physical conditions used in the experiment, that is, flow depth, cross–sectional–averaged flow velocities, and bed material, coincide with conditions previously found in low–energetic lowland streams (Eekhout et al. 2015).

### Flow velocity measurements

Flow velocity measurements were performed with an Acoustic Doppler Velocimeter (ADV, Nortek Vectrino), which is able to measure the flow velocity in three directions (two horizontal and one vertical) at a frequency of 20 Hz. The ADV was mounted on a movable carriage to obtain spatially distributed flow velocity data. The vertical position of the ADV was kept constant at a height of 0.03 m from the bed, which was the vertical position of the ADV closest to the bed without interference with bed forms and leaves. We employed two measurement strategies. First, flow velocities were measured on a coarse grid with 0.05–m intervals, with the aim of obtaining insight into the flow in the area surrounding the test section. These measurements covered the test section and the area surrounding the test section (Fig. 1a). At each grid cell, flow velocities were obtained continuously over a period of 30 s. Second, flow velocities were measured on a detailed grid with 0.025–m intervals. The detailed grid only covered the area of the test section. At each grid cell, flow velocity was obtained continuously over a period of 300 s. The high–resolution velocity measurements aimed at linking mean horizontal flow velocities (time averaged at each grid cell), turbulence kinetic energy (TKE), vertical flow velocities, and Reynolds stress to leaf cover in the test section. After decomposing flow velocity into a mean and a fluctuating component, denoted with a prime, TKE is here defined per unit mass as in

$$TKE = \frac{1}{2}\left(u'^2 + v'^2\right).$$

The vertical fluctuating component $w'$ is left out of the equation, because it is smaller than the horizontal components, and includes comparatively many spikes due to acoustic side lobes from the bed. The main Reynolds stress tensor components are the ones that quantify vertical exchange of momentum, represented by $(\overline{u'w'}, \overline{v'w'})$. We tested the absolute value of the latter vector as a metric controlling positive (upward) and negative (downward) lift forces. The components of the vector can be considered as a co-variance, which is little affected by the outliers in the vertical fluctuations.

### Leaf patch monitoring

European beech (Fagus sylvatica) leaves were used in the experiment, a common Western European species with relatively low variance in leaf shape. Dry fallen leaves were collected, stored, and wetted during 24 hr. Trodden (2012) showed that leaves soaked water to saturation in 10 hr after which their weight remains equal for at least 48 hr. Exactly 600 leaves were positioned in the test section in stagnant water before each run (Fig. 1b). At the start of each experimental run, discharge was slowly increased to the target discharge (1 dm$^3$/s increase every 2 s). Pictures were taken with a digital single–lens reflex camera (CANON EOS 400D) equipped with a polarized lens. The camera was mounted on a frame, 2 m above the leaf patch. Photos were taken at intervals of 1 min over the 75–min

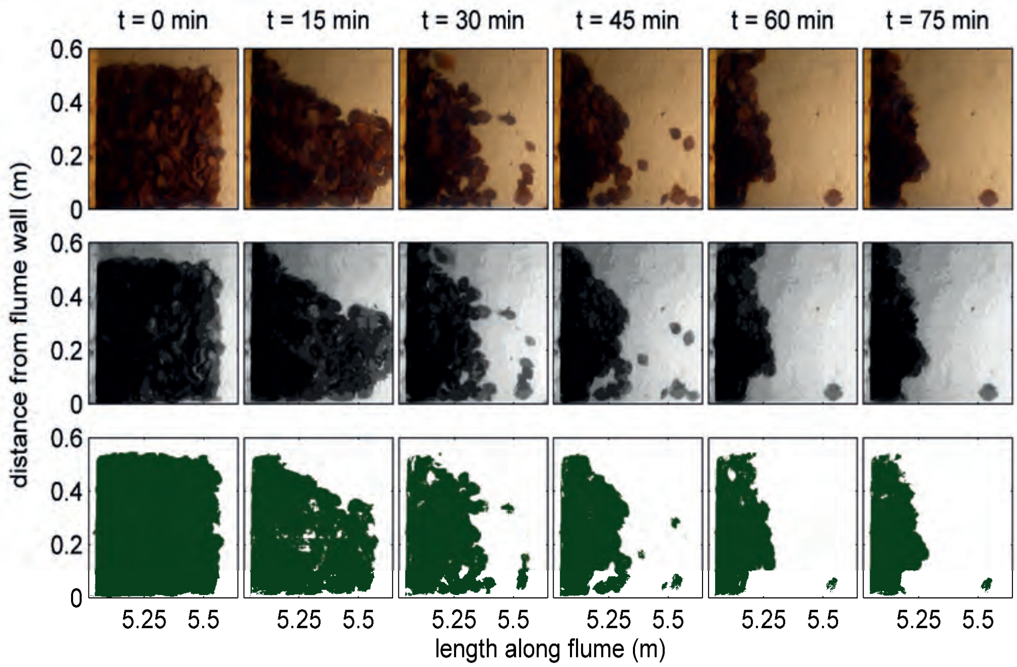

**FIGURE 2** Example of temporal leaf patch development. The figure shows the procedure to distinguish the leaves from the sand and the wood. The example shows data from discharge condition III (0.08 m/s)

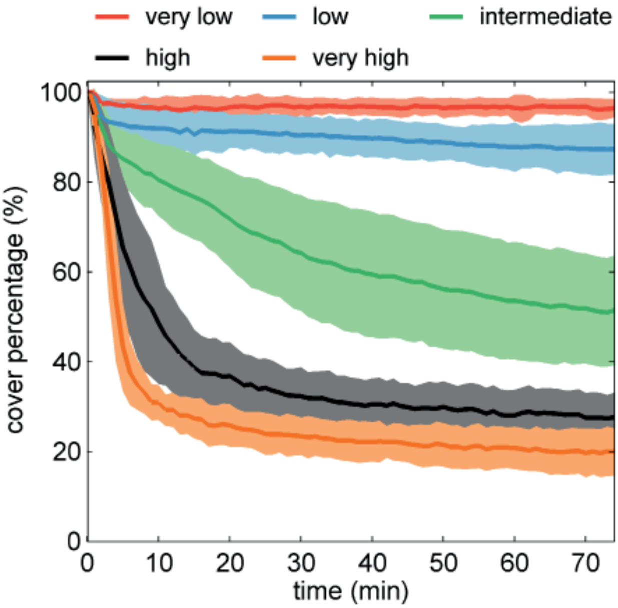

**FIGURE 3** Temporal evolution of the average (n = 15) leaf cover percentage and standard deviation in the test section for the five discharge conditions (see Fig. Supplemental 1 for extended runs for the intermediate discharge condition)

test period. Leaves were distinguished from sand and wood using photo analysis. The photos were transformed to grey scale, and leaves were distinguished from the sand and wood using a threshold value for the grey–scale intensity. Both the temporal and spatial evolution of the leaf patch was analysed from the photos (Fig 2). The percentage leaf cover with respect to the initial cover was determined for each subsequent photo, which allowed obtaining the temporal evolution of the percentage leaf cover for each flow condition. The percentage leaf cover was determined at the locations of the high–resolution velocity measurements. The spatial distribution of leaf cover was obtained at the end of each 75–min test run based on the last photo, when equilibrium conditions were achieved. The spatial distribution was averaged over the 15 replicate runs. This way, we obtained a relationship between leaf cover and the flow parameters TKE, the absolute Reynolds stress |(−uw,−vw)|, mean vertical flow velocity (W), and average flow velocity (U,V). All flow properties apply to the conditions at 0.03 m above the bed.

### Regression curves

The Bayesian P–splines (Appendix I) with credible bands were used to determine the range of entrainment flow velocities for the leaves and to show the stability of leaves on the stream bed at different flow velocities. We hypothesize that leaves are stable at velocities below the lower end of the entrainment range (stability threshold, 85% cover) and highly probable to entrain at the upper end of the entrainment range (entrainment threshold, 15% cover). Credible intervals (CI) for "stable" and "entrainment" were estimated from the intersection points of the 15% and 85% cover levels, with the 95% credible bands of the P–splines. If the level intersects an upper or lower band, twice the average of the intersection points was taken.

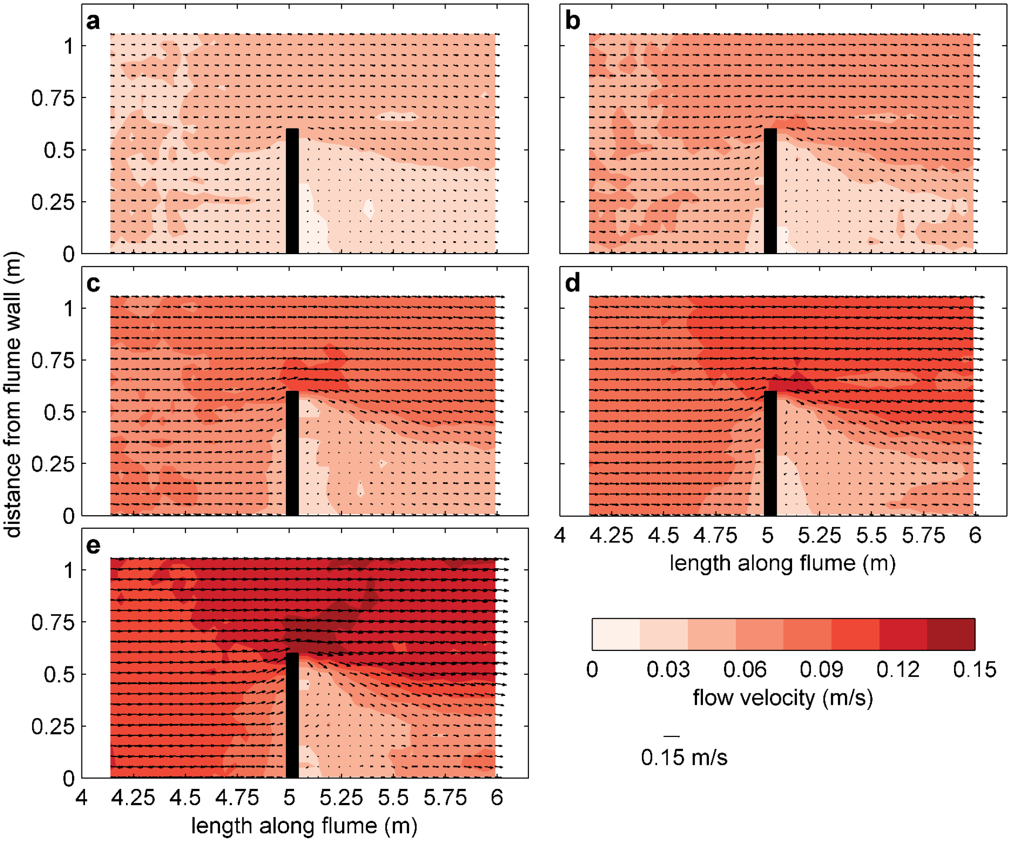

**FIGURE 4** Time-averaged flow velocity from the course grid flow measurements, for the discharge conditions: (a) I (0.04 m/s), (b) II (0.06 m/s), (c) III (0.08 m/s), (d) IV (0.10 m/s), and (e) V (0.12 m/s). The flow vectors show the time-averaged horizontal flow direction. The length of the flow vectors represents the magnitude of the time-averaged flow velocity

## RESULTS

### Leaf patch monitoring

Figure 3 shows the results of the temporal evolution of the leaf patch cover. The leaf patches developed towards a stable equilibrium within 75 min of each experiment. The results from flow condition III differ from this observation and showed more variation among the 15 replicates compared to flow conditions I, II, IV, and V. Figure 3 clearly shows that leaf patch cover developed towards distinct equilibrium values, ranging from 95% cover for flow condition I to 20% for flow condition V.

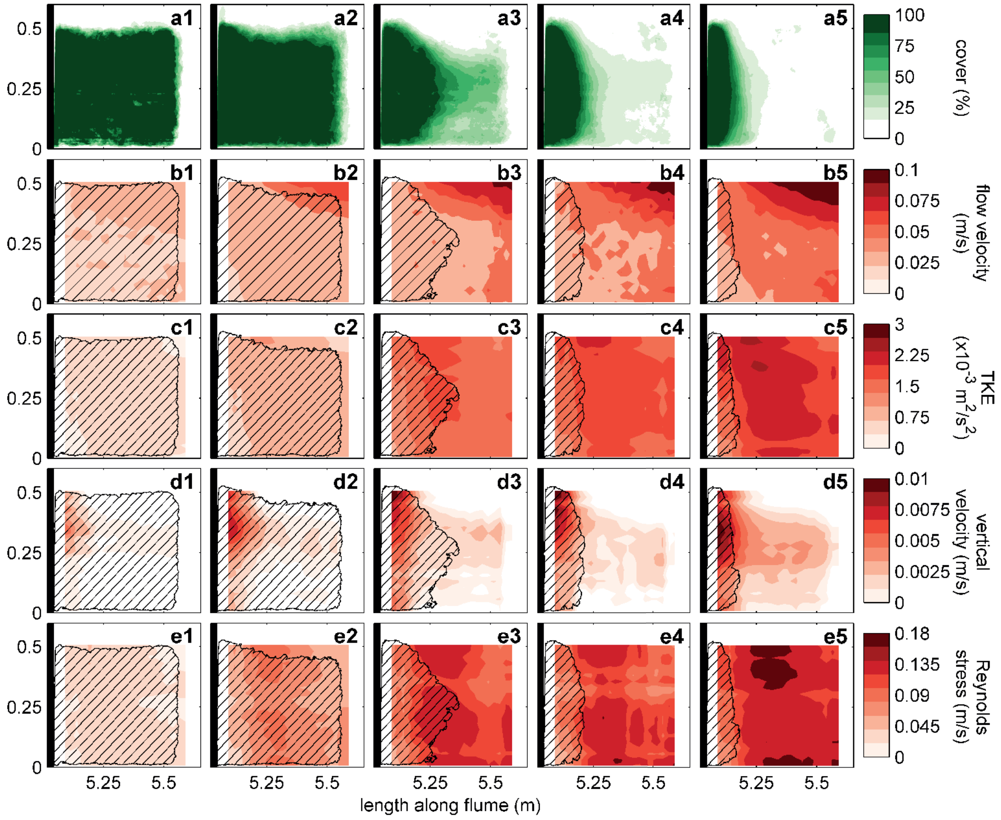

**FIGURE 5** (a) Average (n = 15) leaf cover percentage at the end of the 75-min test runs. (b–e) Detailed flow velocity measurements in the test section, with (b) the time-averaged flow velocity, (c) turbulence kinetic energy (TKE), (d) vertical flow velocity, and (e) Reynolds stress. The shaded area indicates the average leaf cover percentage obtained from the upper panels (a). Indices 1–5 correspond to discharge conditions I (0.04 m/s), II (0.06 m/s), III (0.08 m/s), IV (0.10 m/s), and V (0.12 m/s)

### Flow conditions

Figure 4 shows the results of the course grid flow measurements. The figure shows that under each flow condition, the near uniform flow upstream of the wooden obstacle was deflected by the wood. Near–bed flow velocities downstream of the wood decreased in the test section and created a wake. The flow velocity increased at the tip of the wood, from which a mixed flow expanded downstream and directed towards the side of the channel at an angle of 45° to 85° until it was deflected by the wall. The collision with the wall created a flow towards the wood and circulation, due to interaction with the flow of the water streaming over the wood. The area downstream of the wooden obstacle can be considered a still water zone because of the relatively low flow velocities. However, the test section still showed a wide spectrum of flow velocities.

### Spatial leaf cover in relation to flow conditions

Figure 5 shows the results of the leaf patch monitoring and the detailed–grid flow velocity measurements in the test section. Figure 5a shows the average cover percentage at the end of each experiment. The figure shows that the leaf patches developed towards a stable equilibrium, where size and shape depended on the flow condition, in agreement with the observations on the temporal leaf patch development (Fig. 3). Only the results from flow condition III differed from this observation. In general, most leaves entrained in the mixing layer that extends diagonally downstream from the tip of the wood towards the flume wall. Leaves were most stable in the area near the wood. When visually comparing the final leaf cover and the flow velocity results, it becomes apparent that the time–averaged near–bed flow velocities were consistently low directly downstream of the wood where the leaves accumulated and highest at the downstream end of the test section where the leaves entrained, regardless of discharge (Fig. 5b). Most of the sites where leaves entrained had a relatively high average flow velocity (Fig. 5b), TKE (Fig. 5c), and Reynolds stress (Fig. 5e). Leaf patches were more stable at locations with high vertical flow velocities (Fig. 5d).

### Entrainment conditions

The results obtained from Figure 5 allowed us to relate the final leaf cover to the flow velocity derivatives. From Figure 5a, we obtained the leaf cover at each location where the detailed flow velocity measurements were taken and related these leaf covers to the time–averaged flow velocity, TKE, vertical flow velocity, and Reynolds stress (Fig. 6 and 7). The most consistent relationship was obtained for the time–averaged flow velocity (Fig. 6). A P–spline was fitted to the results of the time–averaged flow velocity (Fig. 6). The P–spline shows a clear entrainment range of near–bed flow velocities: 0.037–0.050 m/s. Leaf cover was high at near–bed flow velocities under the stability threshold (0.037 m/s) and low when the drift threshold was exceeded (0.050 m/s; Tab. 2). The other flow velocity derivatives, that is, TKE, vertical flow velocity, and Reynolds stress, resulted in scattered leaf cover percentages, thus poorly explaining leaf cover (Fig. 7).

**TABLE 2** The near-bed entrainment flow velocity range of beech leaves determined using the Bayesian P-spline method

| | Coverage (%) | U (m/s) | Credible interval |
|---|---|---|---|
| Stability threshold | 85 | 0.0371 | (0.0366-0.0375) |
| Median | 50 | 0.0429 | (0.0424-0.0434) |
| Drift threshold | 15 | 0.0497 | (0.0492-0.0502) |

*Note*. The low end of the range is the stability threshold and the high end is the entrainment threshold

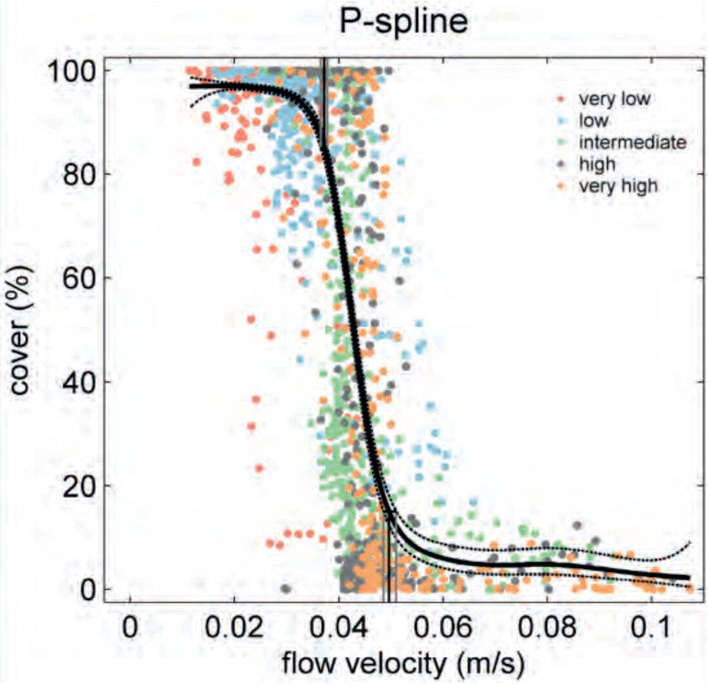

**FIGURE 6** Regression curve (P-spline) to relate the final leaf cover percentage to the time-averaged flow velocity. The straight black lines in contact with the spline at 15% and 85% cover correspond to the boundaries of the entrainment flow velocity range

## DISCUSSION

In this study on leaf entrainment, we showed that near–bed flow velocities better explain leaf patch stability than basic turbulence properties. We defined an entrainment range of near–bed flow velocities between 0.037 to 0.050 m/s. The mean near–bed flow velocity, given the narrow entrainment flow velocity range, proved to be the best indicator of leaf patch stability. Moreover, these entrainment values of near–bed flow parameters can potentially be extrapolated to any lotic waterbody and help to describe and predict stability of leaf patches in natural streams.

Near–bed flow velocity is thus a promising variable to determine conditions for leaf retention, because it induces shear stress forcing on bed load (Nezu & Nakagawa, 1993). The distance from the bed up to which the vertical velocity profile can be described by the law of the wall, implying it to be logarithmic, will be limited in a wake region as created in the experiments. Consequently, we cannot easily infer a depth–averaged flow velocity threshold for leaf entrainment. Strictly speaking, our results on leaf stability require flow velocities at 0.03 m/s above the bed, to be applied. Despite this, the corresponding cross–sectional–averaged velocities for the experiments offer an indication of the range of flow velocities for which leaves may be expected to be cleared from lowland streams.

The physical approach based on driving hydraulic forcing and stabilizing forcing of sediment enabled engineers to produce mathematical models that predict hydraulic and morphologic processes (reviewed in Dey & Papanicolaou, 2008). An analogous approach may seem feasible to explain entrainment of leaves. However, it is not trivial to define a threshold for incipient motion of leaves due to

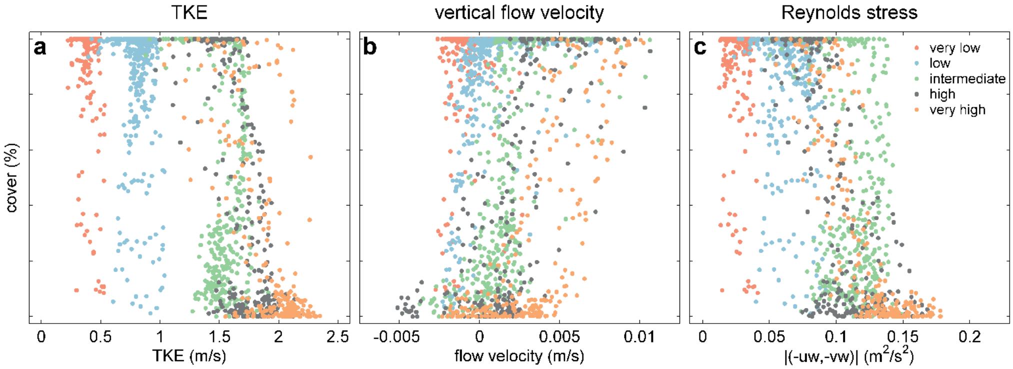

**FIGURE 7** Final leaf cover percentage plotted against flow velocity derivatives: (a) turbulence kinetic energy (TKE), (b) vertical flow velocity, and (c) Reynolds stress

the stochastic nature of entrainment events. Even in sediment transport, particle properties pose difficulty to modelling accuracy, because grains always have some deviation from perfect spheres (Bridge & Bennett 1992, Papanicolaou et al. 2008). Compared to sediment grains, leaves include more complex properties, such as the shape, size, orientation, variable density, stage of decay, and colonization of periphytic diatoms (Hoover et al. 2010, Kochi et al. 2009, Statzner et al. 1988, Steart et al. 2002). The current study shows that mean flow velocities are a better indicator for leaf patch stability than more complex hydraulic parameters. TKE, vertical flow velocity, and Reynolds stress explained the leaf cover poorly, despite their undisputed influence on the entrainment process and the stability of single leaves. Patterns of TKE, vertical flow velocity, and Reynolds stress in the test section differed from patterns of the main flow. In some areas of the grid, a substantial Reynolds stress occurred, despite low mean flow velocities. The leaves can be lifted in such areas without being transported elsewhere, or lifted and dragged towards a more stable area of the wake. In this fashion, the physical flow parameters have a direct effect on leaves without correlating to leaf cover. Only when leaves would be dragged towards the instable edge of the wake Reynolds stress would contribute to a lower leaf cover.

The choice of metrics quantifying the effect of turbulence was restricted to basic descriptors, which can readily be inferred from numerical flow models. Possibly, more complex metrics quantifying accelerations during mutually dissimilar, evanescent turbulent flow events may outperform the mean flow as a predictor for entrainment. Also, the metrics capturing the three-dimensional aspects of the flow may be considered. However, it is likely that such metrics will heavily depend on details of the set-up of the experiment, including leaf type, sediment characteristics, and geometry of the wooden obstacle. Hence, a generic, robust metric that outperforms the predictive capacity of the mean flow is yet to be identified.

Previous studies have presented flow conditions in wakes downstream of obstacles. For example, increased flow velocities in the mixed flow layer directing downstream from the tip of the wood is a phenomenon previously observed near groynes (McCoy et al. 2008; Uijttewaal 2005, Weitbrecht et al. 2008). Studies that showed different flow patterns in wakes behind obstacles used multiple obstacles that caused mixed flow and flow circulation (Brevis et al. 2014, McCoy et al. 2008, Sukhodolov, 2014, Uijttewaal et al. 2001, Weitbrecht et al. 2008). Shape, permeability, and the level of emergence or submergence of obstacles influence the flow field within the wake (Sukhodolov 2014, Uijttewaal 2005). Studies that used submerged single obstacles, or presented flow data of wakes of the last obstacle in line, showed a similar pattern of horizontal flow velocity vectors, despite different dimensions and characteristics of the obstacle, that is, a mixed flow layer towards the side of the channel and a still water zone behind the obstacle (McCoy et al. 2007, Yeo & Kang 2008). Likewise, in the current study, we showed that near–bed flow velocities in the still water zone increases with discharge, as expected, but an area of low flow remained near the wood at all flow conditions allowing the retention of leaf patches.

Our observations thus stress the importance of obstacles for leaf retention, similar to earlier studies that showed how structures contribute to leaf retention during low and high flows, that is, leaves retain in heterogeneous environments (Canhoto & Graça 1998, Hoover et al. 2006, Hoover et al. 2010, Koljonen et al. 2012, Young et al. 1978). Quantified measurements of the flow behind the wood showed that the deflected flow creates a wake of low flow, directed towards the wood. Leaf patches remain locally stable in the low flow areas, regardless of bulk flow conditions. This way, dynamic stream environments that have heterogeneous bed texture and complex structures sustain leaves in a mosaic on the bed sediment, even when cross–sectional–averaged flow velocities exceed entrainment thresholds for leaves.

### Implications for leaf retention

The conditions used in the experiment coincide with conditions found in lowland streams, where leaves are an important food source for macroinvertebrates (Verdonschot et al. 1995). The average flow velocity in natural lowland streams is in the average range of 0.2–0.3 m/s (Tolkamp 1980, Verdonschot, 1995) with frequent low flows down to almost zero and possible high flows up to 0.8 m/s. Channel and catchment modifications in the 20th century, such as channelization, increase of channel dimensions, and increased drainage density, had major consequences for flow velocity patterns (Verdonschot et al. 1995) and caused the discharge to become increasingly flashy (Meijles & Williams 2012). The channel bed of disturbed streams are often homogeneous and are therefore characterized by a uniform flow velocity, causing a low coverage of organic matter (Feld 2013). Restoration measures aim to improve the ecological status of streams, decrease peak discharges, and increase spatial heterogeneity of the channel bed (Eekhout et al. 2015).

The low observed entrainment flow velocity range for stable leaf patches indicates that most leaf coverage is temporary. In morphologically homogeneous streams, the slightest flow velocity increase would thus induce entrainment. The majority of leaves are homogeneous streams with a flashy hydrograph, where leaves would entrain en masse. Moreover, wood and plant removal, often used to “clean” streams, further reduces the structural complexity of the channel bed (Bilby & Ward 1991, Buffington & Montgomery 1997). In contrast, wood addition can restore bed complexity (Davidson & Eaton 2013) and is a promising restoration measure for streams. Adding obstacles to streams can enhance organic matter storage and macroinvertebrate abundance (Negishi & Richardson 2003). Our study shows that obstacles are needed to create local zones of fast flow in combination with still water zones, where leaf patches may retain.

## CONCLUSION

Here, we presented the results of a laboratory experiment on the stability of leaf patches under various flow conditions. The flow was disturbed by a wooden obstacle, which caused the formation of a wake. Our study showed that local stability of a leaf patch and wake size relates to mean flow conditions here measured at 0.03 m above the bed. Cross flow velocity, however, does not explain the spatial coverage in a steady state. Focussing on spatial patterns of cover, our study showed that time–averaged near–bed flow velocity corresponded better to leaf patch cover than more complex flow properties such as TKE, vertical flow velocity, and Reynolds stress. We observed that leaf entrainment occurs within the near–bed flow velocity range of 0.037 to 0.050 m/s. Flow velocities remained stable and low downstream of the wooden obstacle. The low entrainment range and the formation of wakes downstream of the wooden obstacle illustrate the importance of in–stream structures for stable leaf patches in natural environments. Adding instead of removing obstacles may therefore be a key strategy in restoring biodiversity in deteriorated streams.

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## REFERENCES

Abelho M. 2001. From litterfall to breakdown in streams: a review. The Scientific World Journal 1: 656–680.

Brevis W, García-Villalba M, Niño Y. 2014. Experimental and large eddy simulation study of the flow developed by a sequence of lateral obstacles. Environmental Fluid Mechanics 14: 873–893.

Biggs BJF, Smith RA, Duncan MJ. 1999. Velocity and sediment disturbance of periphyton in headwater streams: biomass and metabolism. Journal of the North American Benthological Society 18: 222–241.

Bridge JS, Bennett SJ. 1992. A model for the entrainment and transport of sediment grains of mixed sizes, shapes, and densities. Water Resources Research 28: 337–363.

Brookshire ENJ, Dwire KA. 2003. Controls on patterns of coarse organic particle retention in headwater streams. Journal of the North American Benthological Society 22: 17–34.

Buffington JM, Montgomery DR. 1997. A systematic analysis of eight decades of incipient motion studies, with special reference, to gravel-bedded rivers. Water Resources Research 33: 1993–2029.

Bunn SE, Arthington AH. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. Environmental Management 30: 492–507.

Canhoto C, Graça MAS. 1998. Leaf retention: a comparative study between two stream categories and leaf species. Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie 26: 990–993.

Canhoto C, Graça MAS. 1996. Decomposition of Eucalyptus globulus leaves and three native leaf species (Alnus glutinosa, Castanea sativa and Quercus faginea) in a Portuguese low order stream. Hydrobiologia 333: 79–85.

Clark JM, Lane SN, Chapman PJ, Adamson JK. 2007. Export of dissolved organic carbon from an upland peatland during storm events: implications for flux estimates. Journal of Hydrology 347: 438–447.

Cordova JM, Rosi-Marshall EJ, Tank JL, Lamberti GA. 2008. Coarse particulate organic matter transport in low-gradient streams of the Upper Peninsula of Michigan. Journal of the North American Benthological Society 27: 760–771.

Cummins KW. 1973. Trophic relations of aquatic insects. Annual Review of Entomology 18: 183–206.

Daniels MD, Rhoads BL. 2004. Effect of large woody debris configuration on three-dimensional flow structure in two low-energy meander bends at varying stages. Water Resources Research 40: W11302

Davidson S.L. & Eaton B.C. (2013) Modeling channel morphodynamic response to variations in large wood: Implications for stream rehabilitation in degraded watersheds. Geomorphology 202: 43–50.

Dey S, Papanicolaou A. 2008. Sediment threshold under stream flow: A state-of-the-art review, KSCE Journal of Civil Engineering 12: 45–60.

Ehrman TP, Lambert GA. 1992. Hydraulic and particulate matter retention in a 3rd-order Indiana stream. Journal of the North American Benthological Society 11: 341–349.

Feld CK. 2013. Response of three lotic assemblages to riparian and catchment-scale land use: implications for designing catchment monitoring programmes. Freshwater Biology 58: 715–729.

Fisher SG, Likens GE. 1973. Energy flow in Bear Brook, New Hampshire: An integrative approach to stream ecosystem metabolism. Ecological Monographs 43: 421–439.

Gorecki VI, Fryirs KA, Brierley GJ. 2006. The relationship between geomorphic river structure and coarse particulate (CPOM) storage along the Kangaroo River, New South Wales, Australia. Australian Geographer 37: 285–311.

Graça MAS. 2001. The role of invertebrates on leaf litter decomposition in streams – a review. International Review of Hydrobiology 86: 383–393.

Grimm NB, Fisher SG. 1984. Exchange between interstitial and surface water: implications for stream metabolism and nutrient cycling. Hydrobiologia 111: 219–228.

Hart DD, Finelli CM. 1999. Physical-biological coupling in streams: The pervasive effects of flow on benthic organisms. Annual Review of Ecology and Systematics 30: 363–395.

Hoover TM, Richardson JS, Yonemitsu N. 2006. Flow substrate interactions create and mediate leaf litter resource patches in streams. Freshwater Biololgy 51: 435–447.

Hoover TM, Marczak LB, Richardson JS, Yonemitsu N. 2010. Transport and settlement of organic matter in small streams. Freshwater Biology 55: 436–449.

Hynes HBN. 1970. The ecology of running waters. Liverpool University Press, Liverpool, UK.

James ABW, Henderson IM. 2005. Comparison of coarse particulate organic matter retention in meandering and straightened sections of a third-order New Zealand stream. River Research and Applications 21: 641–650.

Kemp JL, Harper DM, Crosa GA. (2000) The habitat-scale ecohydraulics of rivers. Ecological Engineering 16: 17–29.

Kobayashi S, Kagaya T. 2004. Litter patch types determine macroinvertebrate assemblages in pools of a Japanese headwater stream. Journal of the North American Benthological Society 23: 78–89.

Kobayashi S, Kagaya T. 2005. Hot spots of leaf breakdown within a headwater stream reach: comparing breakdown rates among litter patch types with different macroinvertebrate assemblages. Freshwater Biology 50: 921–929.

Kochi K, Asaeda T, Chibana T, Fujino T. 2009. Physical factors affecting the distribution of leaf litter patches in streams: comparison of green and senescent leaves in a steppool streambed. fHydrobiologia 628: 191–201.

Koljonen S, Louhi P, Mäki-Petäys A, Huusko A, Muotka T. (2012) Quantifying the effects of in-stream habitat structure and discharge on leaf retention: implications for stream restoration. Freshwater Science 31: 1121–1130.

Lancaster J, Hildrew AG. 1993. Characterizing in-stream flow refugia. Canadian Journal of Fisheries and Aquatic Sciences 50: 1663–1675.

Lancaster J, Belyea LR. 1997. Nested hierarchies and scale-dependence of mechanisms of flow refugium use. Journal of the North American Benthological Society 16: 221–238.

Lancaster J. 2008. Movement and dispersion of insects in streamchannels: what role does flow play? In Aquatic Insects: Challenges to Populations, Lancaster J, Briers RA (eds). CAB International: Wallingford: 139–157.

Lancaster J, Downes BJ. 2010. Linking the hydraulic world of individual organisms to ecological processes: Putting ecology into ecohydraulics. River Research and Applications 26: 385–403.

Larrañaga S, Díez JR, Elosegi A, Pozo J. 2003. Leaf retention in streams of the Agüera basin (northern Spain). Aquatic Sciences 65: 158–166.

Li AOY, Dudgeon D. 2011. Leaf litter retention in tropical streams in Hong Kong. Fundamental and Applied Limnology 178: 159–170.

McCoy A, Constantinescu G, Weber L. 2007. A numerical investigation of coherent structures and mass exchange processes in channel flow with two lateral submerged groynes, Water Resources Research 43: W05445.

McCoy A, Constantinescu G, Weber L. 2008. Numerical Investigation of Flow Hydrodynamics in a Channel with a Series of Groynes. Journal of Hydraulic Engineering 134, 157–172.

Manga M, Kirchner JW. 2000. Stress partitioning in streams by large woody debris. Water Resources Research 36: 2373–2379.

Manners RB, Doyle MW, Small MJ. 2007. Structure and hydraulics of natural woody debris jams. Water Resources Research 43: W06432.

Meijles EW, Williams A. 2012. Observation of regional hydrological response during time periods of shifting policy, Applied Geography 34: 456–470

Nakajima T, Asaeda T, Fujino T, Nanda A. 2006. Coarse particulate organic matter distribution in the pools and riffles of a second-order stream. Hydrobiologia 559: 275–283.

Negishi JN, Richardson JS. 2003. Responses of organic matter and macroinvertebrates to placements of boulder clusters in a small stream of southwestern British Columbia, Canada. Canadian Journal of Fisheries and Aquatic Sciences 60: 247–258.

Nezu I, Nakagawa H. 1993. Turbulence in Open-Channel Flows, Balkema, Rotterdam, The Netherlands.

Papanicolaou AN, Elhakeem M, Krallis G, Prakash S, Edinger J. 2008. Sediment transport modeling review—Current and future developments. Journal of Hydraulic Engineering 134: 1–14.

Poff NL, Allan JD, Bain MB, Karr JR, Prestegaard KL, Richter BD, Sparks RE, Stromberg JC. 1997. The natural flow regime. Bioscience 47: 769–784.

Poff NL, Olden JD, Merritt DM, Pepin DM. 2007. Homogenization of regional river dynamics by dams and global biodiversity implications. Proceedings of the National Academy of Sciences of the United States of America 104: 5732–5737.

Richardson JS. 1992. Food, microhabitat, or both? Macroinvertebrate use of leaf accumulations in a montane stream. Freshwater Biology 27: 169-176.

Richardson JS, Bilby RE, Bondar CA. 2005. Organic matter dynamics in small streams of the Pacific Northwest. Journal of the American Water Resources Association 41: 921–934.

Richardson JS, Zhang YX, Marczak LB. 2010. Resource subsidies across the land freshwater interface and responses in recipient communities. River Research and Applications 26: 55–66.

Rowe L, Richardson JS. 2001. Community responses to experimental food depletion: resource tracking by stream invertebrates. Oecologia 129: 473–480.

Speaker R, Moore K, Gregory S. 1984. Analysis of the process of retention of organic matter in stream ecosystems. Verhandlungen der Internationalen Vereinigung fúr Theoretische und Angewandte Limnologie 22:1835–1841.

Statzner B, Gore JA, Resh VH. 1988. Hydraulic stream ecology: observed patterns and potential applications. Journal of the North American Benthological Society 7: 307–360.

Statzner B. 2008. How views about flow adaptations of benthic stream invertebrates changed over the last century. International Review of Hydrobiology 93: 593–605.

Steart DC, Boon PI, Greenwood DR, Diamond NT. 2002. Transport of leaf litter in upland streams of Eucalyptus and Nothofagus forests in southeastern Australia. Archiv für Hydrobiologie. 156. 43–61.

Sukhodolov NA. 2014. Hydrodynamics of groyne fields in a straight river reach: insight from field experiments. Journal of Hydraulic Research. 52: 105–120.

Tank JL, Rosi-Marshall EJ, Griffiths NA, Entrekin SA, Stephen ML. 2010. A review of allochthonous organic matter dynamics and metabolism in streams. Journal of the North American Benthological Society 29: 118-146.

Trodden LRB. 2012. Local physical and hydraulic factors affecting leaf retention within streams. PhD Thesis, Cardiff University.

Tolkamp HH. 1980. Organism-substrate relationships in lowland streams. PhD Thesis, Wageningen University, Wageningen: 211 pp.

Uijttewaal WSJ. 2005. The effects of groyne layout on the flow in groyne fields: Laboratory experiments. Journal of Hydraulic Engineering 131: 782–791.

Uijttewaal WSJ, Lehmann D, van Mazijk A. 2001. Exchange processes between a river and its groyne fields: Model experiments. Journal of Hydraulic Engineering 127: 928–936.

Verdonschot PFM. 1995. Typology of macrofaunal assemblages: a tool for the management of running waters in The Netherlands. Hydrobiologia 297: 99–122

Verdonschot PFM, Driessen O, van der Hoek W, de Klein J, Paarlberg A, Schmidt G, et al. (1995) Beken stromen: Leidraad voor ecologisch beekherstel, Tech. rep., STOWA, Utrecht.

Verdonschot PFM, Nijboer RC. 2002. Towards a decision support system for stream restoration in the Netherlands: An overview of restorationprojects and future needs. Hydrobiologia 478: 131–148.

Sukhodolov AN. 2014. Hydrodynamics of groyne fields in a straight river reach: insight from field experiments. Journal of Hydraulic Research 52: 105-120

Sylvestre S, Bailey RC. 2005. Ecology of leaf pack macroinvertebrate communities in streams of the Fraser River Basin, British Columbia. Freshwater Biology 50: 1094–1104.

Wallace JB, Whiles MR, Eggert SE, Cuffney TF, Lugthart GJ, Chung K. 1995. Long-term dynamics of coarse particulate organic matter in three southern Appalachian streams. Journal of the North American Benthological Society 14: 217-232.

Wallace JB, Eggert SL, Meyer JL, Webster JR. 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. Science 277: 102–104.

Webster JR, Benfield EF, Ehrman TP, Schaeffer MA, Tank JL, Hutchens JJ et al. 1999. What happens to allochthonous material that falls into streams? A synthesis of new and published information from coweeta. Freshwater Biology 41: 687–705.

Webster JR, Benfield EF, Golladay SW, Hill BH, Hornick LE, Kazmierczak RF, et al. 1987. Experimental studies of physical factors affecting seston transport in streams. Limnology Oceanographer 32: 848-863.

Webster JR, Meyer JL. 1997. Organic matter budgets for streams: a synthesis. Journal of the North American Benthological Society 16:141–161.

Weitbrecht V, Socolofsky SA, Jirka GH. 2008. Experiments on mass exchange between groin fields and the main stream in rivers. Journal of Hydraulic Engineering 134: 173–183.

Young SA, Kovalak WP, Del Signore KA. 1978. Distances travelled by autumn-shed leaves introduced into a woodland stream. American Midland Naturalist 100: 217–222.

Yeo HK, Kang JG. 2008. Flow analysis around a submerged groyne. Proceedings of 16th IAHR-APD Congress and 3rd Symposium of IAHR-ISHS: 1762-1766. Beijing: Tsinghua University Press.

## SUPPLEMENTARY APPENDIX

### Appendix I: Bayesian P-splines

The relationship between leaf cover c and average flow velocity was investigated by first transforming the cover % by the logistic transformation y =logc/100-c. This opens up the bounded scale 0-100 of cover. A linear regression of transformed cover y against x and transforming the fitted values back to the percentage scale gave a bad fit. We thus needed a more flexible curve-fitting approach. We chose the penalized spline P-spline approach (Eilers & Marx 1996). In this approach the flexibility is governed by the penalty parameter, with higher penalty giving curves that are smoother and closer to the straight line. We used a Bayesian method to estimate the penalty parameter and fitted a Bayesian P-spline (Lang and Brezger 2004) by integrated nested Laplace approximation (Rue et al. 2009) to the full Bayesian model as implemented in the INLA R package (Rue et al. 2014) and a dedicated R-function available upon request. We used as prior distribution for the penalty parameter a type 2 Gumbel distribution with parameter λ=3 (Martins et al. 2014). The result turned out to be very insensitive to choice of the prior distribution, which is as expected, because there are many data points. Bayesian P-splines average over the posterior distribution of the penalty instead of fitting these once by mixed models/marginal maximum likelihood MML or empirical Bayes. This Bayesian procedure better acknowledges the uncertainty in the smoothing parameters than MML and the uncertainty bands credible intervals around the curves incorporate this uncertainty. We estimated 95% credible intervals for the expected response and transformed fit and intervals back to the cover percentage scale.

### References

Jongman RHG, ter Braak CJF, van Tongeren OFR. 1995. Data analysis in community and landscape ecology. Cambridge University Press, Cambridge.

Eilers PHC, Marx BD. 1996. Flexible smoothing with B-splines and penalties. Statistical Science 1: 89-121.

Martins TG, Simpson DP, Riebler A, Rue H. 2014. Penalising model component complexity: A principled, practical approach to constructing priors. arXiv 1403.4630v2.

Marx BD, Eilers PHC. 1998. Direct generalized additive modeling with penalized likelihood. Computational Statistics & Data Analysis 28: 193-209

Lang S, Brezger A. 2004 Bayesian P-splines. Journal of Computational and Graphical Statistics 13: 183-212.

Rue H, Martino S, Chopin N. 2009. Approximate Bayesian inference for latent Gaussian models by using integrated nested Laplace approximations. Journal of the Royal Statistical Society: Series B (Statistical Methodology) 71: 319-392.

Rue H, Martino S, Lindgren F, Simpson D, Riebler ATK. 2014. INLA, functions which allow to perform full Bayesian analysis of latent Gaussian models using Integrated Nested Laplace Approximaxion. http://www.r-inla.org/:version 0.0-1396629476.

## Appendix II: Formula S-curve

Logistic function: $$LF(x) = \frac{98.62}{1+\left(\frac{x}{0.04271}\right)^{8.247}}$$

5% CI: $$LF(x) = \frac{96.25}{1+\left(\frac{x}{0.04220}\right)^{9.155}}$$

95% CI: $$LF(x) = \frac{101}{1+\left(\frac{x}{0.04322}\right)^{7.339}}$$

## Appendix III: Results extended runs at intermediate the discharge condition

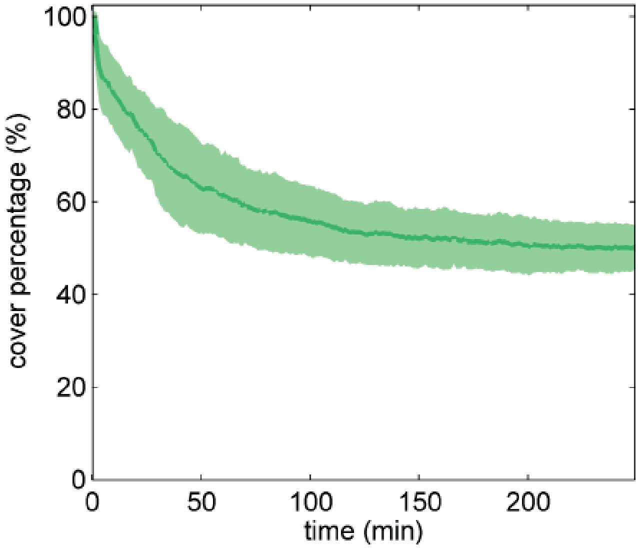

**FIGURE 1** Extended temporal evolution (250 min) of the average (n = 15) leaf cover percentage and standard deviation in the test section for the intermediate discharge condition

# 5

## CHAPTER 5

# MORPHOLOGICAL ASSESSMENT OF RECONSTRUCTED LOWLAND STREAMS IN THE NETHERLANDS

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Eekhout JPC, AJF Hoitink, JHF de Brouwer, PFM Verdonschot

## ABSTRACT

Channelisation measures taken halfway the 20th century have had destructive consequences for the diversity of the ecology in the majority of the lowland streams in countries such as the Netherlands. Re-meandering is the common practice in restoring these lowland streams. Three reconstructed streams were monitored during the initial two years after construction of a new channel. The monitoring program included morphological surveys, sediment sampling, habitat pattern surveys, and discharge and water level measurements. Adjustments of the longitudinal bed profile formed the main morphological response. These adjustments were most likely caused by a lack of longitudinal connectivity of the streams as a whole, interrupting transport of sediment at locations of weirs and culverts. Bank erosion was observed only in a limited number of channel bends, and was often related to floodplain heterogeneity. Longitudinal channel bed adjustments and bank erosion were mainly caused by exogenous influences. In channel bends, the cross-sectional shape transformed from trapezoidal to the typical asymmetrical shape as found in meandering rivers. This behaviour can be attributed to an autogenous response to the prevailing flow conditions. Due to the prevailing fine sediment characteristics, bed material is readily set in motion and is being transported during the entire year. The existing design principles fail to address the initial morphological development after reconstruction. An evaluation of pre-set targets to realise water depth and flow velocity ranges shows the current procedures to be deficient. Based on this unfavourable evaluation, and the two-dimensional nature of habitat patterns needed to improve the conditions for stream organisms, we recommend to predict morphological developments as part of the design procedures for lowland stream restoration in the Netherlands.

*Keywords:* Stream restoration, Lowland streams, Morphodynamics, Re-meandering, Water management

# INTRODUCTION

## Lowland stream degradation

Halfway the 20th century, groundwater management in agricultural areas led to channelisation of a vast number of lowland streams in densely populated agricultural areas. The design of the straightened streams aimed at reducing flood risk and meeting the hydrological requirements for the adjacent agricultural fields. To achieve these requirements, the straightened streams were redesigned to obtain an increased cross-sectional area and to become controlled by weirs. During this period, the drainage density within lowland catchments also increased through the construction of ditches. All these measures were aimed at a fast discharge response during high flows, whereas weirs were in control of groundwater levels during low flows. These measures have seriously affected the hydrological conditions in catchments in the Netherlands (Meijles & Williams 2012). Similar channelisation measures of lowland streams were implemented in Denmark (Brookes 1987, Iversen et al. 1993, Baatrup-Pedersen et al. 2000), Germany (Lorenz et al. 2009), Japan (Nakano & Nakamura 2008), and the UK (Vivash et al. 1998).

The channel modifications of lowland streams in the Netherlands had destructive consequences for the abiotic conditions within the stream and for the stream valley ecosystems (Verdonschot & Nijboer 2002). The construction of straight channelised streams resulted in homogeneous in-channel habitat patterns, often solely consisting of bare sand. In an extensive survey, Verdonschot et al. (1995) conclude that the measures (channelisation, increase of channel dimensions and increase of drainage density) had major consequences for flow velocity, being the key variable of the abiotic environment relevant in running water ecosystems (Fonseca & Hart 2001). During low flows, weirs were closed to increase groundwater levels. This caused flow velocities to drop to nearly zero and fine sediment (e.g. silt) to be deposited on the channel bed. During high flows, weirs were lowered and flow velocities increased dramatically. Eventually, this has caused channel incision and the disappearance of heterogeneous instream habitat patterns. In particular, coarse substrates, such as large woody debris and gravel, were lost (Brookes & Gregory 1988). The homogeneous channel beds consisting of fine sediment in combination with high flow velocities during high discharge events were detrimental for the existing stream organisms. Furthermore, the groundwater management had detrimental effects on the terrestrial stream valley ecosystems.

## Morphological processes in lowland streams

Only a few studies have been presented in the literature focussing on morphological processes in lowland streams. These studies mainly focus on the morphological development after stream restoration measures were implemented in lowland streams. Wolfert (2001) presented the most extensive morphological study on lowland stream restoration in the Netherlands to date. Three reconstructed streams, located in the southern part of the Netherlands, were monitored over a period of two years. Wolfert (2001) showed that the largest sediment production rates were associated with the first bankfull discharge event, which occurred in the first year after construction. Adjustment of the channel bed included local scouring of pools, undercutting of banks, coarsening of bed material and the formation of depositional bedforms. Following the initial morphological response, rates of sediment production declined and the balance of sediment input and output was restored. Similar observations have been made in lowland stream restoration projects in the UK (Sear et al. 1998) and the US (Lindow et al. 2007). These findings confirm the results by Kuenen (1944), who studied the meandering dynamics of several lowland streams in the northern part of the Netherlands. Kuenen (1944) concluded that the majority of streams did not show signs of lateral migration.

The channel bed of lowland streams mainly consists of sand. In natural streams, a mosaic of substrate patterns has been observed covering the sand bed (Tolkamp 1980). The variety of substrates include gravel, leaves, branches, large woody debris and coarse and fine organic detritus. Tolkamp (1980) showed that the substrate pattern is dynamic over time, with distinct differences between the four seasons. Macrophytes are frequently observed in non-shaded lowland streams (Pedersen et al 2006). When macrophytes are present, they can have a strong control over the dynamics of the substrate pattern, by capturing fine sediments (Wolfert 2001, Lorenz et al. 2009) and by reducing the active channel width (Lindow et al. 2007).

## Stream restoration in the Netherlands

The vast majority (96%) of lowland streams in the Netherlands are severely impacted by anthropogenic influences (Nienhuis et al. 2002, Verdonschot & Nijboer 2002), reflecting the need for stream restoration. Wohl et al. (2015) defines stream restoration as: “assisting the establishment of improved hydrologic, geomorphic, and ecological processes in a degraded watershed system and replacing lost, damaged, or compromised elements of the natural system”. An important element of this definition is the focus on the catchment scale. Recently, several stream restoration concepts have been presented focussing on catchment scale measures, such as the ‘erodible corridor’ (Piégay et al. 2005) and ‘espace de liberté' (Kondolf et al. 2012). Until now, stream restoration has mainly taken place adopting reach scale measures (Sudduth et al. 2007, McMillan & Vidon 2014). The common practice in the Netherlands is no exception to this.

Stream restoration in the Netherlands has largely been triggered by the Water Framework Directive (WFD; 2000/60/EC), in which it is stated that all water bodies should achieve a good quality ecological status by 2015, with extensions until 2027. The main objective of stream restoration in the Netherlands is to improve the ecological status. The second objective is to increase the retention of water within the catchment, which follows from the National Water Act (WB21; 2000) Other objectives are related to hydrological conditions, to prevent groundwater damage to crops on agricultural fields and to assure wetland conditions of natural areas, and recreation, to combine measures with an increase of recreational facilities.

Most often, stream restoration in the Netherlands involves the construction of sinuous channels (re-meandering), mimicking the channel planform characteristics before channelisation. The sinuous planform is often based on historical sources. Re-meandering has been widely adopted as a stream restoration measure (e.g., Lorenz et al. 2009, Sear 1998, Kondolf 2006). Positive effects on the habitat diversity have been reported after re-meandering measures were implemented (Lorenz et al. 2009). Re-meandering or other channel reconfiguration measures are often applied at a local scale, in isolated channel reaches. Locally, these measures may be successful in improving the habitat conditions, but recovering the typical stream assemblages may only be successful when taking measures at

**TABLE 1** Hydrological and ecological constraints for the design of the three stream restoration projects. Not all constraints were used in each stream restoration project. The constraints that were not used are denoted with n/a (not available)

| | Period | Hagmolenbeek | Lunterse beek | Tungelroyse beek |
|---|---|---|---|---|
| *Hydrological constraints* | | | | |
| Inundation frequency (days yr$^{-1}$) | | 10-20 | 160-200 | <100 |
| Groundwater level (m - Surface elevation) | Summer | n/a | 1 | n/a |
| | Spring | n/a | n/a | 0.50-0.80 |
| | Winter | n/a | n/a | 0.30-0.50 |
| *Ecological constraints* | | | | |
| Flow velocity (m s$^{-1}$) | Summer | >0.10 | >0.10 | >0.20 |
| | Spring | 0.20-0.40 | n/a | 0.10-0.50 |
| | Winter | n/a | 0.60-0.80 | <1.00 |
| Water depth (m) | Summer | n/a | >0.20 | 0.20-0.70 |

a larger scale, i.e. the catchment (Jähnig et al. 2010).
The design procedure, adopted by the Dutch water authorities, mainly focusses on the design of the cross-sectional shape of the reconstructed streams. The design procedure involves three main requirements of the new channel design: (1) flood risk reduction, (2) optimal groundwater conditions for adjacent agricultural fields and (3) improvement of the conditions beneficial for benthic ecology. Table 1 shows details of the design principles, that served as a basis for the three stream restoration projects here subjected to study. When designing the new cross-sectional shape, the following steps are commonly followed. The channel bed level is adjusted such that existing groundwater levels are maintained. Often a groundwater model is used to predict the future groundwater levels. The cross-sectional shape is adjusted to achieve conditions of water depth and flow velocity that best suit the needs of specific lowland ecosystems (Verdonschot et al. 1995). A 1D-flow model (e.g. SOBEK Channel flow; Deltares 2011) is typically used in this step. Finally, the floodplain level is adjusted to meet the legal requirements of flood risk. The flooding occurrence is related to the bankfull discharge. The bankfull discharge is obtained from a flow duration curve, in which the expected frequency corresponds to the total inundation period. The measures taken to improve the abiotic conditions for benthic ecology and the construction of a floodplain aims at restoring the natural processes in the streams. Although it has been widely used in stream restoration design, 1D-flow modelling may not capture small scale processes related to the benthic ecology appearing in natural lowland streams.

In the design process of lowland stream restoration in the Netherlands, little attention has been paid to the morphological developments that may occur after channel reconstruction. Nevertheless, the Dutch water authorities are concerned with sediment transport and the associated morphological changes after channel

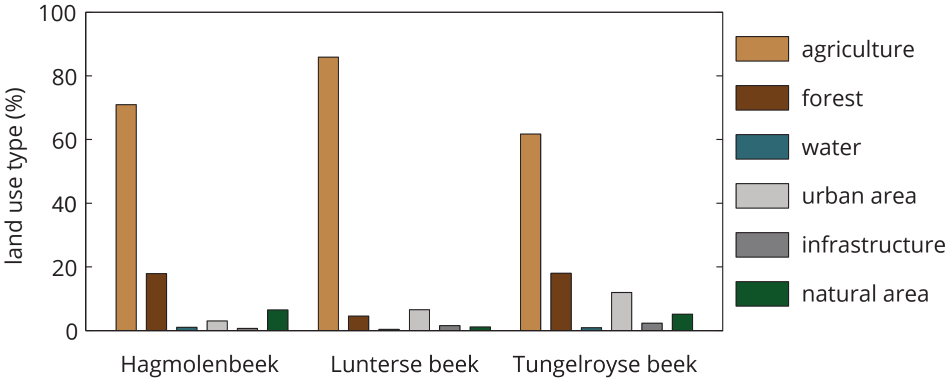

**FIGURE 1** Land use type (%) in each of the three catchments (Hazue et al. 2010)

reconstruction. These concerns mainly address bed slope developments and lateral channel bed adjustments. The objective of this study is to characterise and understand the channel bed adjustments in the three selected lowland streams subject to a stream reconstruction. The selected streams all represent conditions typical for the Netherlands, but are different in bed slope, sediment grain size and channel width.

## STUDY AREAS

The three streams under study are located in three different provinces of the Netherlands (Fig. 2). The catchments are located in aeolian-sand deposits and land use is dominated by agriculture (Fig. 1). Climatological conditions can be considered constant throughout the Netherlands, with the average yearly precipitation amounting to 793 mm (KNMI 2014). Channel reconstruction in all three streams ended between June 2010 and October 2011. The overall stream restoration strategy included the construction of a sinuous channel planform,

**TABLE 2** Characteristics of the study areas, the stream restoration design and the field surveys

| | Hagmolenbeek | Lunterse beek | Tungelroyse beek |
|---|---|---|---|
| *Study area* | | | |
| Longitude | 52° 12'59" N | 52° 4'46" N | 51° 14'42" N |
| Latitude | 6° 43'22" E | 5° 32'37" E | 5° 53'10" E |
| Altitude(m a.m.s.l.) | 17.8 | 5.2 | 23.3 |
| Catchment area (km$^2$) | 59.5 | 63.6 | 116.1 |
| Mean daily discharge (m$^3$ s$^{-1}$) | 0.15 | 0.31 | 1.01 |
| Yearly peak discharge (m$^3$ s$^{-1}$) | 1.00 | 3.55 | 4.77 |
| Annual coeff. of flow variation[a] (-) | 123.2[b] | 138.5[b] | 77.4[c] |
| Sediment size (μm) | 188 | 258 | 141 |
| *Stream restoration design* | | | |
| Total channel length (km) | 1.7 | 1.6 | 9 |
| Channel width (m) | 2.0 | 6.5 | 12.9 |
| Channel depth (m) | 0.4 | 0.4 | 1.4 |
| Channel slope (m km$^{-1}$) | 0.50 | 0.96 | 0.08 |
| Sinuosity (-) | 1.20 | 1.24 | 1.32 |
| Floodplain width (m) | 20-40 | 15-25 | 60-100 |
| Floodplain depth (m) | 0.3 | 0.7 | 1.4 |
| Vegetation management (floodplain) | Sowed[d] | Trees planted[e] | Trees planted[f] |
| *Field surveys* | | | |
| Length of study reach (m) | 385 | 250 | 380 |
| Surveying period (from-to) | Sep 2010 - Jul 2012 | Oct 2011 - Aug 2013 | Jun 2011 - Aug 2013 |

[a] Standard deviation divided by average discharge (Poff & Ward 1989).
[b] Between harsh intermittent and intermittent flashy (Poff & Ward 1989).
[c] Between intermittent flashy and intermittent runoff (Poff & Ward 1989).
[d] With a seed mixture of Perennial ryegrass (*Lolium perenne*), White Clover (*Trifolium repens*), and Timothy (*Phleum pratensis* subsp. *pratensis*).
[e] Alder saplings (*Alnus glutinosa*) and Willow saplings (*Salix alba*, *Salix cinerea*, *Salix repens*).
[f] Alder saplings (*Alnus glutinosa*).

removal of weirs, and lowering of the floodplains. Table 2 shows characteristics of the three projects. Although the same restoration strategy was used in all three projects, the resulting channel characteristics differ. Constructed channel widths range from 2.0 m to 12.9 m, and constructed channel slopes from 0.08 m km$^{-1}$ to 0.96 m km$^{-1}$.

Several site specific characteristics can be observed from the sketches of the study areas (Fig. 2). In the Lunterse beek (panel a), the reconstructed channel crosses the former straightened channel at several locations. A weir is located upstream from the study reach. A peat deposit is located in the upstream part of the study reach. The Lunterse beek was also subject to extensive analyses in (Eekhout et al. 2014). The study reach of the Lunterse beek analysed in the current manuscript includes the reconstructed channel reach upstream from the bend where a cutoff event occurred (Eekhout et al. 2014). This choice was made to facilitate comparison with the morphological processes that occurred in the two other study reaches discussed here. In the Hagmolenbeek (panel b), the reconstructed channel partly follows the former straightened channel, at the location where a bridge was maintained. Here, the channel dimensions increased, compared to the rest of the study reach. The study reach of the Tungelroyse beek (panel c) is located upstream from an area where a straightened channel was maintained, causing an increase of the channel dimensions at the downstream end of this study reach.

## MATERIAL & METHODS

A standardised monitoring scheme was implemented for all three projects. The monitoring focused on morphological and hydrological parameters. Monitoring activities were performed for study reaches with a length between 250 and 380 m. The lengths of the study reaches were chosen such that they captured at least two complete meander wavelengths. Morphological data were collected using Real Time Kinematic (RTK) GPS-equipment (Leica GPS 1200+), with a one-year interval between the surveys. The RTK-GPS equipment allows to measure a point in space with an accuracy of 1 to 2 cm. Morphological data were collected along 30 to 69 cross-sections during each survey. The water level was recorded at each cross-section, from which the water surface slope was determined.

The channel width and channel bed elevation were determined at each individual cross-section. The channel width is defined as the distance between the two channel bank tops. The location of the channel bank tops in each cross-section were marked during the field surveys. The channel bed elevation was obtained by subtracting the hydraulic radius from the average elevation of the two opposing

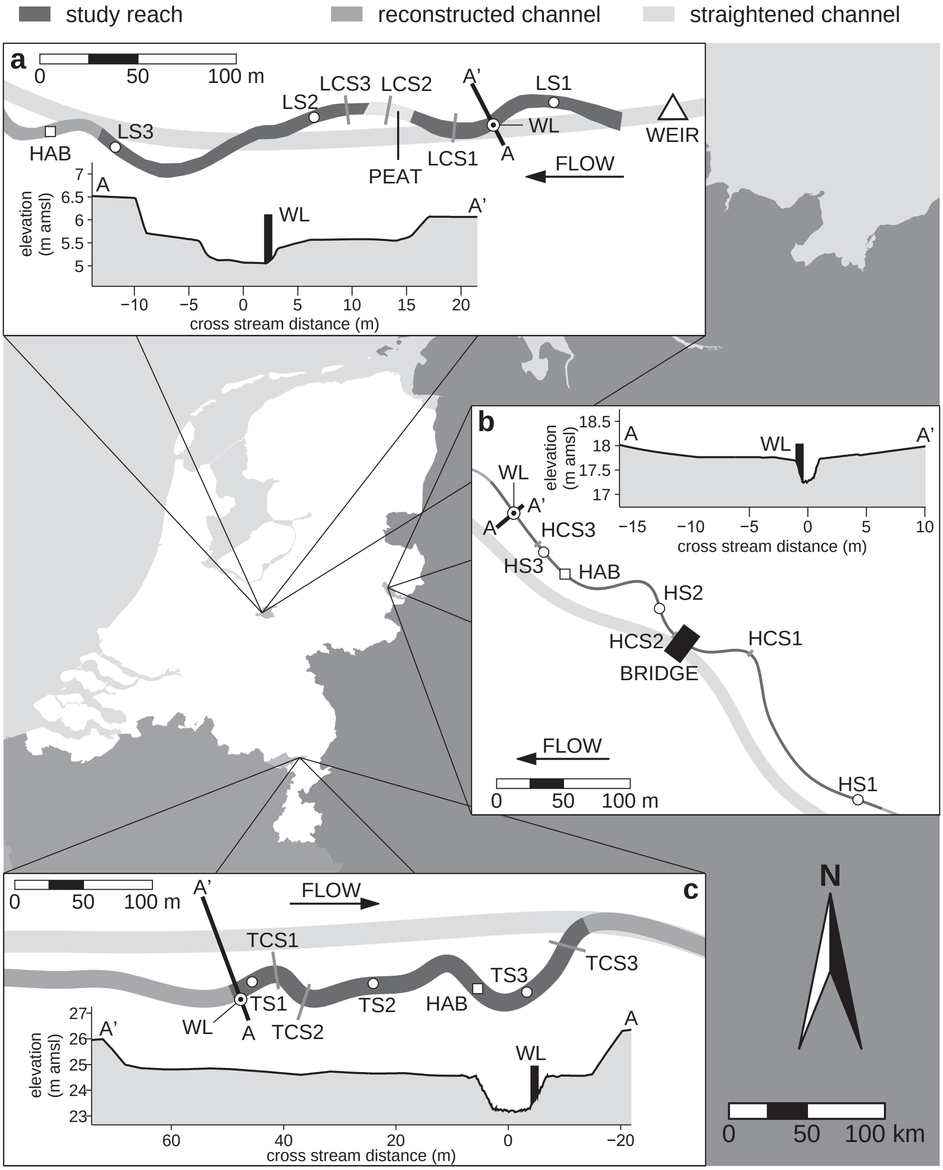

**FIGURE 2** Location and sketches of the study areas in the Netherlands of Lunterse beek (a), Hagmolenbeek (b), and Tungelroyse beek (c). The sketches include the study reach (dark grey), reconstructed channel (grey) and former straightened channel (light grey), the sediment sample locations (S1, S2, S3), the locations of the cross-sections (CS1, CS2, CS3), the location of the habitat survey (HAB), and the location of the water level gauge (WL), including a cross-section (A–A0). The sketches also include the location of a weir and a peat deposit in the Lunterse beek (panel a) and the location of a bridge in the Hagmolenbeek (panel b)

channel bank tops. The hydraulic radius is defined as the cross-sectional area divided by the wetted perimeter. The average channel slope over the total length of the study reach was determined by fitting a straight line through the channel bed elevations.

The in-channel habitat patterns were obtained at 20-m subsections of the three study reaches (HAB; Fig. 2). Each year, three pattern sketches were made of the channel bed, distinguishing substrate (sand, gravel and silt), macrophytes and algae. The inchannel habitat surveys were performed independent from the morphological surveys. In the Lunterse beek, the habitat pattern was obtained at a location downstream of the main study reach (see Fig. 2a), which overlaps with the area where the chute cutoff occurred.

Sediment samples were taken at three locations along the channel, i.e. upstream, half way, and downstream of the study reaches (S1,S2,S3; Fig. 2). Samples were taken during the first and last morphological surveys. Sediment samples were taken with a sediment core sampler (KC Denmark Kajak Model A). At each location, three sediment samples were taken from the top 5 cm of the channel bed. The three samples were combined to obtain the sediment distribution at each location. The sediment samples were dried for 24 h in an oven at 105 $^{0}$C. The dried samples were sieved using a stack of eight sieves, with mesh sizes ranging from 63 to 2000 μm. The weight of each subsample was determined and the cumulative grain size distribution was established. The median grain size was derived from the cumulative grain size distributions.

Discharge was measured continuously at a measurement weir, located outside the study areas. Discharge was sampled at a onehour frequency for the Hagmolenbeek and Lunterse beek and at a 15-min frequency for the Tungelroyse beek. Water level was measured continuously using a water level gauge inside the study reach (WL; Fig. 2). Water level was sampled at a one-hour frequency. Since short-term water level variation may relate to local effects at the water surface, further analysis focusses on the daily-averaged time-series for discharge and water level.

Discharge and water level time-series were combined to determine the cross-sectional averaged flow velocity $\bar{u}$ and dimensionless bed shear stress (Shields stress) $\theta$. The cross-sectional flow area was determined based on the water level and cross-sectional shape at the water level gauge (Fig. 2). Values of $\bar{u}$ were obtained by dividing the discharge by the cross-sectional flow area.

Assuming near-uniform flow conditions, Shields stress θ was estimated according to:

$$\theta = \frac{R\frac{\Delta\zeta}{\Delta x}}{d_{50}S} \tag{1}$$

where *R* is the hydraulic radius (m), $\frac{\Delta\zeta}{\Delta x}$ is the longitudinal water surface slope (-), $d_{50}$ is the median grain size (*m*), and $s=(\rho_s-\rho)/\rho$ is the relative submerged specific gravity of the sediment (-), with $\rho=1000$ kg $m^{-3}$ the density of water and $\rho=2650$ kg $m^{-3}$ the density of sediment. The longitudinal water surface slope $\frac{\Delta\zeta}{\Delta x}$ was based on the average measured longitudinal water level (Tab. 3). The median grain size $d_{50}$ was obtained from the average of the sediment samples from the first survey.

**TABLE 3** Average water surface slope and critical Shields stress for each stream

| | Hagmolenbeek | Lunterse beek | Tungelroyse beek |
|---|---|---|---|
| Water surface slope ($m^{-1}$) | 0.69 | 0.43 | 0.08 |
| Critical Shields stress (-) | 0.052 | 0.042 | 0.067 |

The cross-sectional averaged Shields stress time-series were used to determine the time windows when the Shields stress exceeds the critical Shields stress, corresponding to the periods when sediment may have been actively transported. The critical Shields stress depends on the grain size and is defined as (Van Rijn 1993):

$\theta_{cr}= 0.24D^{-1}$ for $1 < D_* \leq 4$ (2)
$\theta_{cr}= 0.14D^{-0,64}$ for $4 < D_* \leq 10$ (3)

Where $D_*$ is the particle parameter:

$$D_* = \left[\frac{(s-1)g}{v^2}\right]^{1/3} d_{50} \tag{4}$$

where $g=9.81$ m $s^{-2}$ is the gravitational acceleration and $v=10^{-6}$ $m^2$ $s^{-1}$ is the kinematic viscosity of water.

# RESULTS

## Morphological Surveys

Figure 3 shows the temporal changes of the channel width (upper panels) and channel bed elevation (lower panels) along the channel centerline. The figure indicates the location where the reconstructed channel crosses the former straightened channel (Hagmolenbeek and Lunterse beek) and the location of the peat deposit (Lunterse beek).

At two locations in the Hagmolenbeek, changes in channel width and channel bed elevation were observed. One location is situated where the reconstructed channel partly follows the former straightened channel, which coincides with the location of a bridge. The channel bed elevation before reconstruction was partly maintained. During the two-year monitoring period, this section of the channel was filled with sediment. The other location showing pronounced changes is in the bend just upstream from the bridge. Here, a channel width increase and channel incision were observed from year 0 to year 2. A minor form of channel incision is observed in the downstream half of the study reach.

Most variation in channel width and bed elevation was observed in the Lunterse beek. The channel width increased by 1 to 3 m at two sections of the channel. At these two sections, the reconstructed channel crossed the former straightened

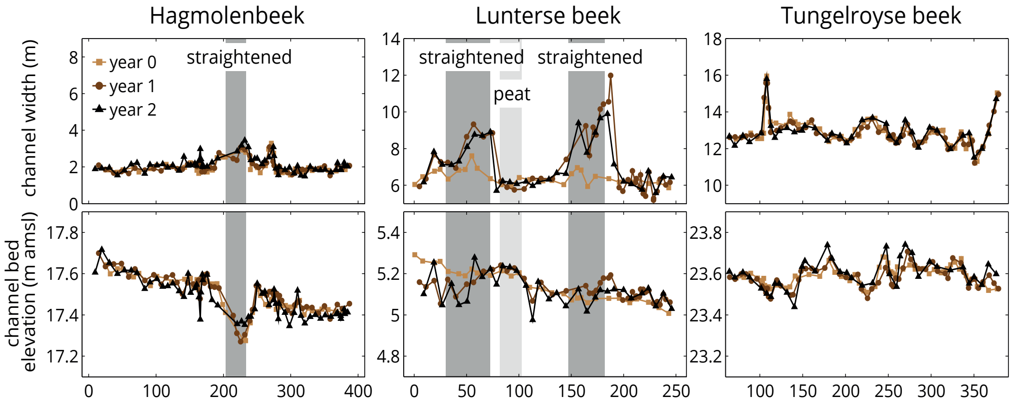

**FIGURE 3** Channel width and channel bed elevation along the channel centerline at year 0 (yellow squares), year 1 (brown circles) and year 2 (black triangles). The location where the reconstructed channels cross the straightened channels are indicated with dark grey (Hagmolenbeek and Lunterse beek). The location of the peat deposit in the Lunterse beek is indicated with light grey. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

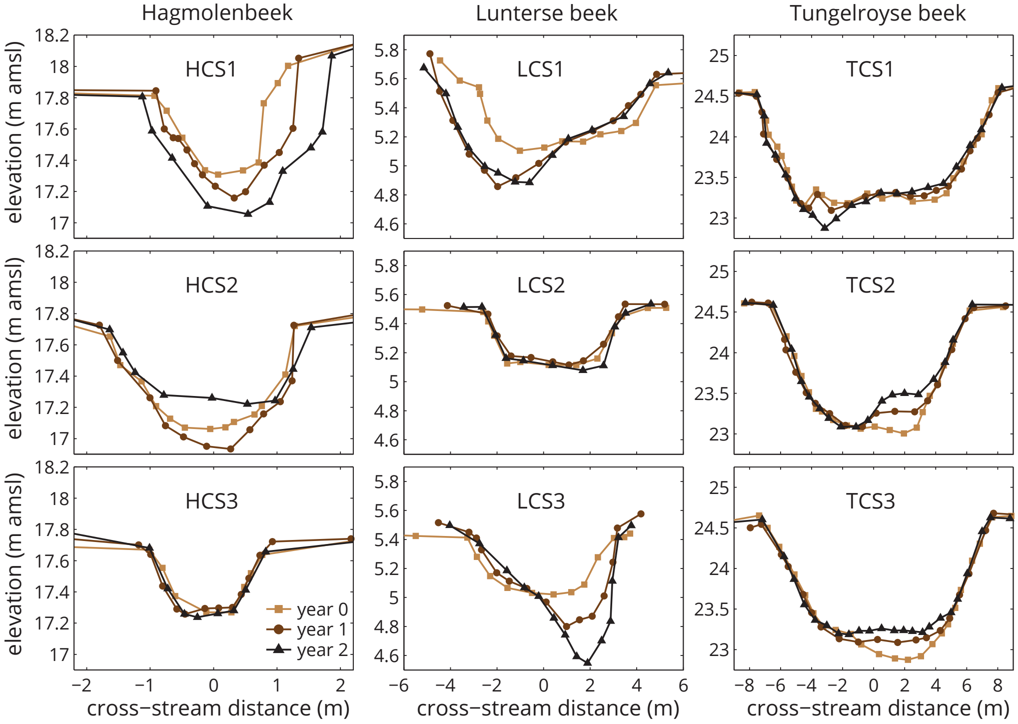

**FIGURE 4** Three examples of the temporal evolution of cross-sections in the three streams at year 0 (yellow squares), year 1 (brown circles), and year 2 (black triangles). The location of the cross-sections correspond to the locations as shown in Fig. 2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

channel. Channel incision occurred at two locations along the channel centerline: upstream and downstream from the peat deposit. Sediment was deposited downstream of the streamwise coordinate 175 m. Most of the changes in channel width and bed elevation occurred during the first year after construction of the reconstructed new channel. In the second year, only minor changes occurred.

During the two-year survey period, hardly any changes in channel width were observed in the Tungelroyse beek. Changes were more apparent in the temporal evolution of the bed elevation. Channel incision occurred between streamwise coordinates 125 and 150 m. Deposition of sediment occurred around streamwise coordinates 175 m and 250 m, and downstream from streamwise coordinate 350 m. The latter is most evident for cross-section TCS3 (Fig. 4).

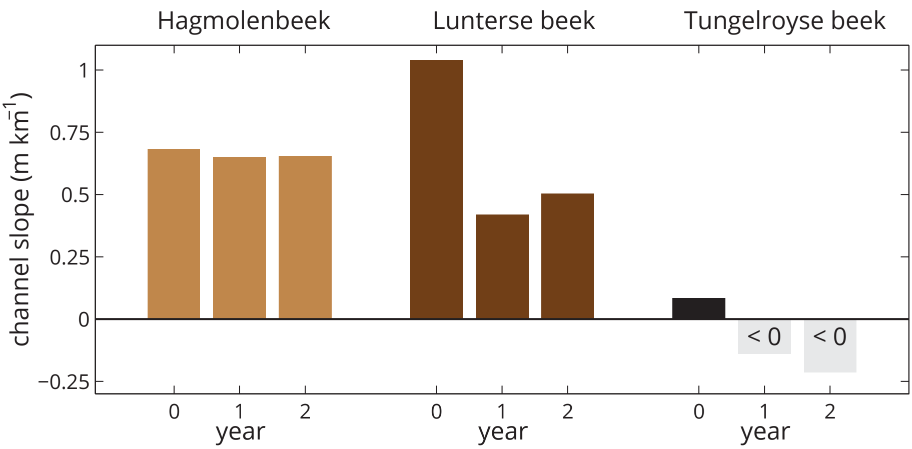

**FIGURE 5** Channel bed slope (m km$^{-1}$) derived from the lower panels of Fig. 3

Figure 4 shows three examples of cross-sections for each study reach and emphasises some of the observations from Figure 3. HCS1 from the Hagmolenbeek shows the bend where both channel widening and channel bed incision occurred. Channel widening is mainly related to bank erosion. Here, bank erosion occurred gradually, from year 0 to year 2, and amounts up to 1.05 m (62% of the channel width). Channel bed incision also occurred gradually and amounted up to 0.25 m (44% of the channel depth). HCS2 shows the rate of sedimentation of the channel near the bridge. Here, the constructed channel width (3.0 m) exceeded the channel width of the rest of the channel. Deposition of sediment locally exceeded 0.29 m (37% of the channel depth). HCS3 shows an example of a cross-section from the downstream half of the study area. Only minor changes occurred here, even though Figure 3 suggests channel incision in this part of the study reach.

In the Lunterse beek, channel widening and incision occurred at a larger scale. LCS1 shows a location along the channel where the reconstructed channel crosses the former straightened channel. It shows a cross-section where bank erosion occurred next to incision of the channel bed near the eroding bank. This resulted in an asymmetric cross-sectional shape, as typically found in meandering rivers. The upstream cross-section also shows that morphological adjustments mainly occurred in the first year. At this location, bank erosion amounted to 1.4 m (19% of the channel width). Channel incision amounted to 0.22 m (55% of the channel depth). LCS2 shows a cross-section within the peat deposit. Few morphological adjustments occurred in this section of the channel. LCS3 shows that just downstream of the peat deposits, channel incision occurred. As opposed to other locations along the channel, here the morphological development took place gradually. In the first year, incision amounted up to 0.22 m and in the second year up to 0.25 m, reaching 130% of the channel depth in total.

Figure 3 shows that few changes in channel width were observed in the Tungelroyse beek. TCS1 shows the cross-section where the channel was constructed, with a channel width exceeding the rest of the channel, viz. 15.7 m against an average of 12.9 m. At this location, located in a bend, channel incision of the outer bank and aggradation of the inner bank occurred. TCS2 shows point bar development in the inner bend. Here, sediment was deposited in the inner bend, resulting in a gradual increase amounting to 0.27 m in the first year and 0.22 m in the second year. TCS3 is located at the downstream end of the study reach and shows the channel bed gradually aggregated over the two-year period, by 0.23 m in the first year and 0.13 m in the second year.

Figure 5 shows the channel slopes for each of the three surveys per stream. The channel slope in the Hagmolenbeek hardly changed over the two-year period. Both the Lunterse beek and the Tungelroyse beek show decreasing channel slopes over time. The decrease of channel slope in the Lunterse beek was most dramatic in the first year. This was mainly caused by channel incision at the upstream end of the study reach. In the second year, a slight increase of the channel slope was observed. The Tungelroyse beek featured negative channel slopes at the time of the surveys that took place one and two years after construction, which can be attributed to local sedimentation in the downstream half of the study area.

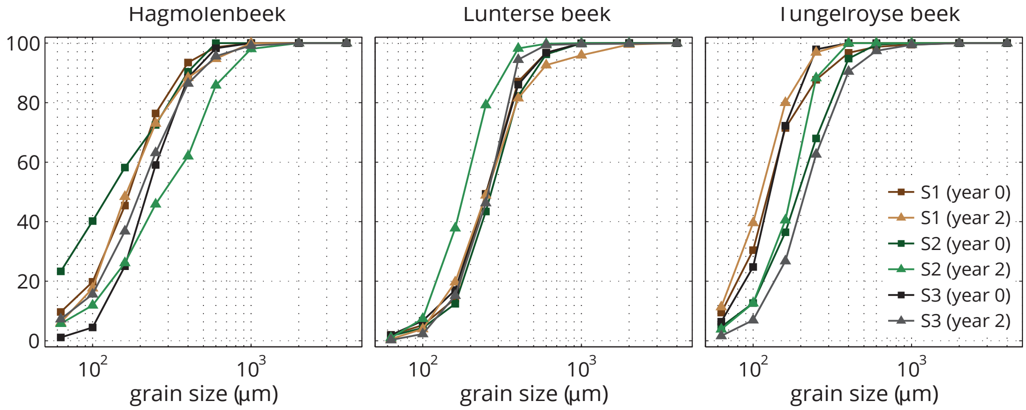

**FIGURE 6** Grain size distributions taken during year 0 (squares) and year 2 (triangles). Samples were taken at three locations along the channel centerline: S1 (brown), S2 (green) and S3 (black). The sample locations are shown in Fig. 2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

### Grain Size Analysis

Figure 6 shows the grain size distributions for the three sample locations in each of the three streams, both at the start and at the end of the monitoring period. Table 4 lists the median grain sizes established from the sediment samples. Only small changes in bed material composition have occurred during the two-year study period. In each of the three streams, two out of three sample locations show negligible changes. Especially in the Lunterse beek, all except one of the grain size distributions remain nearly identical. In each stream, one sample location differs from this observation, i.e. location HS2, LS2, and TS3. Eventually, this caused a change in average median grain size, with an increase in the Hagmolenbeek and Tungelroyse beek and a decrease the Lunterse beek.

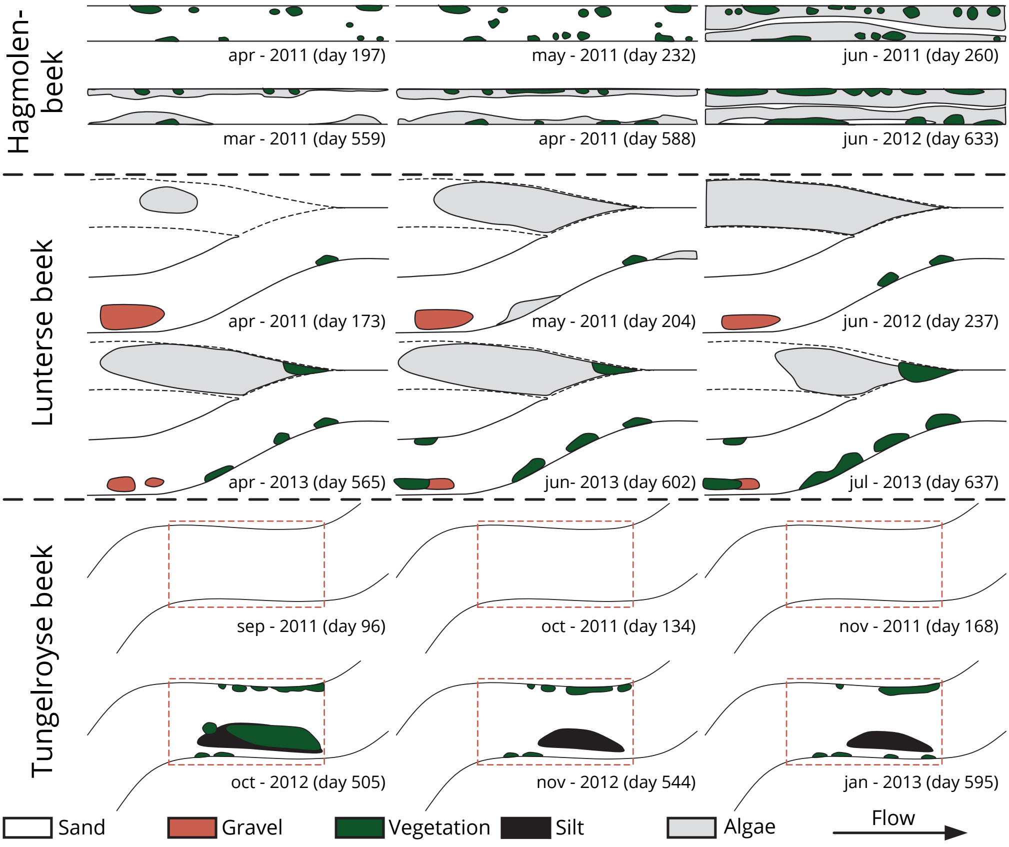

**FIGURE 7** Temporal evolution of the in-channel habitat pattern in a 20-m study reach. The location of the following habitat types were observed: sand (white), gravel (red), vegetation (green), silt (black), and algae (grey). The sample locations are shown in Fig. 2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

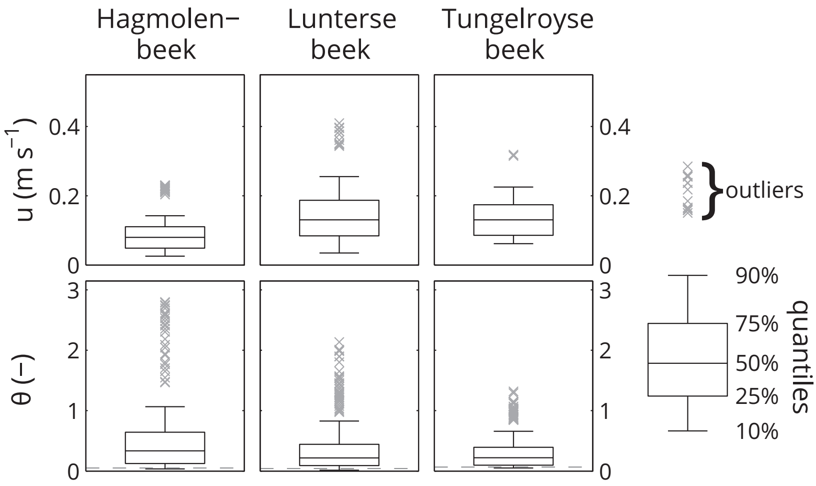

**FIGURE 8** Box-and-whiskers plots (median, 25th and 75th percentiles within the box and 10th and 90th percentiles as whiskers) of the cross-sectional averaged flow velocity u (m $s^{-1}$) and cross-sectional averaged Shields stress $\theta$ (–). The dashed lines in the lower plots indicate the critical Shields stress. A value X is considered to be an outlier when the value is outside the range between $Q_{25}$ - $w(Q_{75}$ - $Q_{25})$ and $Q_{25}$ + $w(Q_{75}$ - $Q_{25})$, with $w$ = 1.5. Outliers are plotted with grey crosses

## Habitat patterns

Figure 7 shows the evolution of the in-channel habitat patterns. All three study reaches were constructed in bare sand. Within the first year several habitat types developed in the Hagmolenbeek and in the Lunterse beek. In the Tungelroyse beek the channel bed still consisted of bare sand after the first year. In each study reach, macrophytes emerged, mainly near the channel banks. Also other habitat types were observed: algae in the Hagmolenbeek and in the cutoff channel of the Lunterse beek, gravel in the Lunterse beek and silt in the Tungelroyse beek. Since the habitat surveys were mainly performed in the summer period in the Hagmolenbeek, the dense cover of algae cover as observed from the figure may not represent the habitat conditions during the entire year.

## Hydrological Results

Figure 8 shows Box-and-whiskers plots of the cross-sectional averaged flow velocity and Shields stress. The lowest cross-sectional averaged flow velocities occurred in the Hagmolenbeek, where the median value amounts to 0.08 m $s^{-1}$. The cross-sectional averaged flow velocities in the Lunterse beek and Tungelroyse beek were similar, with median values amounting to 0.13 m $s^{-1}$. Most variation in cross-sectional averaged flow velocity is observed in the Lunterse beek. Here, values reach up to 0.41 m $s^{-1}$. The least variation is observed in the Hagmolenbeek.

# DISCUSSION

## Longitudinal Adjustments

Longitudinal channel bed adjustments were observed at channel sections where the reconstructed channel either crossed the former straightened channel (Hagmolenbeek), downstream from a weir and a peat deposit (Lunterse beek) or upstream from a straight channel section (Tungelroyse beek). In the Hagmolenbeek, longitudinal channel bed adjustments mainly occurred at a location where the reconstructed channel crosses the former straightened channel. At this location, where a bridge was located, the cross-section was initially both deeper (59%) and wider (34%) than the average values for the rest of the study reach. It is likely that the increase of channel dimensions caused flow velocities to decrease in this area, eventually leading to channel bed aggradation. Geometrical effects may have been responsible for the aggradation of the channel bed at the downstream end of the Tungelroyse beek. Here, the reconstructed channel eventually flows into the straightened channel, resulting in an increase of channel width.

In the Lunterse beek, a weir was maintained upstream from the study reach. At the upstream end of the study reach, channel incision was observed. It is likely that a lack of sediment transport past the weir resulted in an imbalance in sediment transport downstream of the weir. Consequently, more sediment may have been entrained because of the difference between the actual sediment transport and the transport capacity in this section, resulting in channel incision. A similar situation may have occurred downstream of the peat deposit. The peat area may trap sediment from upstream, interrupting the along channel sediment transport. Downstream of the peat deposit, sediment was available and must have been entrained to increase the sediment transport towards the transport capacity of the flow, causing channel bed incision.

It has been recognised that successful stream restoration requires an increase of connectivity (Verdonschot & Nijboer 2002, Wohl 2005, Kondolf et al. 2006). Most restoration projects focus on single, isolated channel reaches and therefore lack connectivity, which is vital for improving the ecosystem. From the three stream restoration projects evaluated in this study, only one project (Tungelroyse beek) involved restoration of the whole stream. The other projects were constructed in isolated channel reaches. This has caused a lack of longitudinal connectivity, affecting the temporal evolution of the longitudinal channel bed profile.

The longitudinal channel bed profile was influenced by backwater effects, caused by widening of the channel width where the reconstructed channel follows the maintained straightened channel (Hagmolenbeek and Tungelroyse beek), and by a lack of upstream sediment input (Lunterse beek). All these influences can be classified as exogenous. Eventually, these exogenous influences caused a decrease of channel slope in two of the studied streams (viz. Lunterse beek and Tungelroyse beek). Similar morphological adjustments have been observed in isolated reconstructed channel reaches of lowland streams in the UK (Sear et al 1998). The discontinuity of sediment transport hampers the use of concepts known from geomorphology such as described by (Schumm 1977, Church 2002) which would allow to predict developments in bed material size, channel gradients and stream flow. To better understand the long-term morphological response to local stream restoration efforts like the ones undertaken, more theoretical knowledge is warranted about the developments under supply limited conditions. In future stream restoration projects it may be worthwhile to aim at increasing the longitudinal connectivity by removing weirs and to anticipate the causes of backwater effects.

### Lateral Adjustments

Lateral channel bed adjustments occurred in each of the three streams. The cross-sections were constructed with a trapezoidal shape. The temporal evolution of the cross-sections shows that after two years an asymmetrical profile emerged, especially in the channel bends. Asymmetrical cross-sectional profiles are typical for meandering rivers and originate from secondary circulation, causing transfer of longitudinal momentum leading to higher flow velocities near the outer bank of a bend. The observations of erosion at the outer bank and deposition at the inner bend, may thus be attributed to an autogenous process.

Not all lateral channel adjustments are autogenous. In the Lunterse beek, bank erosion was observed in areas where the reconstructed channel crosses the former straightened channel. At these locations, the former channel was filled with sediment prior to channel reconstruction. It is very likely that this resulted in a less consolidated floodplain, which was prone to erosion. In the Hagmolenbeek, bank erosion was observed at a location where a non-cohesive sandy layer was overlain by a vegetated upper layer. Erosion of the sandy layer undermined the upper cohesive layer, causing failure of the overhanging upper layer. Furthermore, vegetation may also have played a role in stabilizing the channel banks. Figure 7 shows that macrophytes emerged mainly near the channel banks. Vegetation can have a significant effect on bank stability (Simon & Collison 2002, Pollen-Bankhead & Simon 2009). Our standardised monitoring plan did not include an in-depth analysis on the role of vegetation on bank stability. For future stream restoration analysis, it may be worthwhile to monitor bank stability, since it may have a significant effect on lateral channel development.

Bank erosion, as observed in the Hagmolenbeek and Lunterse beek, was related to spatial variation of the bank material. Recently, the importance of floodplain heterogeneity to meander planform dynamics has been recognised and studied using meander models (Güneralp & Rhoads 2011, Motta et al. 2012). In the Hagmolenbeek and Lunterse beek, the channel bank composition (former channel fills, peat deposit and vegetated upper layer) was a cause of floodplain heterogeneity, and, hence, resulted in spatial variation of the observed lateral development. In future stream restoration projects causes of floodplain heterogeneity can readily be mapped in a field reconnaissance, establishing local seepage and the occurrence of gravel and peat deposits, and former channel fills. Such field reconnaissances may assist in assessing the causes of lateral channel development, and may help to prevent unwanted changes to the new channel topography.

### In-stream ecology

Table 1 lists the principles used by the water authorities involved in the design of the three streams subjected to study. The ecological constraints include minimum and maximum flow velocity and water depth values, which reflect the abiotic conditions relevant for improving the ecological status of the streams. The ecological constraints differ between the seasons. The timeaveraged values for the cross-sectional averaged flow velocity and water depth were estimated based on the discharge and water level time-series. In nearly all cases, the flow velocity conditions in spring and in summer are lower than the design values, with cross-sectional averaged flow velocities around 0.07 m s1 in the Hagmolenbeek and around 0.10 m $s^{-1}$ in the Lunterse beek and Tungelroyse beek. For winter conditions, these values increase to around 0.10 m $s^{-1}$ in the Hagmolenbeek, 0.18 m $s^{-1}$ in the Lunterse beek, and 0.15 m $s^{-1}$ in Tungelroyse beek. The Tungelroyse beek is the only stream meeting the design criterion for flow velocity in winter conditions. The water depths are evaluated for summer conditions only, averaging 0.34 m in the Hagmolenbeek, 0.25 m in the Lunterse beek, and 0.79 m in the Tungelroyse beek. The Lunterse beek is the only stream that meets the design criterion for water depth in summer conditions.

It is likely that these constraints are too much of a simplification of the conditions that best suit the ecology in lowland streams. The habitat of stream organisms mainly occurs just above and below the channel bed and within channel structures, such as patches of leaves, woody debris and macrophytes. At this scale their habitat and mobility can be explained in relation to life resources, including oxygen, food and protection against forces of shear stress (Lancaster & Belyea 2006). At larger spatial scales, the distribution of stream organisms relates to habitat patchiness (Fonseca & Hart 2001), where each habitat (e.g. sand, gravel, leaves, woody debris) forms under different abiotic conditions. Hydraulic conditions play an important role in the formation of each habitat type. Due to their physical characteristics, each habitat type forms under different hydraulic conditions.

Analysis of habitat patterns in the three reconstructed streams show that a gravel bar and a silt bar formed in the Lunterse beek and in the Tungelroyse beek, respectively. These habitat types may be related to the prevailing flow regime. Figure 8 shows that the highest values for the Shields stress were observed in the Hagmolenbeek and the lowest values for the Shields stress in the Lunterse beek and Tungelroyse beek, although the Lunterse beek shows more variation. The low values for the Shields stress in the Tungelroyse beek may explain the formation of a silt bar. Similar habitat dynamics have been observed in other lowland streams, but under different flow conditions Tolkamp 1980, Wolfert 2001). Local variation in hydraulic conditions may result in a mosaic of habitat types, such as the gravel bar in the Lunterse beek. The presence of algae (Hagmolenbeek) and macrophytes (all three streams) may also be related to the flow conditions, although it is likely that nutrient availability and other physical conditions (e.g. temperature, shading) also play an important role in the distribution of these habitat types.

The evaluation of the design principles shows the current design procedure to be deficient for the flow velocity and water depth targets. A channel design procedure based on a one-dimensional flow model may fail to properly represent the abiotic conditions favourable for the typical lowland stream organisms. We recommend to include two- or three-dimensional hydraulic modelling in the design procedure of lowland streams, which yields information required to evaluate the opportunities for habitat development. The design procedure may also involve prediction of the initial morphological development. Morphological models could provide a qualitative view on the initial morphological development of the channel bed and may be able to pin-point locations that are susceptible for channel incision or aggradation.

## CONCLUSION

Three stream restoration projects have been evaluated focusing on morphological developments over a two-year period. During this period, longitudinal and lateral channel adjustments have been observed. Longitudinal channel bed adjustments were significant in each of the three streams, and were related to exogenous influences. Hydraulic structures (e.g. bridges and weirs), channel width variation and heterogeneity of the channel substrate caused channel bed incision and aggradation, and consequently, channel slope adjustments. Bank erosion was only observed in a limited number channel bends and was related to floodplain heterogeneity, which may be considered an exogenous influence. Other lateral channel adjustments were the result of autogenous morphological processes, including point bar formation due to secondary flow, resulting in asymmetrical cross-sectional profiles. In future stream restoration projects it may be worthwhile to anticipate the possible effects of exogenous influences, to prevent unwanted morphological developments.

The fine sediment characteristics (median grain size 125–250 μm) and relatively small flow depths cause the Shields stress to exceed the critical Shields stress more than 81% of the time. Despite this, no significant changes in sediment composition were observed, most likely associated with the uniformity of the prevailing sediment. At the habitat scale, changes occurred that may be related to the flow conditions, leading to the formation of a gravel bar and a silt bar. These observations are particularly relevant for the abiotic conditions determinative to stream ecology, showing that within 2-years' time natural processes cause an increase of the habitat heterogeneity in a reconstructed lowland stream.

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## REFERENCES

Baattrup-Pedersen A, Riis T, Hansen HO, Friberg N. 2000. Restoration of a Danish headwater stream: short-term changes in plant species abundance and composition. Aquatic Conservation: Marine and Freshwater Ecosystems 10:13–23.

Brookes A. 1987. Restoring the sinuosity of artificially straightened stream 575 channels, Environmental Geology and Water Sciences 10: 33–41.

Brookes A, Gregory K. 1988. Channelized rivers: Perspectives for environmental management, Wiley, Chichester: 326 pp.

Church M. 2002. Geomorphic thresholds in riverine landscapes. Freshwater Biology 47(4): 541–57.

Council of the European Communities (2000) Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 establishing a framework for Community action in the field of water policy, Official Journal of the European Communities L327: 1–73.

Deltares. 2011. SOBEK 2.12 user manual, Deltares, Delft, the Netherlands.

Eekhout JPC, Hoitink AJF. 2014. Morphodynamic regime change induced by riparian vegetation in a restored lowland stream, Earth Surface Dynamics Discussions 1: 711–743.

Fonseca DM, Hart DD. 2001. Colonization history masks habitat preferences in local distributions of stream insects. Ecology 82: 2897–2910.

Güneralp I, Rhoads BL. 2011. Influence of floodplain erosional heterogeneity on planform complexity of meandering rivers, Geophysical Research Letters 38: L14401.

Hazeu GW, Schuiling C, Dorland GJ, Oldengarm J, Gijsbertse HA. 2012. Landelijk Grondgebruiksbestand Nederland versie 6 (LGN6); Vervaardiging, nauwkeurigheid en gebruik. Tech. rep. Alerra, alerra-rapport 2012.

Iversen TM, Kronvang B, Madsen BL, Markmann P, Nielsen M. 1993. Reestablishment of danish streams: restoration and maintanance measures. Aquatic Conservation: Marine and Freshwater Ecosystems 3: 73– 92.

Jähnig SC, Brabec K, Buagni A, Erba S, Lorenz AW, Ofenböck T, Verdonschot PFM, Hering D. 2010. A comparative analysis of restoration measures and their effects on hydromorphology and benthic invertebrates in 26 central and southern european rivers. Journal of Applied Ecology 47: 671–680.

KNMI, Langjarige gemiddelden en extremen, tijdvak 1971-2000, http://www.knmi.nl/klimatologie/normalen1971-2000/index.html (accessed 26-01-2014) (2014). URL http://www.knmi.nl/klimatologie/normalen1971-2000/ index.html (accessed 26-01-2014)

Kondolf GM. 2006. River restoration and meanders, Ecology and Society 11: 42.

Kondolf GM. 2012. River Conservation and Management, John Wiley & Sons, Ch. The Espace de Liberté and Restoration of Fluvial Process: When Can the Rive Restore Itself and When Must we Intervene: pp. 225–241.

Kondolf GM, Boulton AJ, O'Daniel S, Poole GC, Rahel FJ, Stanley EH, Wohl E, Bång A, Carlstrom J, Cristoni C, Huber H, Koljonen S, Louhi K, Nakamura P. 2006. Process-based ecological river restoration: Visualizing three-dimensional connectivity and dynamic vectors to recover lost linkages, Ecology and Society 11: 5.

Kuenen PH. 1944. Gedenkboek van Dr. Ir. P. Tesch. Geologische Serie XIV, Verhandelingen van het

Geologisch-Mijnbouwkundig Genootschap voor Nederlandse koloniën, Ch. De Drentsche riviertjes en het meandervraagstuk: pp. 313–336.

Lancaster J, Belyea LR. 2006. Defining the limits to local density: Alternative views of abundance-environment relationships. Freshwater Biology 51: 783–796.

Lindow N, Evans RO, Bass K. 2007. Channel evolution and sediment transport in a restored sand bed stream, in: Restoring Our Natural Habitat - Proceedings of the 2007 World Environmental and Water Resources Congress: 1–10.

Lorenz AW, Jähnig SC, Hering D. 2009. Re-meandering German lowland streams: Qualitative and quantitative effects of restoration measures on hydromorphology and macroinvertebrates. Environ Management 44: 745–754.

McMillan SK, Vidon PG. 2014. Taking the pulse of stream restoration practices: Moving towards healthier streams, Hydrological Processes 28: 398–400.

Meijles EW, Williams A. 2012. Observation of regional hydrological response during time periods of shifting policy, Applied Geography 34: 456–470.

Ministerie van Verkeer en Waterstaat. 2000. Anders omgaan met water; Waterbeleid in de 21ste eeuw, Tech. rep., Ministerie van Verkeer en Waterstaat, Den Haag.

Motta D, Abad JD, Langendoen EJ, García MH. 2012. A simplified 2D model for meander migration with physically-based bank evolution, Geomorphology 163-164: 10–25.

Nakano D, Nakamura F. 2008. The significance of meandering channel morphology on the diversity and abundance of macroinvertebrates in a lowland river in japan, Aquatic Conservation: Marine and Freshwater Ecosystems 18: 780–798.

Nienhuis PH, Bakker JP, Grootjans AP, Gulati RD, de Jonge VN. 2002. The state of the art of aquatic and semi-aquatic ecological restoration projects in the Netherlands. Hydrobiologia 478: 219–233.

Pedersen TCM, Baattrup-Pedersen A, Madsen TV. 2006. Effects of stream restoration and management on plant communities in lowland streams. Freshwater Biology 51: 161–179.

Piégay H, Darby SE, Mosselman E, Surian N. 2005. A review of techniques available for delimiting the erodible river corridor: A sustainable approach to managing bank erosion, River Research and Applications 21:773–789.

Poff NL, Ward JV. 1989. Implications of streamflow variability and predictability for lotic community structure: A regional analysis of streamflow patterns. Canadian Journal of Fisheries and Aquatic Sciences 46: 1805–1818.

Pollen-Bankhead N, Simon A. 2009. Enhanced application of root-reinforcement algorithms for bank-stability modeling. Earth Surface Process and Landforms 34: 471–80.

Schumm SA. 1977. The Fluvial System,Wiley-Interscience, New York: 338 pp.

Sear DA, Briggs A, Brookes A. 1998. A preliminary analysis of the morphological adjustment within and downstream of a lowland river subject to river restoration. Aquatic Conservation: Marine and Freshwater Ecosystems 8:167–183.

Simon A, Collison AJC. 2002. Quantifying the mechanical and hydrologic effects of riparian vegetation on streambank stability. Earth Surface Process Landforms 27: 527–46.

Sudduth EB, Meyer JL, Bernhardt ES. 2007. Stream restoration practices in the Southeastern United

States, Restoration Ecology 15: 573– 583.

Tolkamp HH. 1980. Organism-substrate relationships in lowland streams. PhD Thesis, Wageningen University, Wageningen: 211 pp.

Van Rijn LC. 1993. Principles of sediment transport in rivers, estuaries and coastal seas, Aqua Publications: 700 pp.

Vanoni VA. 2006. Sedimentation engineering. ASCE manuals and reports on engineering practice, No. 54. ASCE Publications.

Verdonschot PFM, Nijboer RC. 2002. Towards a decision support system for stream restoration in the Netherlands: An overview of restoration projects and future needs. Hydrobiologia 478: 131–148.

Verdonschot PFM, Driessen O, van der Hoek W, de Klein J, Paarlberg A, Schmidt G, Schot J, de Vries D. 1995. Beken stromen: Leidraad voor ecologisch beekherstel, Tech. rep., STOWA, Utrecht.

Vivash R, Ottosen O, Janes M, Sørensen HV 1998. Restoration of the rivers Brede, Cole and Skerne: a joint danish and british eu-life demonstration project, ii - the river restoration works and other related practical aspects. Aquatic Conservation: Marine and Freshwater Ecosystems 8:197–208.

Wohl E, Angermeier PL, Bledsoe B, Kondolf GM, MacDonnell L, Merritt DM, Palmer MA, Poff NL, Tarboton D. 2005. River restoration, Water Resources Research 41:W10301.

Wolfert HP. 2001. Geomorphological change and river rehabilitation: case studies on lowland fluvial systems in The Netherlands, Ph.D. thesis, Utrecht University, The Netherlands, Alterra Scientific Contributions 6: 200 pp.

# 6

## CHAPTER 6

# MACROINVERTEBRATE TAXONOMICAL AND TRAIT-BASED RESPONSES TO LARGE WOOD RE-INTRODUCTION IN LOWLAND STREAMS

*Submitted to: **Freshwater Science***

De Brouwer JHF, Verdonschot PFM, Eekhout JPC, Verdonschot RCM

## ABSTRACT

In hydromorphologically degraded lowland streams large wood re-introduction is commonly applied as a stream restoration measure to re-establish instream physical structure, which in turn might benefit biodiversity. However, success rate in terms of positive macroinvertebrate community responses varies. To obtain a better insight into macroinvertebrate-wood relationships macroinvertebrate assemblage composition and associated ecological and functional traits were studied in three lowland streams in the Netherlands where wood was re-introduced.

Using a before-after-control-impact design, stream sections were studied in three subsequent years, one year before and two years after large wood was added and compared to untreated control sections. Changes in physical structure, expressed as substrate diversity, complexity, patchiness and stability, were recorded. Macroinvertebrates were sampled to determine changes in the assemblage composition due to the wood addition and it was assessed whether these changes could be related to taxa preferences for substrate type and flow and the functional traits related to the mode of locomotion and feeding type.

Habitat heterogeneity increased after wood addition and was relatively stable between years. Macroinvertebrate assemblages changed in the two years post-introduction in comparison to the control sections, with 50-58% of the taxa increasing or decreasing in abundance. Despite the changes in substrate composition and habitat heterogeneity most of the assumed functional relationships between macroinvertebrates and large wood could not been demonstrated or were site-specific. Only a high affinity for hard substrates characterized the macroinvertebrate taxa increasing in abundance in all streams.

These findings suggest that an increase in surface area of stable hard substrate was underlying the ecological effect of re-introducing large wood to the stream channel of sand-bed lowland streams, at least on the short term, and only affecting a specific part of the macroinvertebrate community. Because changes in assemblage composition primarily occurred during the first year, colonisation in this early successional stage seems to be limited to the species pool present in the immediate surroundings.

*Keywords:* Stream restoration, Benthic invertebrates, Traits, Habitat heterogeneity, Colonisation

## BACKGROUND

In streams large wood is a key hydromorphological component which to a large extent shapes the instream environment (Gerhard and Reich 2000, Gurnell et al. 2002). It can be a determinant of macroinvertebrate occurrence and abundance by providing, amongst others, habitat substrate, food and shelter (Benke & Wallace 2003, Collier & Halliday 2000, Hax & Golladay 1998, Scealy et al. 2007). Therefore, it is not surprising that the common practice of removing large wood from streams as well as the riparian forests from which it originated negatively impacted the structure and functioning of these ecosystems (Angermeier & Karr 1984, Lepori et al. 2005, Schinegger et al. 2012).

During the last few decades re-introduction of large wood has become a widespread restoration measure, as it will re-establish the instream physical structure and improve biodiversity (Kail et al. 2007, Lester et al. 2007, Roni et al. 2015, Grabowski et al. 2019). Large wood introduction will increase hydraulic variation and contributes to a more diverse physical substrate composition (Gippel et al. 1996). By trapping coarse particulate organic matter in the 'net-structured' wood patches substrate diversity is enhanced (Koljonen et al. 2012). The logs and branches will cause changes in the streams' physical structure and flow patterns, including the formation of pools, riffles, dams and patches with particulate organic matter or mineral material (Harmon et al. 1986, Gerhard & Reich 2000). Furthermore, wood patches will increase resistance against high flow velocities and thereby facilitate retention of water in the upstream reaches, leading to decreased low flow frequencies in the upstream reaches and the levelling off of peak flows (Gippel 1995).

Although increases in diversity and density of stream organisms have been reported following large wood addition, among others, site-specific environmental conditions, time since introduction and wood characteristics result in varying responses, especially by macroinvertebrates (e.g. Gerhard & Reich 2000, Benke & Wallace 2003, Johnson et al. 2003, Scealy et al. 2007). For example, in their review on the effects of introduced large wood, Roni et al. (2015) found that in half of the 21 studies in which macroinvertebrate responses were studied, no change or negative changes in density or diversity were reported. To optimize future restoration efforts it is important to pinpoint the underlying factors responsible for these contrasting responses. It is questionable whether interactions between macroinvertebrates and specific characteristics of the wood patches are responsible for the observed inter-stream differences, or if other instream or watershed environmental conditions have an overriding effect.

This study focusses on the relationship between macroinvertebrate taxonomic and functional composition and wood patch physical structure in terms of diversity, complexity, the level of patchiness and patch stability. Macroinvertebrate communities in stream sections before and after the introduction of large wood in three lowland streams in the Netherlands were investigated and compared to non-restored control sections to evaluate the effects. Among-site comparisons were facilitated by applying a large wood introduction protocol to guide the water managers responsible for the implementation, resulting in a similar layout of the large wood patches in the different streams.

We hypothesized that after large wood has been introduced in-stream physical structure is improved in a similar way in all three streams, increasing substrate diversity, the degree of habitat complexity and the number of different habitat patches present in a given stream section (Fig. 1). With adding large wood three-dimensional physical structures protruding into the water column are introduced in a formerly, in terms of substrate composition, less complex environment. Given the additional attachment and feeding opportunities wood offers, this should be reflected in the ecological and functional traits of the macroinvertebrate communities colonizing the stream sections (Benke & Wallace 2003, Lester et al. 2007). Therefore, we expect an increase in taxa with an affinity for hard substrate types, fast flowing conditions, with passive filter feeder and scrapers/grazer feeding modes and a semi-sessile mode of locomotion. Besides the structure itself, increased coarse particulate organic matter retention within the wood patches should provide additional habitat for detritivores, which we expect to be reflected in an increase in the shredder feeding mode and a preference for patches of particulate organic matter (detritus). Finally, a higher number of predators might

**TABLE 1** Environmental characteristics of the stream reaches studied

| Parameter | Stream Hierden | Stream Tongelreep | Stream Tungelroy |
|---|---|---|---|
| Coordinates | 51°19′51.64″N<br>5°42′41.45″E | 51°22′27.01″N<br>5°29′33.03″E | 51°14′27.67″N<br>5°54′57.33″E |
| Landuse | Forest | Forest | Grassland and forest |
| Reach length with wood patches (km) | 0.9 | 0.7 | 0.5 |
| Number of wood patches (#) | 15 | 6 | 9 |
| Bankfull width reach (min-max, m) | 5-7 | 6-7 | 7-9 |
| Maximum water depth (average, m) | 0.6 (0.2) | 0.6 (0.2) | 1.0 (0.4) |
| Gradient reach (m km$^{-1}$) | 1.9 | 0.4 | 0.5 |
| Flow velocity (average, m/s) | 0.19 (0.10) | 0.24 (0.10) | 0.19 (0.13) |
| Mean annual discharge (m$^3$/s) | 0.3 | 1.0 | 1.1 |
| Total-Nitrogen (yearly average, mg N L$^{-1}$) | 5.97 | 3.27 | 2.46 |
| Total-Phosphorus (yearly average, mg P L$^{-1}$) | 0.11 | 0.25 | 0.27 |

indicate an increase in the complexity of the food web supported by the complex structures. If these links can be defined more clearly it will make information collected in different studies and habitats commensurable in order to increase our understanding of the effects of large wood addition on macroinvertebrate community structure and functioning.

## METHODS

### Study design

Locations where the effects of physical structures on macroinvertebrate communities were examined were situated in three lowland streams in the Netherlands in which water managers had planned large wood introductions as part of larger watershed restoration projects: stream Hierden, Tongelreep and Tungelroy (Tab. 1). Main stressors targeted in these projects were similar in all three streams: eutrophication, peak discharges, degradation of the riparian zone and excessive maintenance of the stream channel (e.g. removal of large wood and vegetation). Large wood addition was carried out as an instream restoration measure aiming at increasing habitat availability for biota.

Although there were inter-stream differences in environmental conditions, amongst others, bankfull width, stream valley land use and discharge, typologically the streams belonged to the same stream type: low-gradient sand-bed middle to lower courses according to the Dutch Water Framework Directive stream typology (Van der Molen et al. 2012). This indicates that the variation in biotic and abiotic conditions between streams fell within the environmental boundaries established for this stream type and is distinctive from other stream types (Hering et al. 2004), facilitating comparisons among streams. Nonetheless we decided to analyse the three streams separately to account for potential effects of differences in environmental conditions. For example, the more open canopy of stream Tungelroy results in extensive macrophyte growth which is absent in the heavily shaded stream Hierden, which might influence physical structure and its associated macroinvertebrate assemblages.

A Before-After-Control-Impact design (BACI) was used to study the effects of the large wood additions. Reaches where wood patches were introduced were compared to adjacent upstream control reaches with similar environmental conditions. The experiment started in autumn 2010 with the sampling of both the control and the impact reaches at each site (before treatment). Within a reach a 20-m-section was selected randomly to determine its physical structure and to collect macroinvertebrate samples. This procedure was repeated three times per reach. After the introduction of the large wood in winter 2010-2011 (Tongel-

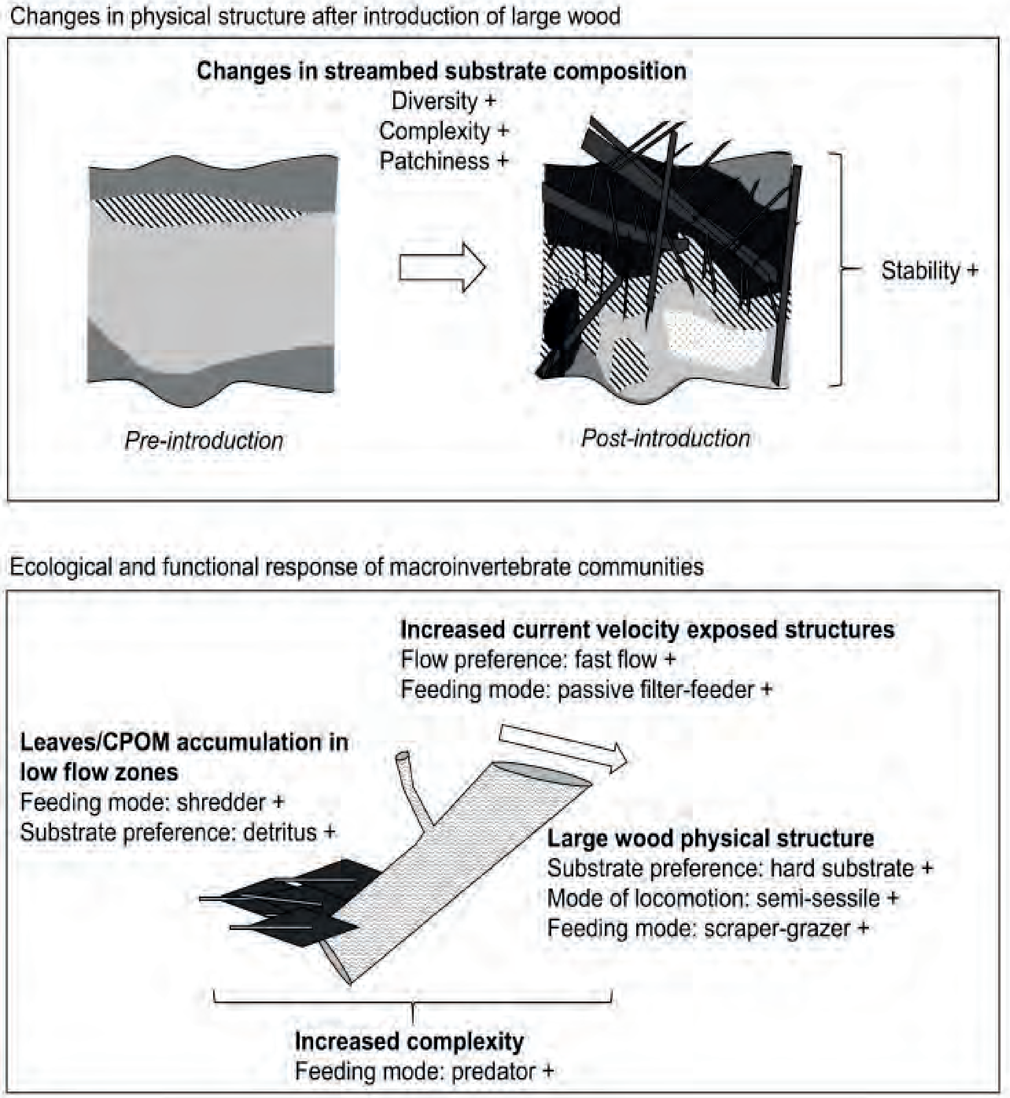

**FIGURE 1** Conceptual diagram illustrating the predicted changes in streambed substrate physical structure and trait-based response of the macroinvertebrate assemblages after large wood was added to the stream channel

reep: December, Hierden and Tungelroy: February), the sampling procedure was repeated in autumn-early winter 2011 (after treatment, year 1) and 2012 (after treatment, year 2). The selected 20-m-sections in the impact reaches after wood introduction always contained a large wood patch.  Each large wood patch covered an area of 25-50 m2 (patch length 10-15 m) and consisted of interwoven logs (diameter >20 cm) and branches (diameter > 5 cm) that covered the full width of the stream (examples for each stream are given in Fig. Supplement 1) . The internal structure of these patches was open, allowing water to flow through the patches at median discharge and over the patch during spates. In terms of substrate cover, the large wood covered approximately 20-25% of the stream bed directly after introduction. Inter-patch distance was at least 25-40 m.

## Sampling

### *Physical structure*

In each stream, three 20-m-sections were surveyed in both the impact and upstream control reach before the large wood was added, after one year and after two years post-introduction. For each 20-m-section the proportional cover of the dominant (>5% coverage in a given section) substrates comprising the stream bed were estimated visually. The substrates were classified according to Hering et al. (2003): sand (including sand and mineral mud with a grain size of >6 µm to 2 mm), wood (including large wood, branches, twigs), leaves (freshly-fallen), CPOM (deposits of coarse particulate organic matter, e.g. leaf fragments), FPOM (deposits of fine particulate organic matter), macrophytes, filamentous algae, and gravel (fine to medium sized gravel with a grain size of >0.2-2 cm).

### *Macroinvertebrates*

Macroinvertebrates were collected using a Surber-sampler (25x25 cm, mesh size 1 mm) by taking 5 sub-samples from the dominant substrates present in the 20-m-section, which were pooled to compose one representative multi-habitat sample of 0.3 $m^2$.  Macroinvertebrate sampling was carried out in the same three impact and control sections surveyed to determine the substrate cover before and after large wood addition. Large wood was sampled by lightly brushing the wood surface (area sampled similar to surface area Surber-sampler). Macroinvertebrate samples were taken to the laboratory and sorted alive. Identification took place to the lowest taxonomical level practical, generally species or genus level.

## Statistical analysis

### *Physical structure*

The spatial component of physical structure was defined using three parameters: habitat diversity, complexity and patchiness. Habitat diversity was calculated using the Simpson's diversity index (Hill 1973): habitat diversity = $1 / \sum(P_i)^2$ , where $P_i$ is the proportion of the $i^{th}$ substrate type.

Habitat complexity was calculated by substituting the relative proportion of each substrate type with a habitat complexity class in the equation of habitat diversity. Habitat complexity classes ranged from 1 for simple to 3 for complex structures, with sand, gravel and FPOM defined as class 1, leaves, CPOM and algae as class 2, and wood and macrophytes as class 3. Habitat patchiness was calculated according to Eadie & Keast (1984): the standard deviation of each substrate cover percentage was divided by its mean percentage and multiplied by the total number of patches recorded. Habitat stability, the temporal component of physical structure, was determined by calculating the Bray-Curtis similarity of the average substrate cover in time between the control and impact sections before, one year and two years after wood addition. Changes in the spatial components of habitat structure were tested by applying randomised intervention analysis (RIA) (Carpenter et al. 1989) using Canoco 5.12 (Ter Braak & Šmilauer 2012). It was evaluated if time dependent changes in physical structure occurred in the sections were large wood was added in comparison to the control sections. Significance in the RIA was calculated with 9999 Monte Carlo random permutations restricted for the temporal structure of the data (cyclic shifts).  To determine if the measures of change in physical structure were due to including the large wood to the reach tests were carried out on the parameters including and excluding the large wood.

### *Macroinvertebrates*

Non-metric multidimensional scaling (NMDS) was conducted to visualize the changes in macroinvertebrate communities before and after the introduction of the large wood. To reduce the effects of rare or highly abundant taxa on the statistical analyses only taxa with a frequency of occurrence >2 were selected for each stream followed by a $\log_2(x+1)$ transformation of the abundances. Non-metric multidimensional scaling was based on a Bray–Curtis dissimilarity matrix and was conducted in PC-ORD for Windows version 4.25 (slow and thorough autopilot mode, 400 iterations, instability criterion of 0.00001, starting number of axes of 6, 40 real runs and 50 runs with randomised data; McCune & Grace, 2002).

To obtain further insight into the changes after wood addition, the macroinvertebrate data were analysed using Principal Response Curve analysis (PRC). This technique is based on the Redundancy Analysis ordination technique, which is the constrained form of Principal Component Analysis (van den Brink & ter Braak 1999). It results in a diagram in which time is displayed on the x-axis and the first Principal Component (PRC-axis 1), which shows the impact of the treatment

**TABLE 2** Before–after control–impact (BACI) analyses on physical structure spatial components using Monte Carlo permutation tests (9999 permutations) based on dependent random shifts of the time series. Tests were carried out including (+) and excluding (-) the large wood

| | | **Parameter** | | | | | |
|---|---|---|---|---|---|---|---|
| | | Diversity | | Complexity | | Patchiness | |
| **Stream** | **Large Wood included** | F | P | F | P | F | P |
| Hierden | + | 46.9 | 0.026 | 84.7 | 0.021 | 44.8 | 0.033 |
| | - | 29.5 | 0.019 | 186.0 | 0.017 | 3.8 | 0.137 |
| Tongelreep | + | 9.4 | 0.047 | 11.6 | 0.015 | 19.3 | 0.003 |
| | - | 8.0 | 0.044 | 13.1 | 0.024 | 35.0 | 0.003 |
| Tungelroy | + | 0.6 | 0.449 | 2.9 | 0.127 | 8.9 | 0.014 |
| | - | 2.8 | 0.070 | 2.8 | 0.070 | 1.4 | 0.323 |

(introduction of large wood) on the community composition on the y-axis. The diagram displays the deviations in community composition over time in the impacted sections compared to those in the control sections. The resulting taxon weights ($b_k$) indicate the fit between the response of the taxon and the overall community response. The PRC analysis was performed using the CANOCO software package, version 5.12 (Ter Braak & Šmilauer 2012).

To relate changes in the macroinvertebrate communities after wood addition to changes in physical structure functional and ecological traits were used. The functional traits mode of locomotion (trait category semi-sessile) and feeding type (trait categories passive filter feeder, shredder, predator and scraper/grazer) were derived from Schmidt-Kloiber and Hering (2015). Substrate preference (trait categories hard substrates and detritus) and flow preference (trait category high flow velocity) were used as ecological traits (Verberk et al. 2012). For Chironomidae additional substrate preference data was included based on Moller Pillot (2009, 2013). The affinity of each taxon for each parameter category was fuzzy-coded, whereby the scores ranged from 0 (avoidance) to 10 (strong preference). Taxon affinities were correlated with the PRC-derived taxon weights ($b_k$) to obtain insight into the relationship between the addition of large wood and the response of the selected traits within the recorded communities in the different streams using Spearman Rank correlations.

## RESULTS

### *Physical structure*

Before the introduction of the large wood, stream beds were dominated by sand (Fig. 2). In the first year after the measure was applied, the mean proportional cover of the different substrate types changed in the impact sections compared

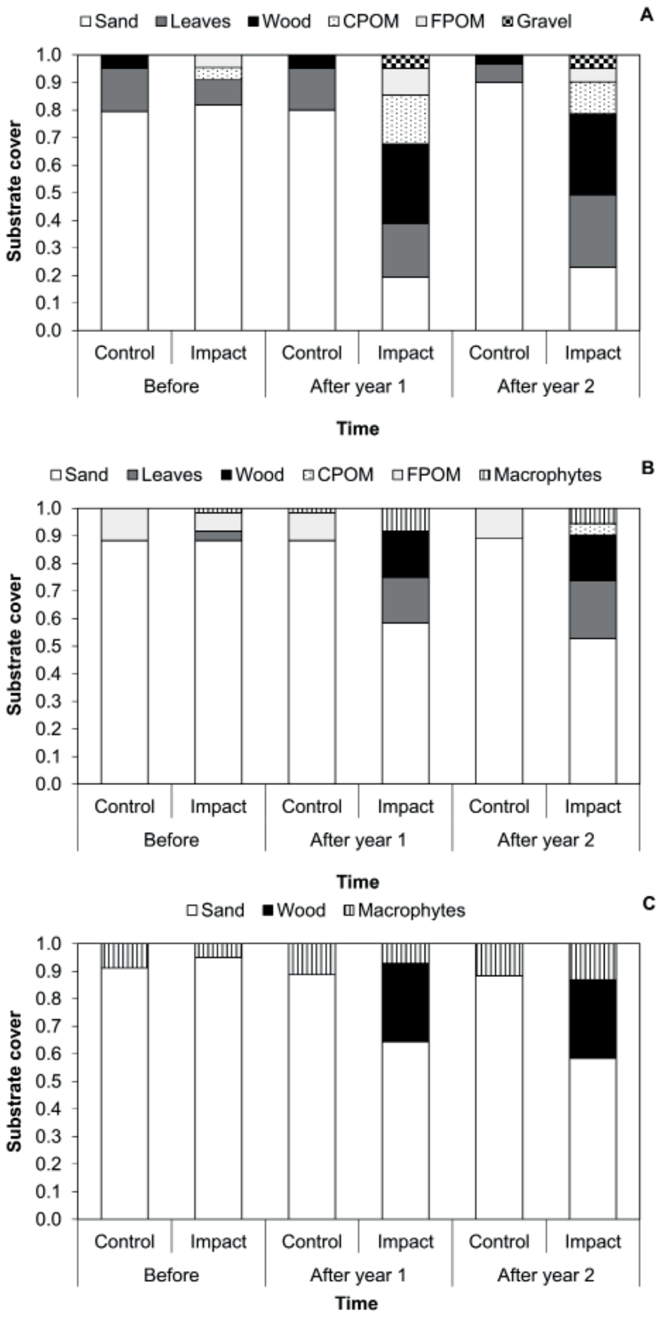

**FIGURE 2** Mean substrate cover (n = 3) on a proportional cover scale (0-1) in the control and impact stream sections before, one year and two years after large wood addition in stream Hierden (A), stream Tongelreep (B) and stream Tungelroy (C)

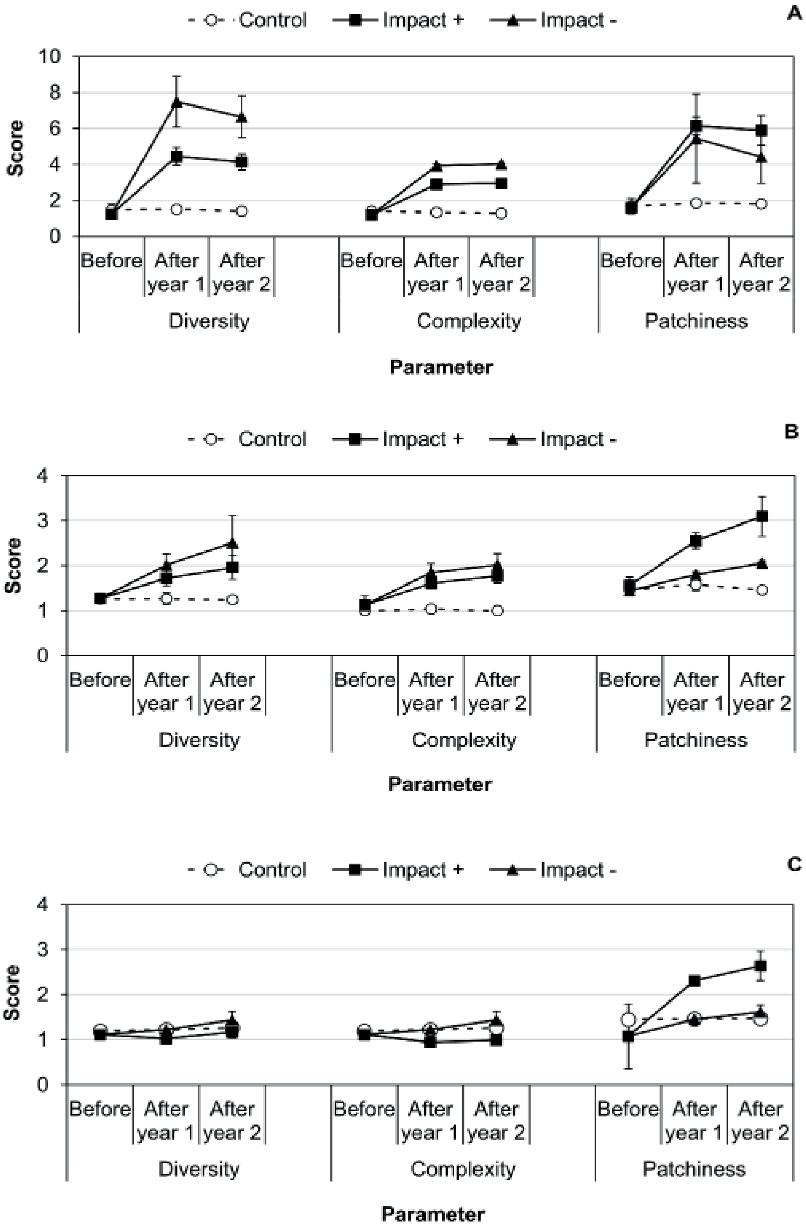

**FIGURE 3** Mean (±1SD) diversity, complexity and patchiness scores in the control and impact 20-m-sections before, one year and two years after large wood addition in stream Hierden (A), stream Tongelreep (B) and stream Tungelroy (C). Both the results including (wood +) and excluding (wood -) the large wood as one of the components of physical structure are given to display the changes due to the added wood

to the control sections in all streams. It was not only the proportional cover of wood which increased, but also the coverage of other substrate types. In stream Hierden and Tongelreep habitat diversity, complexity and patchiness scores of the impacted stream sections increased significantly after the introduction of the large wood (Fig. 3, Tab. 2). In stream Tungelroy only an increase in patchiness was observed in the impacted stream section. Excluding the substrate type wood from the calculations did not affect the outcome of the analyses, except for stream Hierden where the degree of patchiness was not significant in comparison to the control reach. This indicated that in this stream patchiness was primarily generated by the presence of the large wood and not by the other substrate types. Similarity of the proportional cover of stream bed substrate types in the control and impact sections decreased after large wood addition, indicating an increase in substrate heterogeneity during the first year (Fig. 4). When year 1 was compared to year 2, this difference was much smaller, indicating stabilisation of the proportional cover of the different substrate types. In stream Tungelroy, substrate coverage dissimilarity could be contributed to the wood itself, given that excluding this substrate type from the calculations led to an increase in similarity between the control and impact sections over time.

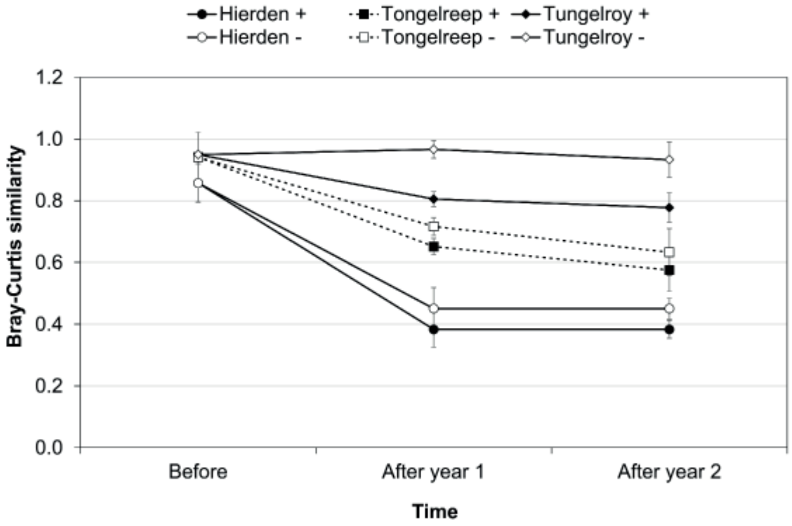

**FIGURE 4** Stability of the stream bed substrate coverage, expressed as Bray-Curtis similarity of the mean (±1SD) substrate composition between control and impact stream sections before and in the years after introduction of large wood. Both the results including (+) and excluding (-) the large wood as one of the components of physical structure are given to display the changes due to the added wood

### *Macroinvertebrates*

Non-metric multidimensional scaling of the macroinvertebrate community composition resulted in an optimal solution incorporating three axes for all streams (final stress ranged from 0.07 to 0.10) (Fig. 5). Macroinvertebrate communities were distinctive relative to the controls after the introduction of the large wood. Dissimilarity differed among streams, with stream Tongelreep displaying the largest deviation in community composition. Also a large effect of time was visible, especially in stream Hierden, given that the different sampling years were clearly separated in the diagram.

PRC showed that before the introduction of the large wood, treatment-control difference in macroinvertebrate community composition in the control and impact sections was relatively small (Fig. 6). After large wood addition community composition changed in the impacted sections compared to the control sections, as deviations in community composition in the impacted sections compared to those in the control sections are observed over time (Monte Carlo permutation tests, PRC-axis 1 Hierden F = 0.7, P = 0.03; Tongelreep F = 1.4, P = 0.002; Tungelroy F =0.8. P = 0.01). Given the smaller treatment-control difference in stream Hierden and stream Tungelroy in the second year, the effect of the wood introduction in these streams decreased over time (Tungelroy PRC-axis 1 16.3% of the variation explained by treatment, Hierden 14.8%), whilst in stream Tongelreep a further increase was observed, indicating an even larger effect in the second year in comparison to the first year (PRC-axis 1 25.3% of the variation explained by treatment).

**TABLE 3** Spearman rank correlation between the taxon weights of the macroinvertebrate communities recorded in the streams, which indicate the response of the individual taxa to the introduction of large wood and the ecological and functional trait category affinities for these taxa. Significance levels: * = P <0.05, ** = P <0.01

| | Taxon weight – trait category affinity correlation (Spearmans' rho) | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Substrate preference | | Mode of locomotion | Feeding type | | | | Flow preference |
| **Stream** | Detritus | Hard substrate | Semi-sessile | Grazer/ scraper | Shredder | Passive filter feeder | Predator | High flow velocity |
| Hierden | -0.185 | 0.460** | 0.189 | 0.126 | -0.313 | 0.253 | 0.062 | 0.184 |
| Tongelreep | -0.225 | 0.331* | 0.100 | 0.320* | 0.172 | 0.263 | -0.055 | 0.421** |
| Tungelroy | 0.055 | 0.323* | -0.091 | 0.248 | 0.128 | 0.041 | -0.177 | 0.212 |

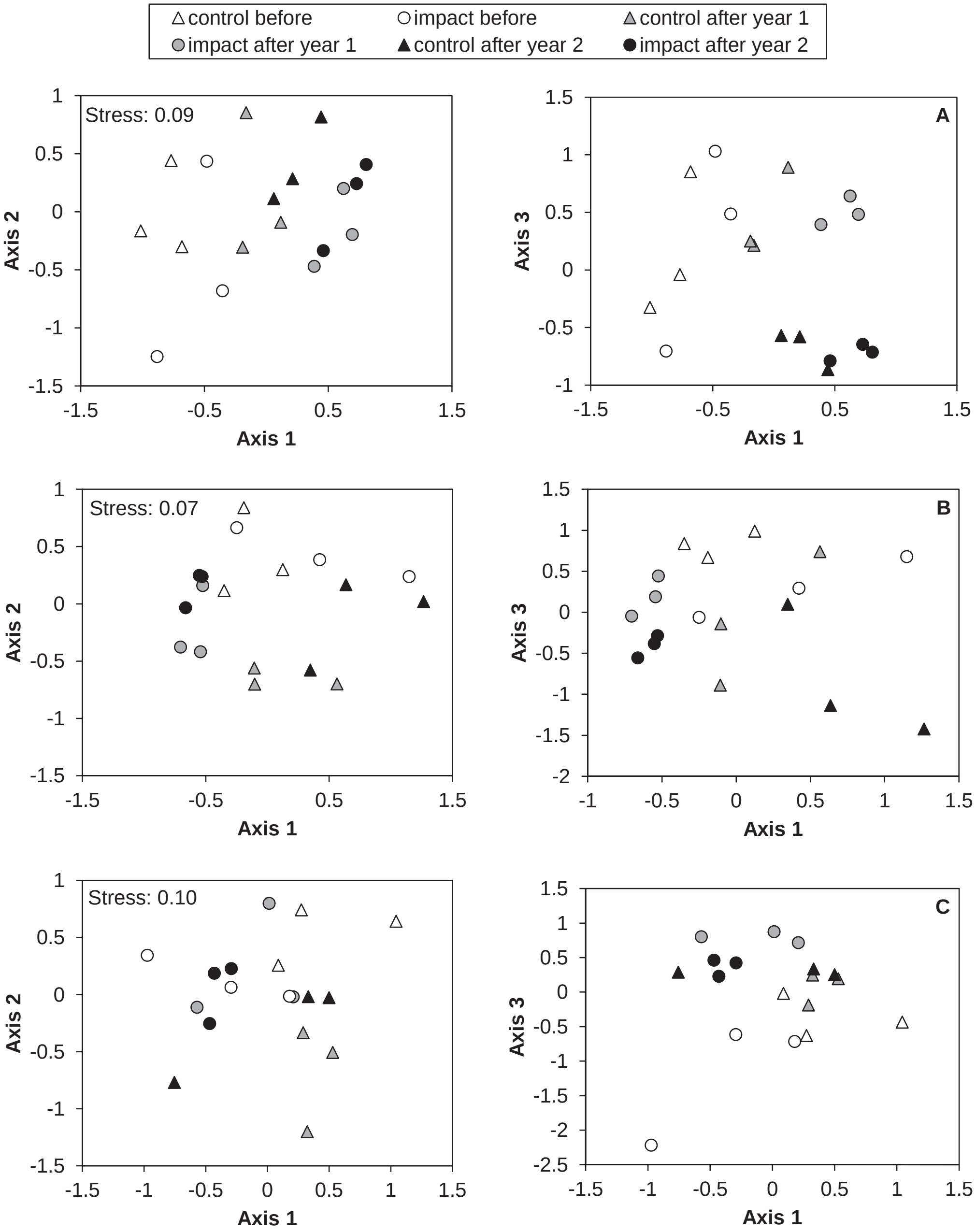

**FIGURE 5** Non-metric multidimensional scaling plots of macroinvertebrate assemblages in the control and impact sections of stream Hierden (A), stream Tongelreep (B) and stream Tungelroy (C) before and after introduction of large wood (n = 3 per year) based on Bray-Curtis dissimilarities

Taxon weights indicate the fit between the response of the observed taxa and the overall community response (Tab. Supplement 1). In total, about half of the taxa (51-58%) displayed an increase or decrease in abundance after wood addition. In stream Hierden 16 out of a total of 41 taxa recorded increased in abundance ($b_k$ >0.5), whilst 5 taxa decreased ($b_k$ <-0.5). For stream Tongelreep (54 taxa in total), 26 taxa increased and only 2 taxa decreased. In stream Tungelroy (55 taxa in total) the number of increasing or decreasing taxa after wood addition was equal, in both cases represented by 16 taxa.

Especially the caddisflies *Hydropsyche pellucidula* and *Lype reducta/phaeopa* and *Simulium* blackflies displayed a strong increase ($b_k$ >2) after wood addition in the streams, as did the caddisfly *Polycentropus irroratus* and the whirligig beetle *Orectochilus villosus* in stream Hierden and the amphipod *Echinogammarus berilloni* and the damselfly *Calopteryx splendens* in stream Tongelreep. More taxa decreased in abundance in stream Tungelroy after wood addition in comparison to the other two streams, ranging from *Neureclipsis bimaculata* and *Mystacides* caddisflies, the mayfly *Cloeon dipterum*, *Microtendipes* chironomids and the bivalve *Corbicula fluminea*.

Correlation of ecological and functional trait parameters to the taxon weights derived from the PRC analyses showed significant relationships between the

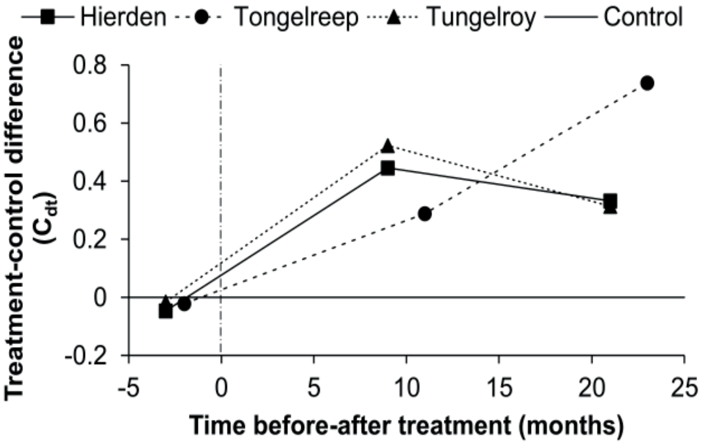

**FIGURE 6** Principal Response Curves of treatment effects ($C_{dt}$, PRC-axis 1) on the macroinvertebrate community for the different streams. The lines represent the effect of the treatment along time, with 0 (vertical broken line) being the moment of wood addition to the streams. Each point represents the mean of 3 replicates per sampling year

response of the macroinvertebrate community and the affinity for the substrate type hard substrate in all streams (Tab. 3). In stream Hierden and Tungelroy no further relationships with the functional traits were found. For stream Tongelreep the addition of large wood matched an increase in the affinity for high flow velocity and a scraper/grazer feeding type.

## DISCUSSION

Examples of an increase in habitat heterogeneity resulting from the introduction of large wood could be found for different stream types (Gerhard and Reich 2000, Lester and Boulton 2008, Pilotto et al. 2014, 2016). Our study is no exception: large wood introduction resulted in an increase in habitat heterogeneity, as the degree of streambed substrate patchiness became larger overall and in two out of three streams an increase in substrate diversity and complexity was observed. Furthermore, the mosaic of streambed substrates resulting from the flow variations induced by the introduced structure and its retention capacity appeared relatively stable, as the degree of change in proportional cover of the different substrate types became smaller in the second year after introduction. Microscale macroinvertebrate distribution is strongly related to these streambed substrate patterns and is largely determined by the functions the patches provide, e.g. as flow refugium, food resource or oviposition/pupation site (Tolkamp 1982, Lancaster 1999). As habitat heterogeneity promotes species diversity via niche and resource availability (Tews et al. 2004), as well as ecosystem functioning and service provisioning (Frainer et al. 2018), it could be an important step towards restoration of degraded stream ecosystems.

Substrate diversity and complexity increased in the two forest streams Hierden and Tongelreep, but not stream Tungelroy. It is expected that to a large extent site-specific or regional factors were underlying these differences. Stream Hierden has a large amount of gravel in the stream-subsurface, leading to faster formation of gravel beds — which were not present at the surface before wood addition — when sand is washed away as a result of large wood induced flow velocity concentrations. As this substrate type was not present pre-restoration, diversity increased. Stream Tungelroy was positioned in a more open, grassland-dominated landscape in comparison to the forested watersheds of stream Hierden and Tongelreep. As leaf retention diversifies the substrate composition of streams (Muotka and Laasonen 2002), the allochthonous inputs of large quantities of coarse particulate organic material, especially leaves, into stream Hierden and to a less extent in stream Tongelreep, might have acted as a catalyst for streambed diversification in and around the large wood patches. These allochthonous inputs were likely to be smaller in stream Tungelroy, where the density of riparian trees was much lower. Furthermore, a lack of effect on complexity in stream Tungelroy might be related to the dimensions of the stream channel. Channel width and depth were larger in comparison to the two other streams, decreasing the trapping efficiency of allochthonous organic matter inputs (Raikow et al. 1995; Larrañaga et al. 2003). At the same time, there was not much space for macrophyte development in stream Tungelroy due to steep banks and high turbidity of the water, which could have acted as an autochthonous source of organic material.

Changes in macroinvertebrate assemblages were observed in all streams, especially in the first year after the measure was applied many taxa increased in abundance. Only in stream Tongelreep the difference in macroinvertebrate assemblage composition with the untreated control section further increased in the second year. Furthermore, the functional response of the macroinvertebrate assemblage in stream Tongelreep differed from the two other streams. Taxa which increased after wood addition showed a strong affinity for hard substrates in all streams. As the sand-bed sediments of lowland streams are very dynamic, re-introducing large wood considerably increases the availability of stable substrate. Pre-introduction this habitat type was only present marginally, especially in the form of tree roots protruding into the stream channel. Given that already within the first year after wood addition considerable changes in assemblage composition took place, we expect that such patches were the primary source of colonists settling on the large wood. Rapid recolonization from local sources is, for example, shown by Westveer et al. (2018) in reconnected lowland stream channels.

Limited availability of species associated with wood or other types of hard substrates within the regional species pool might explain the response pattern in the second year. If all species present in the stream section already colonised the wood during the first year, it is not surprising the degree of change in the second year is less prominent, as a degraded regional species pool could limit recolonization (Spänhoff and Arle 2007, Tonkin et al. 2014). If this is the main mechanism of community assembly on large wood in the lowland streams studied, it would suggest that the potential number of colonists is higher in stream Tongelreep in comparison to the other two streams.

In stream Tongelreep a preference for high flow velocity and a grazer/scraper feeding mode seemed to be associated with large wood or the presence of hard surfaces in general. Pieces of wood which protrude into the water column are exposed to relatively higher flow velocities in comparison to the situation on the stream bottom (Schoen et al. 2013; Pilotto et al. 2016), which facilitates invertebrates preferring fast flow. Scrapers feed on the epixylic biofilm present on the wood surface (Benke and Wallace 2003). As the availability of such surfaces was limited pre-introduction, resource availability for this functional feeding group is strongly expanded with large wood presence in the stream channel. Other traits investigated did not show significant relationships. In general, there is large variability in functional feeding group responses to large wood addition when different studies are compared, which was generally assigned to site-specific environmental conditions (e.g. Johnson et al. 2003, Lester et al. 2007). At the same time its functional structure is directly related to the set of species colonizing the wood and with that dependent on the regional species pool.

Pilotto et al. (2014) stressed the importance of the streambed habitat changes within and surrounding patches with large wood for the taxonomical and functional composition of macroinvertebrate assemblages in contrast to only a minor contribution of the large wood itself. Our results seem to show the opposite, despite having observed considerable changes in substrate cover and patchiness, such as detritus and gravel, this is not reflected in the trait composition of the macroinvertebrate assemblages present in the restored stream sections. In our case it seems that it is the large wood itself which contributes to the differences consistently. This raises the question if provisioning of stable habitat substrate or surface is the main beneficial effect of large wood for macroinvertebrates in lowland streams. Age of the large wood patch might be important here, as the functions provided by the wood and its associated habitats are expected to change with aging of the patch (Benke and Wallace 2003). We only studied large wood patches that were submerged for less than two years, which might not have provided the full spectrum of resources yet. Because of their retention capacity and stability, large wood patches accumulate organic material over time, including leaves, seeds and small branches, but it may require years for these accumulations to develop (Jones 1997; Tank et al. 2010). In time, these organic patches becomes a mixture of organic particles in different stages of decomposition or abrasion towards the core of the patch, and thus, of different food and habitat quality for macroinvertebrates. Also the surface texture of the wood changes in time because of abrasion or decay, potentially influencing the assemblage composition (Molokwu et al. 2014). At the same time, wood aging would not lead to major assemblage changes if the number of potential colonists is limited due to degradation on stream to catchment-scale (Leps et al. 2016). Long term repeated sampling of the macroinvertebrate communities inhabiting the introduced large wood patches could be an interesting follow-up to separate the effects of environmental conditions from that related to the size of the regional species pool.

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## REFERENCES

Angermeier PL, Karr JR. 1984. Relationships between woody debris and fish habitat in a small warmwater stream. Transactions of the American Fisheries Society 113: 716-726.

Benke AC, Wallace JB. 2003. Influence of wood on invertebrate communities in streams and rivers. Pages 149–177 in Gregory S V, Boyer KL, Gurnell AM (editors). The ecology and management of wood in world rivers. American Fisheries Society, Bethesda, Maryland.

Carpenter SR, Frost TM, Heisey D, Kratz TK. 1989. Randomized intervention analysis and the interpretation of whole-ecosystem experiments. Ecology 70: 1142-1152.

Collier KJ, Halliday JN. 2000. Macroinvertebrate-wood associations during decay of plantation pine in New Zealand pumice-bed streams: stable habitat or trophic subsidy? Journal of the North American Benthological Society 19: 94–111.

Eadie JM, Keast A. 1984. Resource heterogeneity and fish species diversity in lakes. Canadian Journal of Zoology 62: 1689-1695.

Frainer A, Polvi LE, Jansson R, McKie BG. 2018. Enhanced ecosystem functioning following stream restoration: The roles of habitat heterogeneity and invertebrate species traits. Journal of Applied Ecology 55: 377-385.

Gerhard M, Reich M. 2000. Restoration of streams with large wood: Effects of accumulated and built-in wood on channel morphology, habitat diversity and aquatic fauna. International Review of Hydrobiology 85: 123–137.

Gippel CJ. 1995. Environmental hydraulics of large woody debris in streams and rivers. Journal of Environmental Engineering 121: 388-395.

Gippel CJ, O'Neill IC, Finlayson BL., Schnatz INGO. 1996. Hydraulic guidelines for the re-introduction and management of large woody debris in lowland rivers. Regulated Rivers Research and Management 12: 223-236.

Gurnell AM, Piégay H, Swanson FJ, Gregory SV. 2002. Large wood and fluvial processes. Freshwater Biology 47: 601-619.

Grabowski RC, Gurnell AM, Burgess-Gamble L, England J, Holland D, Klaar MJ, Morrissey I, Uttley C, Wharton G. 2019. The current state of the use of large wood in river restoration and management. Water and Environment Journal 33: 366-377.

Harmon ME, Franklin JF, Swanson FJ, Sollins P, Gregory SV, Lattin JD, Anderson NH, Cline SP, Aumen NG, Sedell JR, Lienkaemper GW. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15: 133-302.

Hax CL, Golladay SW. 1998. Flow disturbance of macroinvertebrates inhabiting sediments and woody debris in a prairie stream. American Midland Naturalist 139: 210–223.

Hering D, Moog O, Sandin L, Verdonschot PFM. 2004. Overview and application of the AQEM assessment system. Hydrobiologia 516: 1-20.

Hering D, Buffagni A, Moog O, Sandin L, Sommerhäuser M, Stubauer I, Feld C, Johnson R, Pinto P, Skoulikidis N, Verdonschot PFM, Zahrádková S. 2003. The development of a system to assess the ecological quality of streams based on macroinvertebrates – Design of the sampling programme within the AQEM project. International Review of Hydrobiology 88: 345-361.

Hill MO. 1973. Diversity and evenness: a unifying notation and its consequences. Ecology 54: 427 -432.

Johnson LB, Breneman DH, Richards C. 2003. Macroinvertebrate community structure and function associated with large wood in low gradient streams. River Research and Applications 19: 199-218.

Jones JB. 1997. Benthic organic matter storage in streams: influence of detrital import and export, retention mechanisms, and climate. Journal of the North American Benthological Society 16: 109–119.

Kail J, Hering D, Muhar S, Gerhard M, Preis S. 2007. The use of large wood in stream restoration: experiences from 50 projects in Germany and Austria. Journal of Applied Ecology 44: 1145-1155.

Koljonen S, Louhi P, Mäki-Petäys A, Huusko A, Muotka T. 2012. Quantifying the effects of in-stream habitat structure and discharge on leaf retention: implications for stream restoration. Freshwater Science 31: 1121-1130.

Lancaster J. 1999. Small-scale movements of lotic macroinvertebrates with variations in flow. Freshwater Biology 41: 605-619.

Larrañaga S, Díez JR, Elosegi E, Pozo J. 2003. Leaf retention in streams of the Agüera basin (northern Spain). Aquatic Sciences 65: 158-166.

Lepori F, Palm D, Malmqvist B. 2005. Effects of stream restoration on ecosystem functioning: detritus retentiveness and decomposition. Journal of Applied Ecology 42: 228-238.

Leps M, Sundermann A, Tonkin JD, Lorenz AW, Haase P. 2016. Time is no healer: increasing restoration age does not lead to improved benthic invertebrate communities in restored river reaches. Science of the Total Environment 557-558: 722-732.

Lester RE, Boulton AJ. 2008. Rehabilitating agricultural streams in Australia with wood: A review. Environmental Management 42: 310-326.

Lester RE, Wright W, Jones-Lennon M. 2007. Does adding wood to agricultural streams enhance biodiversity? An experimental approach. Marine and Freshwater Research 58: 687–698.

McCune B, Grace JB. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon.

Moller Pillot HKM. 2013. Chironomidae Larvae. Biology and ecology of the aquatic Orthocladiinae. KNNV Publishing, Zeist.

Moller Pillot HKM. 2009. Chironomidae Larvae. Biology and ecology of the Chironomini. KNNV Publishing, Zeist.

Molokwu ND, VazPG, BradshawT, Blake A, Henessey C, Merten E. 2014. Effects of substrate on the benthic macroinvertebrate community: An experimental approach. Ecological Engineering 73: 109-114.

Muotka T, Laasonen P. 2002. Ecosystem recovery in restored headwater streams: the role of enhanced leaf retention. Journal of Applied Ecology 39: 145-156.

Pilotto F, Harvey GL, Wharton G, Pusch MT. 2016. Simple large wood structures promote hydromorphological heterogeneity and benthic macroinvertebrate diversity in low-gradient rivers. Aquatic Sciences 78: 755-766.

Pilotto F, Bertoncin A, Harvey GL, Wharton G, Pusch MT. 2014. Diversification of stream invertebrate communities by large wood. Freshwater Biology 59: 2571-2583.

Raikow DF, Grubbs SA, Cummins KW. 1995. Debris dam dynamics and coarse particulate organic matter retention in a Appalachian mountain stream. Journal of the North American Benthological Society 14: 535-546.

Roni P, Beechie T, Pess G, Hanson K. 2015. Wood placement in river restoration: fact, fiction, and future direction. Canadian Journal of Fisheries and Aquatic Sciences 72: 466-478.

Scealy JA, Mika S J, Boulton AJ. 2007. Aquatic macroinvertebrate communities on wood in an Australian lowland river: experimental assessment of the interactions of habitat, substrate complexity and retained organic matter. Marine and Freshwater Research 58: 153–165.

Schinegger R, Trautwein C, Melcher A, Schmutz S. 2012. Multiple human pressures and their spatial patterns in European running waters. Water and Environment Journal 26: 261-273.

Schmidt-Kloiber A, Hering D. 2015. www.freshwaterecology.info - an online tool that unifies, standardises and codifies more than 20,000 European freshwater organisms and their ecological preferences. Ecological Indicators 53: 271-282.

Schoen J, Merten E, Wellnitz T. 2013. Current velocity as a factor in determining macroinvertebrate assemblages on wood surfaces. Journal of Freshwater Ecology 28: 271-275.

Spänhoff B, Arle J. 2007. Setting attainable goals of stream habitat restoration from a macroinvertebrate view. Restoration Ecology 15: 317-320.

Tank JL, Rosi-Marshall E J, Griffiths NA, Entrekin SA, Stephen ML. 2010. A review of allochthonous organic matter dynamics and metabolism in streams. Journal of the North American Benthological Society 29: 118–146.

Ter Braak CJF, Šmilauer P. 2012. Canoco reference manual and user's guide: software for ordination, version 5.0. Microcomputer Power, Ithaca, New York.

Tews J, Brose U, Grimm V, Tielbörger K, Wichmann MC, Schwager M, Jeltsch F. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. Journal of Biogeography 31: 79-92.

Tonkin JD, Stoll S, Sundermann A, Haase P. 2014. Dispersal distance and the pool of taxa, but not barriers, determine the colonisation of restored river reaches by benthic invertebrates. Freshwater Biology 59: 1843–1855.

Tolkamp HH. 1982. Microdistribution of macroinvertebrates in lowland streams. Hydrobiological Bulletin 16: 133–148.

Van der Molen DT, Pot R, Evers CHM, Van Herpen FCJ, Van Nieuwerburgh LLJ. 2012. Referenties en maatlatten voor natuurlijke watertypen voor de Kaderrichtlijn Water 2014-2021. STOWA report 2012-31. STOWA, Amersfoort.

Verberk WCEP, Verdonschot PFM, Van Haaren T, Van Maanen B. 2012. Milieu- en habitatpreferenties van Nederlandse zoetwatermacrofauna. Van de Garde-Jémé, Eindhoven.

Westveer JJ, Van der Geest HG, Van Loon EE, Verdonschot PFM. 2018. Connectivity and seasonality cause rapid taxonomic and functional trait succession within an invertebrate community after stream restoration. PLOS ONE 13(5): e0197182.

# SUPPLEMENTARY APPENDIX

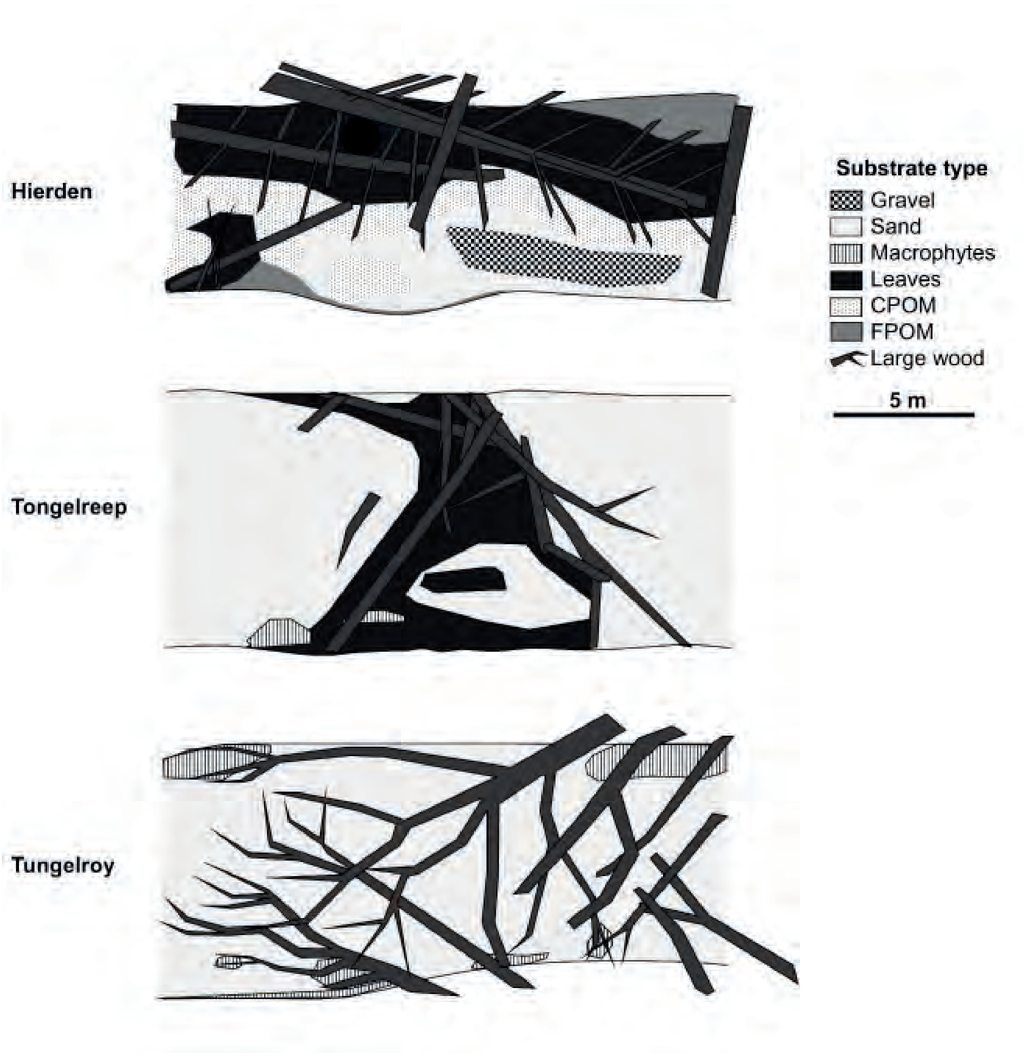

**FIGURE 1** Selection of 20-m-section substrate patterns in November 2011 in the reaches of the three study streams in year 1 after large wood was added. Drawings are on scale

**TABLE 1** Principal Response Curve analysis (PRC) taxon weights ($b_k$) of PRC-axis 1. The taxon weights indicate the fit between the response of an individual taxon to the deviations in community composition over time in the impacted sections where large wood was introduced compared to those in the unimpacted control sections

| | | Stream taxon weight PRC-axis 1 ($b_k$) | | |
|---|---|---|---|---|
| **Taxon** | **Taxonomic group** | Hierden | Tongelreep | Tungelroy |
| *Acroloxus lacustris* | Gastropoda | | | 0.0615 |
| *Ancylus fluviatilis* | Gastropoda | | 1.6126 | |
| *Aphelocheirus aestivalis* | Heteroptera | | | 0.3326 |
| *Apsectrotanypus* | Diptera | 1.1164 | 0.607 | |
| *Asellus aquaticus* | Isopoda | 0.7254 | 1.471 | 0.6004 |
| *Athripsodes cinereus* | Trichoptera | 0.061 | 0.4836 | |
| *Atrichops crassipes* | Diptera | | | -0.7454 |
| *Baetis vernus* | Ephemeroptera | 2 | 1.0538 | 1.8067 |
| *Bathyomphalus contortus* | Gastropoda | -0.884 | 0.192 | |
| *Bithynia tentaculata* | Gastropoda | | -0.155 | -0.1254 |
| *Brillia* | Diptera | | | 0.8136 |
| *Caenis horaria* | Ephemeroptera | | 0.3898 | 0.1368 |
| *Caenis luctuosa* | Ephemeroptera | | | -0.3213 |
| *Calopteryx splendens* | Odonata | | 2.2496 | 1.0248 |
| *Cataclysta lemnata* | Lepidoptera | | 0.0501 | 0.3249 |
| *Ceratopogonidae* | Diptera | 0.1398 | -0.2946 | -0.2049 |
| *Chironomus* | Diptera | | 0.092 | -0.7686 |
| *Cladotanytarsus* | Diptera | 0.9267 | | |
| *Clinotanypus* | Diptera | | -0.3696 | |
| *Cloeon dipterum* | Ephemeroptera | | | -1.6691 |
| *Coenagrionidae* | Odonata | | -0.0513 | -0.1182 |
| *Conchapelopia* | Diptera | 0.1738 | 0.1061 | -0.3903 |
| *Corbicula fluminea* | Bivalvia | | | -1.2825 |
| *Cryptochironomus* | Diptera | | -0.5502 | 0.8068 |
| *Cyrnus trimaculatus* | Trichoptera | | | -0.7578 |
| *Dendrocoelum lacteum* | Tricladida | | 0.8665 | |
| *Dicranota* | Diptera | -0.2084 | 0.3037 | |
| *Dicrotendipes* | Diptera | | | 0.4546 |
| *Echinogammarus berilloni* | Amphipoda | | 2.2202 | |
| *Elmis aenea* | Coleoptera | 0.806 | 1.4624 | |
| *Eloeophila* | Diptera | -0.1844 | 0.198 | |
| *Empididae* | Diptera | 1.7859 | | |
| *Ephemera danica* | Ephemeroptera | -0.5232 | 0.5566 | |
| *Epoicocladius* | Diptera | -0.8529 | | |
| *Erpobdella nigricollis* | Hirudinea | | 0.8597 | |
| *Erpobdella octoculata* | Hirudinea | 1.2789 | 0.9548 | -0.1686 |
| *Gammarus pulex* | Amphipoda | 0 | 1.4059 | 1.3176 |
| *Gammarus roeseli* | Amphipoda | | 1.6192 | 0.1885 |
| *Gammarus tigrinus* | Amphipoda | | 1.1174 | -0.4223 |
| *Glossiphonia complanata* | Hirudinea | -0.0056 | 0.3696 | |
| *Glossiphonia nebulosa* | Hirudinea | 0.0523 | | |
| *Gomphus vulgatissimus* | Odonata | | 0.8338 | 0.0993 |
| *Gyraulus albus* | Gastropoda | | | 0.9197 |
| *Gyrinus* | Coleoptera | | 1.4885 | |
| *Hesperocorixa sahlbergi* | Heteroptera | | | 0.6957 |
| *Hydropsyche angustipennis* | Trichoptera | | 1.8577 | 0.6525 |
| *Hydropsyche pellucidula* | Trichoptera | 2.1238 | 2.0104 | 2.4839 |

| Taxon | Taxonomic group | Stream taxon weight PRC-axis 1 ($b_k$) | | |
|---|---|---|---|---|
| | | Hierden | Tongelreep | Tungelroy |
| *Hydroptila* | Trichoptera | | | 0.3764 |
| *Ilybius fuliginosus* | Coleoptera | -0.0151 | | |
| *Leptophlebia marginata* | Ephemeroptera | 0.1434 | | |
| *Limnephilidae* | Trichoptera | -0.0701 | 1.4037 | -0.5191 |
| *Limnius volckmari* | Coleoptera | -0.4719 | | |
| *Lymnaea stagnalis* | Gastropoda | | | 0.2674 |
| *Lype* | Trichoptera | 2 | 1.7358 | 2.386 |
| *Macropelopia* | Diptera | | 0.478 | |
| *Metriocnemus* | Diptera | | | 0.2674 |
| *Micropsectra* | Diptera | -0.2518 | 0.004 | |
| *Microtendipes* | Diptera | | 0.2811 | -1.7475 |
| *Molanna angustata* | Trichoptera | | -0.1219 | -0.5103 |
| *Mystacides* | Trichoptera | | 0.889 | -1.5234 |
| *Nemouridae* | Plecoptera | -0.3533 | 0.456 | |
| *Neureclipsis bimaculata* | Trichoptera | | 0.013 | -1.8081 |
| *Notidobia ciliaris* | Trichoptera | 0.3061 | | |
| *Notonecta glauca* | Heteroptera | | | -0.567 |
| *Odontomesa* | Diptera | | -0.8075 | |
| *Oligochaeta* | Oligochaeta | 0.9875 | -0.0866 | 0.9569 |
| *Orectochilus villosus* | Coleoptera | 2.5216 | 0.3913 | 0.4625 |
| *Paratanytarsus* | Diptera | | | -0.1648 |
| *Physa fontinalis* | Gastropoda | | | 0.833 |
| *Physella acuta* | Gastropoda | | | 0.3594 |
| *Piscicola geometra* | Hirudinea | | | -0.4235 |
| *Pisidium* | Bivalvia | 0 | -0.0237 | -1.126 |
| *Planorbis* | Gastropoda | | | -0.9171 |
| *Platambus maculatus* | Coleoptera | 0.0087 | | |
| *Platycnemis pennipes* | Odonata | | | -1.0748 |
| *Plectrocnemia conspersa* | Trichoptera | 1.5872 | | |
| *Polycentropus irroratus* | Trichoptera | 2.3435 | | -0.7874 |
| *Polypedilum* | Diptera | 0.5454 | 0.654 | 1.48 |
| *Potamopyrgus antipodarum* | Gastropoda | | | -0.206 |
| *Proasellus coxalis* | Isopoda | | -0.2044 | |
| *Proasellus meridianus* | Isopoda | | 1.1732 | |
| *Procladius* | Diptera | | 0.1792 | |
| *Prodiamesa* | Diptera | 0.8633 | 0.0177 | |
| *Psychoda* | Diptera | -0.6969 | | |
| *Radix balthica* | Gastropoda | | | 0.7777 |
| *Rheocricotopus* | Diptera | 0.2964 | | |
| *Rheotanytarsus* | Diptera | | 0.7722 | |
| *Sialis lutaria* | Megaloptera | -0.5127 | 0.1487 | |
| *Simulium* | Diptera | -0.3507 | 2.2975 | 2.73 |
| *Sphaerium* | Bivalvia | | 0.7127 | 0.3212 |
| *Stictochironomus* | Diptera | 0.187 | | |
| *Tabanidae* | Diptera | 0.7436 | | |
| *Tanytarsus* | Diptera | | | -0.5149 |

# 7

## CHAPTER 7

# SYNTHESIS

## TOWARDS PULSATING PATCHES IN LOWLAND STREAMS

# TOWARDS PULSATING PATCHES IN LOWLAND STREAMS

## Spatiotemporal heterogeneity in lowland streams from a benthic macroinvertebrate perspective

Spatiotemporal heterogeneity is often divided into spatial (Winemiller et al. 2010) and temporal components (Stanley et al. 2010). Spatiotemporal heterogeneity shapes macroinvertebrate communities through spatial habitat filters that include or exclude species (Southwood 1977), followed by disturbances in time (i.e. temporal heterogeneity), which, in turn, could be mitigated by spatial heterogeneity (Townsend & Hildrew 1994). The results presented in this thesis unraveled the key components of this spatiotemporal heterogeneity in lowland streams from a benthic macroinvertebrate perspective at different spatiotemporal scales, showing that the interactions between flow and complex habitat structures shape macroinvertebrate communities.

As a consequence of flow, instream elements move and are modified in time. Hence, disturbance affects many time-related processes, including decomposition and colonization of leaf patches in the lowland stream continuum (Ward 1989). Therefore, the chapters in this thesis included time and time-related retention of habitat structures and the inhabiting macroinvertebrates. It was shown that on the meso- and microhabitat-scale, macroinvertebrates respond strongly to minor changes in flow and habitat structural complexity in time, as discussed below.

## Macroinvertebrate responses to flow

In lowland streams, flow provides rheophilic macroinvertebrates with oxygen and food particles and creates the specific habitat conditions that they require (Lancaster & Downes 2010). At the same time, flow is also a mechanical stressor or habitat filter, affecting the potential occurrence of these rheophilic species. Hydraulic stress can be the offset for dislodgement and the movement of organisms and their habitat and therefore near bed flow velocity may serve as an indicator of species occurrence (Statzner 2008, Gibbins et al. 2010), influenced by species specific flow velocity preferences (Bouckaert & Davis 1998, Wellnitz et al. 2001, Dolédec et al. 2007), as macroinvertebrates tend to occur within a certain flow range (Statzner et al. 1988). Only in case of intentional downstream drift the velocity boundary is deliberately crossed; a proficient, but high-risk behavior to become distributed over larger distances.

Disturbed flow regimes are characterized by frequent spates (Poff et al. 1997). Spates can rapidly change the prevailing microhabitat conditions and induce unintentional dislodgements of macroinvertebrates and their habitat. The consequences of spates for macroinvertebrates on a microhabitat scale and macroinvertebrate responses to counteract dislodgement and habitat loss were poorly understood. Hence, there was a strong need for quantified ecological performance metrics and to determine thresholds for organisms as well as the benthic material (Poff 2017). Yet, until now, our understanding of the process of macroinvertebrates returning to the streambed from drift was based on assumptions. Therefore, this knowledge gap was addressed in several chapters of the present thesis.

Our observations on limnephilid caddisfly species showed that flow velocity thresholds are species specific and are determined by species' traits and their intrinsic abilities to cope with flow, either experienced in their habitat or during drift (**Chapter two**). Though passive, deposited leaves also have distinct flow velocity thresholds (**Chapter four**), from which it can be inferred that each type of bed material has its own flow velocity thresholds as well, resulting in the sorting of different substrate types along a gradient of flow velocities (Kemp et al. 2000). Nonetheless, this direct relationship only holds when there are no structures present on the streambed to retain the transported material, such as large wood, trapping coarse particulate organic matter (**Chapter six**). For macroinvertebrates, movement towards such low flow refuges increases the likelihood of escaping from drift (**Chapter three**). Hence, it is concluded that flow determines the occurrence of benthic macroinvertebrates not only directly, but also indirectly driven by stream bed composition and structural complexity.

## Interactions between flow, organic matter patches and complex habitat structures

### *Complex habitat structures drive spatiotemporal heterogeneity in lowland streams*

Leaf packs comprise, together with fallen trees, branches and other forms of (large) wood, the complex physical structures in lowland streams. At sites where there are gaps in the riparian canopy, or in open landscapes, patches of submerged and emergent macrophytes further add to the complexity of the system. In lowland streams, especially the riparian trees create habitat heterogeneity and drive ecosystem functioning by providing large woody debris and seasonal inputs of different types of particulate organic matter, including twigs, leaves and seeds (Naiman & Décamps 1997, Wallace et al. 1997). In forest streams in the temperate zone the autumn leaf-drop results in large accumulations of particulate organic material on the stream bed (Richardson et al. 2005). Once positioned on the bed, the flow redistributes the material that clusters in patches of which the form, composition and structure are defined by interactions between channel form, bed morphology, complex in-stream structures, flow and biota (Fisher and Likens 1973, Webster et al. 1999).

Complexity is also generated internally within the organic matter patches. The breakdown of litter patches occurs mechanically during scouring and transport, as well as biologically by shredding and decomposition activity of organisms (Gessner et al. 1999, Hoover et al. 2006, Graça et al. 2015). The flow drives the downstream flux of organic material, causing reshuffling, re-aggregating and eventually the loss of organic material (Abelho 2001, Hoover et al. 2010). The same holds for the associated organisms (Lancaster & Hildrew 1993a; Bond & Downes 2000, 2003). As long as the organic substrates are retained in the system, fragmentation and decomposition processes occur and optimal conditions for a high biodiversity of organisms are generated (Bilby 1981, Raikow et al. 1995, Battin et al. 2008).

Complex physical structures define the direction of the flow and its interaction with the stream bed, generating a diverse spatial flow profile (Daniels & Rhoads 2004, Manga & Kirchner 2000, Manners et al. 2007). This way, complex physical structures operate as a regulatory mechanism for flow conditions at the meso- and microscale and thus, directly and indirectly affect the habitat of macroinvertebrates (**Chapter six**, Hoover et al. 2006, Tank et al. 2010). Consequently, lowland streams in which large complex physical structures are present are far less sensitive to larger-scale discharge fluctuations, because the spatial configuration of near bed flow velocities is always diverse (Davidson & Eaton 2013). In these systems patch size and associated flow velocity increases and decreases, both in the faster (rapids) and slower flowing (wakes) stream sections (**Chapter four**, Trodden et al 2012). When viewed on a mesoscale, diversity of flow, substrates and thus suitable flow conditions for macroinvertebrates can persist in these systems regardless of the discharge (Negishi & Richardson 2003, Lepori et al. 2005, Beckman and Wohl, 2014), therewith sustaining species with different preferences (**Chapter six**, Schröder et al. 2013).

### *Consequences of the loss of complex habitat structures in lowland streams*

Nowadays, the loss of complex physical structures is a major problem in lowland streams (Feld et al. 2011), resulting in homogeneous flow patterns and low streambed substrate diversity (Muotka & Laasonen 2001, Haapala et al. 2003, Melody & Richardson 2007). As a consequence, most streams are highly responsive to changes in discharge (spates and droughts) and the inhabiting benthic macroinvertebrates are frequently exposed to extreme conditions. In regulated lowland streams with long periods of very low flow or stagnation, complete coverage with leaves or silt on the stream bed leads to further habitat losses and, with high decomposition rates, to oxygen depletion (Graeber et al. 2013). At the same time, one spate can flush out large amounts of leaves, coarse particulate organic material and silt, including the inhabiting organisms (Petersen & Petersen 1991, Muotka & Laasonen 2001, Haapala et al. 2003). In the case of leaves, this often occurs before the first stages of decomposition are completed (Webster et al. 1999). Under these circumstances the leaf habitat is not durable enough to provide, amongst others, flow refuges for macroinvertebrates, allowing them to avoid being flushed out (**Chapter three**). Obviously, both a complete cover of the streambed by an oxygen depleted organic layer, as well as peak flows resulting in all leaf patches being washed out result in the loss of species (Connolly et al. 2004, Rowe & Richardson 2001, Richardson et al. 2010, Graeber et al. 2013). Hence, either end of the lowland stream flow gradient is potentially detrimental for the benthos. In streams with variable discharges, the duration of the presence of suitable conditions for macroinvertebrate development determines which species can persist in these systems and which species perish, with subsequent effects on community composition and biodiversity.

### *Restoring complex habitat structures in lowland streams*

One of the major challenges in stream ecology is to manage the flow variability and to mitigate the effects of flow extremes on macroinvertebrates in hydromorphologically degraded systems (Feld et al. 2011, Poff 2017). In this thesis, the scientific basis for such restoration efforts was provided. **Chapter five** showed that re-profiling of channelized streams induced only minor changes in streambed morphology and the substrates present. Even though instream vegetation emerged, which could be an alternative source of organic material input in the absence of mature riparian trees in these 'restored' stream stretches, no additional patches of particulate organic matter were observed. Apparently, the way the profiles were designed poorly facilitated organic matter retention and thus, streambed habitat heterogeneity. Oppositely, restoration measures involving the introduction of large wood appeared to be far more efficient in improving organic matter retention and caused a shift in macroinvertebrate assemblages (**Chapter six**). In addition, it was shown that the presence of the wood itself also contributed to biodiversity by facilitating macroinvertebrate taxa with a high affinity for hard substrates.

The present thesis also showed that the interactions between flow and complex physical structures on the microhabitat scale determine the persistence of macroinvertebrates and their habitat (**Chapter two, three and four**). In lowland streams moderate dynamic flow (**Chapter two**), the presence of complex habitat structures (**Chapter three**) and a mixture of more and less durable habitat patches (**Chapter six**) are key to providing benthic macroinvertebrates with resources, oxygen, food and shelter. The interplay of these key components results in a continuously evolving spatially heterogeneous environment suitable for a wide array of species (**Chapter six**). This way, complex habitat structures enable highly biodiverse and resilient macroinvertebrate assemblages, even in stream systems which have a relatively dynamic discharge pattern.

Based on the results obtained in the present thesis it is concluded that the interaction between complex habitat structures and flow dynamics drive the spatiotemporal heterogeneity in lowland streams and that population densities of macroinvertebrates fluctuate in space and time accordingly. For each species, suitable habitat patches expand, shrink and redistribute over time due to changes in discharge. As a consequence, to be able to survive, benthic macroinvertebrates have to track these changes. The interaction between flow and complex habitat structures allow patches to mature, preventing excessive losses of suitable habitat, which in turn results in a high macroinvertebrate biodiversity, given that a high biodiversity is sustained at moderate temporal dynamics and high, but not too high, spatial heterogeneity (Arrington & Winemiller 2004). Hence, the main findings of the present thesis can be seen as an extension of the intermediate disturbance hypothesis (Connell 1978, Shiel and Burslem 2003) and the patch dynamics concept (Townsend 1989), which we have integrated in the concept of pulsating patches in lowland streams.

## THE CONCEPT OF PULSATING PATCHES IN LOWLAND STREAMS

### Introducing the theory of pulsating patches

To describe variations in population density of foraminifera within habitats in space and time, describing density fluctuations within a patch over time and differences between patches, the theory of pulsating patches was introduced, (Buzas & Hayek 2000, 2002; Buzas et al. 2015). Subsequently, this concept was successfully used to explain the distribution, patchiness and densities of the seagrass species Halophila johnsonii (Virnstein et al. 2009). The pulsating patches theory is based on the selective strategy of species to retain stable populations over large spatial and temporal scales in response to variability over small spatial and temporal scales.

The theory of pulsating patches was applied to the findings of this thesis, which showed that variation in flow in space and time results in a dynamic mosaic of organic and mineral habitat patches on the streambed. Organic matter patches become larger or smaller or are completely washed out every time the discharge changes. These changes are tracked by macroinvertebrates to obtain resources or to position themselves along environmental gradients.

## The concept of pulsating patches applied to spatiotemporal heterogeneity in lowland streams

Patches that remain stable enough over time to retain organic matter during high flows are potentially resourceful high-quality habitats for macroinvertebrates. The palatability and complexity of material is related to species specific benthic macroinvertebrate preference (Kaushik & Hynes 1971, Graça 2001, Swan & Palmer 2006, Oliveira et al. 2014, Biasi et al. 2016). Since the breakdown of the leaves deposited on the streambed is strongly related to the retention time (Hoover et al. 2006), the food quality of particulate organic matter increases in time as a result of colonization by bacteria, fungi and diatoms. This increases the palatability of the organic matter during succession through decomposition and fragmentation processes (Fig. 1, Webster & Benfield

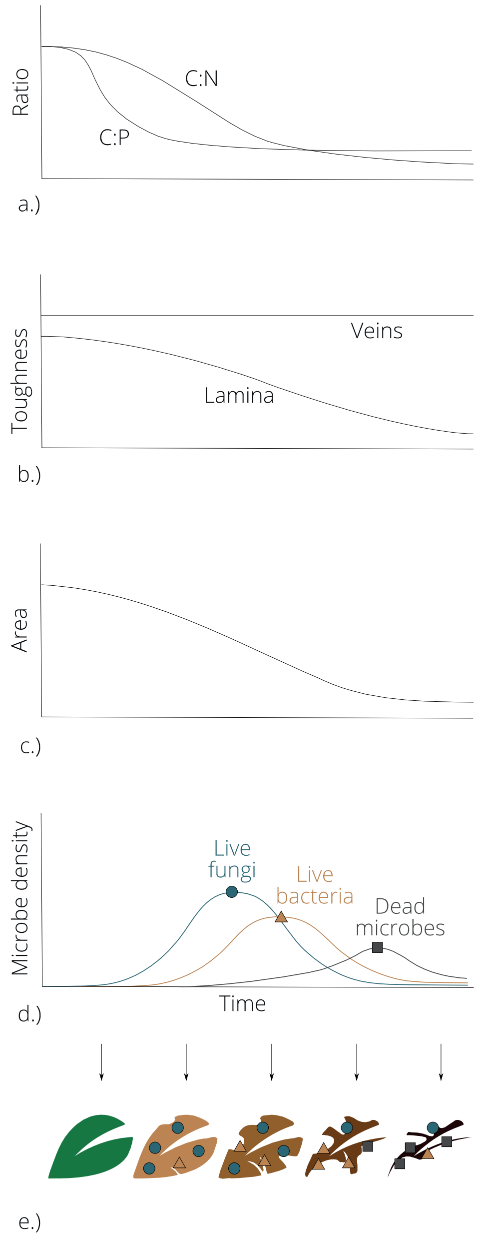

**FIGURE 1** Illustration of leaf breakdown in time. The C:N ratio and C:P ratio decrease in time (a.), the toughness of the lamina decreases in time in contrast to the veins (b.) and fragmentation decreases the area of leaves in time (c.). The microbes colonize the leaves at different rates: in general, the fungi are abundant in the first stage, followed by bacteria, while in the end dead microbes are most abundant (d). The effects of these four factors are combined in a graphical summary of leaf breakdown (e.). Modified from Suberkropp 1998, Webster et al. 2009)

1986, Graça 2001, Tank et al. 2010, Marano et al 2011), that occur at material specific rates (Petersen & Cummins 1974, Cornelissen 1996, Wardle et al. 1997, Cornwell et al. 2008). At the same time the complexity of the entire particulate organic matter patch increases, consisting of a diversity of material each with its own retention time.

Leaf patches are dynamic units in which some parts are more retentive than others (**chapter four**). For macroinvertebrates, the most stable and thus high quality areas within complex structures are here defined as 'core patches'. Because hydraulic forcing is more or less controlled in the core patches, they aid to prevent large losses of macroinvertebrates during spates (Statzner & Higler 1986, Statzner et al. 1988, Hart et al. 1996). During the rising limb of a spate, macroinvertebrates move towards such refuges to prevent dislodgement and passive drift, and thus, loss of populations from the impacted stream sections (Sedell et al. 1990, Hildrew & Lancaster 1993). During average to high discharge, increasingly more instable habitat and macroinvertebrates are dislodged, driving further macroinvertebrate redistribution through passive or active movement towards the remaining low flow refuges (Lancaster 1999, Lancaster 2000, Rice et al. 2008). The risk of dislodgement increases with decreasing level of patch stability. Instable patches are quickly removed, forcing the macroinvertebrates to seek refuge elsewhere.

In pulsating patches that gradually lose leaves with increasing discharge, the macroinvertebrates can move from the instable parts of the patch towards the more stable core. As flow conditions become more critical during spates, the macroinvertebrates need core patches to properly return to the stream bed and prevent secondary dislodgement (**Chapter three**). Even though droughts or complete stagnation always pose risks to species that require water, high oxygen levels and/or flow, within complex instream structures refuges could be present, such as small pools, remnant trickles or moist leaves or wood. Furthermore, strategic positioning in, or movement towards complex structures where flow velocities are highest ensures a continuous supply of small food particles and oxygen, which certain macroinvertebrates need for nutrition or to avoid hypoxic conditions. When discharge returns to normal levels (e.g. median yearly discharge), the core patches could act as a source from which macroinvertebrates can recolonize translocated or newly formed habitats. Hence, within the benthic environment where near-bed flow velocities and streambed substrates which form the habitat of macroinvertebrates pulsate in time in response to discharge changes, these core patches are the 'lifeline' of the system sustaining source populations on the longer term.

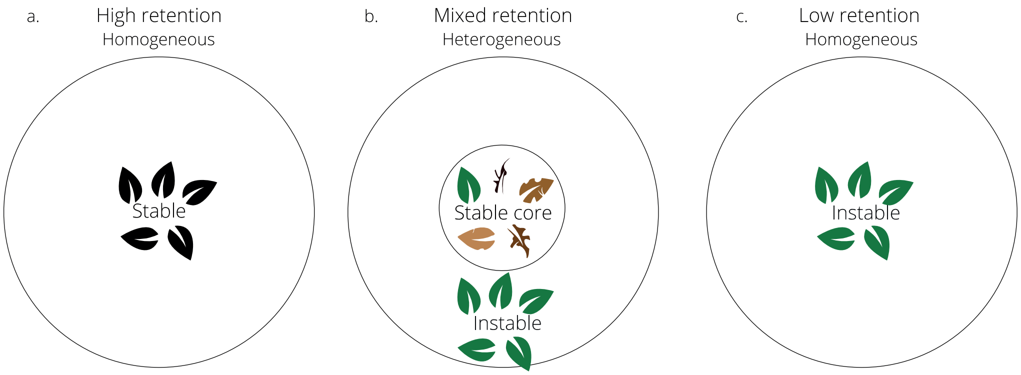

**FIGURE 2** Schematic illustration of particulate organic matter patches differing in stability. Three main types can be distinguished; environmental conditions resulting in very high retention lead to stable patches, but high decomposition rates and low oxygen levels (a), environmental conditions where high retention and entrainment jointly result in patches that pulsate, spatially expanding and shrinking, while maintaining a stable inner core (b), and environmental conditions with very low retention result in short-lived, very mobile patches (c)

In contrast to the surrounding streambed substrate, a core patch persists during extreme flow events, but when the streams' discharge returns to normal levels, the composition of the core patch will often quickly change because of the settling of organic material during the falling limb of a spate. Nevertheless, there will remain a clear distinction between the composition of organic matter in the original core patch and that of the newly deposited parts of the patch (Fig. 2).

This process of 'expanding', 'shrinking' and 'moving around' of organic matter patches re-occurs every time the discharge changes substantially. In time, a patch becomes a mixture of organic particles in different stages of decomposition or abrasion towards the core of the patch, and thus, of different food and habitat quality for macroinvertebrates. This succession sequence is only possible in pulsating patches, in contrast to short-lived patches, which are too instable to develop such gradients.

In terms of flow conditions, the core is without doubt the most stable part of the patch. Observations in this thesis also showed that flow velocities at the edge of shrinking leaf patches remained quite stable, not affected by changes in patch size, regardless of the position of the edge (**Chapter four**). Apparently, also the patch edge is a stable environment in terms of flow conditions. It is likely that the edge attracts other macroinvertebrate species than the actual core, where flow velocities, especially between leaves or leaf fragments are far lower. For example, species that require high oxygen levels may especially occur in the edge-habitat once a patch is matured (Westveer 2018). Species that filter food particles from the current may also prefer the edges of patches. Since the edge is the most exposed part of the patch, to the macroinvertebrates that persist there under variable flow conditions require a well-timed inward movement during the rising limb of a spate, before the outer leaves or leaf fragments are dislodged.

The abovementioned processes occur simultaneously in different patches on the stream bed. Some patches are newly formed, others 'survived' already a few moderate peak flows, while a few core patches already remained in place for months or even longer. Variation in patch longevity potentially causes significant differences in species composition between leaf packs, being essentially different microhabitats. This way, the concept of pulsating patches links spatiotemporal heterogeneity to biodiversity through patch retention, patch development and the differences in quantity and quality of course particulate organic matter in patches that change over time, on a scale that matters for macroinvertebrates.

## THE CONCEPT OF PULSATING PATCHES IN PRACTICE

### Stream restoration: applying the concept of pulsating patches

In stream restoration, the focus on macroscale factors and processes such as sediment transport and discharge levels may not include the ecologically relevant factors for benthic macroinvertebrates, such as the quality of resources including nutritional value and shelter possibilities. Even when there is a focus on the microhabitat scale, it is difficult to determine the links between specific habitat components and biodiversity, especially within a short timeframe (**Chapter six**). Species cope with a continuously changing dynamic environment, which requires tailor made monitoring, substantially differing from the classical monitoring. An important starting point to better establish the link between habitat composition and macroinvertebrate occurrence is incorporating the concept of pulsating patches at the meso- and microhabitat scale in the design of lowland stream restoration projects and the accompanying monitoring efforts.

### Stream restoration: incorporating the concept of pulsating patches

Modern views on stream restoration integrate ecological theory with a catchment scale approach to establish improvement of longitudinal and transversal links, physical habitat conditions, flow dynamics and thus, improve ecosystem functioning and biodiversity (Feld et al. 2011, Palmer 2010, Roni et al. 2008, Verdonschot et al. 2013, Friberg et al 2016). The concept of pulsating patches expands the view on habitat heterogeneity as primary aim of stream restoration. The present thesis showed that the presence of spatial variation in habitat patches in stream sections that differ in stability, durability and quality is essential in order to sustain species with different habitat requirements. The presence of stable core patches, which serve as lifelines during extreme events, preserves source populations in time.

The two most frequently used stream restoration measures, i.e. reprofiling of the channel and the addition of large wood, affect stream hydrology (Stofleth et al. 2008) and habitat heterogeneity (Jähnig et al. 2010, Leps et al. 2016). Large wood addition seems most promising (**Chapter five and six**). In-stream wood is relatively stable over time (Haga et al. 2002, MacVicar et al. 2009, Bertoldia et al. 2013), can last for decades (see Naiman et al. 2002) and is a resourceful hard substrate type (Benke & Wallace 2003, Trainor et al. 2007, 2012). Even though the exogenous organic deposits on the streambed are far more mobile, have higher turnover rates and are subject to annual fluctuations (Webster et al. 1999), in-stream wood can trap large amounts of organic material (Flores et al. 2011, 2013). If positioned strategically on the stream bottom, wood addition results in a mosaic of substrate types (**Chapter six**), that offers food and shelter to a wide variety of species (Fausch 1993, Wallace et al. 1995, Benke and Wallace, 2003; Coe et al. 2009, Nagayama et al. 2012). With the concept of pulsating patches in mind, managers of lowland streams could strategically add wood to the stream and promote the development of riparian trees along the banks to provide a natural input of wood and other forms of organic matter to the stream. At the same time, it is important to cease or extensify the regular maintenance operations to preserve the drainage capacity of streams, which often involves the complete removal of wood and other obstructions from the stream channel.

### Monitoring: measuring pulsating patches and their associated communities

Even though the trend of unfocused standard biological monitoring tends to be hard to break, recent developments direct towards a more targeted monitoring (Friberg et al 2016). These modern views promote long term monitoring applying a before-after-impact-control (BACI) methodology to better link the observed effects to the measures taken and to integrate evidence-based theory into novel stream restoration practice (Feld et al. 2011, Rubin et al. 2017). Still, it is difficult to determine the appropriate focal points of monitoring, because numerous variables, such as variability of configuration, juxtaposition, complexity and composition of habitat patches potentially affect the macroinvertebrate community composition (Pringle et al. 1988). Aiming for pulsating patches adds even more challenges to future monitoring, but this is necessary to match and link environmental and ecological indicators in stream restoration and to better understand the processes which are affected by anthropogenic stressors.

The two main aims of novel monitoring programs should be 1.) to determine if the restoration measure has resulted in the successful establishment of core patches that “pulsate” by expanding and shrinking in time, and 2.) to capture the differentiation in the composition of patches and their longevity and to relate this to species distributions both in time and space. This means monitoring the development of microhabitat patches in time and the occurrence of specific species within these microhabitats, instead of limiting monitoring to snapshots of the macroscale environment and overall abundance.

To be able to appropriately monitor the effects of restoration measures at the microhabitat scale based on the pulsating patches concept, it is a major challenge to recognize core patches and to distinguish high quality habitats from recently formed and recently exposed habitats. Future monitoring should thus focus more on the spatial patterns of patch development in time, to capture pulsing, to distinguish between core areas and edge habitats, to capture the composition and the stages of succession of the patches and to relate these to the macroinvertebrate community composition. Time series of near bed flow patterns can be obtained directly using modern ADCP and ADV techniques, which can be linked to changes in the streambed substrate mosaic. The longevity of the patches and the patch development in time could be captured by polarized camera imaging and differences in longevity could be amplified by using colored markers to distinguish core patches from newly developed patches and to detect periodic changes in patch size and position. It should be noted that this is only feasible in clear water streams as opposed to turbid conditions, where visualization of the streambed substrate patterns is much more challenging.

In conclusion, stream monitoring should be easy and patch longevity is an important overlooked proxy for monitoring stream quality, similar to the presence and quantity of high quality wood structures in streams that capture organic material in core patches. Future studies should turn microhabitat patch characteristics into indicators for patch longevity and patch quality that can be used in more detailed stream monitoring. Measurable characteristics of organic matter patches that change over time, such as overall composition, level of complexity, level of fragmentation, particle size, particle type, toughness of the material, coverage with biofilm, the density and species composition of fungi or bacteria, and overall stage of decomposition are potential proxies for stream quality. However, the links between these proxies and macroinvertebrate and vertebrate diversity should be better established in order incorporate them in standard stream monitoring. However, the stage of decomposition of organic matter patches is already frequently used as functional tool to determine effects of land-use, nutrient enrichment and regulation (Mendoza-Lera et al. 2012, Martinez et al. 2013 & Ferreira et al 2015). As such, relationships between indicators for patch longevity and macroinvertebrate community composition can potentially help to establish space-for-time measurements. Stream monitoring focused on capturing the temporal component of the streambed substrate mosaic as well as the spatial patterns of substrates on the streambed can distinguish microhabitat patches based on durability, define core patches and relate this information to the development of macroinvertebrate communities in time. In other words, the patch could tell the story of the stream.

## CONCLUSIONS

In conclusion, flow and complex habitat structures determine the occurrence of benthic macroinvertebrates. The spatial diversity of flow and changes in flow conditions in time result in a dynamic mosaic of organic and mineral habitat patches on the streambed. According to their life history traits, benthic macroinvertebrates track these substrate patterns on the streambed to obtain resources or to position themselves along environmental gradients. Especially patches of coarse particulate organic matter, such as packs of leaves in various stages of decomposition are important habitats for lowland stream macroinvertebrates.

Spatiotemporal variation in patch stability, largely initiated by near bed hydraulics and the presence of complex habitat structures such as large wood, is an important driver of macroinvertebrate diversity. Core patches, which have a high durability, act as flow refuges during spates. The ability of species to resist flow extremes strongly depends on the availability of these core patches within stream sections. Reintroducing wood to disturbed lowland streams is a promising restoration measure, that stimulates macroinvertebrate biodiversity by providing long-lived core patches of particulate organic matter that expand and shrink in time.

Monitoring of streams should therefore focus on capturing the temporal component of the streambed substrate mosaic next to the spatial patterns of substrates on the streambed. The durability of specific habitat patches should be determined, to be able to define the presence of core patches and to relate this information to the development of macroinvertebrate communities in time. With the concept of pulsating patches in mind lowland stream restoration projects could specifically enhance ecologically relevant stream conditions to optimize conditions for a wide variety of macroinvertebrate species. Focusing stream restoration on the conditions that facilitate the development of pulsating patches might be the key to establish the missing causal link between streambed substrate heterogeneity and macroinvertebrate biodiversity.

## REFERENCES

Abelho M. 2001. From litterfall to breakdown in streams: a review. The Scientific World Journal 1: 656–680.

Arrington DA, Winemiller KO. 2004. Organization and maintenance of fish diversity in shallow waters of tropical floodplain rivers. In Proceedings of the Second International Symposium on the Management of Large Rivers for Fisheries (LARS2). Wellcomme R, Petr T (eds) RAP Publication 2004/16: pp.25–36. Bangkok: FAO Regional Office for Asia and the Pacific.

Battin TJ, Kaplan LA, Findlay S, Hopkinson CS, Marti E, Packman AI, Newbold JD, Sabater F. 2008. Biophysical Controls on Organic Carbon Fluxes in Fluvial Networks. Nature Geoscience 1:95–100.

Beckman ND, Wohl E. 2014. Carbon Storage in Mountainous Headwater Streams: The Role of Old-Growth Forest and Logjams. Water Resources Research 50: 2376-2393.

Benke AC, Wallace JB. 2003. Influence of Wood on Invertebrate Communities in Streams and Rivers. In: Gregory SV, Boyer KL, Gurnell AM (eds) Ecology and Management of Wood in World Rivers. American Fisheries Society Symposium 37, Bethesda.

Bertoldia W, Gurnell AM, Welbera M. 2013. Wood recruitment and retention: The fate of eroded trees on a braided river explored using a combination of field and remotely-sensed data sources. Geomorphology 180–181: 146–155.

Biasi C, Cerezer C, Santos S. 2016. Biological colonization and leaf decomposition in a subtropical stream. Ecologia Austral 26:189-199.

Bilby RE. 1981. Role of Organic Debris Dams in Regulating the Export of Dissolved and Particulate Matter from a Forested Watershed. Ecology 62: 1234–1243.

Bond NR, Downes BJ. 2000. Flow-related disturbance in streams: an experimental test of the role of rock movement in reducing macroinvertebrate population densities. Marine and Freshwater Research 51: 333–337.

Bond NR, Downes BJ. 2003. The independent and interactive effects of fine sediment and flow on benthic invertebrate communities characteristic of small upland streams. Freshwater Biology 48: 455–465.

Bouckaert FW, Davis J. 1998. Microflow regimes and the distribution of macroinvertebrates around stream boulders. Freshwater Biology 40: 77–86.

Buzas MA, Hayek LC. 2000. A case for long-term monitoring of the Indian River, Florida: foraminiferal densities, 1977-1996, Bulletin of Marine Science 67: 805–814.

Buzas MA, Hayek LC. 2002. Foraminiferal densities over five years in the Indian River Lagoon Florida: a model of pulsating patches. Journal of Foraminiferal Research 32(1): 68–93.

Buzas MA, Hayek LC, Jett JA, Reed SA. 2015. Pulsating Patches History and Analyses of Spatial, Seasonal, and Yearly Distribution of Living Benthic Foraminifera. Smithsonian Contributions to Paleobiology. 92 pp. 97. iv-91. 10.5479/si.19436688.97.

Coe HJ, Kiffney PM, Pess GR, Kloehn KK, McHenry ML. 2009. Periphyton and Invertebrate Response to Wood Placement in Large Pacific Coastal Rivers. River Research and Applications 25: 1025–1035.

Connell JH. 1978. Diversity in tropical rain forests and coral reefs. Science 199: 1302–1310.

Connolly NM, Crossland MR, Pearson RG. 2004. Effect of low oxygen on survival, emergence and drift of tropical stream macroinvertebrates. Journal of the North American Benthological Society 23: 251–270.

Cornelissen JHC. 1996. An experimental comparison of leaf decomposition rates in a wide range of temperate plant species and types. Journal of Ecology 84: 573–582.

Cornwell WK, Cornelissen JH, Amatangelo K, Dorrepaal E, Eviner VT, Godoy O, Hobbie SE, Hoorens B, Kurokawa H, et al. (2008). Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. Ecology Letters, 11: 1065–1071.

Daniels MD, Rhoads BL. 2004. Effect of large woody debris configuration on three-dimensional flow structure in two low-energy meander bends at varying stages. Water Resources Research 40: 1–14. W11302. https://doi.org/10.1029/2004WR003181

Davidson SL, Eaton BC. 2013. Modeling channel morphodynamic response to variations in large wood: Implications for stream rehabilitation in degraded watersheds. Geomorphology 202: 43 –50.

Dolédec S, Lamouroux N, Fuchs U, Merigoux S. 2007. Modelling the hydraulic preferences of benthic macroinvertebrates in small European streams. Freshwater Biology 52: 145–164.

Fausch KD, Torgersen CE, Baxter CV, Li HW. 2002. Landscapes to Riverscapes: Bridging the Gap between Research and Conservation of Stream Fishes. BioScience 52: 483–498.

Feld CK, Birk S, Bradley DC, Hering D, Kail J, Marzin A, Melcher A, Nemitz D, Pedersen ML, Pletterbauer F, Pont D, Verdonschot PFM, Friberg N. 2011. From natural to degraded rivers and back again: a test of restoration ecology theory and practice. Advances in Ecological Research 44: 119–209.

Ferreira V, Castagneyrol B, Koricheva J, Gulis V, Chauvet E, Graça MAS. 2015. A meta-analysis of the effects of nutrient enrichment on litter decomposition in streams. Biological Reviews 90: 669–688.

Fisher SG, Likens GE. 1973. Energy flow in Bear Brook, New Hampshire: An integrative approach to stream ecosystem metabolism. Ecological Monographs 43: 421–439.

Flores L, Dıez JR, Larrañaga A, Pascoal C, Elosegi A. 2013. Effects of Retention Site on Breakdown of Organic Matter in a Mountain Stream. Freshwater Biology 58: 1267–1278.

Flores L, Larrañaga A, Dıez JR, Elosegi A. 2011. Experimental Wood Addition in Streams: Effects on Organic Matter Storage and Breakdown. Freshwater Biology 56: 2156–2167.

Friberg N, Angelopoulos NV, Buijse AD, Cowx IG, Kail J, Moe TF, Moir H, O'Hare MT, Verdonschot PFM, Wolter C. 2016. Effective River Restoration in the 21st Century: From Trial and Error to Novel Evidence-Based Approaches. In: Dumbrell AJ, Kordas RL, Woodward G. (eds) Large-Scale Ecology: Model Systems to Global Perspectives. Advances in Ecological Research 55: 535–611.

Gessner MO, Chauvet E, Dobson M. 1999. A perspective on leaf litter breakdown in streams. Oikos 85: 377–384.

Gibbins CN, Vericat D & Batalla RJ. 2010. Relations between invertebrate drift and flow velocity in sand-bed and riffle habitats and the limits imposed by substrate stability and benthic density. Journal of the North American Benthological Society 29: 945–958.

Graça MAS. 2001. The role of invertebrates on leaf litter decomposition in streams – a review. International Review of Hydrobiology, 86: 383–393.

Graça MAS, Ferreira V, Canhoto C, Encalada AC, Guerrero-Bolaño F, Wantzen KM, Boyer L. 2015. A conceptual model of litter breakdown in low order streams. International Review of Hydrobiology 100(1): 1–12.

Graeber D, Pusch MT, Lorenz S, Brauns M. 2013. Cascading effects of flow reduction on the benthic invertebrate community in a lowland river. Hydrobiologia 717(1): 147–159.

Haapala A, Muotka T, Laasonen P. 2003. Distribution of benthic macroinvertebrates and leaf litter in relation to streambed retentivity: Implications for headwater stream restoration. Boreal Environment Research 8: 19-30.

Haga H, Kumagai T, Otsuki K, Ogawsa S. 2002. Transport and retention of coarse woody debris in mountain streams: an in situ field experiment of log transport and a field survey of coarse woody debris distribution. Water Resources Research 38: 1–16.

Hart DD, Clark BD, Jasentuliyana A. 1996. Fine-scale field measurements of benthic flow environments inhabited by stream invertebrates. Limnology and Oceanography 41: 297–308.

Holomzuki JR, Biggs BJF. 2003. Sediment texture mediates high-flow effects on lotic macroinvertebrates. Journal of the North American Benthological Society 22: 542–553.

Hoover TM, Richardson JS, Yonemitsu N. 2006. Flow substrate interactions create and mediate leaf litter resource patches in streams. Freshwater Biololgy 51: 435–447.

Hoover TM, Marczak LB Richardson JS, Yonemitsu N. 2010. Transport and settlement of organic matter in small streams. Freshwater Biology 55: 436–449.

Jähnig SC, Brabec K, Buagni A, Erba S, Lorenz AW, Ofenböck T, Verdonschot PFM, Hering D. 2010. A comparative analysis of restoration measures and their effects on hydromorphology and benthic invertebrates in 26 central and southern european rivers. Journal of Applied Ecology 47: 671–680.

Kaushik NK, Hynes HBN. 1971. The fate of the dead leaves that fall into streams. Archiv für Hydrobiologie 68: 465–515.

Koljonen S, Louhi P, Mäki-Petäys A, Huusko A, Muotka T. (2012) Quantifying the effects of in-stream habitat structure and discharge on leaf retention: implications for stream restoration. Freshwater Science 31: 1121–1130.

Lancaster J, Hildrew AG. 1993. Characterizing in-stream flow refugia. Canadian Journal of Fisheries and Aquatic Sciences 50: 1663–1675.

Lancaster J. 1999. Small-scale movements of lotic macroinvertebrates with variations in flow. Freshwater Biology 41: 605-619.

Lancaster J. 2000. Geometric scaling of microhabitat patches and their efficacy as refugia during disturbance. Journal of Animal Ecology: 69: 442-457

Lancaster J, Downes BJ. 2010. Linking the hydraulic world of individual organisms to ecological processes: Putting ecology into ecohydraulics. River Research and Applications 26: 385-403.

Lepori F, Palm D, Malmqvist B. 2005. Effects of stream restoration on ecosystem functioning: detritus retentiveness and decomposition. Journal of Applied Ecology 42: 228–238.

Leps M, Sundermann A, Tonkin JD, Lorenz AW, Haase P. 2016. Time is no healer: increasing restoration age does not lead to improved benthic invertebrate communities in restored river reaches. Science of The Total Environment 557–558: 722–732.

MacVicar B, Piegay H, Henderson A, Comiti F, Oberline C, Pecorari E. 2009. Quantifying the temporal dynamics of wood in large rivers: field trials of wood surveying, dating, tracking, and monitoring techniques. Earth Surface Processes Landforms 34(15): 2031–2046.

Manga M, Kirchner JW. 2000. Stress partitioning in streams by large woody debris. Water Resources Research 36: 2373–2379.

Manners RB, Doyle MW, Small MJ. 2007. Structure and hydraulics of natural woody debris jams. Water Resources Research 43:1–17. W06432. https://doi.org/10.1029/2006WR004910

Marano AV, Pires-Zottarelli CLA, Barrera MD, Steciow MM, Gleason FH. 2011. Diversity, role in decomposition, and succession of zoosporic fungi and straminipiles on submerged decaying leaves in a woodland stream. Hydrobiologia 659: 93–109. https://doi.org/10.1007/s10750-009-0006-4

Martínez A, Larrañaga A, Pérez J, Descals E, Basaguren A, Pozo J. 2013. Effects of pine plantations on structural and functional attributes of forested streams. Forest Ecology and Management 310: 147–155.

Melody KJ, Richardson JS. 2007. Riparian forest harvesting and its influence on benthic communities of small streams of sub-boreal British Columbia. Canadian Journal of Forest Research 37: 907–918.

Mendoza–Lera C, Larrañaga A, Pérez J, Descals E, Martínez A, Moya O, Arostegui I, Pozo J. 2012. Headwater reservoirs weaken terrestrial-aquatic linkage by slowing leaf-litter processing in downstream regulated reaches. River Research and Applications 28: 13–22.

Muotka T, Laasonen P. 2002. Ecosystem recovery in restored headwater streams: the role of enhanced leaf retention. Journal of Applied Ecology 39:145–156.

Nagayama S, Nakamura F, Kawaguchi Y, Nakano D. 2012. Effects of Configuration of Instream Wood on Autumn and Winter Habitat Use by Fish in a Large Remeandering Reach. Hydrobiologia 680: 159–170.

Naiman RJ, Bfalian EV, Bartz KK, Bilby RE, Latterell JJ. 2002. Dead wood dynamics in stream ecosystems. In: Shea PJ, Laudenslayer WF, Valentine B, Weatherspoon CP, Lisle TE (eds) Symposium on the Ecology and Management of Dead Wood in Western Forests. pp. 23–48. USDA Forest Service, Pacific Southwest Research Station,Albany,CA.

Naiman RJ, Decamps H. 1997. The ecology of interfaces: riparian zones. Annual review of Ecology and Systematics 28: 621–658.

Negishi JN, Richardson JS. 2003. Responses of organic matter and macroinvertebrates to placements of boulder clusters in a small stream of southwestern British Columbia, Canada. Canadian Journal of Fisheries and Aquatic Sciences 60: 247–258.

Oliveira VC, Gonçalves EA, Alves RG. 2014. Colonisation of leaf litter by aquatic invertebrates in an Atlantic Forest stream. Brazilian Journal of Biology 74(2): 267-273.

Palmer MA, Menninger HL, Bernhardt E. 2010. River restoration, habitat heterogeneity and biodiversity: a failure of theory or practice? Freshwater biology 55(s1): 205–222.

Petersen RC, Cummins KW. 1974. Leaf processing in a woodland stream. Freshwater Biology, 4: 343–368.

Petersen LBM, Petersen RC. 1991. Short term retention properties of channelized and natural streams. Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie 24: 1756–1759.

Poff N. 2017. Beyond the natural flow regime? Broadening the hydro-ecological foundation to meet environmental flows challenges in a non-stationary world. Freshwater Biology: 1-11.

Poff NL, Allan JD, Bain MB, Karr JR, Prestegaard KL, Richter BD, Sparks RE, Stromberg JC. 1997. The natural flow regime. Bioscience 47: 769–784.

Pringle CM, Naiman RJ, Bretschko G, Karr JR, Oswood MW, Webster JR, Welcomme RL, Winterbourne MJ. 1988. Patch dynamics in lotic systems: The stream as a mosaic. Journal of the North American Benthological Society 7: 503–524.

Raikow DF, Grubbs SA, Cummins KW. 1995. Debris Dam Dynamics and Coarse Particulate Organic Matter Retention in an Appalachian Mountain Stream. Journal of the North American Benthological Society 14: 535–546.

Rice S, Buffin-Bélanger T, Lancaster J, Reid I. 2008. Movements of a macroinvertebrate (Potamophylax latipennis) across a gravel-bed substrate: effects of local hydraulics and micro-topography under increasing discharge. In: Gravel-bed Rivers: From Process Understanding to River Restoration. H. Habersack, H. Piegay, M. Rinaldi (Eds). Elsevier. pp 637-660.

Richardson JS, Bilby RE, Bondar CA. 2005. Organic matter dynamics in small streams of the Pacific Northwest. Journal of the American Water Resources Association 41: 921–934.

Richardson JS, Zhang YX, Marczak LB. 2010. Resource subsidies across the land freshwater interface and responses in recipient communities. River Research and Applications 26: 55–66.

Roni P, Hansen K, Beechie T. 2008. Global review of the physical and biological effectiveness of stream habitat rehabilitation techniques. North American Journal of Fisheries Management 28: 856–890.

Rowe L, Richardson JS. 2001. Community responses to experimental food depletion: Resource tracking by stream invertebrates. Oecologia 129: 473–480.

Rubin Z, Kondolf GM, Rios-Touma B. 2017. Evaluating stream restoration projects: what do we learn from monitoring? Water 9(3): 174, 1–16.

Schröder M, Kiesel J, Schattmann A, Jähnig SC, Lorenz AW, Kramm S, Keizer-Vlek H, Rolauffs P, Graf W, Leitner P, Hering D. 2013. Substratum associations of benthic invertebrates in lowland and mountain streams. Ecological Indicators 30: 178–189.

Sedell JR, Reeves GH, Hauer FR, Stanford JA, Hawkins CP. 1990. Role of Refugia in Recovery from Disturbances - Modern Fragmented and Disconnected River Systems. Environmental Management 14: 711–724.

Sheil D, Burslem DFRP. 2003. Disturbing hypotheses in tropical forests. Trends in Ecology and Evolution 18: 18–26.

Southwood TRE. 1977. Habitat, the templet for ecological strategies? Journal of Animal Ecology 46:337-365.

Stanley EH, Powers SM, Lottig NR. 2010. The evolving legacy of disturbance in stream ecology: concepts, contributions, and coming challenges. Journal of the North American Benthological Society 19: 67–83.

Statzner B, Gore JA, Resh VH. 1988. Hydraulic stream ecology: observed patterns and potential applications. Journal of the North American Benthological Society 7: 307–360.

Statzner B, Higler B. 1986. Stream hydraulics as a major determinant of benthic invertebrate zonation patterns. Freshwater Biology 16:127–139.

Statzner B. 2008. How Views about Flow Adaptations of Benthic Stream Invertebrates Changed over the Last Century. International Review of Hydrobiology 93: 593–605.

Stofleth J, Shields Jr. FD, Fox GA. 2008. Hyporheic and Total Hydraulic Retention in Small Sand-Bed Streams. Hydrologic Processes 22: 1885-1894.

Suberkropp K. 1998. Microorganisms and organic matter decomposition. – In: Naiman RJ, Bilby RE. River ecology and management: lessons from the Pacific Coastal ecoregion. Springer-Verlag, New York: 120–143.

Swan CM, Palmer MA. 2006. Composition of speciose leaf litter alters stream detritivore growth, feeding activity and leaf breakdown. Oecologia: 147(3): 469-478.

Tank JL, Rosi-Marshall EJ, Griffiths NA, Entrekin SA, Stephen ML. 2010. A review of allochthonous organic matter dynamics and metabolism in streams. Journal of the North American Benthological Society 29: 118–146.

Townsend CR, Hildrew A.G. 1994. Species traits in relation to a habitat templet for river systems. Freshwater Biology 31: 265–275.

Townsend CR. 1989. The patch dynamics concept of stream community ecology. Journal of the North American Benthological Society 8: 36–50.

Trainor AM, Shenk TS, Wilson KR. 2007. Characteristics of Preble's Meadow Jumping Mouse Micro-Habitat Use in Colorado. Journal of Wildlife Management 71: 469–477.

Trainor AM, Shenk TS, Wilson KR. 2012. Spatial, Temporal, and Biological Factors Associated with Preble's Meadow Jumping Mouse (Zapus hudsonius preblei) Home Range. Journal of Mammalogy 93: 429-438.

Trodden LRB. 2012. Local physical and hydraulic factors affecting leaf retention within streams. PhD Thesis, Cardiff University.

Verdonschot PFM, Spears BM, Feld CK, Brucet S, keizer-Vlek H, Borja A,  Elliott M, Kernan m, Johnson RK .2013. A comparative review of recovery processes in rivers, lakes, estuarine and coastal waters. Hydrobiologia 704: 453–474. doi:10.1007/ s10750-012-1294-7.

Virnstein RW, Hayek LC, Mori LJ. 2009. Pulsating patches: A model for the spatial and temporal dynamics of the threatened seagrass Halophila johnsonii. Marine Ecology Progress Series 385: 97–109.

Wallace JB, Eggert SL, Meyer JL, Webster JR. 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. Science 277: 102–104.

Wallace JB, Webster JR, Meyer JL. 1995. Influence of Log Additions on Physical and Biotic Characteristics of a Mountain Stream. Canadian Journal of Fisheries and Aquatic Sciences 52: 2120–2137.

Ward JV. 1989. The four dimensional nature of lotic ecosystems. Journal of the North American Benthological Society 8: 2-8.

Wardle DA, Bonner KI, Nicholson KS. 1997. Biodiversity and plant litter: experimental evidence which doesnot support the view that enhanced species richness improves ecosystem function. Oikos 79: 247–258.

Webster JR, Benfield EF. 1986. Vascular plant breakdown in freshwater ecosystems. Annual Review of Ecology and Systematics, 17: 567-594.

Webster JR, Benfield EF, Ehrman TP, Schaeffer MA, Tank JL, Hutchens JJ, et al. 1999. What happens to allochthonous material that falls into streams? A synthesis of new and published information from coweeta. Freshwater Biology 41: 687–705.

Webster JR, Newbold JD, Thomas SA, Valett HM, Mulholland PJ. 2009. Nutrient uptake and mineralization during leaf decay in streams-a model simulation. International Review of Hydrobiology 94: 372–390.

Wellnitz TA, Poff NL, Cosyleon G, Steury B. 2001. Current velocity and spatial scale as determinants of the distribution and abundance of two rheophilic herbivorous insects. Landscape Ecology 16: 111–120.

Westveer JJ. 2018. Go with the flow: unravelling the ecological mechanisms of dispersal and colonization by aquatic macroinvertebrates in restored lowland streams. PhD Thesis, University of Amsterdam.

Winemiller KO, Flecker AS, Hoeinghaus JD. 2010. Patch dynamics and environmental heterogeneity in lotic ecosystems Freshwater Science 29(1): 84-99.

# 8

## CHAPTER 8

# SUMMARY

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## SPATIOTEMPORAL HETEROGENEITY
## IN LOWLAND STREAMS
## “A BENTHIC MACROINVERTEBRATE PERSPECTIVE”

## SUMMARY

In lowland streams, spatiotemporal heterogeneity of habitat structures and flow together shape the physical environment that affects biota on different scales. However, it is still unclear on which scale these key factors have the strongest effect on benthic macroinvertebrates. At the same time there is an urgent need to improve the ecological quality of lowland streams in terms of biodiversity. Therefore, this thesis aimed at identifying the relevant scales of spatiotemporal heterogeneity for benthic macroinvertebrates in lowland streams. To this purpose, species specific ranges of conditions, thresholds and requirements were studied to test the hypothesis that moderate spatial and temporal heterogeneity at the meso- and micro-scale carries the highest macroinvertebrate diversity in lowland streams and to determine the optimal conditions for characteristic running water species to improve future restoration efforts. In the proceeding chapters, this hypothesis was tested at different scales in laboratory and field experiments.

Chapter 2 aimed to quantify tolerance ranges for flow velocity of six Limnephilidae species based on the process of returning to the stream bottom from drift. The six test species showed different responsiveness, different abilities to cope with flow and thus, different critical flow velocity thresholds that are reflected by their occurrence in the streams. Species on the lotic end of the gradient showed more tolerance to high flow velocities and were able to actively influence their return to the streambed from drift in contrast to species from the lentic end of the gradient.

Chapter 3 showed that stable refuges can increase species' efficiency to return to the streambed after being dislodged. Heterogeneous environments with low flow areas enabled specimens to escape from critical flow velocities in the channel and to persist on site. All of the tested species benefited from the availability of low flow refuges, but especially those more sensitive to high flow velocities. It was concluded that leaves are a resourceful habitat for macroinvertebrates, even though their refuge function highly depends on the stability of the patch.

In chapter 4, the near bed flow velocities reflected leaf retention even better than some more complex hydraulic parameters. Flow velocities that dislodged leaves were far below the critical flow velocities for the macroinvertebrates tested in the previous chapters, thereby highlighting the need for low flow areas to support stable patches and, equally important, chapter 4 also showed that leaf patch size around complex structures shrinks to a constant size, which is related to discharge. Similarly, patches can grow in accordance with discharge, presuming that natural streams transport infalling litter from upstream towards such patches, where leaves accumulate if near bed flow velocities do not dislodge the leaves.

In chapter 5, stream bed-morphology was monitored post re-meandering, so without in-stream complex structures. Longitudinal change occurred in all streams and in some bends typical lateral channel bed adjustments occurred within the study period. After re-meandering, the morphological development was mainly related to exogenous influences. In addition, no course particulate organic matter patches were formed in the studied stretches, while patches of vegetation, silt or gravel emerged, also due to a lack of in-stream structures and riparian trees.

The effects of the addition of large wood to sand-bed lowland streams on the macroinvertebrate assemblage composition of the restored sections and their associated ecological and functional traits were studied in chapter 6. The addition of large wood increased the spatial habitat heterogeneity, which remained relatively stable over years, changing macroinvertebrate assemblages, with 50-58% of the taxa displaying either a positive or a negative response. The species with high affinity for hard substrates characterized the macroinvertebrate taxa displaying a positive response in all streams, suggesting that an increase in surface area of stable hard substrate was underlying the positive ecological effect of re-introducing large wood.

The results presented in this thesis unraveled the key components of spatio-temporal heterogeneity in lowland streams from a benthic macroinvertebrate perspective at different scales, showing that the interactions between flow and complex habitat structures shape macroinvertebrate communities through the persistence of macroinvertebrates and their habitat on a microhabitat scale. In lowland streams moderate dynamic flow, the presence of complex habitat structures and a mixture of more and less durable habitat patches are key to providing benthic macroinvertebrates with resources, oxygen, food and shelter. The interplay of these key components results in a continuously evolving spatially heterogeneous environment suitable for a wide array of species. This way, complex habitat structures enable highly biodiverse and resilient macroinvertebrate assemblages, even in stream systems which have a relatively dynamic discharge pattern.

High biodiversity is sustained at moderate temporal dynamics and high, but not too high, spatial heterogeneity. The main findings of the present thesis can be seen as an extension of the intermediate disturbance hypothesis and the patch dynamics concept, which we have integrated in the concept of pulsating patches in lowland streams. The theory of pulsating patches, based on the strategy to achieve population stability over large spatial and temporal scales in response to variability over small spatial and temporal scales, was here adjusted for lowland streams, extending the relation between spatial heterogeneity and temporal heterogeneity or dynamics.

The mechanism of pulsating patches is driven by the pulse motion initiated by changes in flow. Organic matter patches become larger or smaller or are completely washed out every time the discharge changes. These changes are tracked by macroinvertebrates to obtain resources or to position themselves along environmental gradients. Core patches are the durable parts of patches that remain stable over time, persist during spates and allow individuals to be retained. Core patches serve as a lifeline of stream populations by maintaining source populations that can move to new habitat afterwards.

The retained material starts to decompose once submerged and this processing decreases the size of the particles and increases their palatability and food quality over time. Given the retention time of core patches, they contain a mixture of particles at various stages of decomposition as they are replenished with new material and lose some over time. Over time thus, a patch gains complexity in terms of material- and species composition given that it pulsates, 'expanding', 'shrinking' and 'moving around' with each disturbance event. Such 'matured' pulsating patches differ in quality, biodiversity and level of succession from highly temporal patches in a pioneer stadium or from non-pulsating long-term patches composed of rotting organic material.

The flow around a patch is essential for its development and the oxygen supply. The moving edge of a pulsating patch is a stable environment in terms of flow conditions and, even though size and position may change, a long-term niche suitable for different specific species than the core of the patch. This way, the pulsating behavior of patches may be essential for typical stream species and have an exponential positive effect on biodiversity.

The theory of pulsating patches is potentially useful in the practice of stream restoration. Instead of focusing on the adjustment itself, the focus of stream restoration should be on the processes it drives, starting with patch pulsation that evokes a chain of ecological events in a hydrodynamic environment. Until now, the management focused on habitat heterogeneity as snapshots in time, where it should focus on the pulsating behavior of course particulate organic matter patches and of other habitat types, such as gravel beds or macrophyte patches. The concept of pulsating patches can be used to explain lowland stream functioning. In fact, patch retention and patch pulsation may be the missing link in stream restoration.

PHOTO: PIET VERDONSCHOT
HIERDENSE BEEK

9

# CHAPTER 9

# NEDERLANDSE SAMENVATTING

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RUIMTELIJKE EN TEMPORELE
HETEROGENITEIT IN LAAGLANDBEKEN
GEZIEN VANUIT HET PERSPECTIEF
VAN DE BENTHISCHE MACROFAUNA

## NEDERLANDSE SAMENVATTING

In laaglandbeken is de leefomgeving van benthische macrofauna (ongewervelden die op de beekbodem leven) onderhevig aan continue veranderingen onder invloed van fysische, chemische en biologische processen. De ruimtelijke en temporele heterogeniteit van habitatstructuren vormen samen met de stroming de fysieke leefomgeving van veel soorten en zijn dus sleutelfactoren die de macrofaunagemeenschappen op verschillende schalen beïnvloeden. Het is echter nog altijd onduidelijk op welke manier deze sleutelfactoren op de verschillende schaalniveau’s de benthische macrofauna beïnvloeden. Deze kennis is noodzakelijk om de ecologische kwaliteit in termen van biodiversiteit van laaglandbeken te verbeteren. Daarom zijn in dit proefschrift de relevante ruimtelijke en temporele schalen van heterogeniteit en stroming voor de benthische macrofauna in laaglandbeken onderzocht. Met dit doel zijn soortspecifieke vereisten ten aanzien van stromings- en habitatomstandigheden bestudeerd en is de hypothese getest dat gematigde ruimtelijke en temporele heterogeniteit in structuren en stroming op meso- en microschaal de hoogste diversiteit van macrofauna in laaglandbeken mogelijk maken. Het bepalen van de optimale omstandigheden voor karakteristieke rheofiele (stromingsminnende) aquatische soorten is nodig om succesvol beekherstel te kunnen realiseren. Deze hypothese is getest op verschillende schalen middels laboratorium- en veldexperimenten die zijn beschreven in de verschillende hoofdstukken van dit proefschrift.

In hoofdstuk 2 zijn voor zes soorten kokerjuffers uit de familie Limnephilidae de maximale stroomsnelheden bepaald waarbij de larven nog konden terugkeren naar de beekbodem vanuit drift (het drijven in de waterkolom). Drift komt voor als kokerjufferlarven losraken of loslaten van de bodem, bijvoorbeeld als gevolg van piekafvoeren of door actieve verplaatsing. De zes geteste soorten reageerden verschillend en hadden ieder soortspecifieke kenmerken/aanpassingen om met stroming om te gaan en om vanuit drift de bodem weer te bereiken waar ze habitat, voedsel en bescherming vinden. De soortspecifieke kritische drempelwaarden voor stroomsnelheid weerspiegelden de omstandigheden waar de soorten van nature voorkomen in beken. De rheofiele soorten waren toleranter voor hoge stroomsnelheden dan soorten die meer voorkomen in min of meer stilstaande delen van beken. Bovendien was actief gedrag van rheofiele soorten veel effectiever om bij hoge stroomsnelheden vanuit drift naar de beekbodem terug te keren.

Hoofdstuk 3 bewees dat kokerjufferlarven in aanwezigheid van stabiele refugia (schuilplekken) efficiënter vanuit drift kunnen terugkeren naar de beekbodem.

In een heterogeen leefmilieu fungeren stabiele bladpakketten en luwtes waar de stroomsnelheid laag is als refugia, die de kokerjufferlarven de mogelijkheid bieden om te ontsnappen aan de hoge stroomsnelheid in de stroomdraad en aan predatiedruk. In de refugia konden ze zich veilig schuilhouden tussen de bladeren en stroomden ze minder snel weg. Alle geteste kokerjuffersoorten profiteerden van de refugia en in het bijzonder de soorten die meer voorkomen in stilstaande delen van beken en die gevoeliger zijn voor hoge stroomsnelheden. De bladpakketten leveren naast habitat ook voedsel waar benthische macrofauna en in het bijzonder deze kokerjufferlarven van leven. De rol van een bladpakket als habitat en voedselbron is echter erg afhankelijk van de stabiliteit van het bladpakket.

In hoofdstuk 4 is onderzocht onder welke stromingscondities bladpakketten wegspoelen, waaruit naar voren kwam dat de stroomsnelheden vlakbij de bodem de retentie van bladpakketten zelfs beter weerspiegelden dan enkele meer complexe hydraulische parameters. Stroomsnelheden waarbij de bladpakketten wegspoelden lagen ver onder de kritische drempelwaarden die gevonden waren voor de kokerjuffers. Hiermee onderstrepen de resultaten van hoofdstuk 4 de noodzaak voor de aanwezigheid van luwte plekken die het uitspoelen van kokerjufferlarven helpen voorkomen. In zones met lage stroomsnelheden (luwte), bijvoorbeeld rondom complexe structuren, blijven bladpakketten langer behouden, wat zorgt voor temporele stabiliteit. Dit hoofdstuk illustreerde ook dat het oppervlak van een bladpakket rondom één of meerdere complexe structuren, afhankelijk van de afvoer 'kromp' (hoge afvoer) of ‘groeide’(lage afvoer). Met andere woorden worden bovenstrooms ingevallen bladeren door de stroming getransporteerd naar luwtes en structuren waar ze oude bladpakketten aanvullen totdat kritische stroomsnelheden worden overschreden en de bladeren weer wegspoelen.

Ook het sediment dat de bodemmorfologie van de beek bepaalt wordt beïnvloed door de stroming. In hoofdstuk 5 is de bodemmorfologie bestudeerd in drie laaglandbeken na uitvoering van beekherstel door hermeandering. In delen van deze te herstellen beken werden nieuwe profielen gegraven, maar werden geen complexe structuren ingebracht in de beek. In alle herstelde beken kwamen longitudinale (in de lengterichting van de beek) morfologische veranderingen op gang en in sommige bochten ontstond binnen de onderzoeksperiode een typische laterale vervorming van de bodem in het dwarsprofiel. De morfologische ontwikkelingen na hermeandering ontstonden over het algemeen door exogene invloeden, zoals de aanwezigheid van bruggen en andere structuren in of op de beekbodem en of de beekoever of in de inundatiezone. Er ontstonden ook vegetatie-, slib- en grindplekken in de onderzochte beektrajecten. Bladpakketten of opeenhopingen van grof organisch materiaal werden niet gevormd, juist door 1.) het ontbreken van oevervegetatie, zoals bomen en struiken, die zorgen voor de toevoer van organisch materiaal en 2.) het ontbreken van complexe structuren in de beek die zorgen voor retentie (vasthouden) van het organisch materiaal.

In hoofdstuk 6 is de invloed van complexe structuren van dood hout in laaglandbeken op de samenstelling en ecologische en functionele eigenschappen van de aanwezige macrofaunasoorten bestudeerd. In de drie onderzochte laaglandbeken werden houtpakketten ingebracht, bestaande uit hele bomen verweven in beekbrede netstructuren. Deze houtpakketten zorgden voor een toename van de ruimtelijke habitatheterogeniteit door vorming en opeenhoping van verschillende typen substraat. Het niveau van habitatheterogeniteit bleef na inbrenging van het hout, relatief stabiel gedurende de gehele onderzoeksperiode. De inbreng van dood hout in de beek zorgde voor een verandering in de macrofaunasamenstelling. Voor 50-58% van de soorten werd een significante verschuiving waargenomen, die zich voor sommige soorten uitte in een toename en voor andere in een afname in aantallen. Veel van de verwachtte functionele eigenschappen konden niet worden aangetoond, ondanks de veranderingen in substraatsamenstelling en habitat heterogeniteit. De soorten met hoge affiniteit voor harde substraten vertoonden wel een positieve respons, wat suggereert dat de toegenomen oppervlakte van stabiel hard substraat ten grondslag lag aan het positieve ecologische effect van het herintroduceren van grove structuren van groot dood hout in laaglandbeken.

De resultaten gepresenteerd in dit proefschrift ontrafelden op verschillende schalen de sleutelfactoren voor macrofauna van ruimtelijke- en temporele heterogeniteit in laaglandbeken. De interacties op microhabitatschaal tussen stroming en complexe habitatstructuren zijn erg bepalend voor de macrofaunagemeenschappen. Op macroschaal is vooral het inbrengen van dood hout in laaglandbeken effectief, juist om de processen op microhabitatschaal te sturen.

In laaglandbeken met een matige stromingsdynamiek is de aanwezigheid van complexe structuren en een variatie van meer en minder stabiele bladpakketten de sleutel om macrofauna te voorzien van schuilplaatsen, voedsel en zuurstof. Het samenspel tussen deze sleutelfactoren resulteert in een continue veranderende, maar blijvend ruimtelijk heterogene leefomgeving die geschikt is voor een grote verscheidenheid aan macrofaunasoorten met verschillende eigenschappen. Complexe structuren blijken diverse en veerkrachtige macrofaunagemeenschappen te stimuleren, zelfs in beeksystemen met een relatief dynamisch afvoerregime.

De belangrijkste bevindingen van dit proefschrift kunnen worden gezien als een uitbreiding van de ‘intermediate disturbance hypothesis' en het 'patch dynamics concept', waarbij gesteld wordt dat een hoge biodiversiteit wordt bereikt bij een matige temporele dynamiek en hoge, maar niet te hoge ruimtelijke heterogeniteit. Beide concepten hebben we geïntegreerd in het concept van ‘pulsating patches' in laaglandbeken, dat beoogt om populatiestabiliteit te behalen over grote ruimtelijke en temporele schalen om variatie op kleine ruimtelijke en temporele schaal op te kunnen vangen. Het concept van ‘pulsating patches’ is in dit proefschrift uitgewerkt voor laaglandbeken, waarmee we een nieuwe, uitgebreide kijk op de relatie tussen ruimtelijke en temporele heterogeniteit ofwel dynamiek en tegelijk de randvoorwaarden voor een hoge macrofaunadiversiteit beschrijven.

‘Pulsating patches’ worden aangedreven door de pulserende veranderingen in stroming die een gevolg zijn van veranderingen in de afvoer. Telkens als de afvoer verandert worden pakketten met organisch materiaal groter of kleiner of spoelen volledig weg. De dynamiek van de pakketten heeft invloed op de aanwezigheid van de macrofauna die continu op zoek is naar geschikte schuilplaatsen en voedsel, specifiek passend bij iedere soort. De kern is het meest duurzame deel van een bladpakket, omdat het stabiel blijft in de tijd, aanwezig blijft tijdens piekafvoeren en er dus voor zorgt dat individuen van vooral kwetsbare soorten op die plaats aanwezig kunnen blijven in het beeksysteem. Op deze manier dienen de kernen van de pakketten als levenslijn voor beekpopulaties. Deze populaties fungeren tevens als bronpopulaties voor het behoud van soortendiversiteit op grotere schaal in de beek. Na extreme condities in de rest van de beek. Kunnen vanuit deze bronpopulaties, zich individuen weer verspreiden over het gehele beeksysteem.

Op het moment dat organisch materiaal bezinkt en op de bodem blijft liggen wordt de vertering versneld. Het organisch materiaal wordt afgebroken in kleinere deeltjes waardoor de eetbaarheid en de kwaliteit voor de benthische macrofauna toeneemt. Door de lange verblijftijd van kernen van de bladpakketten ontstaat hierin een mengsel van deeltjes die in verschillende stadia van het verteringsproces verkeren. Steeds opnieuw vindt er aanvulling met vers of minder vers materiaal plaats, maar gaat er ook weer materiaal verloren. Hoe langer een pakket op de beekbodem aanwezig blijft, hoe complexer en diverser dit pakket wordt (voortschrijdende successie) wat betreft materiaalouderdom en macrofaunasoortensamenstelling, mede doordat het pakket in de tijd ook nog pulseert en dus 'groeit' en 'krimpt' met iedere verandering in stroomsnelheid.

Dergelijke gerijpte ‘pulsating patches’ verschillen in voedselkwaliteit, structuurrijkdom en biodiversiteit. Doordat op grotere schaal in de beek zowel zeer tijdelijke pakketten die zich in een pionier stadium bevinden, rijpe complexe en diverse pakketten en niet-pulserende lange termijn pakketten die voornamelijk uit rottend organisch materiaal bestaan, aanwezig zijn vormen ze samen een continue gradiënt die juist tot extra biodiversiteit leidt.

Ook de stroming langs de randen van het pakket is essentieel voor de ontwikkeling ervan en voor de zuurstofvoorziening binnen in het pakket. De bewegende rand van een ‘pulsating patch’ is een steeds aanwezig habitat in termen van stromingscondities wat in grootte en positie steeds verandert en tegelijk een lange termijn niche biedt aan soorten met andere eigenschappen dan die soorten die in de kern van de patch leven. Op microschaal biedt de ‘pulsating patch’ zelf ook een gradiënt aan habitats. Het mechanisme achter ‘pulsating patches’ leidt dus tot het op micro- en macroschaal voorkomen van typische beeksoorten en heeft een sterk positief effect op de biodiversiteit.

De theorie van ‘pulsating patches’ heeft grote potentie om de praktijk van het beekherstel te versterken. Door het creëren van omstandigheden die tot ‘pulsating patches’ op de bodem leiden wordt een kettingreactie van ecologische processen in gang gezet. Tot nu heeft de inrichting en het beheer van beken zich gericht op momentopnames van habitatheterogeniteit, terwijl de aandacht zich zou moeten richten op het dynamische gedrag van grof organisch materiaal en van andere habitattypen, zoals pulserende detritusafzettingen, grindbedden en waterplantpakketten. We concluderen dat het concept van ‘pulsating patches’ de ruimtelijke en temporele heterogeniteit in laaglandbeken goed beschrijft en verklaart. Sterker nog, de ‘pulsating patches’ zouden wel eens de missende schakel in succesvol beekherstel kunnen zijn.

PHOTO: PIET VERDONSCHOT
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# APPENDICES

# APPENDICES

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ACKNOWLEDGEMENTS
AUTHOR CONTRIBUTIONS
LIST OF PUBLICATIONS

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## AUTHOR CONTRIBUTIONS

**Chapter 2:** AA Besse-Lototskaya[1], CJF ter Braak[2], MHS Kraak[3], PFM Verdonschot[1,3]
JHFDB, AABL and PFMV conceived the study. JHFDB, AABL and PFMV were involved in the study design. JHFDB performed the experiments. JHFDB and CJFTB analyzed the data. JHFDB wrote the manuscript with contributions from PFMV and MHSK.

**Chapter 3:** MHS Kraak[3], AA Besse-Lototskaya[1], PFM Verdonschot[1,3]
JHFDB, PFMV and AABL conceived the study. JHFDB performed the experiments. JHFDB and PFMV analyzed the data. PFMV, AABL and MHSK supervised JHFDB. JHFDB, PFMV and MHSK drafed the manuscript. All authors contributed to improve the manuscript and approved the final version of the manuscript.

**Chapter 4:** JPC Eekhout[4], AA Besse–Lototskaya[1], AJF Hoitink[5], CJF ter Braak[2], PFM Verdonschot[1,3]
JHFDB, AABL, AJFH and PFMV conceived the study. JHFDB, AABL, AJFH and PFMV were involved in the study design. JHFDB performed the experiments. JHFDB, JPCE and CJFTB analyzed the data. JHFDB wrote the manuscript with contributions from JPCE, AJFH and PFMV.

**Chapter 5:** JPC Eekhout[4], AJF Hoitink[5], PFM Verdonschot[1,3]
JPCE, AJFH, JHFDB and PFMV conceived and designed the field experiments. JPCE and JHFDB collected the data, JPCE and JHFDB analyzed the data, JPCE wrote the manuscript with contributions from the other authors.

**Chapter 6:** PFM Verdonschot[1,3], JPC Eekhout[4], RCM Verdonschot[1]
JHFDB was involved in the study design, acquired and analysed data and wrote parts of the manuscript text. PFMV was involved in the study design, analysed data and critically revised the manuscript. JPCE was involved in the study design, acquired data and added to the revision of the manuscript. RCMV analysed data and wrote parts of the manuscript text.

1 Wageningen Environmental Research, Wageningen University and Research. P.O. Box 47, 6700 AA Wageningen, The Netherlands.
2 Department Statistical Analysis, Biometris, Wageningen University Research. P.O. Box 47,6700 AA Wageningen, The Netherlands.
3 Department of Freshwater and Marine Ecology, Institute for Biodiversity and Ecosystem Dynamics (IBED), University of Amsterdam. P.O. Box 94248, 1090 GE, Amsterdam, The Netherlands.
4 Department of Soil and Water Conservationand Organic Waste Management, Centro de Edafología y Biología Aplicada del Segura (CEBAS-CSIC). P.O. Box 164, 30100 Murcia, Spain.
5 Department of Environmental Sciences, Wageningen University and Research. P.O. Box 47, 6700 AA Wageningen, TheNetherlands.

# LIST OF PUBLICATIONS

**De Brouwer JHF**, Verdonschot RCM, Eekhout JPC, Verdonschot PFM. Macroinvertebrate taxonomical and trait-based responses to large wood re-introduction in lowland streams. Freshwater Science, 2020, In press.

**De Brouwer JHF**, Kraak MHS, Besse-Lototskaya AA, Verdonschot PFM. 2019. The significance of refuge heterogeneity for lowlandstream caddisfly larvae to escape from drift. Scientific Reports, 2019, 9(1), 2140.

**De Brouwer JHF**, Besse-Lototskaya AA, ter Braak CJF, Kraak MHS, Verdonschot PFM. 2017. Flow velocity tolerance of lowland stream caddisfly larvae (Trichoptera). Aquatic Sciences, 2017, 79(3), 419–425.

**De Brouwer JHF**, Eekhout JPC, Besse–Lototskaya AA, Hoitink AJF, Ter Braak CJF, Verdonschot PFM. 2017. Flow thresholds for leaf retention in hydrodynamic wakes downstream of obstacles. Ecohydrology, 2017, 10(7), e1883.

Eekhout JPC, Hoitink AJF, **de Brouwer JHF**, PFM Verdonschot. Morphological Assessment of Reconstructed Lowland Streams in the Netherlands. Advances in Water Resources, 2015, 81, 161-171.

Govers LL, **de Brouwer JHF**, Suykerbuyk W, Bouma TJ, Lamers LPM, Smolders AJP, van Katwijk MM. 2014. Toxic effects of sediment nutrient and organic matter loading on the seagrass Zostera noltii. Aquatic toxicology 155; 253-260.

Govers LL, Lamers LPM, Bouma TJ, **de Brouwer JHF**, Hendriks AJ, Huijbers CM, van Katwijk MM. 2014. A global benchmark list of seagrasses as bioindicators for coastal trace metal loading and a Caribbean case study. Environmental pollution 195; 210-217.

Govers LL, Lamers LPM, Bouma TJ, **de Brouwer JHF**, van Katwijk MM. 2014. Eutrophication threathens Caribbean seagrasses - an example from Curaçao an Bonnaire. Marine Pollution Bulletin 89(1-2):481-486.

Huber H, **de Brouwer JHF**, von Wettberg EJ, During HJ & Anten NPR. 2014. More cells, bigger cells or simply reorganization? Alternative mechanisms leading to changed internode architecture under contrasting stress regimes. New Phytologist 201:193-204.

Huijbers CM, Nagelkerken I, Govers LL, van de Kerk M, Oldenburger JJ, **de Brouwer JHF**. 2011. Habitat type and schooling interactively determine refuge-seeking behaviour in a coral reef fish troughout ontogeny. Marine Ecology Progress Series 437; 241-251.

Huber H, **de Brouwer JHF**, de Caluwe H, Wijschedé J & Anten NPR. 2008. Shade induced changes in biomechanical petiole properties in the stoloniferous herb Trifolium repens. Evolutionary Ecology 22:399–416

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KLEINE DOMMEL