# Large wood as trigger for invertebrate habitat diversity in lowland rivers

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# The SMART Joint Doctorate Programme

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(v) Submission of a thesis within 3 years of commencing the programme.

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# Summary

Large wood (LW) forms a key element in the morphology of river channels. Its presence can significantly influence the hydromorphological processes shaping the river channel by increasing hydraulic roughness, and thus modify prevailing flow patterns and sediment transport. The surface of LW has often been described as a hotspot of macroinvertebrate diversity and abundance, since it represents a hard and stable substrate suitable for animal attachment and oviposition, and it may additionally offer more diverse food resources. Such effects of LW are expected to be especially conspicuous in lowland sandy rivers, where LW logs represent the main roughness elements within the river channel, and also the unique stable substratum for colonization within the otherwise homogeneous and loose sandy or muddy river bottom. Despite this, previous studies on LW have focused on mountain streams with coarser sediments, and did thereby also hardly consider the effects of LW on the benthic macroinvertebrates colonizing the surrounding riverbed sediments.

This thesis thus analysed the effects of the presence of in-channel pieces of LW on the physical habitat conditions and macroinvertebrate benthic assemblages of lowland sandy rivers. The study was based on field observations in river channels that were subjected to little human disturbances only, and were hence naturally rich in LW. The field records of hydraulic, morphological and biotic variables allowed for the identification of the mechanistic linkages between the changes in the physical and biotic components of the river ecosystems that were induced by the presence of LW. The effects of LW on macroinvertebrate communities were analysed in terms of taxonomic and functional composition, and of alpha and beta diversity.

Results show that in the studied lowland rivers LW induced consistent patterns of habitat variability within the otherwise homogeneous sandy river channel, as e.g. a 57%-126% increased coefficient of variation of key abiotic variables such as mean flow velocity, turbulence, median grain size and organic content of the sediments. In particular, the presence of LW was associated with the appearance of both erosion and sedimentation areas, which resulted in the formation of habitat patches with distinct combinations of sediment composition, organic matter content and flow patterns. E.g., median sediment grain size decreased by up to 53% in the sedimentation patches whereas it increased by up to 243% in scouring patches, compared to adjacent river sections without LW. The changes in abiotic conditions and the persistence of the LW logs as stable substrata also increased the diversity of the trophic resources available for macroinvertebrate assemblages by enhancing both autochthonous primary production and the retention of allochthonous organic matter. This resulted in a 1.9-5.5 fold increased contributions of autochthonous primary production and a 1.3 fold increased contribution of allochthonous organic matter to the diet of local macro-invertebrate assemblages. The elevated diversity of trophic resources and abiotic conditions in the river bed areas surrounding the LW pieces was paralleled by elevated values of alpha diversity (on average 45% higher in sites with LW) and beta diversity of the communities (on average 31% higher in sites with LW).

Hence, it may be concluded that in sandy lowland rivers even single wood logs that affect a substantial part of the channel width will trigger the formation of much more heterogeneous habitat conditions in the surrounding channel areas extending at least 60 cm upstream and 160 cm downstream of the LW. Higher habitat and resource diversity will subsequently enable a diversification of benthic invertebrate communities colonizing streambed sediments. This elevated physical and biological diversity is likely to lead to increased temporal stability of the aquatic communities, especially to higher ecosystem resilience during disturbance events. River management practices should thus avoid to remove LW from river channels. On the other hand, the addition of even simple LW structures into degraded river sections represents an effective measure to significantly enhance ecosystem functions and health.

# Zusammenfassung

Totholz stellt ein Schlüsselelement der Morphologie von Flussläufen dar. Seine Anwesenheit kann die hydromorphologischen Prozesse, die die Flussbetten gestalten, durch Erhöhung der Gerinnerauheit und damit auch durch die Veränderung der bestehenden Strömungsmuster und des Sedimenttransports wesentlich beeinflussen. Die Totholz-Oberfläche ist bereits oft als Hotspot der Makrozoobenthos-Diversität und -Abundanz beschrieben worden, da sie ein hartes und stabiles Substrat für das Festhalten und die Eiablage der Tiere darstellt, und sie kann zusätzlich vielfältige Nahrungsressourcen bieten. Solche Wirkungen von Totholz sollten in Tieflandsflüssen besonders deutlich werden, weil Totholzstämme dort die hauptsächlichen Rauheitselemente innerhalb des Flussgerinnes darstellen, und außerdem das einzige stabile Siedlungssubstrat auf der dort sonst homogenen und unbeständigen sandigen oder schlammigen Flusssohle bilden. Trotz dieser möglichen großen Bedeutung haben bisherige Arbeiten zu Totholz sich auf Bergbäche mit Grobsedimenten konzentriert, und haben dabei auch kaum die Wirkungen des Totholzes auf die benthischen Wirbellosen der umliegenden Flussbettsedimente betrachtet.

Diese Doktorarbeit soll somit die Auswirkungen der Anwesenheit von großen Totholzstücken auf die abiotischen Lebensbedingungen in Flussgerinnen sowie auf die Lebensgemeinschaften des Makrozoobenthos in sandigen Flachlandflüssen aufzeigen. Die Studie basiert auf Felduntersuchungen in vom Menschen wenig gestörten Flussgerinnen, die daher von Natur aus reich an Totholz sind. Die Feldmessungen der hydraulischen, morphologischen und biotischen Variablen erlauben die Darstellung der durch Totholzvorkommen induzierten mechanistischen Zusammenhänge zwischen den Veränderungen der physikalischen und biotischen Komponenten der Flussökosysteme. Die Wirkungen des Totholzes auf die Makrozoobenthosgemeinschaften wurden im Hinblick auf ihre taxonomische und funktionelle Zusammensetzung analysiert sowie hinsichtlich ihrer Alpha- und Beta-Diversität.

Die Ergebnisse zeigen, dass in den untersuchten Tieflandflüssen die Anwesenheit von Totholz konsistente Muster der Habitatheterogenität in dem sonst homogenen Sandflussgerinne induzierte wie z.B. ein um 57%-126% erhöhter Variationskoeffizient bei abiotischen Schlüsselvariablen wie mittlere Fließgeschwindigkeit, Turbulenz, mittlere Sedimentkorngröße und organischer Sedimentanteil. Insbesondere war das Vorhandensein von Totholz mit dem Auftreten von Flächen sowohl der Erosion und Sedimentation verbunden, was zur Bildung von Kleinlebensräumen mit bestimmten

Kombinationen von Ausprägungen der Sedimentzusammensetzung, organischem Gehalt und Strömungsmustern führte. Beispielsweise verringerte sich die mediane Sedimentkorngröße um bis zu 53% in den Sedimentationszonen, während sie in Auskolkungszonen um bis zu 243% anstieg im Vergleich zu benachbarten Flussabschnitten ohne Totholz. Die Änderungen der abiotischen Bedingungen und die Persistenz der Totholzstämme als stabile Substrate erhöhten außerdem die Vielfalt der trophischen Ressourcen, die für die Makrozoobenthosgemeinschaften zur Verfügung stehen, indem sowohl die autochthone Primärproduktion als auch die Retention allochthoner organischen Stoffe erhöht wurde. Dies führte zu einer 1.9-5.5 fach erhöhten Zunahme der autochthonen Primärproduktion sowie einer 1.3 fach erhöhten Zunahme des allochthonen organischen Materials in der Nahrung der dort vorhandenen Makrozoobenthosgemeinschaften. Die erhöhte Vielfalt der trophischen Ressourcen und der abiotischen Bedingungen im Gewässerbett in der Umgebung der Totholzstücke wurde begleitet von erhöhten Werten der Alpha-Diversität (an den Holz-Probestellen um im Durchschnitt 45% erhöht) und Beta-Diversität der Lebensgemeinschaften (an den Holz-Probestellen um im Durchschnitt 31% erhöht).

Es kann somit geschlussfolgert werden, dass in sandige Tieflandflüssen bereits einzelne Baumstämme, die einen wesentlichen Teil der Gerinnebreite einnehmen, die Ausbildung von wesentlich heterogeneren Lebensbedingungen in einem Umfeld von mindestens 60 cm flussaufwärts und 160 cm flussabwärts auslösen. Diese erhöhte Habitat- und Ressourcenvielfalt ermöglicht anschließend eine Diversifizierung der benthischen Wirbellosengemeinschaften. Diese erhöhte physische und biologische Vielfalt führt dann wahrscheinlich auch zu größerer zeitlicher Stabilität der aquatischen Lebensgemeinschaften, insbesondere zu höherer Resilienz der Ökosysteme während Störungsereignissen. In der Praxis der Flussbewirtschaftung sollte daher vermieden werden, Totholz aus Flussgerinnen zu entfernen. Auf der anderen Seite stellt die Zugabe selbst einfacher Totholzstrukturen in degradierte Flussabschnitte eine wirksame Maßnahme dar, um dort Ökosystem-Funktionen und -Zustand erheblich zu verbessern.

# Thesis outline

This thesis is composed of three manuscripts that are either accepted for publication, or ready to be submitted to peer-reviewed journals. Each manuscript has an introduction, methodology, results and discussion and forms a chapter of the thesis. A general introduction section provides the general context of the thesis and the results are discussed coherently a the general discussion section. The layout of the three manuscripts was modified and figures and tables were renumbered through the text to ensure a consistent layout throughout the entire thesis. The references of the general introduction, each manuscript, and general discussion were merged in an overall reference section. The research aims of Chapters 2, 3 and 4 are described in Paragraph 1.4.

### Chapter 1:

General introduction

### Chapter 2:

**Pilotto F.**, Bertoncin A., Harvey G.L., Wharton G. & Pusch M.T. (2014) Diversification of stream invertebrate communities by large wood. Freshwater Biology. doi: 10.1111/fwb.12454

*Author contributions:*

F. Pilotto designed the study, organized and performed field and laboratory work, analysed the data and compiled the manuscript. A. Bertoncin co-performed field and laboratory work and contributed to data analysis. G.L. Harvey, G. Wharton and M.T. Pusch co-designed the study and contributed to the text.

## Chapter 3:

**Pilotto F.**, Harvey G.L., Wharton G. & Pusch M.T. (to be submitted) Wood triggers consistent patterns of habitat variability and invertebrate diversity in lowland rivers.

*Author contributions:*

F. Pilotto designed the study, organized and performed field and laboratory work, analysed the data and compiled the manuscript. G.L. Harvey, G. Wharton and M.T. Pusch co-designed the study and contributed to the text.

## Chapter 4:

**Pilotto F.**, Cashman M.J., Harvey G.L., Wharton G. & Pusch M.T. (to be submitted) Enhanced resource availability by the presence of large wood in a lowland river as demonstrated by combined FA and SIA analyses.

*Author contributions:*

F. Pilotto and M.J. Cashman contributed equally to this work. They both designed the study, organized and performed field work and compiled the manuscript. F. Pilotto performed the laboratory work and data analysis for stable isotope analysis, M.J. Cashman performed the laboratory work and data analysis for fatty acid analysis. G.L. Harvey, G. Wharton and M.T. Pusch co-designed the study and contributed to the text.

## Chapter 5:

General discussion

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# 1. General introduction

## 1.1 Large wood in rivers: research history and management approaches

Large wood (LW) is conventionally defined as wood material larger than 0.1 m in diameter and 1 m in length (Gippel *et al.*, 1996) which may enter into river channels due to natural events, beaver and human activities. In mountain streams, wind-throw, soil and snow avalanches constitute the main natural input processes, while in lowland streams LW is mostly transported from upstream or may arrive through bank undercutting (Keller & Swanson, 1979; Harmon *et al.*, 1986; Montgomery *et al.*, 1996). LW may exhibit different degrees of size and spatial complexity, from simple pieces of wood to whole trees with branches and roots, and wood structures can range from isolated LW pieces to accumulations that span the entire channel width and are packed with leaves, organic debris or sediments (Gregory *et al.*, 1993). The size and shape of the wood piece, channel morphology, flow regime and sediment transport regime are the main factors that determine the transport and trapping of drifting wood, as well as its burial and stability (Gurnell *et al.*, 2002). Within small to medium sized rivers, the most important characteristic for wood dynamics is wood length in relation to channel size. There, wood is mostly aligned perpendicular to the flow direction and not accumulated by flow. In intermediate-sized channels, wood frequently forms conspicuous accumulations that may span the entire channel width. With increasing channel size and stream power wood pieces become increasingly oriented parallel to flow direction. In large rivers with high stream power wood mainly accumulates at the margins and outside the active channel (Bilby & Likens, 1980; Montgomery *et al.*, 1996; Gurnell *et al.*, 2002).

The traditional approach to river channel management involves the removal of in-channel LW, mainly because the additional roughness due to LW is supposed to significantly decrease the water conveyance capacity of the river and thus to increase the risk of flooding the banks (Gurnell & Linstead, 1998). Moreover, transported wood may block or damage man-made structures such as bridges, hamper boating tourism or fill up reservoirs. Moreover, the input of LW is reduced by harvesting most trees through forestry before they may fall into a river, or by removal of natural riparian forests. Both the removal of trees on the banks and of LW in the channels have led to a substantial decrease of the amount of wood in the water bodies, and subsequently to a homogenization of in-stream habitats (Gippel *et al.*, 1996).

The role of dead wood in freshwater ecosystems has been reappraised during the last decades, with the scientific interest in this topic starting at the end of the 1970s and in the 1980s, after the seminal publications by Anderson *et al.* (1978), Keller and Swanson (1979), Bilby and Likens (1980) Wallace and Benke (1984) and Harmon *et al.* (1986) (Figure 1). Since then an increasing amount of studies showed that large wood plays key roles in rivers by influencing both abiotic and biotic features of the ecosystem.

As a consequence, the purposeful addition of wood to channels has been increasingly applied as in-stream habitat restoration technique recently (Reich *et al.*, 2003), especially in North America (Kauffman *et al.*, 1997; Gregory & Wildman, 1998; Roni *et al.*, 2002), but also in Europe (Gerhard & Reich, 2000; Kail & Hering, 2005; Kail *et al.*, 2007), in Australia (Lester & Boulton, 2008) and Japan (Nakano *et al.*, 2008).

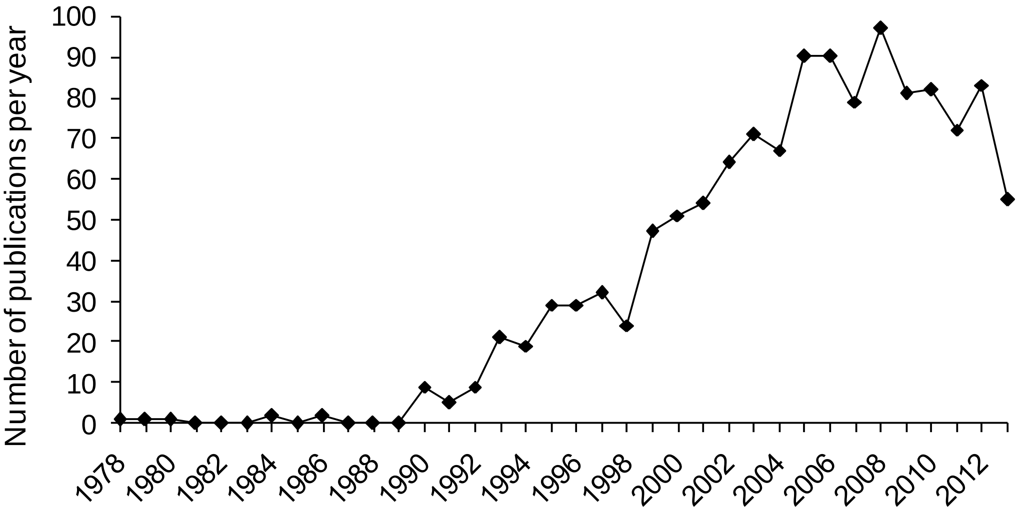

**Figure 1 Temporal dynamic between 1979 and 2013 of scientific publications dealing with large wood in rivers. Publications were selected by searching within the ISI Web of Knowledge database for the index: "large wood" OR "woody debris" OR "wood log" OR "wood dam" AND "river" OR "stream".**

## 1.2 Effects of large wood on the hydrogeomorphology of the river system

The characteristics of LW structures, their quantity, position and orientation within the river channel affect flow resistance, flow patterns and the longitudinal profile of the water surface (Figure 2). Thus, LW may profoundly influence hydromorphological processes (Young, 1991; Gippel *et al.*, 1996; Wallerstein & Thorne, 2004) by inducing changes in the flow pathways, water and sediment storage, dissipation of energy and attenuation of flood peaks.

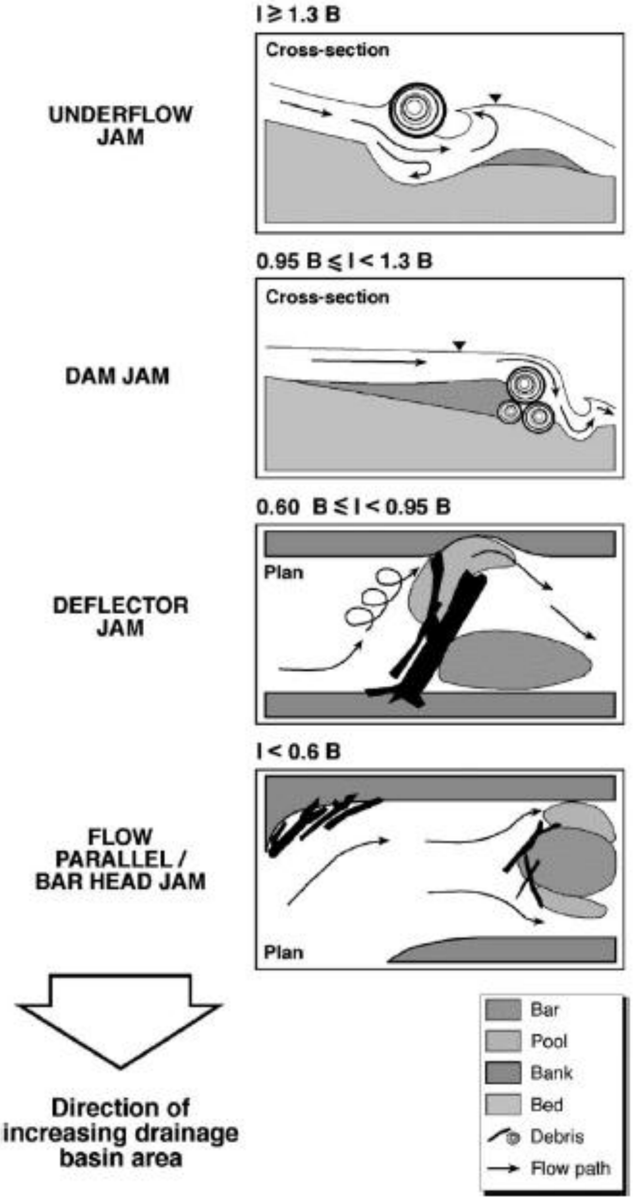

**Figure 2 Examples of deposition and erosion processes induced by different wood jam structures, from Wallerstein and Thorne (2004). l= mean LW log length; B= mean channel width.**

LW structures (single logs or LW accumulations) constitute major controls on the dissipation of the river energy by acting as roughness elements and creating log steps (Gregory *et al.*, 1985). For example, Keller & Swanson (1979) reported that wood accumulations were responsible for the 80% of waterfalls and cascades in steep mountain streams in Oregon, through which major parts of river energy was dissipated.

Also, LW diverts the water flow and concentrates it in restricted portions of the channel cross-section. This creates pressure gradients along the streambed which creates turbulences, thus driving vertical water fluxes across the streambed that enhance the vertical hydraulic exchange with the hyporheic zone (Mutz *et al.*, 2007; Sawyer *et al.*, 2011). If the LW log or jam occupies a large portion of the channel cross-section it may also produce significant water afflux and increase water storage (Gippel *et al.*, 1996; Gurnell & Linstead, 1998). This leads to an increase in water table levels in the adjacent riparian zone, too, which may induce there the formation of wetland areas (Gurnell *et al.*, 1995). During high flow, the damming effect induced by LW will enhance the connectivity between the river and floodplain by causing overbank flows into the floodplain (Wohl, 2013). Sometimes LW may even cause permanent flow diversions, thus forming side channels (Keller & Swanson, 1979).

In mountain streams, accumulations of LW enhance the formation of a step-pool sequences. There, river channels with higher wood loading generally exhibit lower distances among pools, (Gurnell & Linstead, 1998; Montgomery *et al.*, 2003), and thereby the size of pools is related to the size of LW structures (Wallerstein, 2003). Wood-induced pools support water storage even at low flows, and thus sustain surface water for longer periods during drought conditions (Gurnell & Linstead, 1998).

As a consequence of energy dissipation, creation of pools, backwaters and water storage in side channels, the presence of LW accumulations generally decreases overall flow velocity, and thus increases the travel time of river water, including flood peaks. This hydraulic retention will cause an attenuation of flood hydrograph shape (Gregory *et al.*, 1985; Ehrman & Lamberti, 1992) and a more intense recycling (shorter spiralling lengths) of nutrients transported by the stream (Bilby, 1981; Smock *et al.*, 1989). Such effects seem stronger at low-medium flow and decrease at very high flow, when water level exceeds the LW and dams are drowned (Gregory *et al.*, 1985).

### *1.2.1 Local influences of large wood on the physical conditions of the river channel*

Around pieces of LW, flow patterns in the river channel are more complex and average flow velocities are generally lower (Ehrman & Lamberti, 1992; Gippel *et al.*, 1996). This enhances the retention of fine inorganic sediments and organic matter (Smock *et al.*, 1989; Ehrman & Lamberti, 1992; Daniels, 2006; Cordova *et al.*, 2008), which leads to a more heterogeneous distribution and sorting of the sediments (Montgomery *et al.*, 2003).

These effects of LW on the local physical conditions are well documented for rivers with high-gradient and/or coarse sediments and massive accumulations of LW (Keller & Swanson, 1979; Buffington & Montgomery, 1999; Gurnell *et al.*, 2002). On the contrary, only few studies investigated the influence of isolated LW logs in sandy lowland rivers (Daniels, 2006). However, the effects of LW on the local physical conditions are potentially more important in such rivers, because they are characterized by lower stream power, more homogeneous flow patterns and more unstable substrata. Therefore, in such systems, LW may represent the most important trigger creating more diverse flow and habitat conditions (Mutz, 2000; Kail, 2003; Webb & Erskine, 2005; Daniels, 2006).

## 1.3 Effects of large wood on macroinvertebrate assemblages

In freshwater systems macroinvertebrates play a key role in nutrient cycling and transfer of carbon and energy from primary producers and detrital deposits to higher trophic levels, as fish and terrestrial predators (Wallace & Webster, 1996).

LW pieces are generally colonized by a distinct macroinvertebrate community compared to benthic habitats. Abundance, biomass and diversity are usually higher on wood (Smock *et al.*, 1989; Hoffmann & Hering, 2000; Benke & Wallace, 2003). Wood provides a stable substratum for invertebrate attachment and oviposition (Hoffmann & Hering, 2000; Benke & Wallace, 2003; Schröder *et al.*, 2013). As LW often protrudes into the water column, it may intercept drifting egg masses and macroinvertebrates which then will colonize its surface (Spänhoff *et al.*, 1999). Especially the complex micro-structure of bark offers many refugia for invertebrates against predation (Everett & Ruiz, 1993; Czarnecka *et al.*, 2014), and can also trap transported fine particulate organic matter, which may then be exploited by gatherer collector taxa (Benke & Wallace, 2003). Moreover, LW constitutes a stable substratum for the growth of periphyton, which may be utilized by grazer taxa (Golladay & Sinsabaugh, 1991), while xylophages may feed on the wood tissue itself (Hoffmann & Hering, 2000). Passive filter feeders, as simulids and net-spinning trichopterans, often use the stable wood as attachment points for their nets or for the passive filterer activity (Benke & Wallace, 2003; Schröder *et al.*, 2013). Thus, the presence of LW may significantly increase the availability of food resources for invertebrates. However previous studies so far did not demonstrate such a shift in the trophic basis of the macroinvertebrate assemblages colonizing the LW log surface and the riverbed sediments in its surrounding areas, compared to other channel areas.

Most of previous studies on the effects of LW on macroinvertebrates have been conducted in mountain streams in North America, while only few studies have dealt with European rivers or lowland reaches (Gerhard & Reich, 2000; Hoffmann & Hering, 2000). Furthermore, most studies have focused on the wood-dwelling benthic invertebrate assemblages (Hoffmann & Hering, 2000; Benke & Wallace, 2003), whereas few (Wallace *et al.*, 1995; Hilderbrand *et al.*, 1997; Gerhard & Reich, 2000) have investigated the potential effects of LW on benthic communities colonizing the streambed sediments around a piece of LW. In mountain streams studied in Europe, the addition of LW results in sediment deposition upstream of the logs, which increases overall benthic invertebrate densities and taxa richness (Gerhard & Reich, 2000). More specifically, the abundance and biomass of collectors and predators was increased, while those of scrapers and filterers were decreased (Wallace *et al.*, 1995). In low-gradient rivers, the presence of LW was observed to increase the number of pool habitats (Hilderbrand *et al.*, 1997).

### 1.4 Approach, aims and structure of this thesis

Notably, previous study that investigated the effects of LW on benthic habitats in the surrounding channel areas have considered upstream effects only (Wallace *et al.*, 1995). So far, the effects of the presence a single LW structure on nearby channel areas, or the distance to the next LW on a given point of a stream channel have never been analysed. Thus, there is an obvious knowledge gap concerning the effects of LW on physical habitat conditions and on benthic invertebrate communities in surrounding channel areas.

In particular little is known about the mechanistic linkages between the changes in the hydromorphological features of the river channel and the availability of trophic resources induced by the presence of large wood, together resulting in changes in the macroinvertebrate assemblages colonizing the riverbed sediments.

Thus, this thesis aims to identify the effects of large wood on the physical habitat conditions and on the structure of macroinvertebrate assemblages in sand-dominated lowland rivers. Wood provides hard and stable substrata, which are generally rare in lowland rivers. Thus, wood is expected to lead to the formation of a mesoscale mosaic of flow velocity and sediment composition in the surrounding areas of the river channel, and also to enhance the availability and quality of trophic resources for macro-invertebrates. As a consequence, the presence of LW pieces would significantly increase the abundance and diversity of benthic invertebrates.

Thus, in the second chapter of the thesis I aimed to quantify the effects of LW on the structural and functional composition of benthic invertebrate assemblages in the riverbed sediments around the LW logs, and to relate those effects to the hydromorphological changes induced by single LW pieces. For this purpose I studied a reach of a lowland sandy river which was naturally rich in in-channel large wood. There, I systematically analysed the effects of four LW logs (replicates) on the surrounding channel areas at the spatial scale of the mesohabitat (centimetres to meters) and along a gradient of distance from the next LW piece.

The third chapter aims to test the general validity of the findings in the previous chapter by involving a whole set of study reaches from several sandy lowland river reaches, and investigating more LW pieces. In that study I was especially interested in quantifying the effects of the presence of LW on the alpha and beta diversity of the macroinvertebrate assemblages settled on the LW, and on the sediments in its surrounding areas. Also, this study aims to relate those effects to the variability of abiotic habitat conditions in its surroundings areas. For that, I gathered data on abiotic variables and macroinvertebrates in five reaches of three lowland rivers, and compared habitat and community diversity among sites that were rich in LW and nearby sites without LW in a paired-site study design.

The fourth chapter aims to demonstrate and quantify the differences in the utilization of several possible food resources by the macroinvertebrates settling on the surface of LW logs, on the riverbed sediments in its surrounding area, and on riverbed sediments in a site without LW. The study hypothesizes that the contribution of epixylic and terrestrial material would represent a larger proportion of the diet of specific taxa, and as a consequence the whole assemblage would be sustained by more diverse trophic resources in the proximity of LW than in the area without LW.

These studies were based on field surveys in near-natural river reaches with abundant in-channel large wood that are not prone to significant human disturbances. These river reaches thus may also represent reference scenarios for river restoration projects in impacted lowland rivers.

# 2. Diversification of stream invertebrate communities by large wood

Francesca Pilotto, Andrea Bertoncin, Gemma L. Harvey, Geraldene Wharton and
Martin T. Pusch

(Freshwater Biology, http://dx.doi.org/10.1111/fwb.12454)

# 3. Wood triggers consistent patterns of habitat variability and invertebrate diversity in lowland rivers

Francesca Pilotto, Gemma L. Harvey, Geraldene Wharton and Martin T. Pusch

## 3.1 Abstract

The presence of large wood (LW) in river channels does not only add an important habitat for benthic invertebrates, but also triggers the formation of complex hydromorphological patterns in the surrounding channel area. This study aimed to quantify the effects of LW pieces on channel habitat characteristics and on the diversity of the macroinvertebrate communities in sandy lowland rivers, seeking for common patterns among a set of river sections where sites rich in LW were compared with nearby sites without LW. As expected, the presence of LW induced greater heterogeneity in channel hydromorphology, as e.g. the coefficients of variation of flow velocity and sediment grain size were 85% and 126% times higher in the wood sites compared to non-wood sites, whereas the mean values did not differ. In parallel, macroinvertebrate beta diversity was on average 31% higher in the wood sites than in the non-wood sites, and positively correlated with the number of LW structures in the site. The hotspots of diversity were located in the river-bed areas surrounding the LW, where taxa richness was 30% higher and Shannon-Wiener diversity 45% higher compared to non-wood sites, and which was even higher than the values recorded for the LW surface. This effect of LW could be related to the increased variability of abiotic variables recorded in the surroundings of LW, in particular to the increased coefficients of variation of sediment grain size and of flow velocity. Thus we could demonstrate that the presence of LW pieces triggers consistent patterns of benthic habitat variability in the surrounding channel areas, which significantly enhances alpha and beta diversity of macroinvertebrate communities in the whole area.

## 3.2 Introduction

In freshwater ecosystems, spatial heterogeneity of physical conditions is usually followed by a higher diversity and taxonomic richness of various biotic components (Baattrup-Pedersen & Riis, 1999; Beisel *et al.*, 2000; Passy & Blanchet, 2007). This can also result in changes in ecosystem functions, such as changes in the primary productivity of stream algae and respiration of benthic biofilms (Cardinale *et al.*, 2002), and in the provision of refugia for biota during disturbances (Townsend & Hildrew, 1994), thus increasing the temporal stability of aquatic communities (Brown, 2003). In streams and rivers, the presence of large wood (LW) induces complex flow patterns (Ehrman & Lamberti, 1992; Gippel *et al.*, 1996) which often lead to changes in channel depth and width and to a more heterogeneous distribution and sorting of sediments (Gurnell & Linstead, 1998; Montgomery *et al.*, 2003; Wohl, 2013) including particulate organic matter (Ehrman & Lamberti, 1992; Daniels, 2006) in the surrounding channel areas. In low-gradient rivers with fine bed material LW can represent a key hydraulic roughness element, which is only paralleled by the seasonal appearance of submerged macrophyte stands (Hilderbrand *et al.*, 1997; Mutz, 2000; Kail, 2003; Webb & Erskine, 2005).

Although the surface of LW logs is widely recognized as a hotspot of macroinvertebrate abundance, biomass and diversity (O'Connor, 1991; Everett & Ruiz, 1993; Drury & Kelso, 2000; Hoffmann & Hering, 2000; Benke & Wallace, 2003), less is known about the effects of LW on the benthic communities colonizing river habitats in the surrounding channel areas. A shift in invertebrate community composition in response to the addition of LW logs has been recorded in a high gradient stream, associated with the formation of depositional areas upstream (Wallace *et al.*, 1995), and in a low gradient stream, related to the formation of pools (Hilderbrand *et al.*, 1997). These studies, however, do not report any significant effect of LW on invertebrate total abundance or diversity. There is some evidence that LW triggers the formation of new mesohabitats known to host diverse macroinvertebrate communities, but this has only been shown for one high-gradient stream (Gerhard and Reich, 2000) and one low-gradient river (Pilotto *et al.*, 2014) so far. Moreover, previous studies do not demonstrate the effect of LW on the compositional heterogeneity of the macroinvertebrate assemblages (beta diversity).

The aim of this study was to examine the relationship between LW, channel hydromorphology and macroinvertebrate diversity across a set of lowland river reaches. In particular, this study investigated (i) whether LW increases the variability of abiotic habitat conditions in the surrounding channel areas, (ii) whether the changes in abiotic conditions result in changes in the taxonomic composition and local (alpha) diversity of the macroinvertebrate assemblages, and (iii) whether the compositional heterogeneity of the macroinvertebrate assemblages (beta diversity) increases with increasing frequency of LW in the river channel. Data on abiotic variables and macroinvertebrates were collected from five reaches of three lowland rivers, and habitat variability and community diversity were compared among sites that were rich in LW and nearby sites without LW in a paired-site research design.

## 3.3 Methods

### *3.3.1 Study area*

This study was carried out in five reaches of three near-natural rivers in Western Poland, the Płociczna, Korytnica and Pliszka Rivers (Figure 11). All three rivers are low gradient, sand dominated lowland rivers with largely forested floodplains. The Płociczna (length: 51 km) and Korytnica (length: 37 km) Rivers are tributaries of the Drawa River, while the Pliszka River is a 56-km long tributary of the Oder River (Figure 11).

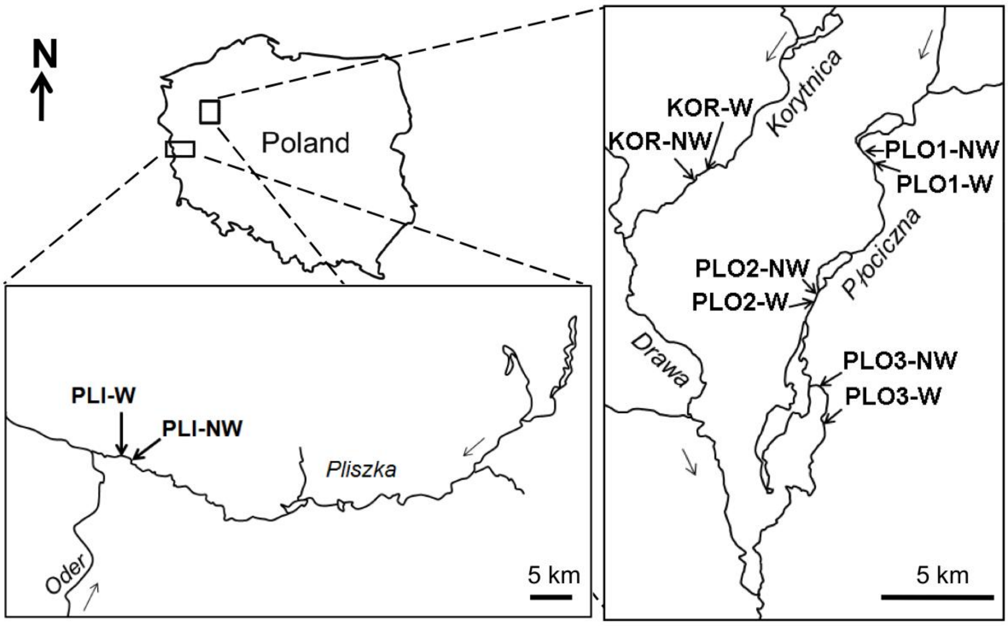

**Figure 11 Map of the study area.**

For our study, we selected one reach of Korytnica (KOR) and Pliszka River (PLI), and three reaches in the Płociczna River which are separated by lakes (PLO1, PLO2 and PLO3, Figure 11). These reaches allowed a paired-site research design: within the same river reach, a 100-m-long site naturally rich in in-channel LW (‘wood site’) was compared in terms of hydromorphology and stream macroinvertebrate assemblages to a nearby site without (or with a low amount of) LW (‘non-wood site’). Due to the low gradient of the studied reaches, LW pieces falling into the channel are not transported downstream or re-oriented and thus remain in place mainly as single logs, mostly aligned across the channel perpendicular to the flow direction. Only few accumulations of LW (jams; Table 5) were recorded within the studied reaches, which were composed of smaller wood pieces trapped by a complex key element (i.e. wood stem with branches). All selected study sites were relatively straight (to avoid the confounding effect of meanders on channel geomorphology), with forested banks (mainly alder [*Alnus glutinosa*]) and similar bankfull width, discharge and sandy sediments (Table 5).

### *3.3.2 Study design*

Field work was carried out in April-May 2012, under near bankfull discharge conditions. In each reach, six in-channel pieces of LW were selected at the respective wood site (except PLO2 where three LW were selected) as replicates. Single LW pieces with similar characteristics representative of the wood structures in the study area were selected. These ranged between 12 and 41 cm in diameter and were larger than 2 m in length (range: 2.5 - 18.8 m), were oriented perpendicular to river flow, and were partially in contact with bed sediment. The selected LW were separated by distances > 5 m in order to avoid overlapping effects.

For each selected LW piece, abiotic and biotic data were collected from three substrata: the surface of the LW (W1), the river-bed sediment around the LW (at ca. 10 cm from the LW; W2), and the river-bed sediment outside the direct hydrological influence of the LW log (> 5 m from the LW; W3). We set one sampling point in the W1 and W3 substratum of each selected LW piece, and three sampling points in the W2 substratum, one upstream, one downstream and one lateral to the LW. In each non-wood site we set six sampling points covering the range of water depths present there (NW). At each sampling point environmental variables and macroinvertebrates were sampled as outlined below.

**Table 5 Geographical position and hydromorphological characteristics of study sites. KOR= Korytnica, PLI= Pliszka, PLO1= Płociczna reach 1, PLO2=Płociczna reach 2; PLO3= Płociczna reach 3; W= wood site, NW = non-wood site.**

| | KOR | | PLI | | PLO1 | | PLO2 | | PLO3 | |
|---|---|---|---|---|---|---|---|---|---|---|
| | W | NW | W | NW | W | NW | W | NW | W | NW |
| Latitude (North) | 53°10'10" | 53° 9'58" | 52°14'58" | 52°14'41" | 53°10'29" | 53°10'38" | 53°07'21" | 53°07'28" | 53°04'38" | 53°05'32" |
| Longitude (East) | 15°55'20" | 15°54'59" | 14°44'18" | 14°45'20" | 16°01'14" | 16°01'01" | 15°59'18" | 15°59'25" | 15°59'37" | 15°59'27" |
| Bankfull width (m) | 15.8 | 10.9 | 9.6 | 7.9 | 12.1 | 15.4 | 16.4 | 16.6 | 12.3 | 14.1 |
| Mean water depth (m) | 0.48 | 0.53 | 0.58 | 0.83 | 0.5 | 0.56 | 0.38 | 0.54 | 0.7 | 0.38 |
| Near-bankfull discharge ($m^3/s$) | 2 | 2.1 | 1.6 | 1.8 | 1.4 | 1.5 | 2 | 3.2 | 3.4 | 2.9 |
| Water level slope ($x10^{-3}$) | 1.3 | 0.2 | 0.5 | 0.1 | 0.5 | 0.4 | 1.4 | 0.2 | 1.4 | 1.1 |
| River-bed slope ($x10^{-3}$) | 4.9 | 1.6 | 1.5 | 6.2 | 2.1 | 0.8 | 1.9 | 2 | 0.1 | 1.4 |
| Number of wood logs (log jams) in 100m | 22 (0) | 1 (0) | 19 (0) | 3 (0) | 20 (5) | 7 (2) | 27 (3) | 15 (1) | 31 (2) | 8 (0) |
| Number of wood logs and jams with blockage ratio > 0.10 in 100m | 10 | 1 | 9 | 2 | 9 | 5 | 14 | 10 | 15 | 4 |
| Mean diameter of wood logs (m) | 0.26 | 0.17 | 0.25 | 0.22 | 0.16 | 0.17 | 0.2 | 0.17 | 0.24 | 0.24 |
| Mean length of wood logs (m) | 6.39 | 7.76 | 5.35 | 6.02 | 6.47 | 7.51 | 7.07 | 8.8 | 7.3 | 5.24 |
| Ratio logs volume / Channel bankfull area ($m^3/ha$) | 65.2 | 1.7 | 36 | 5.8 | 94.4 | 22.9 | 53.7 | 32.7 | 165.8 | 9.9 |

### 3.3.3 Environmental variables

Channel bed elevation was recorded across three to five cross-sections within each site, using a total station (TCRA 1205+, Leica, Heerburgg, Switzerland), and water depth was measured at 1-m intervals. Two cross-sections were located at the beginning and end of the site, the others were set to be equally distant one to the other. In case one cross-section overlapped a LW piece, that cross-section was moved downstream to avoid the measurements of channel bed elevation being affected by the LW piece. The locations of the LW pieces were surveyed using the total station, too. Mean channel width, the channel area, and the orientation angle of each LW relative to the channel, were calculated using ArcGIS 9.2. The slope of the riverbed and the slope of the water level were calculated along the thalweg line as the difference in the elevation between the most upstream and downstream cross-sections divided by the reach length (i.e. 100 m). In order to estimate the volume of LW in each site, we measured the length of each in-channel LW piece and its diameter at its ends, assuming a nearly cylindrical shape. The blockage ratio (B) was defined as the partial cross-sectional area occupied by each piece of LW and computed as $B = L\,d/A$, where A is the cross-sectional area, d is the diameter of the LW piece and L is the projected length of the LW against the flow (Gippel *et al.*, 1996).

Near-bed (5 cm above the sediment) 3D flow measurements were recorded in each sampling point for 1 minute (Buffin-Bélanger & Roy, 2005) at 1 Hz, using a FlowTracker (SonTek) Acoustic Doppler Velocimeter, in order to assess the hydraulic conditions experienced by benthic invertebrates (Jowett, 2003). From those measurements, mean flow velocity was computed as $\text{MeanV}=\sqrt{Vx^2+Vy^2+Vz^2}$ , with Vx, Vy and Vz being the average velocity values over 1 minute of the streamwise, transverse and vertical component. The standard deviation of Vx was used as proxy for turbulence (Enders *et al.*, 2003).

A sediment core (diameter 10 cm, depth 5 cm) was collected at each benthic sampling point. Sediment samples were dried in the laboratory at 60°C for 36 h and sieved through a 12-level sieving cascade with a sieve shaker. Each fraction was then re-dried at 60° and weighed. Organic content was determined by loss on ignition (the samples were burnt at 550° for 5h). From the dry weight of the 12 fractions, distribution curves and the median grain size ($D_{50}$) were calculated.

### *3.3.4 Macroinvertebrates*

Benthic macroinvertebrates colonizing the river-bed sediments were sampled using a Surber sampler (frame size = 23x23 cm, mesh size: 500 μm). The material from five Surber samplers was pooled to produce one sample, which thus represented a total area of 0.26 $m^2$. Invertebrates sampled from the LW surface were dislodged by brushing a surface area of 0.26 $m^2$ and collecting the material in a net. Samples were preserved in 70% ethanol and processed in the laboratory, where they were sorted and animals counted and identified to the lowest taxonomic level possible under a binocular microscope with 10x magnification. Samples were mostly identified to species or genus level, Gammaridae (with the exception of *Gammarus roeselii*) and some Trichoptera to family, Chironomidae to subfamily, Oligochaeta as class. The taxonomic level was the same across all the samples.

Taxa abundances from the three sampling points on the river-bed sediments surrounding the same LW (upstream, downstream and lateral) were averaged in order to obtain a composite sample (W2) for the area surrounding each of the six replicate LW. Thus, in each reach we obtained six replicate NW samples, six replicate W1 samples, six replicate W2 samples and six replicate W3 samples. In the reach PLO2 we had three replicates each substratum instead of six. Based on the invertebrate taxonomic abundances, we computed the Shannon-Wiener diversity index and the taxa richness after rarefaction per each sample, using R software package 'Vegan' (R Core Team, 2013) (Oksanen *et al.*, 2013). Beta diversity was computed as global multivariate dispersion, which is a multivariate measure of compositional heterogeneity in groups of samples (Clarke & Warwick, 2001; Anderson, 2006). The multivariate dispersion was calculated for the wood and non-wood sites within each reach as the mean distance of the samples from their group centroid, again using package 'Vegan' (Oksanen *et al.*, 2013) in R, this computation was based on the log(x+1) transformed invertebrate taxonomic abundances and the binomial distance (Anderson & Millar, 2004). Since the number of samples differed between the two groups (i.e. 6 samples for non-wood sites, 18 for wood sites at all reaches, except PLO2 where the respective numbers were 3 and 9) we applied the sqrt(n/(n-1)) correction to the estimated distances to centroid within each group (Stier *et al.*, 2013).

### *3.3.5 Data analysis*

Hydromorphological characteristics and the amount of LW in the wood and non-wood sites were compared using Student’s paired t-test. Spatial variability of the abiotic variables was computed as their coefficient of variation (Minshall & Robinson, 1998; Gostner *et al.*, 2013).

In order to account for the nested study design and investigate the common patterns among the different study reaches, we fitted a series of linear mixed effect models (LME). The models included the factor of interest as fixed factor, and random intercepts for the reach (random effect). Those models were used to test for differences in the values and variability of the environmental variables (i.e. mean flow velocity, turbulence, organic matter and median grain size) between site types (fixed factor with levels: wood site and non-wood site) and among substrate types (fixed factor with levels: NW, W1, W2 and W3). LME models were also used to test for differences in the values of macroinvertebrate metrics (abundance, taxa richness and Shannon-Wiener diversity) among substrate types (fixed factor with levels: NW, W1, W2 and W3) and beta diversity between site types (fixed factor with levels: wood site and non-wood site). All the LME models were tested by likelihood ratio tests against the reduced model (without the fixed factor), and the residuals where checked for normality by applying the Wilk-Shapiro test. The relationship between beta diversity and the amount of LW in the sites was analysed using linear regression.

LME models were also used to investigate the relationship among the two invertebrate metrics of alpha diversity (taxa richness and Shannon-Wiener diversity index) recorded on benthic habitats (NW, W2 and W3) and the mean value and variability of the abiotic variables recorded there, as mean flow velocity, turbulence, median sediment grain size and sediment organic content. If two or more abiotic variables were highly correlated with each other (i.e. Pearson's product-moment correlation >0.6; Table 6), only one of those was included in the models to avoid collinearity. As above, the models included the reach as random factor and were tested by likelihood ratio tests against the reduced models (without the fixed factors).

**Table 6 Matrix of correlations among the studied abiotic variables (mean values and coefficients of variation, CV). The Pearson's product-moment correlations are reported, with values > 0.60 indicating strong correlation in bold.**

| | Mean flow velocity CV | Mean flow velocity | Turbulence CV | Turbulence | Organic matter CV | Organic matter | Median grain size CV |
|---|---|---|---|---|---|---|---|
| **Mean flow velocity** | -0.31 | | | | | | |
| **Turbulence CV** | 0.54 | -0.22 | | | | | |
| **Turbulence** | 0.07 | **0.83** | 0.05 | | | | |
| **Organic matter CV** | **0.78** | -0.21 | 0.47 | 0.07 | | | |
| **Organic matter** | 0.21 | 0.22 | 0.49 | 0.25 | 0.36 | | |
| **Median grain size CV** | 0.39 | 0.07 | 0.55 | 0.42 | 0.32 | 0.09 | |
| **Median grain size** | -0.2 | **0.83** | -0.24 | **0.85** | -0.22 | -0.04 | 0.24 |

For multivariate analyses, we first log(x+1) transformed invertebrate taxonomic abundances, and used the binomial distance (Anderson & Millar, 2004) for analyses that required computation of matrices of dissimilarity among samples or sites. The effects of reach (as KOR, PLI, PLO1, PLO2 and PLO3) and substratum (as NW, W1, W2 and W3) in shaping the invertebrate taxonomic composition were tested by a permutational multivariate ANOVA, perMANOVA (Anderson (2001). This involved 999 permutations which were constrained within each river reach in order to account for the nested study design (i.e. substrata nested in reaches). Invertebrate taxonomic composition in the study reaches and on the various substrata was then plotted using non-metric multidimensional scaling (nMDS).

The LME analyses were run in the R package “lme4” (Bates *et al.*, 2012), post-hoc multiple comparisons tests were performed by using the function testInteractions of the R package “phia“ (Rosario-Martinez, 2013), the perMANOVA and nMDS analyses were run in the R package “Vegan“ (Oksanen *et al.*, 2013).

## 3.4 Results

### *3.4.1 Environmental variables*

Wood and non-wood sites within each reach were not statistically different for most hydromorphological variables (paired t-test: $p > 0.05$; Table 5), except for the number of wood pieces (paired t-test: $p < 0.05$; Table 5), the LW volume:bankfull channel area ratio (paired t-test: $p < 0.05$; Table 5) and the gradient of the water level ($p = 0.05$). Wood sites exhibited a higher water surface gradient, while the longitudinal gradient of the channel bed did not differ significantly between wood and non-wood sites (paired t-test: $p > 0.05$; Table 5).The wood sites exhibited on average 11.4 structures with a blockage ratio higher than 0.10, compared to only 4.4 in non-wood sites (Table 5).

Flow velocity, turbulence, median sediment grain size and percentage of sediment organic matter showed no consistent differences between wood and non-wood sites (LME analysis, likelihood ratio test: $p > 0.05$; Figure 12A, C, E and G). However, their variability, as described by the coefficient of variation, was on average 85%, 98%, 126%, and 57% larger in the wood sites than in the non-wood site respectively and LME analysis confirmed significant differences in the coefficients of variation for mean flow velocity, turbulence and median grain size (likelihood ratio test: $p < 0.05$; Figure 12B, D and H).

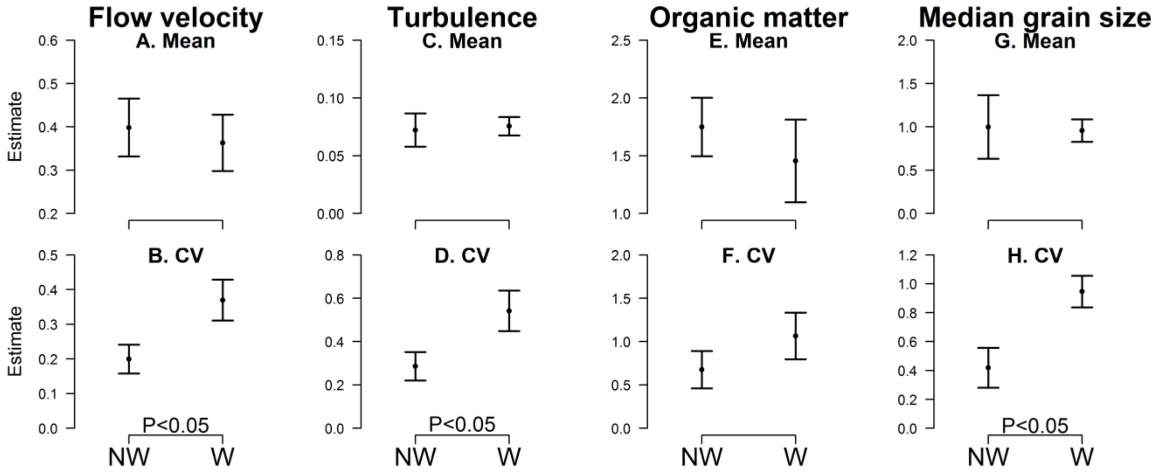

**Figure 12 Estimates (mean ± SE) of the mean (A, C, E and G) and coefficient of variation CV (B, D, F and H) of the environmental variables (mean flow velocity, turbulence, sediment organic matter, median grain size) after linear mixed effect models (LME, fixed factor= site type, random factor= reach) in the non-wood and wood sites (NW, W). $P < 0.05$ indicates significant differences after likelihood ratio test.**

The higher variability of the environmental variables in the wood sites was due to the high variability recorded in the measurement points near the wood logs (W2) within all the studied reaches. The coefficients of variation for mean flow velocity, turbulence, median grain size and organic matter were significantly higher there than in all the other substrata (NW, W1 and W3; LME analysis, likelihood ratio test: $p < 0.05$; Figure 13), in particular they were 101%, 89%, 148% and 57% higher there than in the non-wood measurement points (NW).

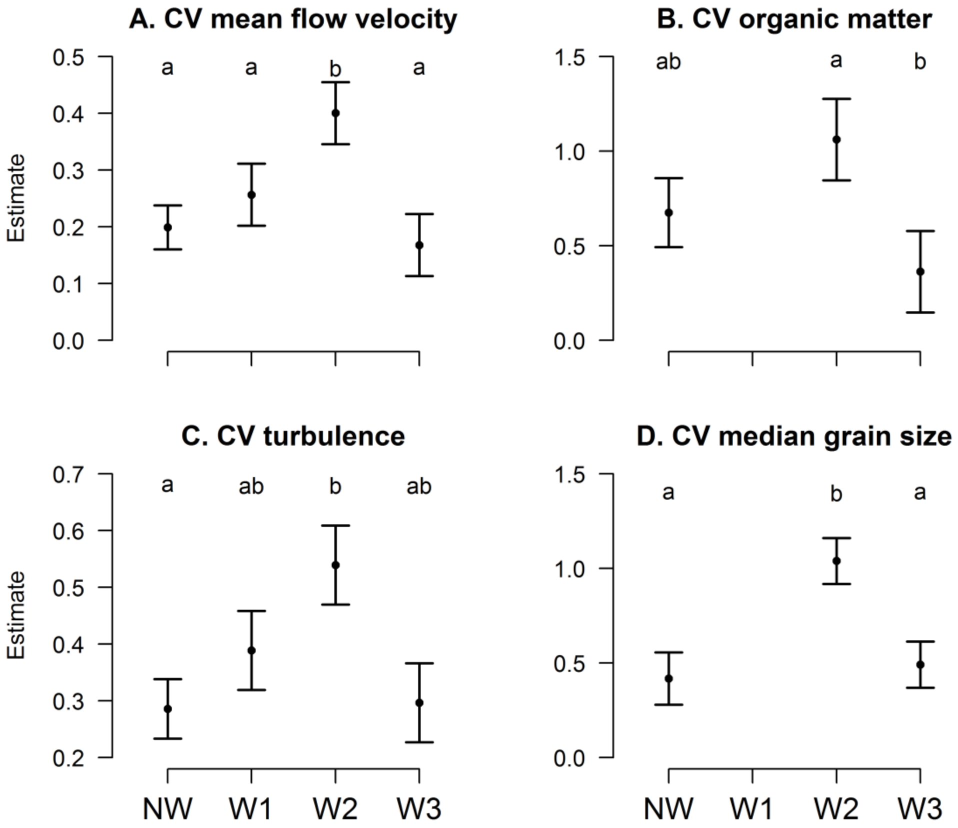

**Figure 13 Estimates (mean ± SE) of the coefficients of variation of the environmental variables (A: mean flow velocity, B: sediment organic matter, C: turbulence, D: median grain size) after linear mixed effect models (LME, fixed factor= substratum, random factor= reach) in the substratum types (NW, W1, W2 and W3). W1= surface of the wood logs, W2= sediment around the wood logs, W3= sediment outside the direct influence of wood logs, within the wood sites, NW= sediment in the non-wood site. Different letters (a and b) indicate significant differences (p < 0.05) after multiple comparisons test.**

### 3.4.2 Macroinvertebrates

In total we collected ca. 137,000 macroinvertebrates, belonging to 138 taxa, the most abundant groups were Diptera (65%), Trichoptera (9%) and Ephemeroptera (9%). Invertebrate communities showed a consistent pattern of differences between wood and non-wood sites in terms of taxonomic composition and diversity.

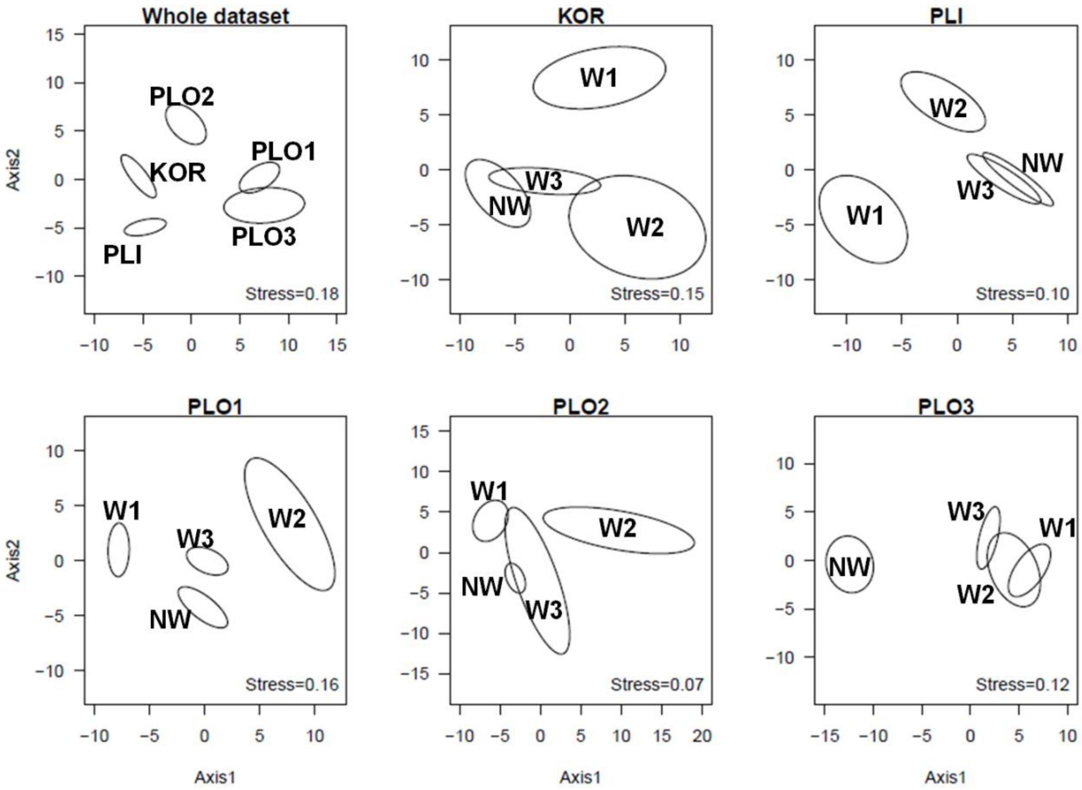

**Figure 14 Non-metric multidimensional scaling run on log(x+1) transformed invertebrate data and binomial distances for the whole dataset, and for the five reach datasets, respectively: KOR= Korytnica, PLI= Pliszka, PLO1= Płociczna reach 1, PLO2= Płociczna reach 2; PLO3= Płociczna reach 3. W1= samples from the surface of the wood logs, W2=samples from the sediments around the wood logs, W3= samples from the sediment outside the direct influence of wood logs, within the wood sites, NW= samples from the non-wood site. Ellipses show the 95% confidence interval per each group of samples.**

Within each reach, different communities colonized the sediments in the non-wood sites (NW) and the sediments around the wood logs (W2, Figure 14). Also the community inhabiting the wood logs (W1) differed from the others in all the reaches, except at PLO3 where it was similar to that inhabiting the sediments around the logs. W3 showed overlaps with W2 (KOR) and NW samples (KOR, PLI) and generally was located in between those two substrata in the ordination plots (Figure 14). The taxonomic composition of the invertebrate community was significantly influenced by both reach and substratum. Thereby, reach explained the 39 % (perMANOVA, F(4) = 22.27, $p<0.01$) of the taxonomic variance, and substratum the 17 % (perMANOVA, F(4) = 12.48, $p<0.01$).

Beta diversity was on average 31% higher in the wood sites than in the non-wood sites, such difference was significant and consistent across the studied reaches (LME analysis, likelihood ratio test: $p<0.01$; Figure 15A). Moreover, beta diversity was positively correlated with the number of LW structures in the site, although with some scatter (regression analysis: Beta diversity=0.07 Number of LW + 5.4, $R^2= 0.43$, F(1,8)=5.97, p=0.04; Figure 15B).

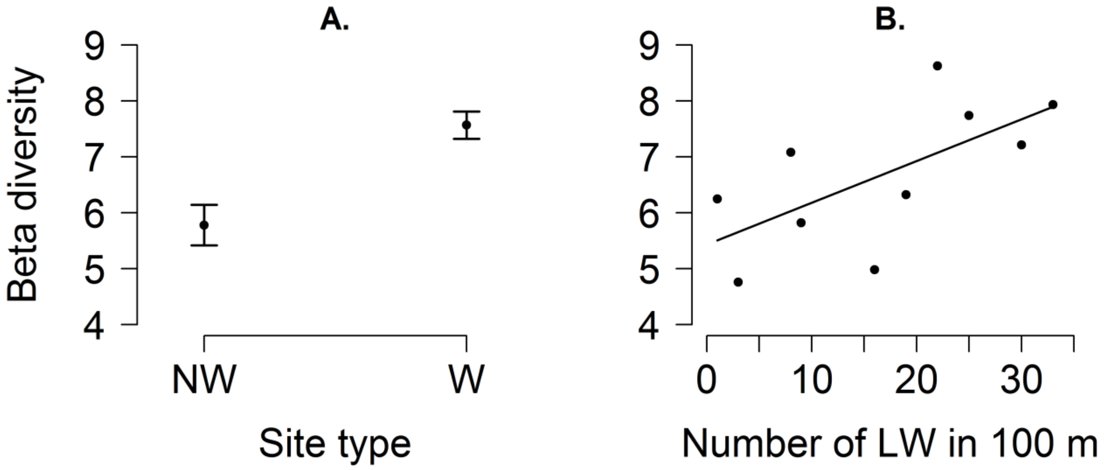

**Figure 15 Beta diversity of the invertebrate communities (A) in the non-wood sites (NW) and in the wood sites (W) after linear mixed effect models (LME, fixed factor= site type, random factor= reach; likelihood ratio test: $p<0.01$) and (B) its correlation with the number of LW pieces in the 100-m study sites, regression analysis: Beta diversity=0.07 Number of LW + 5.4, $R^2$= 0.43, F(1,8)=5.97, p=0.04. See text for the method used for the computation of beta diversity.**

The highest values of taxa richness and Shannon-Wiener diversity index were consistently recorded on the sediment around the wood logs (W2), where in average 30% and 45% higher values were recorded in comparison to the non-wood site (NW; LME analysis, likelihood ratio test: $p < 0.01$; Figure 16). The highest macroinvertebrate abundances were recorded on the surface of the wood logs (LME analysis, likelihood ratio test: $p < 0.01$; Figure 16).

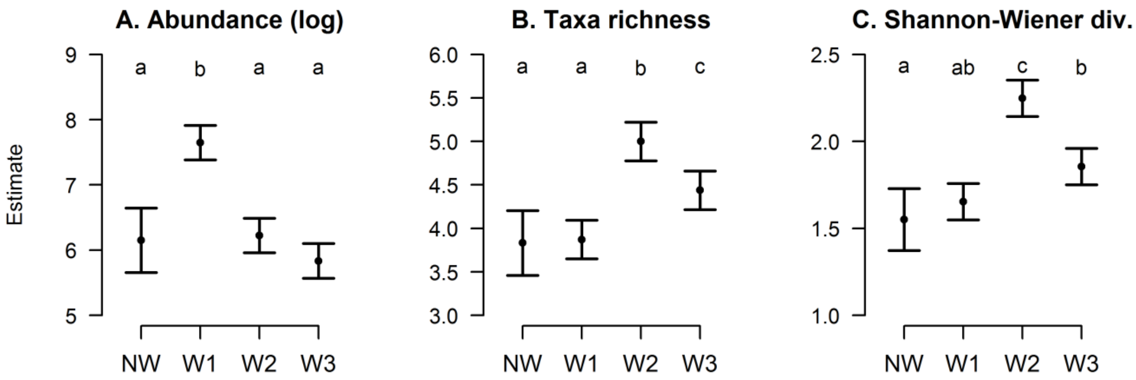

**Figure 16 Estimate (mean ± SE) of the invertebrate metrics (A: abundance, B: rarefied taxa richness, C: Shannon-Wiener diversity index) after linear mixed effect models (LME, fixed factor= substratum, random factor= reach) in the substratum types (NW, W1, W2 and W3). W1= surface of the wood logs, W2= sediment around the wood logs, W3= sediment outside the direct influence of wood logs, within the wood sites, NW= sediment in the non-wood site. Different letters (a, b and c) indicate significant differences ($p<0.05$) after multiple comparisons test.**

### *3.4.3 Mechanisms contributing to the effect of wood on macroinvertebrate alpha diversity*

The metrics of alpha diversity, taxa richness and Shannon-Wiener diversity were positively correlated with the variability of the environmental variables. In particular, they significantly increased with increasing coefficient of variation of the median grain size of the riverbed sediments (Table 7; LME, $p<0.05$), and the values of Shannon-Wiener diversity with increasing coefficients of variation of mean flow velocity and of organic matter, too (Table 7).

**Table 7 Relationships among the values of the invertebrate metrics and the mean and coefficient of variation (CV) of the environmental variables, as resulting from linear mixed effect models. The estimated coefficients and model statistics are reported. The mixing models included the reach as random factor and the studied environmental variables as fixed factors. Only one environmental variable within each group of correlated variables (Table 6) was included in the analysis to avoid collinearity. *= p< 0.05, **= p < 0.01.**

| | **Taxa richness** | **Shannon-Wiener diversity** |
|---|---|---|
| *Model estimates* | | |
| Mean flow velocity (correlated with turbulence and median grain size) | 14.83 | 1.13 |
| Mean flow velocity CV (correlated with organic matter CV) | 16.2 | 1.98* |
| Turbulence CV | 4.58 | -1.5 |
| Organic matter | -2.87 | -0.02 |
| Median grain size CV | 10.51** | 0.65* |
| *Likelihood ratio test* | | |
| $\chi^2$ | 18.84** | 13.32* |

## 3.5 Discussion

The results of this study demonstrate a consistent pattern of increasing invertebrate diversity and compositional heterogeneity associated with LW-induced habitat variability across a set of lowland river reaches.

### *3.5.1 Effects of LW on river channel hydromorphology*

The hydromorphology of the river channel areas surrounding the LW was consistently characterized by much more diverse abiotic conditions than channel areas lacking LW, as shown by e.g. the coefficients of variation of flow velocity and sediment grain size which were 85% and 126% times higher than in the non-wood site. This variation was produced by the complexity of flow patterns generated by the LW in its surroundings, as reduced levels of flow velocity within the roughness projection area of the LW, and increased velocities where flow was concentrated in the remaining part of the channel cross-section (Wallace *et al.*, 1995; Gurnell & Linstead, 1998; Mutz, 2000; Montgomery *et al.*, 2003). In mountain streams such hydraulic patterns are easily detectable, as these are associated to a shift from erosional to depositional processes where flow is reduced by the LW, with subsequent deposition of silt and sand (Wallace *et al.*, 1995;

Buffington & Montgomery, 1999). In sand-dominated lowland rivers lacking coarse gravel or stones on their channel bottom, LW triggers both depositional and erosional processes, as the sediments exhibit less resistance to increased shear stress. This results in the formation of depositional patches of fine sediments and scouring patches of coarser sediments in the surrounding channel areas (Mutz, 2000; Pilotto *et al.*, 2014), which creates the variability in abiotic conditions that was consistently recorded in this study.

The hydraulic roughness induced by LW additionally changes river hydromorphology at a larger spatial scale, as it can cause an upstream increase in the water level (water afflux; Gippel *et al.*, 1996 ). The extent of this impounding effect mainly depends on the proportion of the channel cross-section area blocked by the LW, as LW pieces with a blockage ratio higher than 0.10 have been shown to be responsible for significant water afflux (Gippel *et al.*, 1996; Gurnell & Linstead, 1998). Accordingly, within each of the reaches studied here, the water surface slope was considerably steeper ($1.0 \pm 0.2\ 10^{-3}$ m) in the wood sites, which showed higher loadings of LW with blockage ratio >0.10, compared to the non-wood sites ($0.4 \pm 0.2\ 10^{-3}$ m), although the channel bed slope was similar across paired wood ($2.1 \pm 1.7\ 10^{-3}$) and non-wood ($2.4 \pm 2.2\ 10^{-3}$ m) sites. This higher water surface gradient indicates that LW significantly influenced the hydraulics of the sites.

### *3.5.2 Effects of LW on macroinvertebrate communities*

It is well-known that macroinvertebrate community composition is driven by factors acting at different spatial scales (Frissell *et al.*, 1986; Brosse *et al.*, 2003; Townsend *et al.*, 2003). Accordingly our results showed that a large part of the taxonomic variance of the macroinvertebrate assemblages was explained by the factor ‘reach’, which syntheses the large-scale variables that differ among reaches, but the factor ‘sub-stratum’, which syntheses the substratum-specific variations at local scale, also constituted a significant driving factor for macroinvertebrate assemblages. As the studied substrata were defined based on their location relatively to the next LW piece, these results demonstrate that the taxonomic composition of the macroinvertebrate assemblages was significantly influenced by the LW-induced changes in abiotic conditions.

Consistent and significant differences between the communities colonizing the soft sediments in proximity to the LW (W2) and those colonizing the sediments in the sites without LW (NW) were recorded throughout the five studied reaches, despite the fact that they hosted different macroinvertebrate communities. Moreover, the communities inhabiting the sediments outside the direct influence of LW in the wood sites (W3) generally were located in between those two communities (W2 and NW) in the ordinations plots. This indicates that LW acted in our study as the main driver of macroinvertebrate community composition even in channel areas outside its direct influence. This may be due to short-distance dispersals from nearby LW-related assemblages (Beisel *et al.*, 2000), which thus likely act as sources for colonization for larger river-channel areas.

Previous studies have demonstrated that taxonomic richness, abundance and biomass of aquatic invertebrates are higher on wood than on other benthic habitats (Smock *et al.*, 1989; Hoffmann & Hering, 2000; Benke & Wallace, 2003). Accordingly, in this study the highest macroinvertebrate abundances were found on the LW surface compared to the other benthic substrata. In contrast, however, taxa richness and diversity were significantly higher on other soft substrata, in particular on the sediments around the LW, compared to the LW surface.

The communities colonizing the sediment around the LW logs consistently showed the highest values of alpha diversity in the study reaches, i.e. taxa richness and Shannon-Wiener diversity index were on average 30% and 45% higher there than in the non-wood site. This result, which is consistent with the results of a previous study on the Pliszka River (Pilotto *et al.*, 2014), is also reflected by the significant correlation of both taxa richness and Shannon-Wiener diversity with the variability of abiotic conditions, in particular with the variability of sediment median grain size and flow velocity. According to general niche theory (Hutchinson, 1961), heterogeneous environments can sustain larger invertebrate alpha diversity by enabling a larger number of niches for macroinvertebrates, and by supporting short-distance dispersal of biota among neighbouring habitats compared to homogeneous environments (Beisel *et al.*, 2000).

The positive effect of LW on alpha diversity was paralleled by a concomitant effect on beta diversity, which was on average 31% higher in the wood sites than in the non-wood sites, and positively correlated to the amount of LW in the site. Thus, LW-induced habitat heterogeneity offers longer environmental gradients even at larger spatial scales. Those gradients increase proportionally to the amount of LW and support higher compositional heterogeneity of biotic assemblages at the reach scale, too. This finding also confirms that beta diversity constitutes a possible suitable measure for the appraisal of restoration programs (Passy & Blanchet, 2007).

During the last few decades, numerous attempts have been undertaken to restore hydromorphological heterogeneity in degraded aquatic systems, with the ultimate aim to increase biodiversity (Pretty *et al.*, 2003; Kail *et al.*, 2007). However, such restoration projects have often failed to generate desired responses in terms of fish and macroinvertebrate abundance and diversity (Brooks *et al.*, 2002; Pretty *et al.*, 2003; Lepori *et al.*, 2005). The results presented in this study show that in sandy lowland rivers even simple LW structures (single logs) may constitute an effective measure to increase habitat heterogeneity and benthic diversity, at least where water quality and nearby sources of colonization do not represent limiting factors.

### *3.5.3 Conclusions*

Freshwater ecosystems worldwide are subjected to an overarching trend of biotic homogenization, which has been associated with several human-induced pressures: loss of habitat heterogeneity (Passy & Blanchet, 2007), introduction of invasive species (Olden *et al.*, 2006), nutrient enrichment (Donohue *et al.*, 2009) and land-use pressure (McGoff *et al.*, 2013). This study demonstrates that in near-natural lowland rivers the presence of LW consistently increased hydromorphological heterogeneity in its surrounding channel areas, which resulted in elevated levels of both alpha and beta diversity of macroinvertebrates. Therefore, large wood constitutes a crucial element supporting aquatic biodiversity in lowland rivers, and thus should remain in river channels wherever possible. In degraded rivers, introduction of LW for restoration purposes can represent an effective measure with desirable effects even on surrounding channel areas, and thus should be encouraged (Piégay & Landon, 1997).

## Acknowledgements

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# 4. Enhanced resource availability by the presence of large wood in a lowland river as demonstrated by combined FA and SIA analyses

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## 4.1 Abstract

As large wood (LW) may profoundly modify the hydromorphology of rivers, we tested if it may also influence the availability of trophic resources for benthic macroinvertebrates. For that, we quantified the contribution of trophic resources to the diet of macroinvertebrates colonizing the surface of LW logs and surrounding river-bed sediments in a lowland river with those in the sediments of a nearby control site with minimal amounts of LW. We estimated diet contributions through a combination of both stable isotope (SIA) and fatty acid (FA) analyses. SIA analysis showed that the macroinvertebrate food web was mostly sustained by seston, likely exported from a nearby lake, in all three substrata. Although the diet of single taxa only differed slightly between the non-wood and the wood site, the trophic bases of the community clearly differed among substrata. The contribution of local autochthonous primary producers increased of 1.9-5.5 times from the non-wood site to the sediment around the LW and to the wood surface. Similarly, the contribution of terrestrial material was 1.3 times higher on the sediment around the wood than in the non-wood site. FA analysis demonstrated the higher nutritional value of autochthonous (aquatic) primary producers. Despite the high seston contribution estimated by SIA to many taxa, FA profiles indicate that diets were based on a more equilibrated range of basal resources. Hence, our study demonstrated that the presence of LW in the river channel significantly increases the diversity and quality of food resources for the

macroinvertebrate community, primarily through increased autochthonous primary production on the wood.

## 4.2 Introduction

Large wood (LW) constitutes a fundamental component in the health and integrity of river ecosystems. LW functions as an element of structural complexity in the channel, increasing the heterogeneity of physical habitat conditions (Ehrman & Lamberti, 1992; Gregory *et al.*, 1995; Montgomery *et al.*, 1995; Gurnell & Linstead, 1998). LW has been shown to increase macroinvertebrate assemblage diversity by providing a stable and hard substratum for colonization (Hoffmann & Hering, 2000; Benke & Wallace, 2003; Schröder *et al.*, 2013) and by providing diverse habitats in nearby river-bed sediments (Pilotto *et al.*, 2014). These effects may be particularly notable in lowland sandy rivers, where in the otherwise loose and instable river-bed sediments, LW represents the main roughness structure due to its stability and persistence in the river-channel (Mutz, 2000; Kail, 2003; Montgomery *et al.*, 2003; Daniels, 2006).

In addition to the positive effects of increased physical heterogeneity on biotic assemblages, LW may also influence the local abundance and composition of macroinvertebrates by affecting the availability and quality of food resources. LW can serve directly as a food source for xylophilic macroinvertebrate species, however the proportion of these taxa is generally relatively low (Anderson *et al.*, 1984; Anderson, 1989; Hoffmann & Hering, 2000). Also, wood may alter the availability of both allochthonous (terrestrial) and autochthonous (aquatic) food resources present in the channel. Previous studies demonstrated that LW increases organic matter retention by trapping fine sediment, leaves, twigs, and other transported matter (Bilby & Likens, 1980; Bilby, 1981). In addition, the erosion and decay of the wood surface itself can contribute to increased allochthonous organic matter within the reach (Ward & Aumen, 1986). LW also directly increases the total surface area of hard substrate for biofilm colonization (Wondzell & Bisson, 2003). This may be particularly important in sand-bed rivers, as stable and hard surfaces besides LW may be limited in the channel. Although previous studies documented that the presence of LW increases the availability of potential food resources for invertebrates, none investigated whether there were resulting shifts in the autochthonous versus allochthonous trophic bases of the macroinvertebrate assemblages, which may explain alterations in the taxonomic structure of the community.

Food webs of stream ecosystems with dense riparian shading, limiting in-stream production and promoting terrestrial inputs, should be primarily supported by allochthonous production (Vannote *et al.*, 1980; Smock *et al.*, 1989). Similarly, lowland sand-bed rivers with high terrestrial inputs and low in-stream production could be expected to have their trophic base mostly derived from terrestrial matter. However, recent work has demonstrated that terrestrial matter may function as only a relatively minor part of the diet, and that macroinvertebrates are mostly dependent on autochthonous matter, even for species considered shredders (Torres-Ruiz *et al.*, 2007; Lau *et al.*, 2008; Lau *et al.*, 2009a).

Allochthonous carbon is mostly recalcitrant, while autochthonous production, although less plentiful, is more labile and contains higher concentrations of nitrogen, phosphorus, and specifically highly unsaturated fatty acids (HUFAs) (Torres-Ruiz *et al.*, 2007; Lau *et al.*, 2008; Brett *et al.*, 2009; Lau *et al.*, 2009b; Torres-Ruiz & Wehr, 2010). The efficient transfer of energy from basal resources to consumers depends on a high-quality food base rich in HUFAs, and a lack of these important components may lead to trophic decoupling, where increased primary production does not result in increases in higher trophic levels (Sterner & Hessen, 1994; Brett & Müller-Navarra, 1997; Müller-Navarra *et al.*, 2000; Rosemond *et al.*, 2000; Urabe *et al.*, 2002; Hill *et al.*, 2010; Gladyshev *et al.*, 2011; Perhar *et al.*, 2013). While the increased residence time and increased quantity of organic matter trapped by LW may increase microbial processing and the quality of allochthonous matter for the food web (Smock *et al.*, 1989; Fry & Fuller, 1991), even limited increases in autochthonous production associated with LW may have large proportional effects on the trophic base of the macroinvertebrate community.

Stable isotope analysis (SIA) of carbon and nitrogen retention and fractionation has become a standard method in evaluating aquatic food webs, with Bayesian mixing models providing quantitative estimates of mixed diet composition (Gannes *et al.*, 1997; Finlay, 2001; Phillips *et al.*, 2005; Benstead *et al.*, 2006; Moore & Semmens, 2008; Parnell *et al.*, 2008; Lau *et al.*, 2009b). Combining bulk stable isotope data with fatty acid (FA) biomarker data can facilitate the interpretation of the food web structure, particularly when relevant primary production sources have distinct signatures, or in cases of mixed trophy (El-Sabaawi *et al.*, 2009b; Allan *et al.*, 2010; Galloway *et al.*, 2012). Basal resources produce specific fatty acid biomarkers, which are retained in consumers. Rather than the two source signals (C/N) used in traditional stable isotope analysis, FA analysis allows for more than a dozen biomarkers to be used to evaluate the feeding relationships. The advantages of the combination of SIA and FA approaches to the analysis of aquatic food webs have been shown in an increasing amount of studies. Those previous studies however, focused on marine, tidal or estuarine systems (Kharlamenko *et al.*, 2001; Alfaro *et al.*, 2006; Schmidt *et al.*, 2006; El-Sabaawi *et al.*, 2009a; Van den Meersche *et al.*, 2009; Allan *et al.*, 2010; Carreón-Palau *et al.*, 2013; Bergamino *et al.*, 2014; Connelly *et al.*, 2014), whereas only few studies considered river food webs and they were generally restricted to a limited number of consumers (Lau *et al.*, 2009a; Heissenberger *et al.*, 2010; Gladyshev *et al.*, 2012; Wang *et al.*, 2014).

This work aims to quantify the effect of LW on the trophic base of a river ecosystem by combining the analyses of stable isotopes and fatty acid biomarkers of possible food resources for macroinvertebrates settled on the surface of LW logs, river-bed sediments surrounding the LW, and on river-bed sediments in a nearby control site with minimal amounts of LW. We hypothesized that the presence of LW would support the growth of epixylic primary producers, this increased availability of autochthonous organic material would result in increased autochthonous dependence in the average diet of the whole benthic invertebrate assemblage in river-channels rich in LW.

## 4.3 Methods

### *4.3.1 Study area*

Field work was carried out in April 2012 in the Płociczna River, a lowland, minimally-disturbed sand-bed river in Western Poland (Figure 17). The Płociczna River (length: 51 km) runs through the forested Drawienski National Park, where it joins the Drawa River. Although there were pine plantations in the catchment, the dominant riparian vegetation consisted of broad-leaved trees, mainly alder (*Alnus* sp.). We conducted the study in two forested reaches (bankfull width: 12-15 m; near-bankfull discharge: 1.4-1.5 $m^3s^{-1}$), with varying levels of LW, near the outflow of the Lake Sitno. The upstream reach (ca. 700 m from the lake outflow) was poor in in-channel LW (9 wood structures in 100 m, with a total volume of 22.9 $m^3$ $ha^{-1}$ of channel area), hereby “non-wood site”, while the downstream reach (ca. 1000 m from the lake outflow) was rich in in-channel LW (25 wood structures in 100 m, with a total volume of 94.4 $m^3$ $ha^{-1}$ of channel area), hereby “wood site”. Due to the low gradient and limited discharge of the studied reach, LW pieces falling into the channel are not transported or re-oriented by flow, and thus remain in place as single logs, mostly aligned perpendicular to the flow.

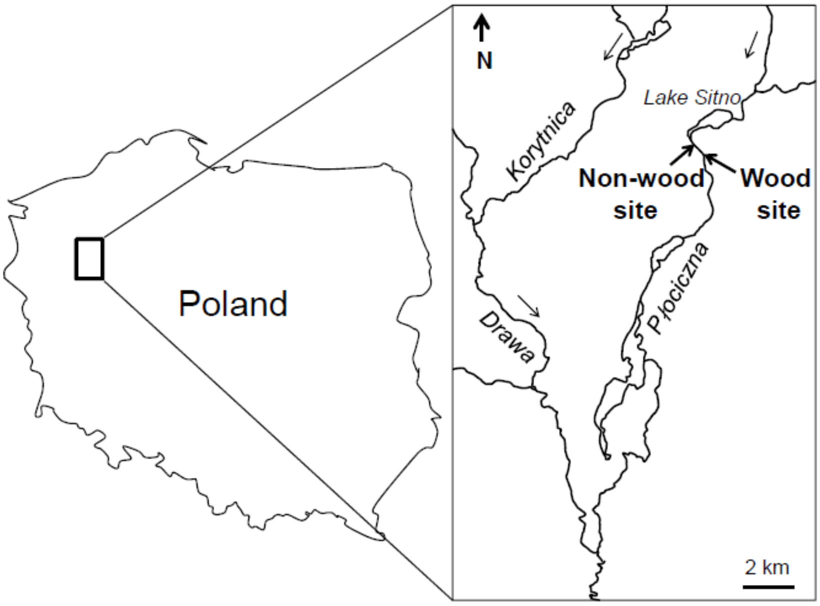

**Figure 17 Map of the study area**

### *4.3.2 Sampling for macroinvertebrates*

Macroinvertebrates were collected from the LW surface (WW samples) and the sediment surrounding the LW (within 20 cm from the LW; WS samples) in the wood site and from the sediment in the non-wood site (NW samples).

For the analysis of the macroinvertebrate taxonomic composition, we selected 6 replicate pieces of LW within the wood-site. We collected one sample from the LW surface of each LW log by brushing an area of 0.26 $m^2$ into a hand net. We collected benthic samples from the sediment around each selected LW in three sampling points, one upstream, one downstream and one lateral to the LW. We additionally collected six replicate benthic samples in the non-wood site. Each benthic sample consisted of the pooled material from five Surber samplers (frame size = 23x23 cm, mesh size: 500 µm; total sampled area for each sample: 0.26 $m^2$). Samples were preserved in 70 % ethanol. In the laboratory animals were identified to species or genus, Chironomidae were identified to subfamily and Oligochaeta to class. The identification level was consistent across all the samples. Taxa abundances from the three sampling points on the river-bed sediments surrounding the same LW (upstream, downstream and lateral) were averaged in order to obtain a composite sample for the area surrounding each of the six replicate LW.

We collected three additional replicate invertebrate samples from the LW surface (WW), three from the LW surrounding (WS) and three from the non-wood site (NW) for isotope and fatty acid analyses. The samples were sorted in the field and transported in filtered river water to the laboratory where they were identified under 10x microscope and left for 24 h for gut clearance. Where the number of animals was enough, half of the sample of each taxon was processed for stable isotope analysis and half for fatty acid analysis (Table 8).

**Table 8 Taxa collected on the three substrata in the Płociczna river, along with the dominant functional feeding group (Tachet *et al.*, 2000; Schmidt-Kloiber & Hering, 2012), and assimilation analysis test conducted. NW=river-bed sediments in the non-wood site; WS=river-bed sediments in the wood site; WW=wood surface. Shr=shredders; Grz=grazers; Prd=predator; Gat=gatherers; AFF=active filterers; PFF=passive filterers; Min=miners. Ad=adult; Lv=larvae.**

| Taxon | Functional Group | Analysed for SIA | Analysed for FA | NW | WS | WW |
|---|---|---|---|---|---|---|
| *Anodonta anatina* | AFF | X | X | X | | |
| *Aphelocherius aestivalis* Ad | Pred | X | X | | X | |
| *Aphelocherius aestivalis* Lv | Pred | X | X | X | X | X |
| *Baetis* sp. | Grz/Gat | X | X | | X | X |
| *Bithynia tentaculata* | AFF/Grz/Gat | X | X | X | X | |
| *Caenis* sp. | Gat | X | X | X | X | X |
| Chironomidae | Gat/AFF/Grz/Min/Prd | X | X | X | X | X |
| *Dreissena polymorpha* | AFF | X | X | X | X | |
| *Ephemera danica* | AFF/Gat | X | X | X | X | X |
| *Gammarus pulex* | Shr/Gat/Grz/Prd | | X | | X | |
| *Gammarus roselii* | Shr/Gat/Grz/Prd | | X | | X | |
| *Glossiphonia* | Prd | X | X | X | | |
| *Gomphus* sp. | Prd | X | X | X | X | |
| *Hydropsyche pellucidula* | PFF/Prd/Grz | X | X | X | X | X |
| Nemouridae | Shr/Gat | X | X | X | | |
| Oligochaeta | Gat | X | | X | X | |
| *Ophiogomphus cecilia* | Prd | X | X | X | | |
| *Orectochilus villosus* | Prd | X | X | X | X | X |
| *Platycnemis* sp. | Prd | X | X | X | | |
| *Polycentropodidae* | Prd / PFF | X | X | X | X | X |
| *Potamopyrgus antipodarum* | Oth/Gat/Shr/Graz | X | X | X | | |
| Sphaeriidae | AFF | X | X | X | X | X |
| Tabanidae | Prd | X | X | X | X | |
| *Theodoxus fluviatilis* | Grz | X | X | | | |
| *Unio pictorum* | AFF | X | X | X | X | |
| *Unio tumidus* | AFF | X | X | X | X | |

### *4.3.3 Sampling for food resources*

We sampled the same set of trophic resources in the two study reaches, with three replicates within each reach, including transported matter, periphyton collected from wood (“wood periphyton”), periphyton collected from mussel shells (“mussel periphyton”), filamentous algae, wood, bryophytes, sediments, riparian grass, and leaf litter. Small pieces of woody debris (*i.e.* bark, branches) were present on the riverbed in the non-wood section and provided wood periphyton samples in the non-wood reach. Filamentous green algae, i.e. *Cladophora* sp., was only found in the wood site and periphyton on mussel shells were sampled only in the non-wood site.

Periphyton was collected from submerged pieces of wood and from the shells of unionid mussels, which were gently rinsed with filtered water and cleaned with a toothbrush. Periphyton slurries were then collected in vials and put on ice until return to the lab. The filamentous green alga, *Cladophora* sp., was removed from submerged pieces of wood. The top 5-cm layer of sediment (sand and organic matter deposits) was collected using a Perspex sediment corer. Leaves (mainly alder) and grass were collected from the riparian zone. Samples of transported organic matter in seston (TOM) were collected with a 125 µm phytoplankton net over 30 minutes for each replicate. The isotopic signature of total seston was also inferred from the isotopic signature of unionid mussels (i.e. *Unio tumidus* and *Unio pictorum*) which were collected in the two study sites. Unionid mussels are often used to trace back the temporal integrative signature of seston (Cabana & Rasmussen, 1996; Gippel *et al.*, 1996; Atkinson *et al.*, 2014) since they are long – lived sestonic filter feeders, and thus their tissue is less sensitive to seasonal fluctuations in the values of $\delta^{13}C$ and $\delta^{15}N$.

All the samples were brought to the laboratory, where they were washed under filtered water, checked under microscope (20x) in order to remove animals or inorganic material and prepared for stable isotope and fatty acid analysis. Periphyton and TOM samples were filtered onto pre-ashed Whatman 25-mm GF/F Filters (Sigma-Aldritch).

### *4.3.4 Sample processing for stable isotope analysis*

Trophic resources and single (large animals as e.g. Odonata) or pooled (small animals as e.g. Chironomidae) macroinvertebrate individuals belonging to the same taxon were dried separately at 60 °C for 48 h, weighed and grinded to fine powder. Subsamples of ~1mg for animals and from 1 to 30 mg for food resources were placed in tin caps and sent for analysis at the UC Davis Stable Isotope Facility, where they were analysed through mass spectrophotometry.

Stable isotope data are expressed as the relative difference between ratios of samples and standard gases (Vienna PeeDee Belemnite and air for carbon and nitrogen, respectively), as:

$$\delta\, R(‰) = \left(\frac{R_{sample}}{R_{standard}} - 1\right) x\; 10^3$$

Where R = $^{13}C/^{12}C$ or $^{15}N/^{14}N$, and $\delta^{13}C$ and $\delta^{15}N$ are the deviation (‰) of the sample from the corresponding isotope standards.

### *4.3.5 Sample processing for fatty acid profiles*

For fatty acid analysis, all samples were stored at -80°C under $N_2$ until extraction following a method adapted from Torre-Ruiz et al. (2007), and originally modified from Parrish (1999). Samples were extracted in two washes of chloroform:methanol (2:1 v/v), sonicated on ice, and the chloroform phase was separated for methylation into fatty acid methyl esters with $BF_3$ (10 -14% w/v in methanol) at 80°C. Fatty acid methyl esters were suspended in hexane and measured on an Agilent 6890 gas chromatograph with a Agilent 5973-N mass selective detector that was fitted with a CP Sil 88 for FAME fused-silica capillary column (100m x 250 µm x 39 µm) set in splitless mode. Carrier gas (He) flow rate was constant at 0.2 mL $min^{-1}$. Inlet temperature was 300°C, with initial temperature 70°C with an increase of 720°C $min^{-1}$. Detector temperature was set at 280°C. The temperature program started at 80°C for 1 min, increased at a rate of 4°C $min^{-1}$ until reaching a temperature of 220°C. This was maintained for 4 min, heated at 4°C $min^{-1}$ until 240°C, where it was maintained for a final 15 min. Total temperature program lasted for 60 minutes. Fatty acid methyl esters were identified by retention times and mass spectra in full scan mode previously calibrated with standards: 37-Component FAME Mix (47885-4), PUFA No1; Marine Source (47033) and PUFA No3; Menhaden Oil (47085-4; all Supelco, Germany).

### *4.3.6 Data analysis*

#### *Composition of the macroinvertebrate assemblages*

Community composition of the macroinvertebrate assemblages colonizing the three substrata (NW, WS and WW) was compared by non-metric multidimensional scaling (nMDS) and analysis of similarities (ANOSIM) in the R (R Core Team, 2013) package ‘vegan’ (Oksanen *et al.*, 2013). These analyses were run on log(x+1)-transformed macroinvertebrate data with Bray-Curtis distance among samples.

From the macroinvertebrate assemblage data, we computed the Shannon-Wiener diversity index and the rarefied taxonomic richness by using the functions implemented in the R package ‘vegan’. The values of those metrics and the total abundances were compared among the three groups of samples (NW, WS and WW) through analysis of variances (ANOVA).

### *Analysis of stable isotope data*

We estimated the relative importance of the trophic sources to the diet of the studied macroinvertebrate taxa by using mixing models implemented in the R package ‘SIAR’ (Parnell *et al.*, 2008; Parnell *et al.*, 2010). Such models are based on a Bayesian approach and estimate the probability distributions to a consumer diet starting from the $\delta^{13}C$ and $\delta^{15}N$ signature of each consumer, that of each resource (mean ± standard deviation) and the trophic enrichment factor (TEF). We used the TEF values reported by Post (2002), i.e. 0.4 ± 1.3 ‰ for $\delta^{13}C$ and 3.4 ± 1.0 ‰ for $\delta^{15}N$. For predator taxa we doubled the TEF values, to account for the double trophic transfer (Lau *et al.*, 2009a). Since *Hydropsyche* sp. can show both primary consumer’s and predatory behaviour we included in the model both TEF and doubled TEF values, and the results were *a-posteriori* combined. We run the models for each taxon including all trophic resources present at the site. If two sources are located in the same isotopic space, it may be impossible for the model to determine the differences in their contributions (Ward *et al.*, 2011; Parnell *et al.*, 2013). To account for that, the models were checked for correlations among resources (by using the function “siarmatrixplot” of the R package SIAR) and the resources that showed strong negative correlations (<-60) in at least one model were *a-posteriori* combined (Ward *et al.*, 2011; Parnell *et al.*, 2013). Thus, seston inferred from the isotopic signature of unionid mussels was combined to filamentous algae because negatively correlated in several models, thus forming the group “seston and filamentous algae”. Similarly, “wood periphyton” and bryophytes were combined because negatively correlated in several models (“periphyton and bryophytes”). Finally grass and leaves were combined because ecologically similar (i.e. “allochthonous terrestrial material”).

The results obtained for the single taxa were up-scaled to the community level by integrating the diet composition of the single taxa (output of the SIA mixing models) weighted by their biomass within the assemblage (Junger & Planas, 1994; Choy *et al.*, 2009). The mean biomass of each taxon was computed from the mean dry weight of the samples, multiplied by the mean abundance of that taxon.

*Analysis of fatty acid data*

Fatty acids profiles were examined as percentages of total fatty acids based on all fatty acids identified. Less than 1% of all quantified fatty acids were excluded from the analysis. Fatty acid profiles were ordinated with non-metric multidimensional scaling in the R package 'vegan'. Overall profiles were compared using ANOSIM analyses and followed by SIMPER tests, all in the R package 'vegan', to determine the fatty acid species responsible for differences in the profiles.

### 4.4 Results

The three studied substrata were colonized by different macroinvertebrate assemblages (ANOSIM: R= 0.92, p= 0.001; Figure 18). The highest total invertebrate abundances were recorded on the LW surface (in average 3326 ± 1788 individuals), followed by the sediments around the LW (1925 ± 740) and by the non-wood site (1658 ± 1054), although this was not significantly different (ANOVA: p= 0.08). The highest rarefied taxa richness (ANOVA, F= 43.68, df= 2, p<0.01) was recorded on the sediment around the LW (25.5 ± 4.0) followed by the non-wood site (16.3 ±1.9) and by the LW surface (11.0 ± 1.7). The highest values of Shannon-Wiener diversity index (ANOVA, F= 12.36, df= 2, p<0.01) were recorded on the sediment around the LW (1.53 ± 0.18) followed by the non-wood site (1.17 ± 0.18) and by the LW surface (1.11 ± 0.06). Chironomidae (subfamilies: Chironominae and Orthocladiinae) was the dominant taxonomic group in all three datasets, representing on average 72 %, 72 % and 80 % of the total abundances in the non-wood site, on the sediment around the LW and on the LW surface respectively. The second most abundant group was *Caenis* sp. in the non-wood site and WS samples (respectively 16 % and 7 % of the total abundances), Oligochaeta on the LW surface (14 % of the total abundance).

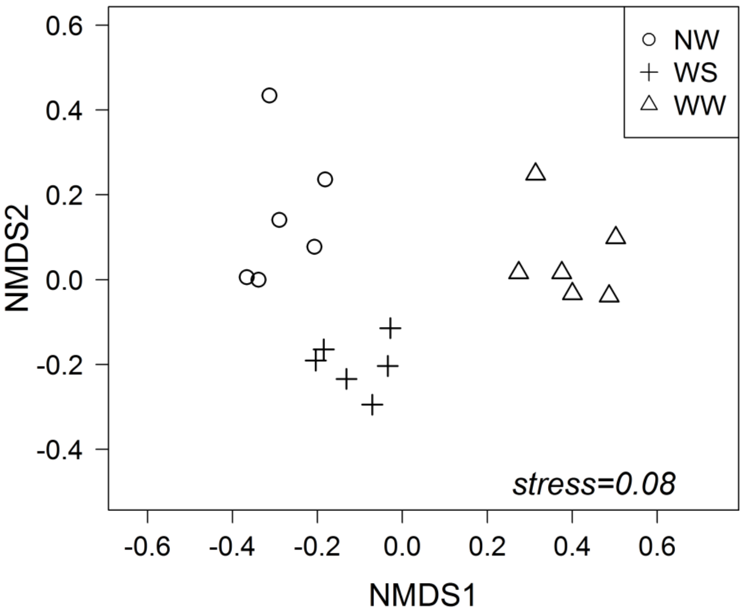

**Figure 18 Non-metric multidimensional scaling of the community composition, performed on log(x+1)-transformed abundances and with Bray-Curtis distance. NW= river-bed sediment in the non-wood site; WS= river-bed sediment in the wood site; WW= wood surface.**

### *4.4.1 Stable isotope analysis*

The isotopic signature of macroinvertebrates was generally more depleted in $\delta^{13}$C than most of the food resources (Figure 19). SIA mixing models showed that seston and filamentous algae were the dominant trophic resources for most of the taxa on the three substrates, while transported organic matter, detritus, wood and mussel periphyton had only a minor (<10%) contribution to their diet (complete SIA results are reported in Table S2 in Appendix). The exceptions were Oligochaeta on the sediment around the LW, which fed more on periphyton and bryophytes than on seston and filamentous algae (Figure 20D), and two snail taxa *Theodoxus fluviatilis* and *Potamopyrgus antipodarum*, which were sampled only in the non-wood site. The diet of *T. fluviatilis* and *P. antipodarum* mainly based on periphyton and bryophytes (33% and 34% of the diet), both had larger contribution of transported organic matter (12%) than the other studied taxa and the diet of *T. fluviatilis* included larger contribution of mussel periphyton (25%).

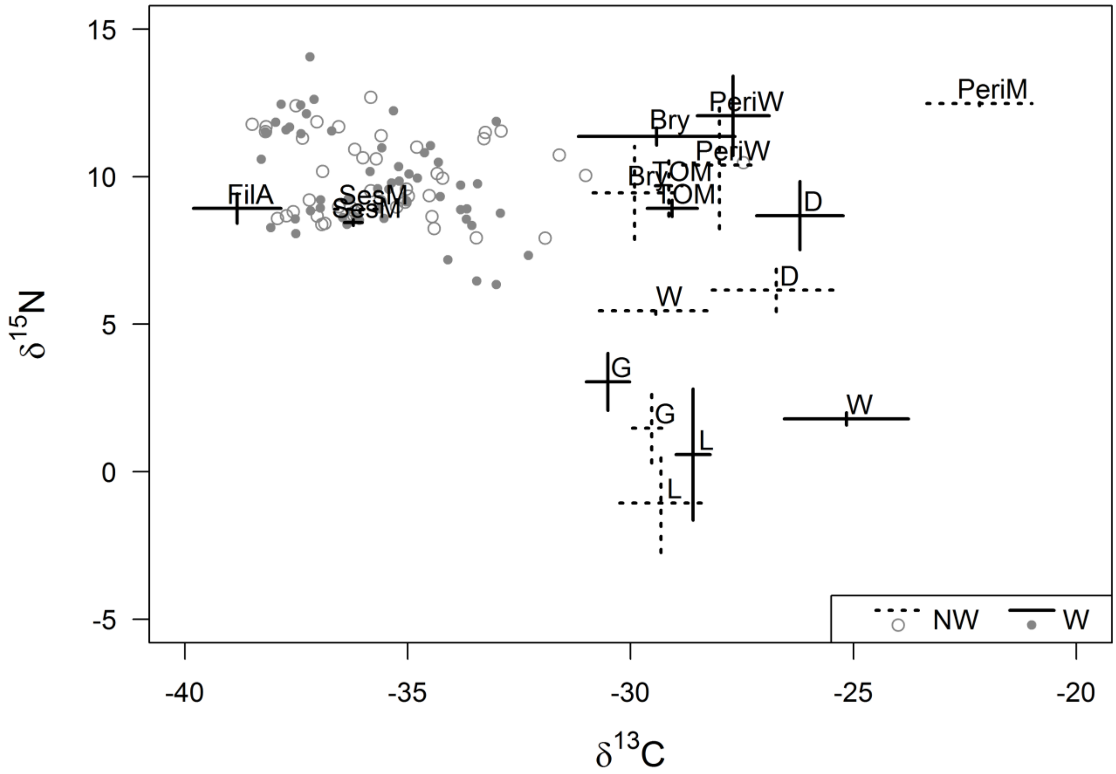

**Figure 19 Stable isotope signature of resources (lines, mean ± s.d.) and macro-invertebrates (circles) in the non-wood site (NW, dotted lines and open circles) and in the wood-site (W, solid lines and solid circles). The isotopic signatures of resources were corrected by the trophic enrichment factor: 0.4 ± 1.3 ‰ for $\delta^{13}C$ and 3.4 ± 1.0 ‰ for $\delta^{15}N$ (Post, 2002). FilA= filamentous algae; Bry= bryophytes; TOM= transported organic matter; SesM= seston inferred from the isotopic signature of unionid mussels (see text for explanation); PerW= periphyton on wood; PeriM= periphyton on the shells of unionid mussels; D= detritus; W= wood; G= grass; L= leaves.**

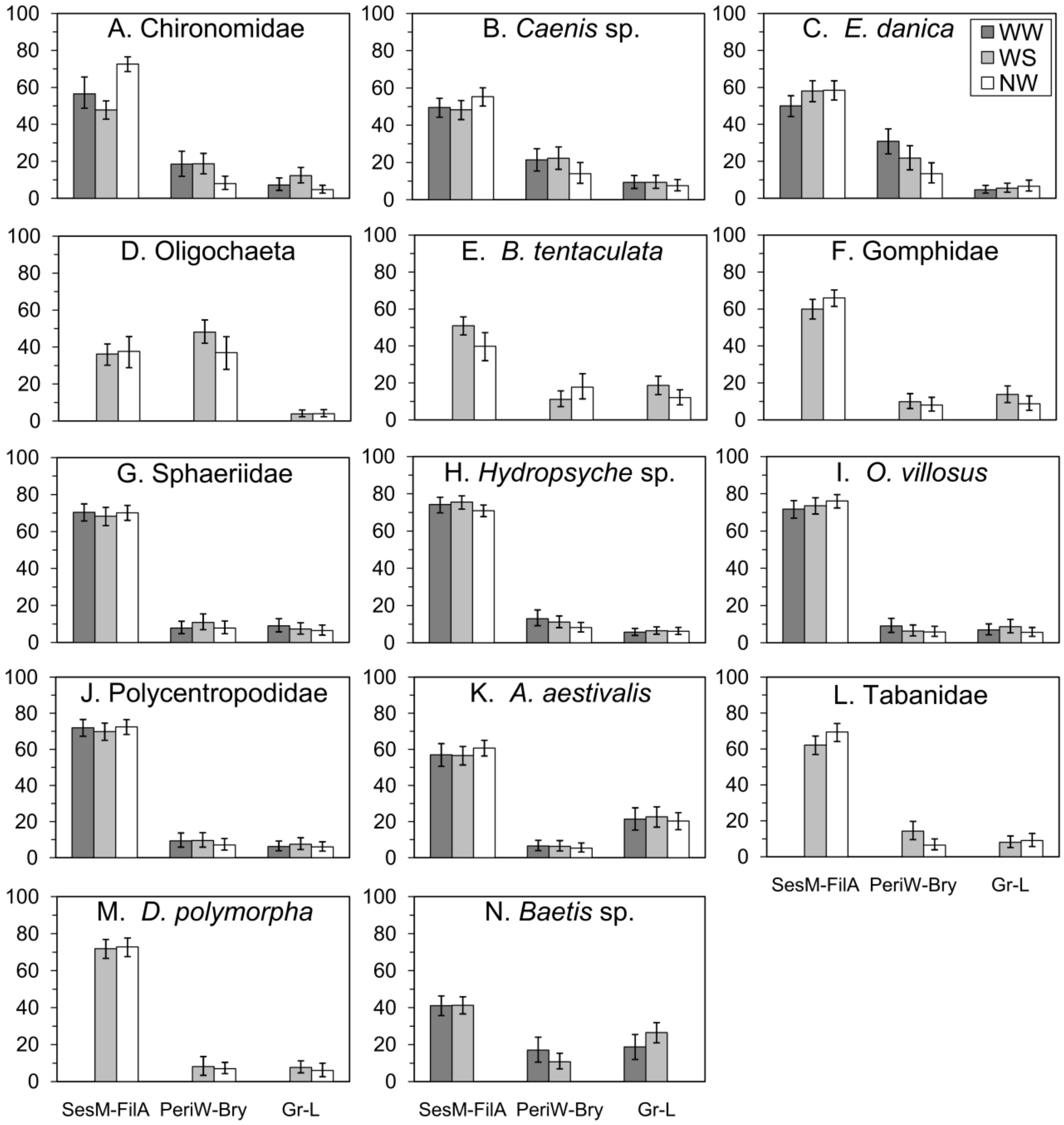

**Figure 20 Percent contributions of the trophic resources to the diet of the studied taxa (median and 75% credible interval) in the three substrata, as resulting from the mixing models applied to the stable isotope data. The plots show only the results obtained for the taxa that were analyzed for both wood and non-wood sites, and the trophic resources which contributed >10% to diet of at least one taxon. NW=river-bed sediment in the non-wood site, WS=river-bed sediment in the wood site, WW=wood surface. SesM-FilA= seston inferred from Unionids and filamentous algae (see text for explanation), PeriphW-Bry=periphyton on wood and bryophytes, Gr-L=grass and leaves. A=Chironomidae, B=*Caenis* sp., C=*Ephemera danica*, D=Oligochaeta, E=*Bithynia tentaculata*, F=Gomphidae, G=Sphaeriidae, H=*Hydropsyche* sp., I=*Orecthochilus villosus*, J=Polycentropodidae, K=*Aphelocheirus aestivalis*, L=Tabanidae, M=*Dreissena polymorpha*, N=*Baetis* sp.**

The diet of filter feeders (i.e. Sphaeriidae  and *Dreissena polymorpha*), the generalist *Hydropsyche* sp. and most of the predators (i.e. *Aphelocheirus aestivalis*, Polycentropodidae, *Orectochilus villosus*) was highly dominated (<70%) by seston and filamentous algae and did not differ among the three mesohabitats (Figure 20). On the contrary other consumers slightly shifted their diet from one substratum to another (Figure 20). In general, they fed more on seston and filamentous algae and less on periphyton and bryophytes in the non-wood site in comparison to the wood site (LW surface and sediment around the LW; Figure 20). This general trend was particularly evident for Chironomidae and *Ephemera danica*, for which the credible intervals (at 75%) of the estimates of diet composition did not overlap (Figure 20A and C). Chironomidae fed 22% and 34% more on seston and filamentous algae and 1.3 - 1.4 times less on periphyton and bryophytes in the non-wood site than in the wood site (LW surface and sediments near the LW respectively), and *Ephemera danica* fed 130% and 62% less on periphyton and bryophytes there. Periphyton and bryophytes contributed 120% less also to the ultimate trophic bases of the predator Tabanidae in the non-wood site than on the sediments around the LW (Figure 20L). Conversely, *Bithynia tentaculata* showed the opposite trend, with higher contribution of seston and filamentous algae and lower contribution of periphyton and bryophytes on the river-bed sediments around the LW than in the non-wood site, although probably not significant (overlapping credible intervals; Figure 20E). Chironomidae and *Bithynia tentaculata* showed also higher proportions of terrestrial allochthonous material (i.e. grass and leaves) in their diets on the sediment around the LW than on the other substrates (Figure 20A and E).

The analysis at community level showed that, although seston and filamentous algae were the most important resources in both wood and non-wood sites, the contribution of the different trophic resources greatly differed among the studied substrata (Figure 21). The contribution of epixylic autochthonous material (i.e. periphyton and bryophytes) to the biomass of the macroinvertebrate assemblages clearly increased (as show by the non-overlapping credible intervals of the estimates) from the non-wood site to the sediment around the LW (1.9 times higher) and to the LW surface (5.5 times higher). The contribution of allochthonous material (i.e. grass and leaves) was 1.3 times higher on the river-bed sediments around the LW than in the non-wood site.

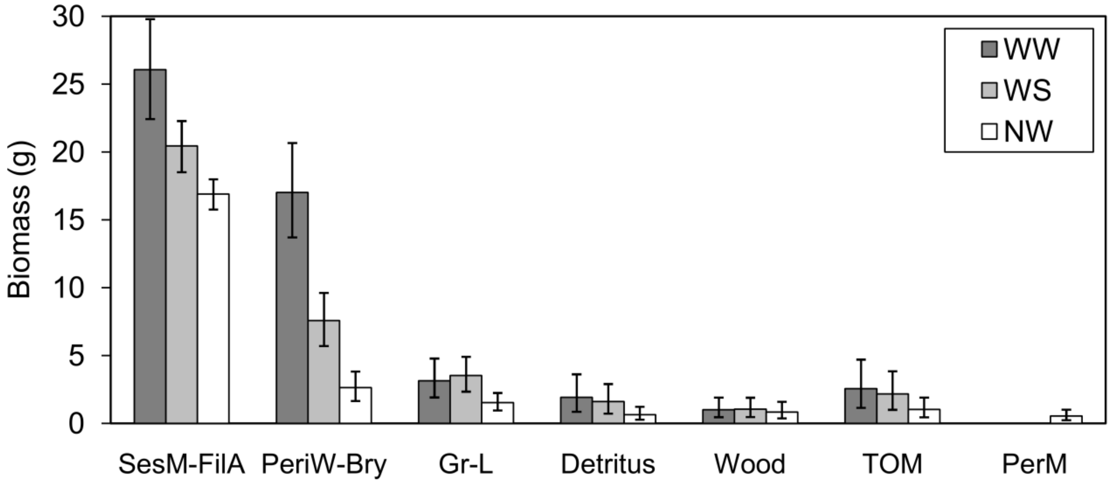

**Figure 21 Contributions of the studied trophic resources to the biomass of the macro-invertebrate assemblages on the three substrata, median and 75% credible interval. NW= river-bed sediment in the non-wood site, WS= river-bed sediment in the wood site, WW= wood surface. SesM-FilA= seston inferred from Unionids (see text for explanation) and filamentous algae, PeriW-Bry= periphyton on wood and bryophytes, Gr-L= grass and leaves, TOM=transported organic matter, PeriM= periphyton on the shells of unionid mussels.**

### *4.4.2 Fatty acid analysis*

The major fatty acid constituents, 14:0, 16:0, 18:0, 18:1ω9c (oleic acid, OA), and 20:5ω3 (Eicosapentaenoic acid, EPA) represented on average the 60% of the total fatty acids present in the study. However, the proportion of these FAs, and other important FA biomarkers, varied considerably across the food resources and taxa examined.

The fatty acid content by weight of the various basal resources was highly variable, with the greatest amount of fatty acids recorded in autochthonous sources, lower levels in terrestrial sources, and the least in sediment sources (Figure 22). The filamentous green algae (*Cladophora sp*.) had on average the greatest fatty acid content by weight; in contrast, sand had fatty acid concentrations 2 orders of magnitude smaller (Figure 22A). Saturated fatty acids (SAFAs) were the most abundant fatty acid class across all food sources (48-68%), and highly unsaturated fatty acids (HUFAs) were on average the least abundant fatty acid class (2.5-21%), although HUFA content varied extensively based on the origin of the food source. By weight, HUFA availability was greatest in all aquatic food resources (periphyton on mussels and wood, filamentous algae, bryophytes; mean: ~6.4 mg $g^{-1}$), while this was substantially lower in allochthonous and sediment material (mean: 0.9 mg $g^{-1}$; Figure 22A).

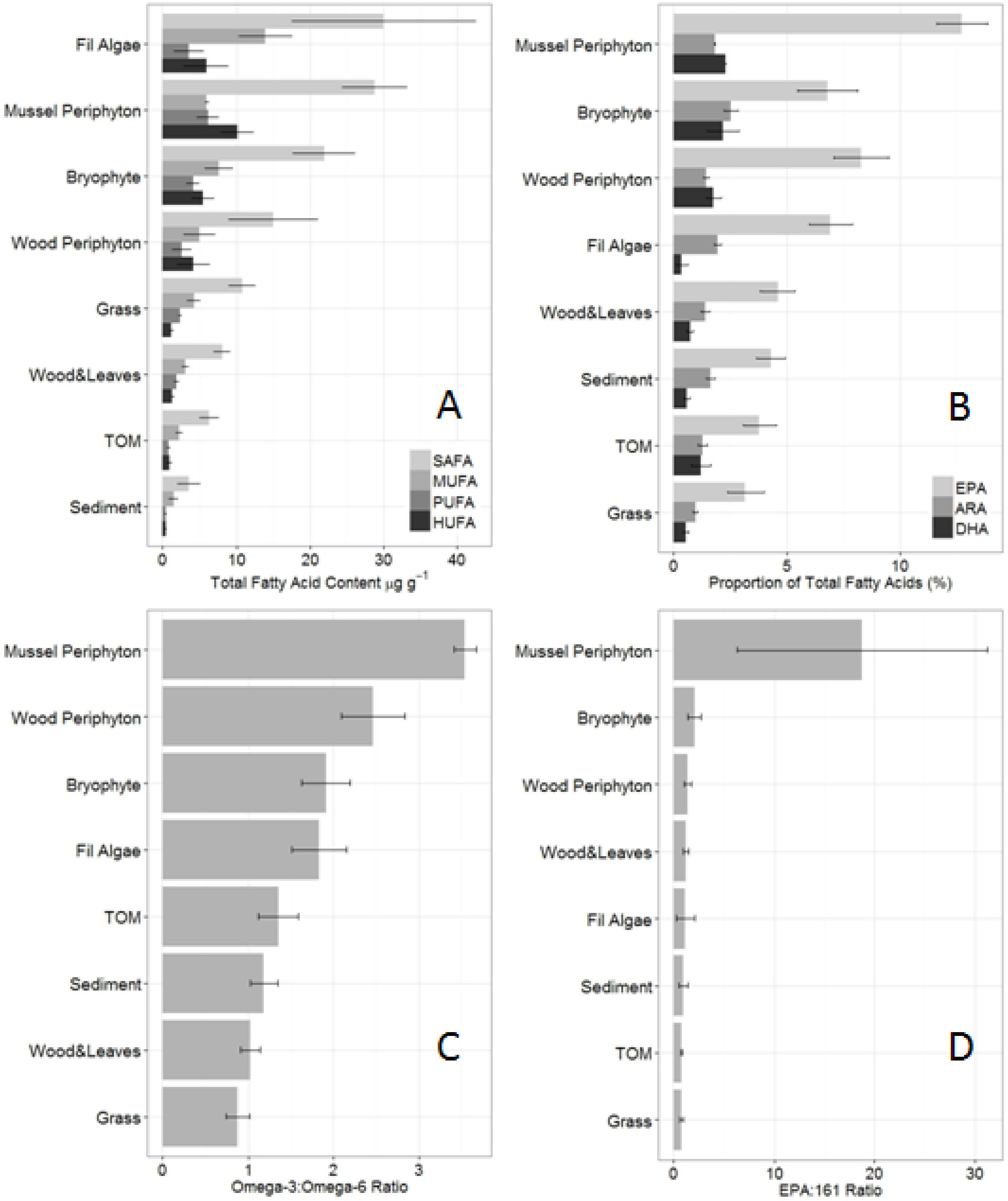

**Figure 22 Fatty acid composition for the various food resources collected in the study. A= total fatty acid content per class by weight (μg mg-1); B= proportion of physiologically important highly-unsaturated fatty acids by weight; C= ratio of omega-3:omega-6, an indicator of autochthony/allochthony dominance; D= overall proportion of the ratio of eicosapentaenoic acid (EPA; 20:5ω3) to 16:1, an indicator of diatom dominance.**

Eicosapentaenoic acid (EPA: 20:5ω3) was the most abundant HUFA and it was most abundant in mussel periphyton. Bryophytes and mussel periphyton had similarly high levels of docosahexaenoic acid (DHA: 22:6ω3, Figure 22B), and bryophytes had the greatest amount of arachidonic acid (ARA: 20:4ω6; Figure 22B). The ratio of EPA/16:1, commonly used as an indicator of diatom dominance, was greatest in mussel periphyton, indicating diatom dominated biofilms (Figure 22B). The ratio of omega-3:omega-6 fatty acids (ω3:ω6), which is a proxy for the relative influence of autochthony/allochthony, was predictably greatest in autochthonous sources, and lowest in allochthonous sources, although rarely below 1 (Figure 22C). Mussel periphyton had the greatest ω3:ω6 ratio (3.5) of all food sources, with wood periphyton containing less ω3 fatty acids (2.5). Transported organic matter (TOM) showed a ratio of 1.3 indicating a high influence of allochthonous sources.

A non-metric multidimensional scaling (nMDS) ordination of the fatty acid profiles separated the available basal resources into roughly three groups (Figure 23): 1) mussel periphyton, 2) wood periphyton and bryophytes, and 3) filamentous algae, terrestrial matter (wood, leaves and grass), and sediment (sand/organic matter). No basal resource profile was significantly different between wood and non-wood reaches. Mussel periphyton and the grouping of filamentous algae, terrestrial matter, and sediment had substantially different profiles (ANOSIM: R=0.864, P=0.002), mussel periphyton contained greater 12:0, EPA, and ALA (α-linoleic acid; 18:3ω3), while the terrestrial and sediment group contained greater 16:0, 16:1, and 18:0 (66% of variation, SIMPER). Wood periphyton and bryophytes occupied an intermediate area of the nMDS plot, and contained medium levels of HUFA and EPA/16:1. Wood periphyton exhibited a mixed signature between the diatom-dominated signal of mussel periphyton, and the grouping of wood and filamentous algae. Bryophytes appeared to group differently from wood periphyton, but this was not significant (ANOSIM: R = 0.020, P = 0.42). Sand and sediment organic matter, while containing different amounts of fatty acids, showed very similar fatty acid profiles, and were clustered *a-posteriori* for the ordination plot. Wood and leaves, being *Alnus* sp., had highly similar profiles between trunk and leaves, and were also *a-posteriori* grouped for the ordination. Transported organic matter had a highly variable signature, with most samples being very similar to sediment, although two samples were more algal based, with fatty acid profiles similar to bryophytes and wood periphyton. Filamentous algae, which were collected only in the wood site, showed fatty acid profiles that were similar to terrestrial material (grasses, wood, and leaves), but had one sample which contained a profile similar to wood periphyton.

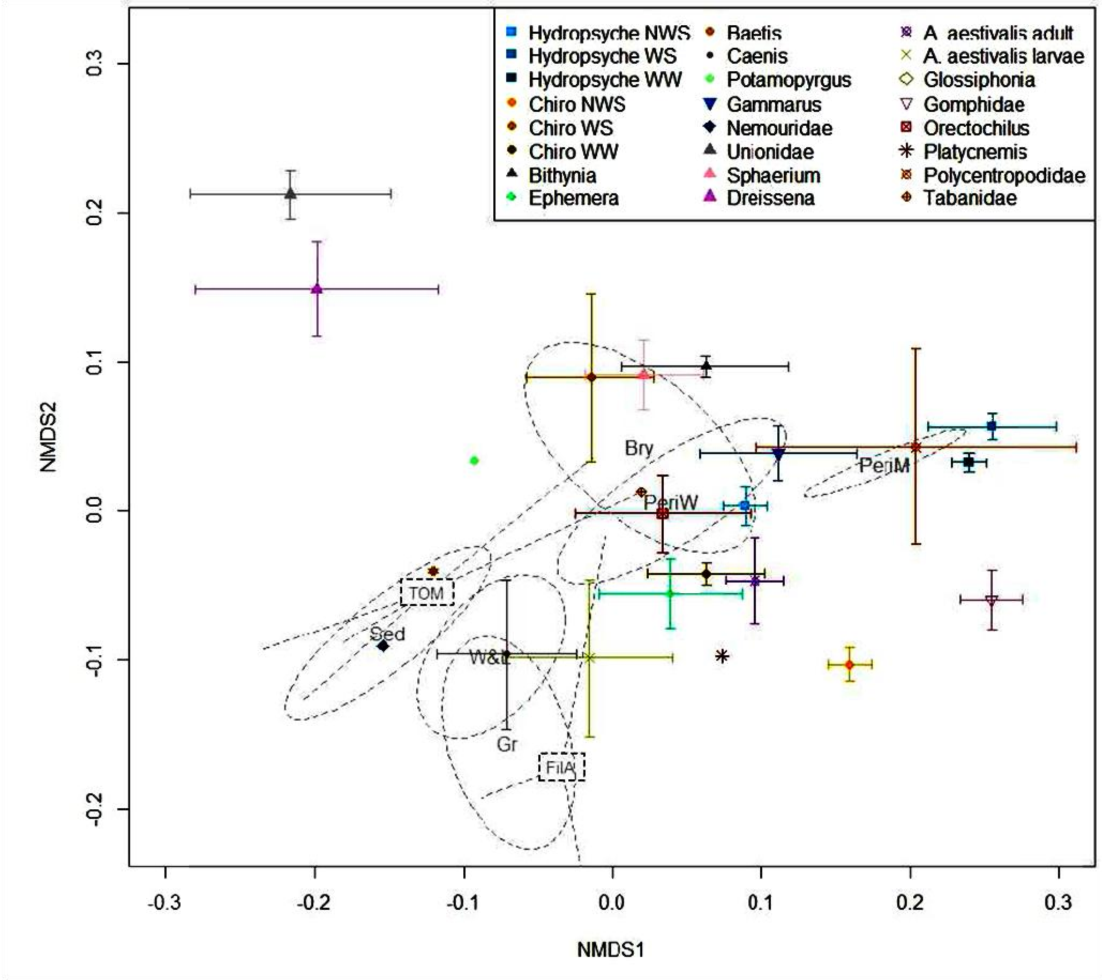

**Figure 23 Non-metric multidimensional scaling of all food resources and collected macroinvertebrates from the site locations. Ellipses represent 95% confidence intervals for each basal food resources. Ordispider lines are used for filamentous algae (Fil A) and transported organic matter (TOM) to indicate the variability in the samples. Bry = bryophytes; PeriM = mussel periphyton; PeriW = wood periphyton; Gr = grass; W&L = wood and leaves. Chiro=Chironomidae.**

Most macroinvertebrate taxa had fatty acid profiles similar to specific food resources or between multiple resources, with several notable exceptions. Unionidae (*Unio* and *Anodonta*) and *Dreissena polymorpha* contained high levels of long-chain and branched fatty acids (*e.g.* 24:0, 22:2) and grouped separately from all measured food resources. Despite feeding on seston, Unionidae and *Dreissena* are known to retain and possibly elongate commonly present fatty acids into long-chain branched forms which are not present or are rare in seston (Gladyshev *et al.*, 2011). The leech *Glossiphonia complanata*, which was collected in only one sample, had a distinct fatty acid profile with extremely high levels of ARA (~26% of total FA), and was highly different from all food resources (outside plot viewing area).

Overall, there were few observed differences in consumers' profiles among substrata, with the notable exception of the net-spinning caddisfly *Hydropsyche pellucidula* and Chironomidae, which were collected in all three locations. *Hydropsyche* had substantially different fatty acid compositions in wood and non-wood locations. Both samples from the LW surface and from the sediments around the LW grouped closely with mussel periphyton, containing high levels of HUFA and ω3 fatty acids, and were significantly different from the samples from the non-wood site (Figure 23; ANOSIM: $R = 0.682$, $P = 0.002$). Compared to both wood-related *Hydropsyche* populations, *Hydropsyche* in the non-wood site had decreased 12:0, ~50% lower EPA, 16:1, ALA, and 50% decreased DHA, but increased 16:0, 18:0, OA, and 14:1 (SIMPER: 80%, descending order of importance; Figure 24). However, *Hydropsyche* ω3:ω6, even though lower than in both wood habitats, was still extremely high also in the non-wood site, indicating a diet dominated by autochthonous production (Figure 24). Chironomidae were significantly different among all three wood and non-wood locations, although this separation was not along any clear resource gradient (Figure 23; ANOSIM: $R = 0.589$, $P = 0.006$). Chironomidae from the LW surface were located centrally in the plot near wood periphyton, while those from the non-wood site were located to the bottom right, and those from the sediments near the wood were located to the upper left, overlapping with the bryophyte signal. In comparison to the samples from the LW surface, those in the non-wood site had increased 16:1ω9, 14:0, 18:2ω6c and ALA, but decreased concentrations of 16:0, 18:0, 14:1, EPA, and 12:0 (SIMPER NW-WW: 82%). In comparison to the samples from the sediments near the LW, the samples in the non-wood site contained higher 16:1ω9, 40% greater EPA content, 18:2ω6c, 14:0, and 18:3ω3, but lower 16:0, 18:0, 85% less DHA, ARA and 17:0 (SIMPER NW-WS: 79%). Chironomidae profiles in both wood locations (WS and WW) differed quite strongly from one another, with the samples from the sediments around the LW having decreased EPA, 18:2ω6c and 14:0 but greater 16:1ω9, DHA, and ARA (SIMPER WS-WW: 57%).

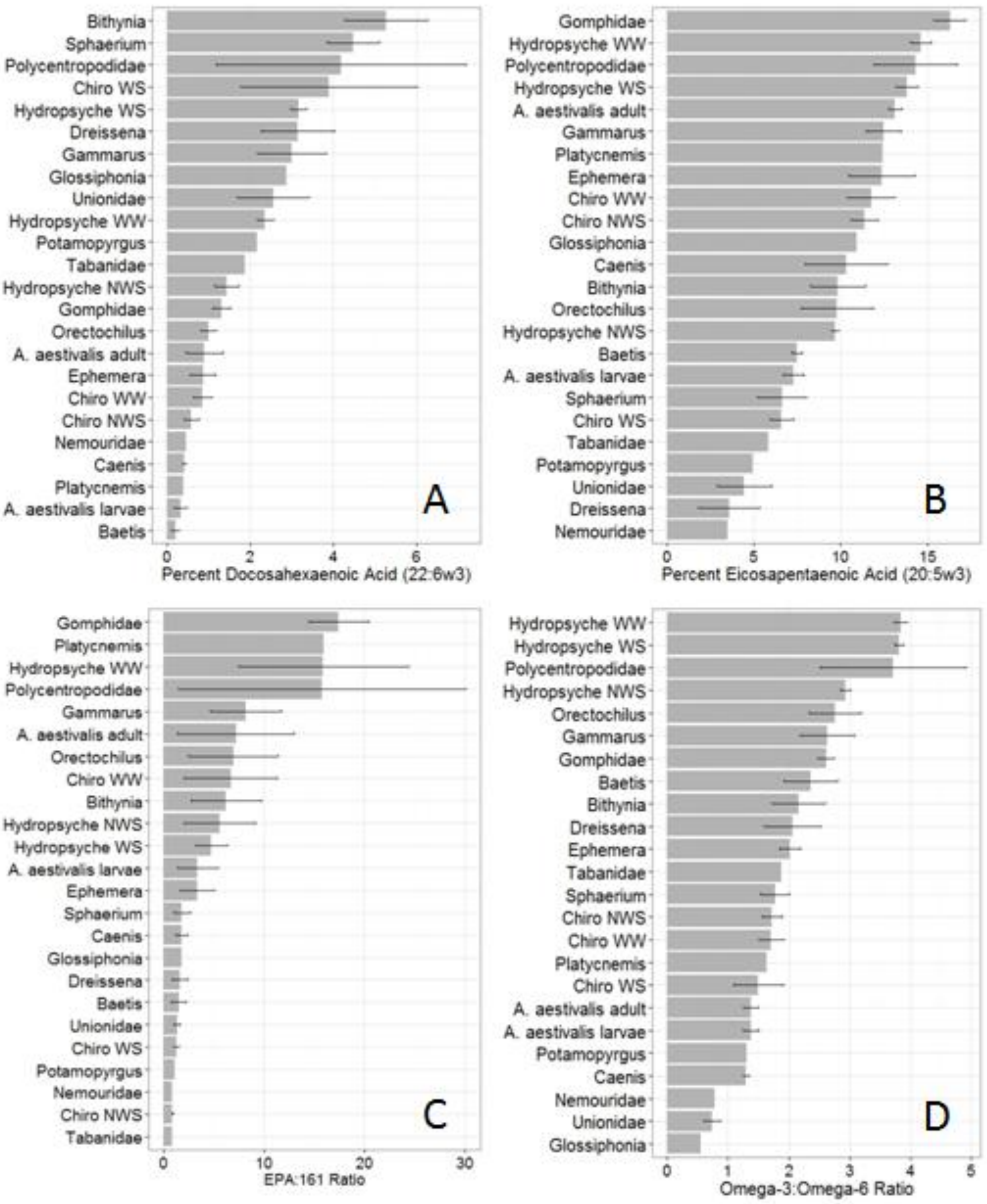

**Figure 24 Various biomarker data for all stream consumers analysed for fatty acids A= total proportion of docosahexaenoic acid (DHA; 22:6ω3); B= total proportion of eicosapentaenoic acid (EPA; 20:5ω3); C= ratio of eicosapentaenoic acid (EPA; 20:5ω3) to 16:1, an indicator of diatom dominance D= ratio of omega-3:omega-6, an indicator of autochthony/allochthony dominance.**

Although other consumers were not significantly different among mesohabitat locations, they showed distinct fatty acid profiles indicative of their diet. The caddisfly *Polycentropodidae* had the largest variability in profile, possibly indicating several different dietary patterns, but generally contained a high algal signature with a high ω3:ω6 ratio, and although extremely variable, a high EPA/16:0 indicating a high diatom component of the diet (EPA/16:0; Figure 24). This HUFA enriched, high algal influence is also seen in *Gammarus roeselii*, while considered a shredder/gatherer, has a signal located between mussel periphyton and wood periphyton (Figure 23). The snail *Bithynia tentaculata*, had a mainly autochthonous signature, in contrast to the New Zealand Mud Snail, *Potamopyrgus antipodarum*, which had a signature between bryophytes and sediment/TOM (Figure 23). *Potamopyrgus* had very low concentrations of HUFA, especially ARA, in comparison to other consumers (Figure 24). *Ephemera danica* is located near wood periphyton and slightly towards the cluster of filamentous green algae, grass, and wood and leaves, and its intermediate ω3:ω6 ratio supports this mixed diet of autochthonous and allochthonous sources. *Sphaerium* sp. grouped with bryophytes and had a similar signature to *Bithynia tentaculata* and Chironomidae from the sediments around the LW (Figure 23).

A few taxa showed similar profiles to the cluster of terrestrial matter, sediment, and filamentous algae. *Nemouridae*, a shredder/gatherer stonefly, which was only collected in NW, had a strong sediment signature, plotting directly above the combined sediment profile (Figure 23). *Baetis* sp., which was collected in WW locations, was similar to transported organic matter, suggesting feeding on deposited transported matter. *Caenis* sp., known to be a gatherer, had a relatively wide variability in its fatty acid signature but was centrally located in the wood-leaves and grass signatures.

Generally, predator profiles did not as closely match basal energy resources as did primary consumers, likely due to a fatty acid trophic integration factor (FA-TEF), where fatty acid profiles may shift with increasing trophic level, and may vary due to species-specific physiological demands. Unfortunately, unlike for stable isotopes, this has not yet been explored for benthic consumers in the literature, and cannot be corrected for within this study. Some taxa, most notably Gomphidae and *Glossiphonia complanata*, were most separated from any potential food resources, likely exhibiting the largest FA-TEF from their diets. Gomphidae likely fed on nearby Chironomidae or *Hydropsyche* sp., and retained their high algal signature with a high ω3:ω6 ratio and diatom dominance with a high EPA/16:1 (Figure 23 and Figure 24). *Orectochilus villosus* profiles were most similar to the profiles of consumers found near wood periphyton and bryophytes, and contained relatively high ω3:ω6 ratios (Figure 23 and Figure 24).

*Platycnemis* sp. and Tabanidae, while single samples, were located within the wood-associated cluster, but *Platycnemis* sp. maintained a high diatom signature with a high EPA/16:1 (Figure 23 and Figure 24). *A. aestivalis* adults also clustered near periphyton growing on wood and bryophytes, and were likely consuming Chironomidae, while larvae had profiles more similar to filamentous algae and terrestrial matter.

## 4.5 Discussion

The results of this study show that invertebrate assemblages in the wood site were less dependent on seston subsidies and had a greater support from autochthonous production (periphyton and bryophytes), despite an increase in both epixylic and terrestrial food resources there.

### *4.5.1 Taxa-specific trophic bases*

#### *Stable isotope analysis*

The combined seston and filamentous algae resource was the most important trophic resource for most of the studied taxa, and supported a large portion of the assemblages both in the wood-related substrata (LW surface and river-bed sediment in the surrounding of the LW) and in the non-wood site. However, filamentous algae were only found in the wood reach, and were relatively rare in the channel, isolated to a few small patches in over 100 m of channel. Therefore, even though seston and filamentous algae were combined isotopically, seston would likely be the dominant basal support. This is probably due to the proximity to a lake (Lake Sitno, located 700-1000 m upstream the non-wood and wood sites), as the lake seston exported to downstream channels is able to sustain large biomasses of filter feeders (Richardson & Mackay, 1991; Hillbricht-Ilkowska, 1999). Thus lacustrine subsides likely have a high influence on the studied low-productivity sand-bed river. The combined periphyton and bryophyte signal represented the second-most important resource, with the greatest support occurring in the reach with higher wood loadings, and especially on the wood surface itself. On the contrary, even in the sediment around the wood, the accumulations of grass, leaves, detritus, and fine organic matter contributed relatively little to overall community biomass.

We obtained the isotopic signature of seston with two methods, as we collected one-size fraction (>125 µm) seston samples during the sampling time (transported organic matter), and second we inferred total seston from the isotopic signature of unionid mussels. The value of $\delta^{13}C$ greatly differed between the seston signatures obtained with those two methods. Such difference may be due to the high seasonal variability of the isotopic signature of lacustrine seston, with bulk isotopic values depending by its successional change in composition, which generally results in more $\delta^{13}C$ depleted in winter and more enriched in spring (Zohary *et al.*, 1994). The isotopic composition of the tissues of Unionid mussels integrates the seasonal variation in the isotopic signature of seston (Cabana & Rasmussen, 1996; Atkinson *et al.*, 2014). According to that, we found that the 125 µm seston collected at the time of sampling (April) was more $\delta^{13}C$ enriched than that inferred from mussels, which may retain a $\delta^{13}C$ depleted winter signature. Alternatively, the difference in the isotopic values of seston may be due to a selective feeding behaviour, or to the recently detected pedal feeding behaviour of mussels (Makhutova *et al.*, 2013). Unionid mussels may behave as selective filter feeders, preferring ultra-fine nutritive particles, as are $\delta^{13}C$ depleted bacteria, thus their isotopic signature may be representative only of that component of the seston (Nichols & Garling, 2000), which may have not be detected by the isotope analysis of the bulk 125-µm samples of seston. This hypothesis however seems is in contrast to other studies that report that unionid mussels feed on particles of a broad size range, up to 250 µm, e.g. Vaughn *et al.* (2004). Further studies on the seasonal shifts in the isotopic signature of seston and unionid mussels and a species-specific analysis of the isotope ratio in the different components of the seston may help in disentangling this issue.

Non-filterer taxa, as *Baetis* sp. (mostly grazer and gatherer-collector), *Caenis* sp. (mostly gatherer-collector), Chironomidae (mostly gatherer-collectors, but with genus- or species-specific differences in feeding behaviours) and, to a lesser extent, Oligochaeta (mostly gatherer-collector), also showed a strong sestonic isotopic signature. They probably fed on deposited seston on the sediments, which might be enhanced by the presence of LW (Smock *et al.*, 1989; Ehrman & Lamberti, 1992; Daniels, 2006; Cordova *et al.*, 2008), and by the benthic-pelagic coupling role by filter feeders (Vaughn *et al.*, 2004; Howard & Cuffey, 2006). However, the isotopic signature of detritus greatly differed from that of seston (Figure 19), especially from the isotopic signature of seston inferred from unionid mussels. As we collected the first 5-cm layer of river-bed sediments for detritus signatures, it is possible that deposited seston only represented the first millimetres of sediment and thus its isotopic signature was masked by that of deeper layers. Alternatively, other macroinvertebrates may also show preferences for only part of the (deposited or pelagic) seston, i.e. the small-sized fractions, as discussed for unionid mussels (see above), or this pattern may be due again to seasonal differences in the isotopic signature of seston. The isotopic signature of macroinvertebrates at the time of the sampling might have been still largely affected by the isotopic signature of the winter (deposited or pelagic) seston, which, due to seasonal variations, was not more detectable in the spring sediments. In fact seasonal variations in carbon isotopic ratios of the trophic resources are paralleled by shifts in carbon isotopic ratios of the tissues of macroinvertebrate consumers (Zah *et al.*, 2001). Changes in isotope ratios in macroinvertebrate consumers lags behind the changes in isotope ratios of algae (McCutchan & Lewis, 2002), being this time lag related to the turnover time of the tissues of the consumers, which is faster in small sized animals and slower in large-sized animals, e.g. the turnover time of muscles tissues of shrimps has been reported to be 15 days (Fry *et al.*, 2003).

*Fatty acid analysis*

The results of the fatty acid biomarker profiles, in contrast do not explicitly show a dominant seston signature supporting the macroinvertebrate assemblage. Consumer fatty acid profiles generally coincide with the collected basal food resources, and ω3:ω6 ratios are sufficiently variable to suggest that while many consumers are supported by autochthonous production, others are supported by allochthonous production. Seston derives from a mix of allochthonous and autochthonous sources, including phytoplankton, bacteria, and processed terrestrial matter that may be present in various size fractions. As a result, while consumers may exhibit a uniformly depleted seston stable isotope signature, they may be preferentially utilizing different autochthonous/allochthonous resources in the seston. For example, *Caenis* sp. fatty acid profiles show a distinct sediment and terrestrial signature, and a low ω3:ω6 ratio to support this allochthonous dominance. *Caenis* sp., for which stable isotopes show to have a high seston signal, might thus feed on the allochthonous component of the seston that, while originating in the lake upstream from the sample location, is deposited within the study reach. On the other side, the net-spinning caddisfly *Hydropsyche* was uniformly estimated to feed mostly on seston while fatty acid profiles indicate a high algal and specifically diatom diet. This would suggest that *Hydropsyche* would be preferentially trapping and eating from their nets a diet rich in algae.

### *4.5.2 Changes in the trophic bases at taxon level*

#### *Stable isotope analysis*

Stable isotope analysis showed differences in the trophic bases of some consumers (i.e. Chironomidae, *Ephemera* sp. and Tabanidae) among the three substrata. Seston and filamentous algae seem to contribute less while periphyton and bryophytes seem to contribute more to the diet of macroinvertebrates in the wood site in comparison to the non-wood site. This may be due to an actual shift in the diet of those taxa (Chapman & Demory, 1963; Rosi-Marshall & Wallace, 2002), or it may be due to a different taxonomic composition of the studied taxa on the three substrata, as a response to the different availability of food resources. For example, Chironomidae show large genus- or species-specific differences in feeding behaviors (Ehrman & Lamberti, 1992), thus the changes in diet that we recorded might have been the result of a within-family shift in taxonomic composition.

#### *Fatty acid analysis*

Mesohabitat differences in Chironomidae resulted also from the FA analysis. However, the differences in specific FA biomarkers were not clearly indicative of a shift in diet towards increased seston in the non-wood site, as instead resulted from SIA. Fatty acid profiles of the various size-fractions of the seston could have provided better insight on this.

While not detected in the stable isotope data, fatty acid profiles showed a difference in the quality of the diet of *Hydropsyche pellucidula* between the wood and non-wood sites. In the wood-related mesohabitats the *Hydropsyche* FA signal was similar to that of the periphyton growing on the shells of mussels, which suggests that the seston collected and consumed in their nets was overall more diatom-dominated and overall enriched in EFAs. This may be due to a direct subsidy by wood substrates, as periphyton scours and is dislodged from the wood, enriching the diet of *Hydropsyche* in the nearby sediments. Wood also provides an elevated place for attachment in the water column, and may allow *Hydropsyche* to collect a greater fraction of phytoplankton, which stay higher in the water column.

### *4.5.3 Changes in the trophic bases at assemblage level*

Lake Sitno, which was located only 1 km upstream of the sampling reaches, clearly provided strong subsidies for the macroinvertebrate production in the studied area of the Płociczna River. However, the presence of large wood altered the way in which downstream macroinvertebrate assemblages were dependent upon these lake subsidies. In sediments near LW, lake subsidies were still prevailing, while the invertebrate assemblage had increased subsidies from periphyton and bryophyte sources, as well as slight increases from terrestrial matter and detritus, although in low absolute amounts. Furthermore, for the assemblages on the wood surface, filamentous algae, periphyton and bryophytes supplemented nearly double the amount of biomass that would be sustained by seston subsidies alone. Although the relationship between resources availability and consumers biomass might not be linear and consistent across the various resources (e.g. algal production provides limiting FA, and thus has likely larger impacts on the consumers biomass), such results suggest that macroinvertebrates benefitted from the autochthonous primary producers growing on the wood surface.

In a sandy-bed river, there normally exists little in-stream autochthonous or even organic matter to support overall ecosystem productivity. Sediment instability is one of the main limiting factors for primary producers, as the surface layer of sand is in continuous motion even at low flow (Atkinson *et al.*, 2008). In contrast, large wood represents a stable substratum for periphyton growth and a long lasting source of carbon for the development of the heterotrophic biota within this biofilm (Golladay & Sinsabaugh, 1991), and thus it acts as hotspot of autochthonous primary production within otherwise low productive sandy river channels.

LW can also trap allochthonous inputs, as fallen leaves from the riparian zone, and thus represent important an storage of coarse particular organic matter (CPOM). Smock *et al.* (1989) found that about 85% of annual CPOM storage on the channel surface in a low-gradient headwater stream occurred at wood dams and that the concentration of organic matter storage on channel sediments greatly increased in proximity to the wood dams and with increasing dam abundance. In our study, however, in contrast to other food resources, terrestrial matter was a minor component of the diet, despite the large abundance of these food resources, and thus supported for less biomass than autochthonous aquatic production, even in sediment habitats.

### 4.5.4 Conclusions

Our study showed that SIA and FA analyses complement each other and thus may improve studies of freshwater food webs, particularly where resources may be a mix of lacustrine and riverine origins. Since stable isotopes are subjected to seasonal and local phenomena, SIA allows to distinguish among the contribution of food resources with different spatial origin (i.e. riparian zone, lake and river), but may give inconsistent results due to the seasonal changes in the signature of food resources, or as resources do not have clearly distinct isotopic signatures. On the other hand, fatty acids can be used to accurately estimate taxonomic groupings even with variations in season and abiotic conditions (Dethier *et al.*, 2013; Taipale *et al.*, 2013), although may not be able to distinguish between lacustrine or riverine origins (e.g. a "diatom signature" is similar whether from periphyton or phytoplankton sources).

This study also showed that, although not sustaining the majority of production in the reach, the presence of large wood resulted in distinct increases of autochthonous epixylic material, as periphyton and bryophytes, and, to a minor extent, of allochthonous (i.e. terrestrial) material in the production of the macroinvertebrate community of the Płociczna river. Even in a sandy-bed river, with low quantities of autochthonous production due to the low amounts of hard substrate available for periphyton and other phytobenthos, autochthonous production has a disproportionate influence on supporting ecosystem productivity. As the influence of lake subsides decreases at increasing distance from the lake (Richardson & Mackay, 1991; Hillbricht-Ilkowska, 1999), the role of large wood is likely to increase with lake distance, as secondary production would be entirely dependent on the remainder of the food resources.

Hence, large wood in rivers increases the diversity and quality of basal trophic resources available for the food web. This, together with an increase in habitat heterogeneity, enhances the abundances and diversity of macroinvertebrates. Thus, any type of river management that would limit the availability of wood and its effects on the habitat heterogeneity of these ecosystems would also severely limit both the quantity and quality of food resources available to stream biota, and ultimately ecosystem productivity.

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# 5. General discussion

## 5.1 Rationale and research aims

Freshwater ecosystems continue to be subjected to general abiotic and biotic homogenization (Moyle & Mount, 2007; Rahel, 2007; Donohue *et al.*, 2009; McGoff *et al.*, 2013). On the other side, my studies provided new evidence that the presence of large wood constitutes an effective trigger to increase both physical and biotic diversity in rivers. Several studies have already shown that large wood exerts important effects on the hydrogeomorphology of river systems (e.g. Gurnell *et al.*, 2002; Wohl, 2013) and hosts a diverse fauna (e.g. Hoffmann & Hering, 2000; Benke & Wallace, 2003). However, there has been a clear knowledge gap on how the LW-induced alterations of local physical conditions affect benthic fauna colonizing the river bed sediments around the LW. Previous studies have mostly focused on headwater streams with high gradient, coarse sediments, and massive accumulations of LW. However, single LW pieces potentially drive even more important changes to the local physical conditions in lowland sandy rivers, which are characterized by more homogeneous flows and more unstable and loose substrata. In these rivers, LW represents the most important trigger creating more diverse flow and habitat conditions (Mutz, 2000; Kail, 2003; Webb & Erskine, 2005; Daniels, 2006), which will have concomitant effects on benthic communities. Thus, a comprehensive knowledge of the LW-driven changes in the abiotic conditions and their linkages with changes in biotic diversity is fundamental to understanding the full effects of the presence of LW in streams, as well as the effectiveness of potential introductions of LW pieces within river restoration projects.

Therefore, this thesis aimed to fill the aforementioned research gap by: characterising the mesohabitats that typically appear in proximity to LW logs (Chapter 2); investigating the linkages between the variability in the physical conditions induced by LW and macroinvertebrate alpha and beta diversity (Chapter 3); and by investigating whether the presence of LW logs drives changes in the trophic bases of the invertebrate food web (Chapter 4).

The data for this thesis were gathered during field surveys at 10 sites within 5 near-natural lowland river reaches in western Poland. Each study included in this thesis was based on a paired-site study design, where river reaches that were naturally rich in in-channel LW pieces were compared to adjacent river reaches that were poor in wood.

Macroinvertebrate samples included ca. 152,000 specimens of invertebrates in total, belonging to 175 taxa.

## 5.2 Effects of large wood on the hydrogeomorphology of sandy lowland rivers

The results of this study demonstrated a consistent effect of the presence of LW on the abiotic conditions in the river channel areas surrounding the LW, which are much more diverse than those in the channel areas without LW (Chapters 2 and 3).

Flow patterns around LW are known to be highly heterogeneous and variable (Montgomery *et al.*, 2003), that is, flow velocity is reduced within the roughness projection area of the LW, and it is increased in the remaining part of the channel cross-section, where the water flow is concentrated (Wallace *et al.*, 1995; Gurnell & Linstead, 1998; Mutz, 2000). In mountain streams this induces in a gradual shift from erosional to depositional processes, which results in the local deposition of fine sediments and organic matter (Wallace *et al.*, 1995; Buffington & Montgomery, 1999). In contrast to that, Mutz (2000) found that in sandy lowland rivers the presence of LW pieces was associated with erosional processes. The results of this thesis confirm Mutz (2000) finding, as scouring pools with coarser sediments were recorded around LW pieces. However, depositional patches of fine sediments and organic matter were also recorded (Chapter 2), showing that in sandy lowland rivers the presence of LW pieces drives both depositional and erosional processes. The loose sandy sediments of lowland rivers may be moved by much smaller shear forces than the coarser sediment material present in mountain streams. Thus, in lowland sandy rivers even simple LW structures such as single wood logs can significantly change local habitat conditions, whereas in systems with coarser grain size, as mountain streams, more complex structures are probably necessary to obtain significant shifts in habitat characteristics.

The LW-driven sedimentation and erosion processes created a high heterogeneity of abiotic conditions in the river-channel areas surrounding the LW logs, which was consistently recorded throughout this research (reported in Chapters 2 and 3). Such heterogeneity of abiotic conditions could be effectively summarized by the coefficients of variation of key abiotic parameters, as median sediment grain size, mean flow velocity, turbulence and organic matter content in the sediments, which were significantly higher at the sites rich in LW logs (Chapter 3). The presence of LW also increased the retention of organic matter in the nearby river-bed sediments (Chapter 2), which is likely to shorten the spatial scale of carbon and energy transfers within the food web, and of nutrient spiralling (Smock *et al.*, 1989). This effect will increase energy and nutrient availability for local biotic communities, thus enhancing the overall intensity of ecosystem functions and processes.

In the studied river reaches, the hydraulic roughness induced by LW changed river morphology at a larger spatial scale, too, as river reaches where in-channel LW blocked a large proportion of the channel cross-section area exhibited steeper water lever gradients, indicating a substantial water afflux upstream (Gippel *et al.*, 1996; Gurnell & Linstead, 1998).

## 5.3 Effects of large wood on macroinvertebrate communities

The results of this thesis demonstrated that the presence of in-channel large wood changed the taxonomic and functional composition of the macroinvertebrate assemblages in a wider area, and thus enhanced both macroinvertebrate alpha and beta diversity. Not only the wood surface, but also the nearby river-bed sediments were colonized by distinct and more diverse macroinvertebrate communities.

The wood surface consistently exhibited the highest values of total macroinvertebrate abundances compared to the benthic habitats throughout the study (Chapters 2, 3 and 4). High abundances on the wood were also reported by Hoffmann and Hering (2000), Benke and Wallace (2003) and Smock *et al.* (1989). The wood-dwelling community included taxa that are known to be closely associated with wood (Hoffmann & Hering, 2000; Schröder *et al.*, 2013), such as the xylophages *Macronychus quadrituberculatus* (Coleoptera) and *Lype* sp. (Trichoptera), grazer and scraper taxa, for example, the elmid beetle larvae *Oulimnius* sp. and *Elmis* sp., and collector gatherer taxa such as Chironominae and *Baetis* sp.(Ephemeroptera) (Chapter 2).

Although the wood surface hosted the most abundant communities, the hotspot of macroinvertebrate diversity was found to be the area of river-bed sediments in proximity to the LW logs. There, the typical flow patterns generated by the presence of the LW created distinct habitat patches that were colonized by distinct and diverse macroinvertebrate assemblages which reflected the taxa-specific preferences for particular abiotic conditions (Chapter 2). Thus the scouring patches were preferentially colonized by taxa that prefer coarser sediment grain sizes and faster flows (Schröder *et al.*, 2013), for example, the trichopteran *Hydropsyche pellucidula* and the heteropteran *Aphelocheirus aestivalis*. The patches with slower flows and accumulation of organic matter were colonized by taxa that prefer shallower water and moderate flows such as the mussels *Sphaerium* sp. and *Pisidium* sp. (Hamill *et al.*, 1979; Schröder *et al.*, 2013), while the detritus accumulations again supported especially high macroinvertebrate densities. Shredder taxa such as gammarids generally benefit from the increased organic matter contents in the sediments surrounding the LW logs (Dobson & Hildrew, 1992).

Such heterogeneous abiotic conditions potentially provide refugia for biota during disturbances (Townsend & Hildrew, 1994). This applies both to floods, by providing sheltered areas with reduced flows, and to low flow conditions, by providing areas with local peaks in mean flow velocity.

Besides increasing the heterogeneity of abiotic conditions, LW also increases the availability of more diverse trophic resources. As LW constitutes an obstacle to flow, it traps transported coarse organic matter deriving from the riparian zone, such as leaves, and enhance the sedimentation of fine particulate organic matter (Chapter 2). As LW represents the unique hard and persistent substratum in sandy river channels, it allows for the growth of periphyton and bryophytes, which are high quality autochthonous trophic resources. Thus, LW also represents a hotspot of primary production in an otherwise low productive system. The availability of diverse trophic resources thus resulted in a higher diversification of the trophic basis of the macroinvertebrate assemblages colonizing the surface of LW pieces and the surrounding river-bed areas (Chapter 4).

Overall, the LW-induced higher variability of abiotic conditions (Chapters 2 and 3) and the availability of more diverse trophic resources (Chapter 4) could sustain a higher invertebrate diversity by offering a larger number of potential ecological niches (Hutchinson, 1961). Invertebrate communities are also likely to benefit from the improved options for short-distance dispersal of organisms among the diverse neighbouring habitats (Beisel *et al.*, 2000). This effect may have substantially contributed in this study to the higher values of local alpha diversity and of compositional heterogeneity in those assemblages (beta diversity; Chapter 3).

The diverse mesohabitats provided by LW are likely to increase the temporal stability of the aquatic communities (Brown, 2003) and to lead to a higher resilience, by offering sources for re-colonization after disturbances (Figure 25). The elevated invertebrate production around LW is likely to enhance the presence of higher trophic levels in the river food web, thus representing an abundant and nutritive food resource for fish. As emergent aquatic insects that had developed near LW provide an important energy resource for riparian predators (Baxter *et al.*, 2005), the abundant LW-associated macroinvertebrate assemblages are likely to increase the ecological connectivity between aquatic and terrestrial biota, too.

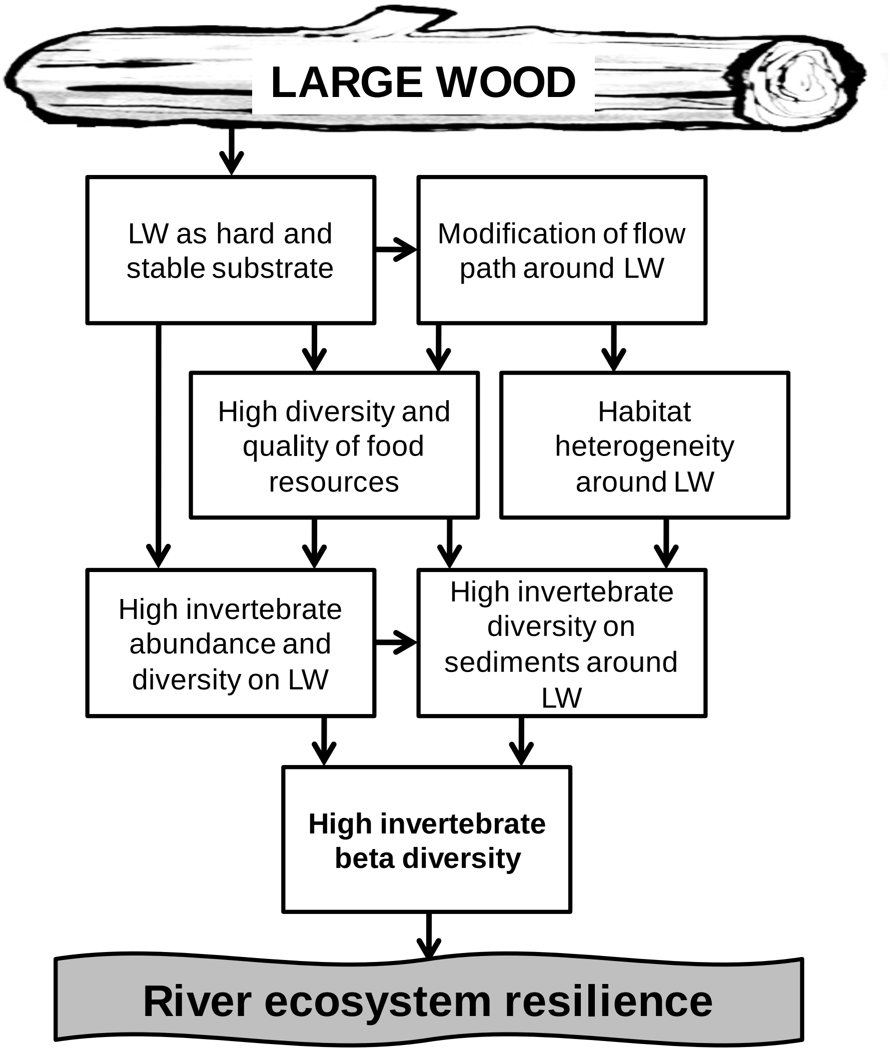

**Figure 25 Conceptual representation of the cascading ecological effects of large wood (LW, as a tree trunk) in sandy lowland rivers. The presence of the LW will trigger the formation of more diverse abiotic conditions in its proximity (see Chapters 2 and 3) and this will increase the availability of more diverse food resources (see Chapter 4). The highly diverse and abundant macroinvertebrate assemblages on the LW surface will thus act as hotspots which may serve as species reservoirs for the colonization of nearby habitats. These hotspots will thus lead to more diverse invertebrate assemblages in wider areas of the river-bed sediments around the wood logs. The increased beta diversity within the river reach will then produce an elevated level of resilience against disturbances in the respective river section.**

## 5.4 Implications for river management

The results presented in this thesis show the key role of LW for habitat heterogeneity and biotic diversity in lowland rivers, which can also increase ecosystem resilience to disturbance events. During floods, stable LW tends to attenuate flood peaks and to increase their travel time (Gregory *et al.*, 1985; Ehrman & Lamberti, 1992). Despite that, the traditional approach to river channel management consists of the removal of in-channel LW, with the aim to increase water conveyance and thus reduce the risk of floods (Gurnell & Linstead, 1998). The active removal of in-channel LW and the depletion of natural riparian vegetation that has occurred during the last centuries have led to a decrease in in-channel wood stocks, and to a concomitant decrease in the natural sources of dead wood for water bodies, which has eventually resulted in a substantial loss of ecological and hydromorphological functions (Gippel *et al.*, 1996).

To reduce the potential risks for human populations on one side, and maintain the beneficial hydromorphological and ecological role of LW on the other side, it is necessary to develop and implement integrated approaches to wood management along the entire river continuum (Wohl *et al.*, 2005). Within this context, Piégay and Landon (1997) recommended to identify different sectors along the river channel and to tailor the management measures to the type of river sector. Thus, the removal of wood pieces should be carried out only in particularly vulnerable sectors, such as upstream of bridges or weirs, in order to reduce the risk of damage to human populations and infrastructures, while in the other sectors in-channel LW should be preserved and natural riparian vegetation restored to increase the natural recruitment of in-channel LW pieces (Kauffman *et al.*, 1997). There, the largest and most stable wood pieces would trap the smaller and highly mobile pieces, thus reducing the load of transported wood. Thus, the effects of LW on hydrological processes would be maintained, which would lead to a more efficient and sustainable flood risk management strategy (Piégay & Landon, 1997). An integrated approach to river management at the catchment scale, such as the one described above, would also result in increased frequency of LW structures along the river network. Within this context, projects that aim to restore biotic diversity in degraded channel reaches would have more options for effective measures and an increased chance of success in comparison to isolated restoration projects, as the in-channel LW would also serve as potential sources of biotic colonization for the newly formed habitat patches.

## 5.5 Conclusions

River ecosystems are subjected worldwide to a variety of human-induced pressures, such as channelization, nutrient enrichment, land-use pressure and introduction of invasive species, which together lead to substantial physical and biotic homogenization of these ecosystems (Olden *et al.*, 2006; Donohue *et al.*, 2009; McGoff *et al.*, 2013). This thesis has shown that in near-natural lowland rivers large wood not only represents a hotspot of invertebrate diversity itself, but additionally it triggers a higher diversity of habitats, trophic resources, and thus of biota in the surrounding river-channel areas. This elevated physical and biological complexity is likely to lead to increased temporal stability of the aquatic communities, and to higher ecosystem resilience during disturbance events. Thus, in-channel large wood should remain in river channels wherever possible, and the addition of even simple LW structures, such as single wood logs, into degraded systems has the potential to substantially enhance ecosystem functions and health.

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# Appendix

**Table S1** Complete list of taxa.

| Group | Family | Taxon |
|---|---|---|
| Turbellaria | Dendrocoelidae | *Dendrocoelum lacteum* |
| | Dugesiidae | *Dugesia* sp. |
| Oligochaeta | | Oligochaeta gen. sp. |
| Hirudinea | Erpobdellidae | *Erpobdella* sp. |
| | Glossiphoniidae | *Glossiphonia complanata* |
| | Glossiphoniidae | *Glossiphonia concolor* |
| Crustacea | Asellidae | *Asellus aquaticus* |
| | Corophiidae | *Corophium curvispinum* |
| | Gammaridae | Gammaridae Gen. sp. |
| | Gammaridae | *Gammarus roeselii* |
| Ephemeroptera | Baetidae | *Baetis* sp. |
| | Caenidae | *Brachycercus harrisella* |
| | Ephemeridae | *Ephemera danica* |
| | Heptageniidae | *Heptagenia flava* |
| | Heptageniidae | *Heptagenia longicauda* |
| | Heptageniidae | *Heptagenia sulphurea* |
| | Leptophlebiidae | *Paraleptophlebia submarginata* |
| Plecoptera | Chloroperlidae | *Isoptena serricornis* |
| | Leuctridae | *Leuctra* sp. |
| | Nemouridae | *Nemoura avicularis* |
| | Nemouridae | *Nemoura cinerea* |
| | Perlodidae | *Perlodes dispar* |
| | Taeniopterygidae | *Taeniopteryx nebulosa* |
| Odonata | Calopterygidae | *Calopteryx* sp. |
| | Gomphidae | *Gomphus* sp. |
| | Gomphidae | *Ophiogomphus cecilia* |
| Heteroptera | Aphelocheiridae | *Aphelocheirus aestivalis* |
| | Corixidae | *Micronecta* sp. |
| Planipennia | Sisyridae | *Sisyra fuscata* |
| Diptera | Athericidae | *Atherix ibis* |
| | Athericidae | *Atrichops crassipes* |
| | Athericidae | *Ibisia marginata* |
| | Ceratopogonidae | Ceratopogoninae gen. sp. |
| | Chironomidae | Chironominae gen. sp. |
| | Chironomidae | Orthocladiinae gen. sp. |
| | Chironomidae | Tanypodinae gen. sp. |
| | Culicidae | Culicidae gen. sp. |
| | Empididae | *Chelifera* sp. |
| | Empididae | *Hemerodromia* sp. |

**Table S1 (cont.)**

| Group | Family | Taxon |
|---|---|---|
| Diptera | Limoniidae | Limoniidae gen. sp. |
| | Muscidae | Muscidae gen. sp. |
| | Pediciidae | *Dicranota* sp. |
| | Psychodidae | Psychodidae gen. sp. |
| | Ptychopteridae | *Ptychoptera* sp. |
| | Simuliidae | Simuliidae gen. sp. |
| | Tabanidae | Tabanidae gen. sp. |
| | Tipulidae | Tipulidae gen. sp. |
| Trichoptera | Brachycentridae | *Brachycentrus* sp. |
| | Hydropsychidae | *Hydropsyche guttata* |
| | Hydropsychidae | *Hydropsyche pellucidula* |
| | Hydropsychidae | *Hydropsyche siltalai* |
| | Hydroptilidae | Hydroptilidae gen. sp. |
| | Lepidostomatidae | *Lepidostoma basale* |
| | Leptoceridae | Leptoceridae gen. sp. |
| | Limnephilidae | Limnephilidae gen. sp. |
| | Polycentropodidae | *Holocentropus* sp. |
| | Polycentropodidae | *Plectrocnemia* sp. |
| | Polycentropodidae | *Polycentropus* sp. |
| | Psychomyiidae | *Lype* sp. |
| | Psychomyiidae | *Psychomyia pusilla* |
| Coleoptera | Elmidae | *Elmis* sp. Ad. |
| | Elmidae | *Elmis* sp. Lv. |
| | Elmidae | *Limnius* sp. Ad. |
| | Elmidae | *Limnius* sp. Lv. |
| | Elmidae | *Macronychus quadrituberculatus* Ad. |
| | Elmidae | *Macronychus quadrituberculatus* Lv. |
| | Elmidae | *Oulimnius* sp. Lv. |
| | Elmidae | *Riolus* sp. Ad. |
| | Elmidae | *Riolus* sp. Lv. |
| | Gyrinidae | *Orectochilus* sp. Lv. |
| | Hydraenidae | Hydraenidae gen. sp. |
| Lepidoptera | Pyralidae | *Acentria ephemerella* |
| | Pyralidae | *Nymphula stagnata* |
| Hydrachnidia | | Hydracarina gen. sp. |
| Gastropoda | Bithyniidae | *Bithynia tentaculata* |
| | Hydrobiidae | *Potamopyrgus antipodarum* |
| | Planorbidae | *Ancylus fluviatilis* |
| Bivalvia | Sphaeriidae | *Pisidium* sp. |
| | Sphaeriidae | *Sphaerium* sp. |
| | Unionidae | *Anodonta anatina* |
| | Unionidae | *Unio* sp. |

**Table S2** Percent contributions of the trophic resources to the diet of the studied taxa (median ± 75% credible interval), as resulting from the mixing models applied to the stable isotope data of each taxon within each mesohabitat. SesM-FilA= seston inferred from Unionids (see text for explanation) and filamentous algae, PeriW-Bry= periphyton on wood and bryophytes, Gr-L= grass and leaves, TOM=transported organic matter, Det= detritus, PeriM= periphyton on the shells of unionid mussels. Lv.=larvae.

| | **SesM-FilA** | **PeriW-Bry** | **Gr-L** | **TOM** | **Detritus** | **Wood** | **PerM** |
|---|---|---|---|---|---|---|---|
| **Non-wood site** | | | | | | | |
| *Anodonta anatina* | 55 (50-60) | 19 (12-26) | 5 (3-7) | 6 (3-11) | 3 (1-5) | 3 (1-6) | 4 (2-7) |
| *Aphelocheirus aestivalis* Lv. | 61 (56-65) | 5 (3-8) | 20 (16-25) | 2 (1-4) | 2 (1-4) | 4 (2-7) | 1 (1-2) |
| *Bithynia tentaculata* | 40 (32-47) | 18 (11-25) | 12 (8-16) | 8 (4-14) | 5 (2-9) | 7 (3-13) | 3 (1-6) |
| *Caenis* sp. | 55 (50-60) | 14 (9-20) | 8 (5-11) | 6 (3-10) | 3 (1-7) | 5 (2-9) | 3 (1-5) |
| Chironomidae | 73 (69-77) | 8 (5-12) | 5 (3-7) | 3 (1-6) | 2 (1-4) | 3 (1-5) | 2 (1-4) |
| *Dreissena polymorpha* | 73 (69-77) | 7 (4-11) | 6 (4-9) | 3 (1-5) | 2 (1-4) | 3 (1-6) | 2 (1-3) |
| *Ephemera danica* | 58 (53-64) | 13 (8-19) | 7 (4-10) | 5 (2-10) | 3 (1-6) | 4 (2-8) | 3 (1-5) |
| *Glossiphonia complanata* | 53 (49-58) | 9 (5-13) | 17 (13-22) | 4 (2-7) | 3 (1-6) | 6 (2-11) | 2 (1-3) |
| Gomphidae | 66 (61-70) | 8 (5-12) | 9 (5-13) | 3 (1-6) | 3 (1-5) | 4 (2-7) | 2 (1-3) |
| *Hydropsyche* sp. | 71 (68-74) | 8 (6-11) | 6 (4-8) | 4 (2-6) | 1 (1-2) | 1 (1-3) | 1 (0-2) |
| *Nemoura* sp. | 57 (52-62) | 15 (10-22) | 6 (4-8) | 6 (3-11) | 3 (1-6) | 4 (2-7) | 3 (1-6) |
| Oligochaeta | 38 (29-46) | 37 (28-46) | 4 (2-6) | 6 (3-12) | 2 (1-5) | 3 (1-5) | 4 (2-7) |
| *Orectochilus villosus* | 76 (72-80) | 6 (3-9) | 6 (3-8) | 2 (1-5) | 2 (1-4) | 2 (1-5) | 1 (1-3) |
| *Platycnemis* sp. | 59 (54-63) | 10 (6-14) | 11 (8-15) | 4 (2-7) | 3 (1-6) | 5 (2-9) | 2 (1-4) |
| Polycentropodidae | 72 (68-77) | 7 (4-11) | 6 (4-9) | 3 (1-6) | 2 (1-4) | 3 (1-6) | 2 (1-3) |
| *Potamopyrgus antipodarum* | 26 (20-32) | 34 (25-42) | 6 (4-9) | 12 (5-20) | 4 (2-7) | 5 (2-9) | 7 (3-12) |
| Sphaeriidae | 70 (66-74) | 8 (5-12) | 6 (4-9) | 3 (1-6) | 2 (1-5) | 3 (1-6) | 2 (1-3) |
| Tabanidae | 69 (64-74) | 7 (4-10) | 9 (6-13) | 3 (1-5) | 2 (1-5) | 3 (1-7) | 1 (1-3) |
| *Theodoxus fluviatilis* | 7 (3-11) | 33 (25-41) | 6 (4-10) | 12 (6-19) | 6 (3-11) | 5 (2-9) | 25 (19-31) |
| **Wood site - sediment** | | | | | | | |
| *Aphelocheirus aestivalis* | 57 (51-62) | 6 (4-10) | 23 (17-28) | 3 (1-6) | 3 (1-5) | 4 (2-8) | - |
| *Baetis* sp. | 41 (37-46) | 11 (7-15) | 27 (21-32) | 6 (3-10) | 4 (2-8) | 7 (3-12) | - |
| *Bithynia tentaculata* | 51 (46-56) | 11 (7-16) | 19 (14-24) | 6 (3-10) | 4 (2-7) | 5 (2-9) | - |
| *Caenis* sp. | 48 (43-53) | 22 (16-28) | 9 (6-13) | 7 (3-13) | 5 (2-10) | 3 (1-5) | - |
| Chironomidae | 48 (43-53) | 19 (13-24) | 12 (8-17) | 7 (3-13) | 5 (2-10) | 4 (2-7) | - |
| *Dreissena polymorpha* | 72 (67-76) | 8 (5-12) | 8 (5-11) | 3 (1-6) | 3 (1-5) | 2 (1-4) | - |
| *Ephemera danica* | 58 (52-64) | 22 (15-28) | 5 (3-8) | 5 (2-9) | 4 (2-7) | 2 (1-3) | - |
| Gomphidae | 60 (55-65) | 10 (6-14) | 14 (9-18) | 5 (2-8) | 3 (2-6) | 4 (2-7) | - |
| *Hydropsyche* sp. | 76 (72-79) | 11 (8-14) | 6 (5-9) | 4 (3-7) | 3 (2-5) | 2 (1-3) | - |
| Oligochaeta | 36 (30-42) | 48 (42-55) | 4 (2-6) | 4 (2-7) | 3 (1-6) | 1 (1-3) | - |
| *Orectochilus villosus* | 74 (69-78) | 6 (4-10) | 9 (5-13) | 3 (1-5) | 2 (1-4) | 2 (1-4) | - |
| Polycentropodidae | 70 (65-75) | 9 (6-14) | 7 (5-11) | 4 (2-7) | 3 (1-5) | 2 (1-4) | - |
| Sphaeriidae | 68 (63-73) | 11 (7-15) | 7 (5-11) | 4 (2-8) | 3 (1-6) | 2 (1-4) | - |
| Tabanidae | 62 (57-67) | 14 (10-20) | 8 (5-12) | 5 (2-9) | 4 (2-7) | 2 (1-4) | - |

## Table S2 (cont.)

| | SesM-FilA | PeriW-Bry | Gr-L | TOM | Detritus | Wood | PerM |
|---|---|---|---|---|---|---|---|
| **Wood site - wood surface** | | | | | | | |
| *Aphelocheirus aestivalis* Lv | 57 (51-63) | 7 (4-10) | 21 (15-28) | 3 (2-6) | 3 (1-5) | 4 (2-8) | - |
| *Baetis* sp. | 41 (36-46) | 17 (11-24) | 19 (12-26) | 8 (3-13) | 5 (2-10) | 5 (2-9) | - |
| *Caenis* sp. | 48 (44-55) | 22 (15-27) | 9 (6-13) | 7 (3-13) | 5 (2-9) | 3 (1-5) | - |
| Chironomidae | 57 (49-66) | 18 (12-26) | 7 (4-11) | 5 (2-10) | 4 (2-7) | 2 (1-4) | - |
| *Ephemera danica* | 50 (44-56) | 31 (24-38) | 5 (3-7) | 5 (2-9) | 4 (2-8) | 2 (1-3) | - |
| *Hydropsyche* sp. | 74 (70-78) | 13 (9-18) | 6 (4-8) | 4 (3-6) | 3 (2-5) | 2 (1-3) | - |
| *Orectochilus villosus* | 72 (67-76) | 9 (6-13) | 7 (4-10) | 3 (2-7) | 3 (1-5) | 2 (1-4) | - |
| Polycentropodidae | 72 (67-77) | 9 (6-14) | 6 (4-9) | 4 (2-7) | 3 (1-5) | 2 (1-4) | - |
| Sphaeriidae | 70 (66-75) | 8 (5-12) | 9 (6-13) | 3 (2-7) | 3 (1-5) | 2 (1-5) | - |