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Age matters: substrate-specific colonization patterns of benthic invertebrates on installed large wood

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Abstract Large wood (LW) is an indispensable element in riverine ecosystems, especially in lower river parts. The presence of LW significantly shapes local hydraulics, morphology, the nutrient budget; promotes overall river dynamics; and additionally presents a unique habitat for numerous benthic invertebrate species. Therefore, LW is recognized as valuable asset for river restoration measures. Experiences from previous projects show that ecological responses on LW implementation measures vary greatly. That complicates comparisons and estimations on the success of planned measures. Methodological inconsistencies and thus reduced transferability of the results is one major issue. Additionally, wood quality aspects are suspected to be important factors affecting benthic invertebrate colonization patterns. The focus of this study is therefore to consistently assess the ecological significance of installed LW and concrete samples of similar size and shape in terms of benthic invertebrate colonization and to further test, if the condition of wood affects the benthic invertebrate colonization. Our results show that (1) installed LW serves as an abundantly and heterogeneously colonized habitat, (2) the state of decay of LW pieces significantly affects benthic invertebrate colonization in terms of density and diversity and (3) even rare or threatened taxa closely associated to LW were abundantly present on the installed logs, emphasizing the suitability of the chosen approach.

Keywords Macroinvertebrates · Xylal · State of decay · River gradient · LW · Wood condition

Introduction

Large wood (LW) is a key component of natural river ecosystems. Previous studies have already stressed the beneficial effects of instream wood structures on local river hydraulics (e.g., Shields et al. 2001; Mutz 2003; Manners et al. 2007), hydromorphology (e.g., Gurnell et al. 1995, Kail et al. 2007, Blanckaert et al. 2014), nutrient balance (e.g., Bilby and Bisson 1998; Gurnell et al. 2005; Flores et al. 2011) and habitat diversity (e.g., Dudley and Anderson 1982; Hering and Reich 1997). Submerged LW provides essential habitats which are existential for many xylobiont species (Anderson et al. 1978; Hoffmann and Hering 2000) and are of increasing importance along the river course (Dossi et al. 2018). LW further offers vital aquatic–

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terrestrial interface areas and oviposition sites, significantly promoting the reproductive success of merolimnic invertebrate species (Dudley and Anderson 1982; Sweeney 1993; Hoffmann and Hering 2000). Due to the wide variety of beneficial aspects, LW is known to generally promote the density and diversity of fish and aquatic invertebrate species (e.g., Dudley and Anderson 1982; Copp 1992; Hering and Reich 1997; Hoffmann and Hering 2000; Pilotto et al. 2014, 2016) and therefore presents a valuable and cost-effective asset for river restoration measures, especially given the large amount of morphologically degraded river sections and comparably low costs to conventional measures (Kail and Hering 2005; Kail et al. 2007). Rough estimates assume that even in densely populated areas such as Central Europe, approximately one-third of the degraded river sections could be restored by reintroducing LW structures (Kail and Hering 2005).

A profound understanding of LW and ecosystem interactions is a prerequisite for efficient implementations in river management practices. Even though LW and its function in river ecosystems have been extensively investigated, knowledge gaps and therefore implementation shortcomings still persist. Kail et al. (2007) evaluated 50 restoration projects in Germany and Austria involving LW placement and found that only approximately 58% were successful. The authors concluded that the key to success lied in the consideration of site-specific characteristics. Hence, profound knowledge on river type specific wood characteristics is one important criterion to promote the success of measures. One challenge, hard to come by, is the lack of knowledge of the pristine state of LW and related ecological aspects in many European streams due to the long history of active wood removal (Hering and Reich 1997; Hering et al. 2000). Additional studies in different areas with remaining intact riparian vegetation and at least near-natural LW dynamics are therefore of utter most importance to improve the understanding of LW and biota interactions.

Benke and Wallace (2003) called attention to additional difficulties regarding comparability and transferability of results from different studies. Fundamental information such as reported invertebrate densities span wide apart from several hundred (e.g., O'Connor 1992; Rabeni and Hoel 2000) to many (ten-) thousands of individuals per square meter (e.g., Smith and Smock 1992; Benke 1998). Besides natural fluctuations of densities due to riverine characteristics on local up to regional scales or methodological inconsistencies, especially regarding the quantification of LW pieces and related individual densities, variations due to differing wood quality aspects, such as hardness, species and condition, were discussed as potentially important factors (Benke and Wallace 2003). That suggests a type specific colonization of wood substrate, especially considering general substrate selection processes of invertebrates substantially determining species richness, composition and density in freshwater ecosystems (Minshall 1984). Wood quality aspects were focused by only a limited number of studies, but most results indicate that the type and quality of instream LW affect invertebrate colonization patterns (e.g., Anderson et al. 1978; Kaufman and King 1987; Magoulick 1998; McKie and Cranston 1998; O'Connor 1991; Spänhoff et al. 2000).

The aim of this study is therefore (1) to consistently assess the general ecological value of LW structures of installed wood and concrete samples of comparable size and shape in terms of species richness and density, (2) to investigate colonization patterns based on the condition of the introduced LW pieces and (3) to test if the results are consistent within different river stretches along the longitudinal gradient of a medium-sized lowland river in Austria.

Materials and methods

Study sites

Four sites along the Lafnitz River have been investigated. The Lafnitz River is one of the last medium-sized meandering rivers in the Central Europe with near-natural flow-regime and morphodynamics, riparian vegetation and LW accumulations along large parts of its course. It is therefore well suited to study the importance of LW and its interactions with biota. The Lafnitz lies within the Danube catchment, located in the southeastern part of Austria (Fig. 1). The river course has an approximate length of 112 km and drains into the Raab River, in Hungary. The Lafnitz River has a catchment size of approximately 2000 km^2 at the border of Austria, making it the 13th largest river in Austria (BMLFUW 2002; Cejka et al. 2005). The spring is located in the federal state of

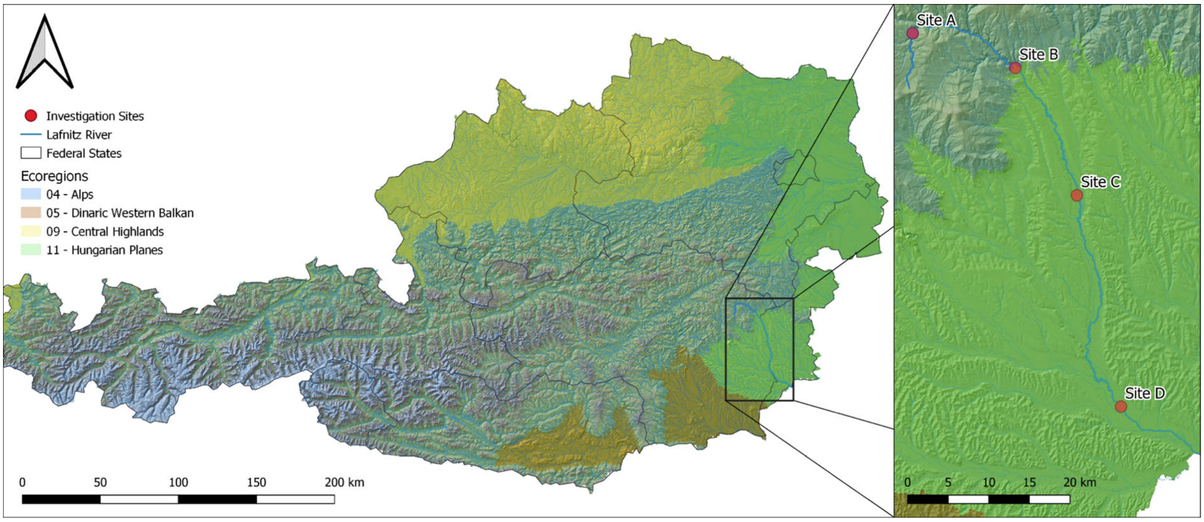


Fig. 1 Overview of the project area and location of the Lafnitz River in Austria (left) and location of the investigation sites along the river course (right); overlay: Ecoregions according to Illies (1978)

Styria and originates at an altitude of 940 m above sea level (m a.s.l.). Following Illies (1978), the first 36 river kilometers are situated in the ecoregion 4-Alps, whereas the following section lies in ecoregion 11-Hungarian Plains (Fig. 1). The mean annual discharge of the Lafnitz River spans from 2.6 m^3/s in the upper section (near Site A) to approximately 6.3 m^3/s in the lower section near the town Dobersdorf (near Site E).

The sampling sites were chosen to cover a variety of different river characteristics along the longitudinal gradient to (1) allow general statements on the potential ecological benefits of installed wood structures as well as to (2) assess possible variations in different river sections. At all four sites naturally deposited large wood accumulations were present to ensure a comparable colonization potential.

Samples have been taken at four sites along the river course (see Table 1), whereas the most upstream site is located at 648 m a.s.l. and the most downstream site at 244 m a.s.l. The sites were chosen based on significant changes of river characteristics such as slope, discharge (stream order according to Strahler (1957)), substrate composition and morphological characteristics. Figure 1 gives an overview of the site locations along the river course. Site-specific characteristics are shown in Table 1.

Abiotic characteristics at each site including mean flow velocity, mean water depth and dominant grain size at each site were assessed in March 2014 prior to the installation of the samples. Mean flow velocities and water depths were derived from averaged transect measurements. Grain size distribution were based on the choriotope assessment (Multi-Habitat-Sampling-Method (MHS), AQEM Consortium 2002).

Sample characteristics, sampling design and laboratory work

For this colonization experiment three different types of substrate, comparable in size, were installed at each sampling site: (1) concrete bars, (2) fresh logs and (3) rotten logs (Figs. 2, 3).

The concrete bars were used to mimic lithal substrates of comparable size and shape to the logs. The dimensions of each piece were 50 cm × 5 cm × 20 cm (length × width × height). In each concrete bar, a whole was drilled and a rope was attached to be fixed at nearby trees (see Figs. 4, 5).

All xylal substrate samples (fresh and rotten) originate from the Lafnitz River and were sampled in February 2014 near the village of Neustift, in the middle section of the river. To ensure comparability, only previously submerged logs with a diameter between 200 mm and 300 mm were used in this study. Each log was cut to a length of 630 mm and analogous to the concrete bars; a hole was drilled in each sample log and a rope was attached to fix the log

Table 1 Overview of site characteristics including altitude (meters above sea level), distance from spring (km), mean river slope (%), dominant grain size (cm), Strahler number (Strahler 1957), average water depth (m), average flow velocity (m/s) and average river width (m)

Site	Altitude (m asl)	Distance from Spring (km)	Slope (%)	Dominant grain size (cm)	Strahler Number	Average water depth (m)	Flow Velocity (m/s)	Average River width (m)
A	648	8.7	1.7	6.3–20	4	0.2	0.3	8
B	438	26.1	0.9	6.3–40	5	0.3	0.6	15
C	324	52.1	0.3	2–6.3	5	0.5	0.3	10–20
D	244	100.4	<0.1	2–6.3	6	0.6	0.35	20

Fig. 2 Picture of the Lafnitz River at site A (left) and site B (right)

Fig. 3 Picture of the Lafnitz River at site C (left) and site D (right)

at the chosen sites (see Fig. 4). All sampled logs were classified into the categories "rotten" and "fresh" on site (examples see Fig. 6). Wood classification was based on the summarized decay categories of Robinson and Beschta (1990) (class 1–3: fresh; class 4–5: rotten) and Grette (1985) (class 1–4 fresh; class 5–6:

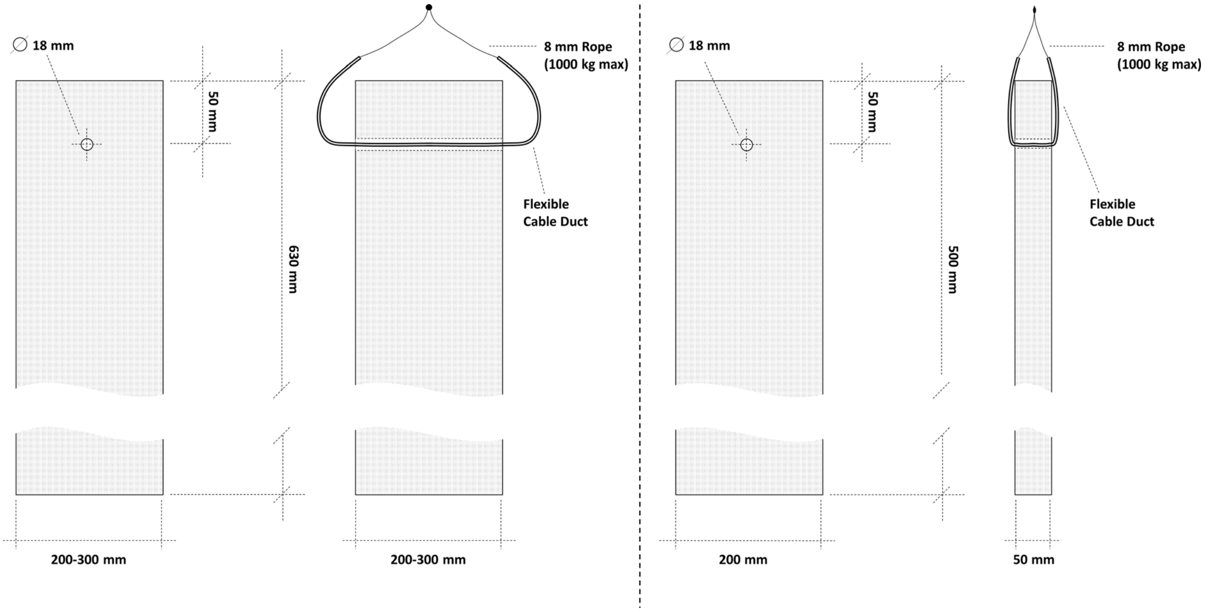


Fig. 4 Sample schematics and dimensions for fresh and rotten logs (left) and concrete samples (right)

Fig. 5 Example of one installed concrete bar at site A

rotten). Details on the classification characteristics of wood pieces are shown in Annex see Table 5, 6. Length, width and volume of each LW piece was measured, and the surface area was calculated using the formula of a simplified shape of a truncated cone:

$$S = r^2 * \pi + \pi * R^2 + \pi * h * (r + R)$$

where S = surface area, r = radius 1, R = radius 2, h = sample height.

The surface area of the sampled LW pieces varied between 0.16 m^2 and 0.32 m^2. The volume of each LW piece was measured in an overflow tank and varied between 2.8 dm^3 and 10.2 dm^3. In total, there were 24 wood samples, corresponding to a total surface area of approximately 5.2 m^2 (12 rotten logs: 2.5 m^2; 12 fresh logs: 2.7 m^2). All wood sample characteristics are summarized in Table 2. After classification and preparation of the samples, all wood samples were rinsed, cleaned and carefully examined

Fig. 6 Example of fresh (left) and rotten logs (right) installed at the Lafnitz River

for remaining organisms to ensure a comparable precolonization state of all samples. The logs were then stored in black plastic bags until installation.

The logs and concrete bars were installed in a similar manner at each site. At each of the four sites, three concrete bars and six logs (three fresh/three rotten) were installed in early March 2014. Three long guiding ropes (approximately 15–20 m) were tied to riparian trees, and three substrate samples (either logs or concrete bars) were subsequently bound to each guiding rope. The allocation of logs and concrete bars on the guiding ropes was randomized, and all samples were installed in comparable orientations, parallel to the flow. However, a slight displacement or motion of the samples was possible. The location and orientation of the guiding ropes was chosen to ensure comparable habitat characteristics for each sample within each site (e.g., flow velocity, surrounding substrate composition).

Details on the habitat parameters at each concrete bar or log are given in Table 2. All single logs and concrete bars were installed with a minimum distance of 2 m to each other to allow undisturbed sampling conditions at each log or concrete bar. To ensure comparable colonization potentials, all samples had contact with the river bottom.

Sampling was performed in spring 2014 and 2015. To ensure comparable exposition times, all logs and concrete bars were cleaned and carefully examined 6 weeks prior to each sampling run. All attached organisms were removed, and each log or concrete bar was subsequently reintroduced to the river. Benthic samples were taken on three different dates in April 2014, June 2014 and March 2015. All samples were taken within 1 day. Due to the long exposition time and the high morphodynamics at the Lafnitz River, not all samples were consistently available for analysis. Single logs or concrete bars which occasionally stranded or were entirely covered with sediments were excluded from subsequent analysis (Details see Table 2).

Sampling was performed with a standardized 500-µm mesh-size kick-net with a frame size of 25 × 25 cm (surface area per single sample: 0.0625 m^2) and a net length of 1.2 m. Prior to sampling, all LW pieces were carefully put into the kick-net to avoid organisms from drifting. Benthic invertebrates were then carefully brushed and washed from the LW piece into the kick net. All organisms were preserved with formaldehyde (4%) (Table 3).

The Screening-Taxa list (Ofenböck et al. 2010) was used as a basis for identification. In many cases Ephemeroptera, Plecoptera and Trichoptera taxa could be identified to a lower taxonomic level (genus/species), whereas Diptera taxa were mainly identified to family level. Oligochaeta were not identified further. All taxa were counted and weighed (wet weight). Specimens were then fixed in 70% ethanol and stored.

Table 2 Overview of the sample characteristics including sample ID, the site, volume (dm^3), surface (cm^2), the state (f-fresh, r-rotten, c-concrete), the flow velocity (mean flow velocity at exact sampling point in m/s), dominant substrate at exact sampling point and the availability (only fully submerged samples from each sampling date were considered for analysis) of samples at the each sampling date (1-23.04.14, 2-28.06.14, 3-18.03.15)

Sample ID	Site	Volume (dm^3)	Surface (cm^2)	State	Flow velocity (m/s)	Substrate	1	2	3
W01	A	4.8	2161	r	0.3	Psammal	+	+	+
W02	A	5.1	2131	r	0.3	Microlithal	+	+	+
W03	A	7.2	2416	r	0.1	Psammal	+	+	+
W04	A	3.9	1981	f	0.4	Psammal/Akal	+	+	+
W05	A	6.1	2462	f	0.2	Psammal	+	+	+
W06	A	10.2	3178	f	0.3	Psammal	+	+	+
C01	A	5	2700	c	0.7	Akal/Microlithal	+	+	+
C02	A	5	2700	c	0.1	Psammal	+	+	+
C03	A	5	2700	c	0.7	Akal/Microlithal	–	+	+
W07	B	4.5	2027	r	0.8	Microlithal	+	+	+
W08	B	4	1911	r	0.8	Microlithal	+	+	+
W09	B	3.9	1880	r	0.8	Microlithal	+	+	+
W10	B	5.2	2314	f	0.8	Akal/microlithal	+	+	+
W11	B	7	2594	f	0.4	Microlithal	+	+	+
W12	B	4.9	2123	f	0.7	Akal/microlithal	+	+	+
C04	B	5	2700	c	0.8	Akal/microlithal	+	+	+
C05	B	5	2700	c	0.7	Akal/microlithal	–	+	+
C06	B	5	2700	c	0.7	Akal/microlithal	+	+	+
W13	C	6	2350	r	0.2	Psammal	–	+	+
W14	C	5.9	2332	r	0.5	Akal/psammal	+	–	+
W15	C	4	1927	r	0.3	Psammal	+	+	+
W16	C	7.1	2600	f	0.2	Psammal	–	+	+
W17	C	2.8	1678	f	0.3	Psammal	+	+	+
W18	C	4.2	1952	f	0.2	Psammal	+	+	+
C07	C	5	2700	c	0.4	Akal	–	+	+
C08	C	5	2700	c	0.5	Akal/microlithal	+	–	+
C09	C	5	2700	c	0.5	Akal	+	–	+
W19	D	3.6	1811	r	0.6	Psammal/akal	+	+	+
W20	D	4	1898	r	0.6	Psammal/akal	+	+	+
W21	D	3	1629	r	0.6	Psammal/akal	+	+	+
W22	D	4.8	2129	f	0.6	Psammal/akal	+	+	+
W23	D	6.8	2559	f	0.6	Psammal/akal	+	+	+
W24	D	4.1	1944	f	0.6	Psammal/akal	+	+	+
C10	D	5	2700	c	0.6	Psammal/akal	+	+	–
C12	D	5	2700	c	0.6	Psammal/akal	+	+	+
C13	D	5	2700	c	0.6	Psammal/akal	+	+	+

Data analysis

Statistical analyses were performed with the Software R-Studio 1.1.456. The Levene's test was applied to test equality of variances between the substrate groups and the Shapiro–Wilk Test to test on normality of the data. All abundance and biomass data (from all substrates) were converted to densities (Ind/m^2).

Table 3 Overview of the total number of specimen, taxa and families observed at each site and substrate type

	A	B	C	D
No of specimen				
Concrete	3338	2578	796	1918
Fresh	2221	3270	3887	3562
Rotten	3154	5819	6703	4746
No of taxa				
Concrete	33	29	32	42
Fresh	36	36	34	48
Rotten	42	49	43	47
No of families				
Concrete	22	19	22	27
Fresh	27	24	23	32
Rotten	30	30	23	31

Abundances for cluster and NMDS analyses were log (n + 1) or presence/absence transformed. For cluster analysis "Bray–Curtis" distance measure and "Ward.D2" linkage method was applied. NMDS analysis (Kruskal, 1964) was performed with "Sørensen (Bray–Curtis)" distance measure.

The affinity of species or taxa to a particular substrate type was performed combining two different methods:

1. Identification of taxa exclusively present on one substrate type and
2. identification of taxa which were significantly more abundant on one substrate type based on the results of an "Indicator species Analysis (ISA). All taxa with an Indicator value (IV) > 25 (Dufrene and Legendre 1997) and a p value of ≤ 0.05 were considered as significantly overrepresented on the corresponding substrate type.

This two-level approach was chosen in order to consider that even though some taxa significantly benefit from the presence of wood are not necessarily limited to wood as a habitat. The sole information on exclusive occurrences would therefore be insufficient.

Results

In total ~ 43,000 benthic invertebrate specimen and 108 taxa from 52 families and 12 orders were collected (see Annex in Table 7). The most abundant orders were Diptera (~ 32%; mainly Chironomidae), Crustacea (~ 27%; only *Gammarus fossarum*) and Trichoptera (22%; mainly Limnephilidae). Ephemeroptera comprised a share of ~ 13% and Plecoptera of ~ 3%. Benthic invertebrate species richness gradually increased along the river course from 49 taxa at site A to 71 taxa at site D. Taxa richness per sample ranged from 4 to 27 taxa. Details on the number of specimens, taxa and families at each site and substrate type are summarized in Table 3.

Density and diversity differences between substrate types

Benthic invertebrate colonization showed significant differences between the substrate types (see Fig. 7). Abundance, biomass and species richness were significantly higher (Wilcoxon test: $\alpha = 0.01$) on wood samples (Ind/m^2: $\mu = 2436.9 \pm 241.3$; g/m^2: $\mu = 31.7 \pm 5.5$; No. of taxa: $\mu = 15.5 \pm 0.6$) compared to concrete samples (Ind/m^2: $\mu = 1102.2 \pm 139.0$; g/m^2: $\mu = 8.1 \pm 1.4$; No. of taxa: $\mu = 11.8 \pm 0.6$). Wood sample showed a generally wider variation, as shown by the higher standard errors. Further, significant differences between fresh (Ind/m^2: $\mu = 1723.9 \pm 219.8$; g/m^2: $\mu = 23.7 \pm 4.8$; No. of taxa: $\mu = 13.9 \pm 0.8$) and rotten wood samples (Ind/m^2: $\mu = 3194.5 \pm 401.6$; g/m^2: $\mu = 40.2 \pm 10$; No. of taxa: $\mu = 17.3 \pm 0.9$) were evident. Only biomass differences between fresh and rotten wood did not show significant results. Still, a consistent pattern with lowest benthic invertebrate density and diversity on concrete, followed by fresh wood and peak values on rotten wood, was clearly visible.

The most prominent density differences among the substrate types were found for *Gammarus fossarum* (concrete: $\mu = 102.2$ Ind/m^2; fresh: 648 Ind/m^2; rotten: 1086 Ind/m^2) (see Fig. 8: left). Diptera (mainly represented by Chironomidae taxa) showed comparable densities on concrete bars (487 Ind/m^2) and fresh logs (418 Ind/m^2) while being distinctly more abundant on rotten logs (1206 Ind/m^2). Lowest Trichoptera densities were recorded on concrete (167 Ind/m^2), followed by fresh (433 Ind/m^2) and highest on rotten

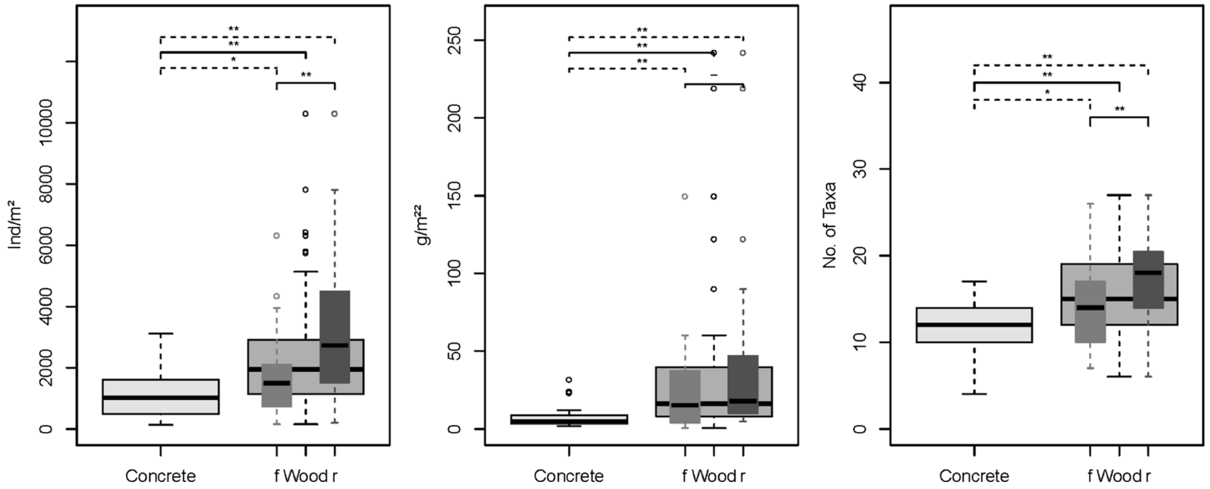


Fig. 7 Boxplot based on the number of individuals/m^2 (left), biomass/m^2(middle) as well as the number of taxa (right) recorded at each single log or concrete bar; f—fresh wood, r—rotten wood; *$p \le 0.05$, **$p \le 0.01$, -$p \ge 0.05$

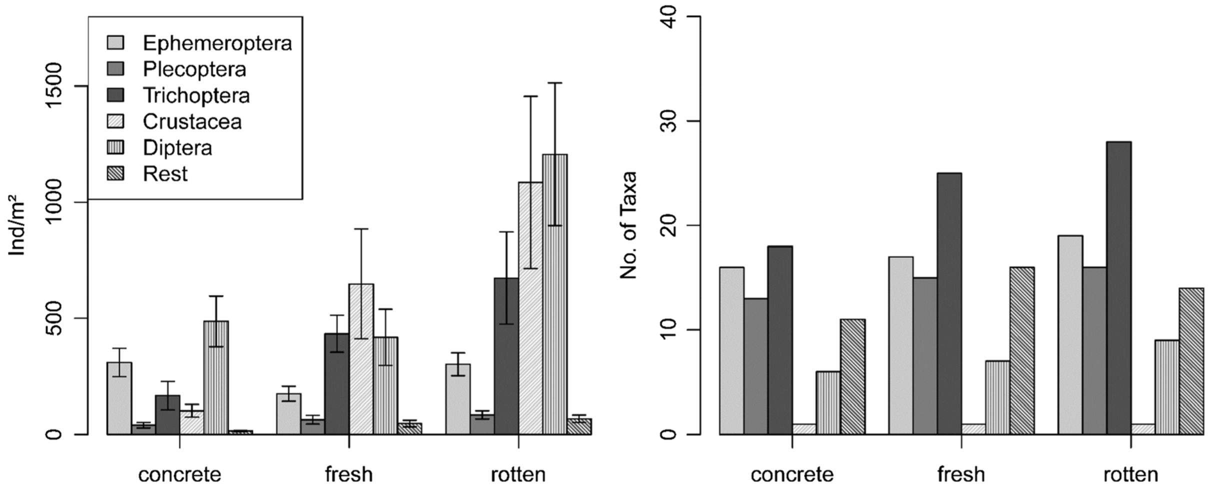


Fig. 8 Mean number of individuals of each order found on concrete bars (c), fresh (f) and rotten logs (r) with additional display of the standard error of the mean (left) and total number of taxa in each order (right)

logs (673 Ind/m^2). For Ephemeroptera and Plecoptera taxa no particular trend was visible. The number of taxa for all orders except for Crustacea (*G. fossarum*) showed a minor but consistent pattern as shown in Fig. 8: right. The number of taxa for Ephemeroptera, Plecoptera, Trichoptera and Diptera gradually increases from concrete bars to fresh and rotten logs (see Fig. 8: right).

Differences in species distribution between the substrate are well reflected in the number of substrate-specific taxa (see Table 4). Considering all samples, three taxa were exclusively present on concrete bars (e.g., Ephemeroptera: *Epeorus alpicola* and Trichoptera: *Glossosoma* sp.). In total, 39 taxa were only found on wood samples (e.g., Plecoptera: *Agnetina elegantula* and Coleoptera: *Macronychus quadrituberculatus*). A further differentiation between fresh and rotten wood samples showed nine taxa exclusively present on fresh (e.g., Trichoptera: *Rhyacophila tristis* and *Silo pallipes*) and 17 exclusively on rotten wood samples (e.g., Trichoptera *Hydropsyche bulbifera* and *Lype phaeopa*) (see Fig. 9: left). Results from each site and run separately reveal a comparable pattern to the overall analysis (see Fig. 9: middle). Lowest number of exclusive taxa were found on concrete ($\mu = 2.7 \pm 0.6$) followed by fresh-

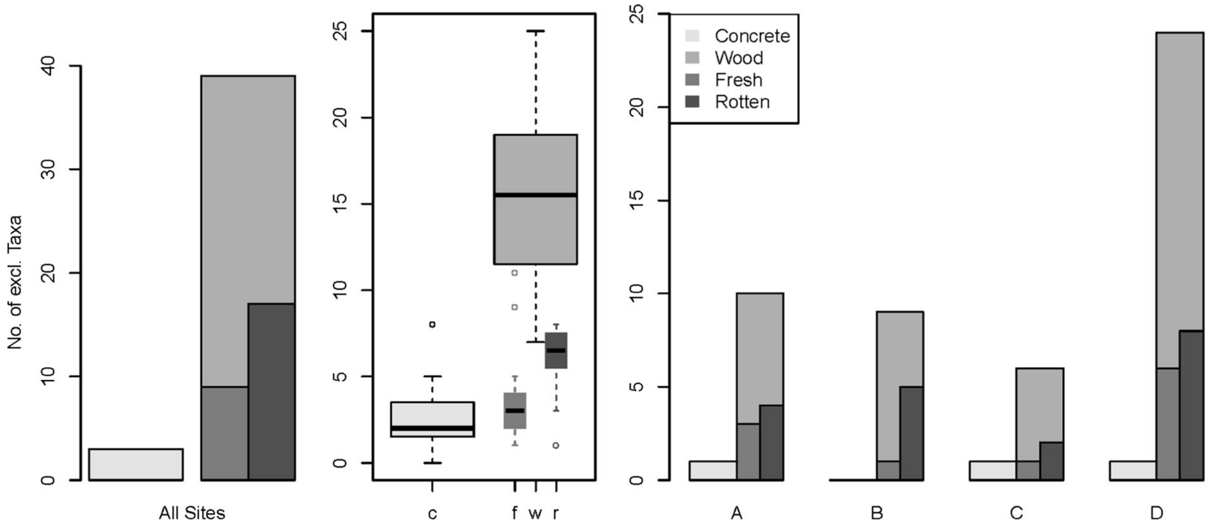


Fig. 9 Bar chart showing the number of exclusive taxa on each substrate type from all sites (Site A to Site C) (left); number of exclusive taxa on each substrate type for each single sampling run, c—concrete, w—wood, f—fresh wood, r—rotten wood (middle); number of exclusive taxa on each substrate type at each site (Site A to Site C) (right)

($\mu = 3.8 \pm 0.9$) and rotten wood samples ($\mu = 6 \pm 0.6$).

The results of the indicator species analysis are shown in Table 4. The analysis was performed based on different taxonomic resolutions (family, genus and species level), and results of all three taxonomic levels showed consistent results. Seven families were identified, mainly represented by one dominant taxon which was significantly more abundant on fresh and rotten wood, respectively (e.g., Trichoptera: Lepidostomatidae: *Lepidostoma basale*; Limnephilidae: *Halesus* sp., Rhyacophilidae: *Rhyacophila* s.str.sp.) and two families/genera significantly more abundant exclusively on rotten wood samples (Coleoptera: Hydraenidae: *Hydraena* sp.; Crustacea: Gammaridae: *Gammarus fossarum*). On genus/species level one additional taxon was found to be significantly more abundant on concrete samples (Plecoptera: Perlidae: *Perla* sp.) and one on fresh and rotten wood samples (Ephemeroptera: Heptageniidae: *Heptagenia longicauda*).

Community composition

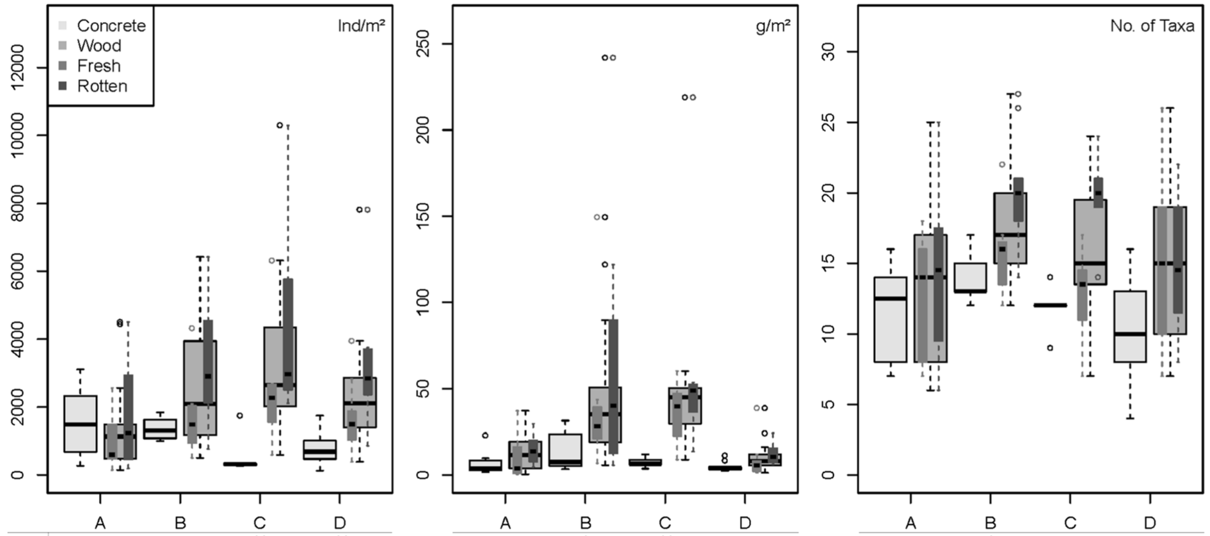
Community analysis shows a clear separation of samples per site (see Fig. 11) indicating that site-specific river characteristics are the predominant factors determining the benthic community. In addition, a distinct longitudinal pattern as well as allocations patterns based on the substrate type are visible. Wood samples (fresh and rotten) are mainly distributed in the middle of the NMDS plot, with rotten wood samples being generally allocated within closer proximity to each other compared to the other substrate types. Concrete samples are generally oriented to the left side of the plot within each site group and rotten wood samples to the right. Fresh wood samples are generally oriented in between concrete and rotten wood samples.

Comparable results are obtained by the cluster analysis (see Fig. 12) identifying four distinct groups. One group comprises all substrate types from the two upstream investigation sites (A and B), one the concrete samples from both lower investigation sites (C and D), one the fresh and rotten wood samples from site C and the last one both wood samples from site D. The slight separation of the rotten wood samples at site B in the second cluster are mainly caused by distinctly higher invertebrate densities on the samples compared to those at sites A and B. Following the allocation of samples within the groups from the NMDS analysis, the cluster analysis shows a closer allocation of the concrete samples from site C and D to the samples of the first two sites A and B.

Table 4 Overview of exclusive taxa (Type 1) and taxa significantly more abundant on concrete bars and fresh/rotten logs (Type 2)

Order	Family	Genus	Species	Preference	Type
Coleoptera	Corixidae	Corixidae	Gen. sp.	C	1
	Dytiscidae	Dytiscidae	Gen. sp.	R	1
	Elmidae	*Esolus*	sp.	F + R	1
	Elmidae	*Macronychus*	*quadrituberculatus*	F + R	1
	Gyrinidae	*Orectochilus*	*villosus*	F + R	1
	Hydraenidae	*Hydraena**	sp.*	R	2
Crustacea	Gammaridae*	*Gammarus**	*fossarum**	R	2
Diptera	Empididae	Empididae	Gen. sp.	R	1
	Psychodidae	Psychodidae	Gen. sp.	R	1
	Tipulidae	Tipulidae	Gen. sp.	R	1
Ephemeroptera	Ephemeridae	*Ephemera*	*danica*	R	1
	Heptageniidae	*Epeorus*	*alpicola*	C	1
	Heptageniidae	*Heptagenia*	*coerulans*	R	1
	Heptageniidae	*Heptagenia**	*longicauda**	F + R	2
	Leptophlebiidae	*Habroleptoides*	sp.	R	1
	Leptophlebiidae	*Habrophlebia**	*confusa**	R	2
Mollusca	Tateidae	*Potamopyrgus*	*antipodarum*	F	1
Odonata	Calopterygidae	*Calopteryx*	sp.	F	1
	Gomphidae	*Ophiogomphus*	*cecilia*	R	1
	Platycnemididae	*Platycnemis*	*pennipes*	F	1
Plecoptera	Chloroperlidae	*Chloroperla*	sp.	F	1
	Perlidae	*Agnetina*	*elegantula*	F + R	1
	Perlidae	*Perla**	sp.*	C	2
	Perlodidae*	*Isoperla**	sp*	F + R	2
	Taeniopterygidae	*Rhabdiopteryx*	*navicula*	R	1
Trichoptera	Glossosomatidae	*Glossosoma*	sp.	C	1
	Goeridae	*Goera*	*pilosa*	R	1
	Goeridae	*Silo*	*pallipes*	F	1
	Hydropsychidae	*Hydropsyche*	*bulbifera*	F	1
	Hydropsychidae	*Hydropsyche*	*dinarica*	F + R	1
	Hydropsychidae	*Hydropsyche*	*siltalai*	R	1
	Hydropsychidae*			F + R	2
	Hydroptilidae	*Hydroptila*	sp.	F	1
	Lepidostomatidae*	*Lepidostoma**	*basale**	F + R	2
	Leptoceridae	*Ceraclea*	*dissimilis*	R	1
	Leptoceridae	*Ylodes*	*simulans*	R	1
	Limnephilidae*	*Anabolia*	furcata	F + R	1
	Limnephilidae*	*Chaetopteryx*	sp.	F + R	1
	Limnephilidae*	*Halesus**	sp.*	F + R	2
	Limnephilidae*	*Melampophylax*	*melampus*	R	1
	Polycentropodidae	*Cyrnus*	*trimaculatus*	F	1
	Polycentropodidae	*Polycentropus*	*flavomaculatus*	R	1
	Psychomyiidae	*Lype*	*phaeopa*	R	1
	Psychomyiidae	*Psychomyia*	*pusilla*	F + R	1
	Rhyacophilidae	*Rhyacophila*	s.str.sp.*	F + R	2
	Rhyacophilidae	*Rhyacophila*	*tristis*	F	1

*Marks the taxonomic level of a significant overrepresentation ($p \leq 0.05$)



	A	B	C	D	A	B	C	D	A	B	C	D
c – w	-	-	**	**	-	*	**	-	-	*	-	-
c – f	-	-	**	*	-	-	**	-	-	-	-	-
c – r	-	*	**	**	*	*	**	**	-	**	**	-
r - f	-	*	-	-	-	-	-	-	-	*	**	-

Fig. 10 Overview of the number of individuals and biomass per m^2 as well as the number of taxa on each substrate type for each investigation site separately (**a**–**d**); significant differences between the substrate types are shown in the table below: c—concrete, w—wood, f—fresh wood, r—rotten wood; *$p \leq 0.05$, **$p \leq 0.01$, -$p \geq 0.05$

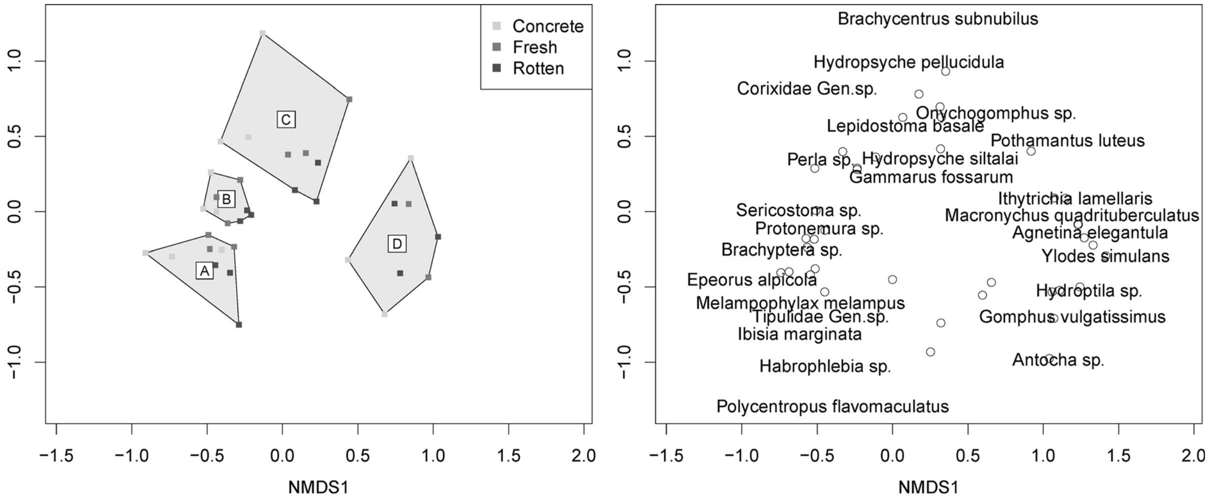


Fig. 11 Ordination graph of NMDS analysis based on the species composition and density from all concrete bars as well as fresh and rotten logs (sites A to D) (left) and display of species allocations in the ordination graph (right); species with best fit are shown by name; all other species are only indicated by solid circles to ensure readability; final stress for 2-dimensional solution = 0.1912

Site-specific analysis

A site-specific approach gives comparable results to the pooled data. Abundance, biomass and taxa richness at each site and on each substrate type consistently follow the patterns found in the overall dataset (see Fig. 10). Significant differences (Wilcoxon test: * = 0.05; ** = 0.01) are shown in Fig. 10. Lowest values were generally found on concrete samples, followed by fresh and rotten wood samples.

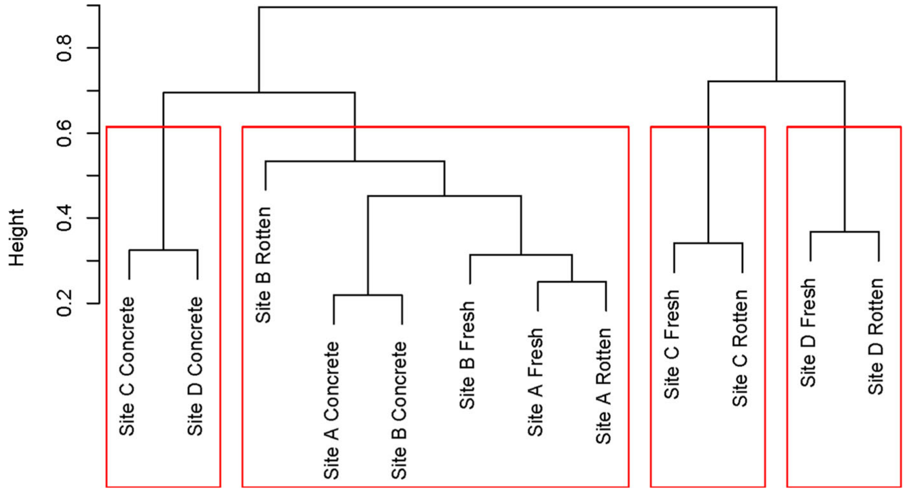


Fig. 12 Cluster dendrogram (distance measure: Bray–Curtis; group-linkage-method: Ward.D2) based on the species composition at each site (A-D)

One sole exception is evident at site A showing higher abundance on concrete than on wood samples. Highest abundance, biomass and taxa richness, regardless of the substrate types, were evident at the sites B and C. The most considerable colonization differences between the substrate types are evident at site C.

The number of exclusive taxa found at each site is illustrated in Fig. 9 (right). Lowest values were consistently observed on concrete samples with only one exclusive taxon at site A, C and D and none at site B. The number of exclusive wood taxa varies from site A to C between seven to ten taxa. At site D, a considerably higher amount of 24 exclusive wood taxa was evident. Fresh wood samples mark an increase from three taxa at site A to six at site D, while only one exclusive taxon was found at site B and C. On rotten wood samples, an increase of exclusive taxa from four at site A to eight at site D was found.

Discussion

Previous studies already stressed the general ecological importance of instream wood structures but most of them focused on naturally deposited logs or wood accumulations of varying sizes. Further, wood characteristics such as the state of decay received little attention. Detailed results varied greatly but nonetheless consistently showed higher benthic invertebrate densities and diversities on wood compared to adjacent lithal habitats (e.g., Benke et al. 1984; Smock et al. 1989, 1992; O'Connor 1991; Piegay and Gurnell 1997; Hoffmann and Hering 2000; Spänhoff et al. 2000; Grafahrend-Belau and Brunke 2005; Milner and Gloyne-Phillips 2005; Coe et al. 2009; Pilotto et al. 2016; Dossi et al. 2018).

The high variability of invertebrate density on wood is difficult to compare and interpret. Main reasons for these differences comprise the lack of a common experimental and quantification approach as well as general river types or regional differences (Benke and Wallace 2003). The aim of this study therefore was to assess the ecological significance of installed large wood compared to uniform concrete structures for benthic invertebrate communities, with particular attention on the wood condition. To overcome difficulties in the quantification of heterogenous instream LW pieces, we conducted our study with concrete, fresh and rotten LW of comparable size and shape.

Our results generally agree with the above-mentioned findings. A discrimination between lithal and xylal substrates showed distinctly higher benthic invertebrate density, biomass and diversity on xylal samples.

Besides similar patterns, the majority of the above-mentioned studies reported higher invertebrate density on xylal substrates, especially considering those from North America (see Benke and Wallace 2003). A potential underestimation due to an insufficient exposition time can be ruled out in our study. Samples were exposed for 6 weeks and previous studies showed that colonization on installed substrates peaks at approximately two to 6 weeks the latest (e.g., Nilsen and Larimore 1973; O'Connor 1992; Spänhoff et al. 2000). Comparisons with a previously conducted study at the Lafnitz River, which focused on natural instream wood (see Dossi et al. 2018) further support our results. Recorded invertebrate density and biomass were on a comparable level but on average higher in the present study on the installed logs (1655 Ind/m^2 vs. 2437 Ind/m^2; 19.2 g/m^2 vs. 29.6 g/m^2). Similar differences between installed and natural substrates have already been observed and discussed. While Spänhoff and Cleven (2010) generally referred to rapid initial colonization processes of newly introduced substrates resulting in above-average invertebrate densities in the first weeks, Spänhoff et al. (2000) added another aspect that was also observed in the Lafnitz River. Due to the longer residence time of naturally deposited, compared to installed logs, larger parts of their surface tend to be covered by sediments which are therefore not (or only partially) suitable for benthic invertebrate colonization. That affects surface density calculations and leads to a slight underestimation of benthic invertebrate abundance on naturally deposited logs.

Site characteristics and the natural longitudinal zonation of aquatic communities along the river course were identified as the dominant factor governing the overall composition of the benthic invertebrate community. However, overall species richness and density of invertebrates further depended on the wood condition as already indicated by previous studies (e.g., Magoulick 1998; Spänhoff et al. 2000). An additional distinction of our samples between different substrates revealed discrete benthic invertebrate density and diversity differences, with lowest values on concrete, followed by fresh and peak values on rotten wood. Only at site A, no clear differences were evident between the substrate types, which emphasizes the results of Dossi et al. (2018). Their study showed that the importance of LW as unique habitat structure significantly changes along the longitudinal gradient of a river. While invertebrate species showed no significant preference for a specific substrate type in upper river sections, an increasing diversification of the benthic communities among xylal and lithal substrates was evident along the river course.

Information on determining factors of specific benthic invertebrate colonization patterns on logs of different decay stages is still sparse, but the results of previous studies suggest that wood surface characteristics present a decisive aspect (e.g., Kaufman and King 1987; O'Connor 1991; Phillips 1993; Phillips and Kilambi 1994; Magoulick 1998; Spänhoff et al. 2000). LW further develops a productive epixylic biofilm which is an essential food source for grazing taxa (Golladay and Sinsabaugh 1991; Sinsabaugh et al. 1991), which might depend on log surface characteristics. Conditioned wood has a softer and more diverse, 3-dimensional, structure compared to most other habitats. It therefore provides a comparably large, smooth and more importantly complex habitat on a small spatial scale compared to rocks and fresh LW which is potentially beneficial for benthic invertebrate colonization (Kaufman and King 1987; O'Connor 1991; Magoulick 1998). The consistently higher densities and diversities on rotten logs compared to fresh logs and concrete bars support these assumptions. Besides overall quantities, consistent statements on taxa-specific colonization patterns are only possible to a limited extend. Even though most taxa were found in higher quantities on rotten wood, only a few taxa showed significant preferences. The most prominent differences were found for *G. fossarum* being significantly more abundant on rotten logs. *G. fossarum* being a shredder with preferences for low flow velocities might benefit most from the more complex surface structure of rotten wood. It provides flow protection as well as retention areas for organic matter on a small spatial scale. The softer surface might further facilitate the fragmentation and processing of the woody material itself as well as epixylic biofilm growth. Most taxa labeled as closely associated to wood such as *L. basale*, *M. quadrituberculatus*, *O. villosus* or *A. elegantula* (Anderson et al. 1978; Hoffmann and Hering 2000; Dossi et al. 2018) were found to be significantly more abundant on wood but did not show any preference for either fresh or rotten logs. Assumptions on possible differences due to varying biofilm developments on the tested substrate types could not be verified. Grazer taxa were equally dominant on the tested substrate types.

Our results further show that artificial LW introduction, even of comparably small logs as used in our study, comprise a valuable element in river restoration measures. All samples were consistently colonized by heterogenous invertebrate taxa throughout the sampling period and also threatened or rare species, closely associated to wood (e.g., *M. quadrituberculatus, H. longicauda*; *A. elegantula)*, were frequently found on the installed logs (Graf 1997; Bauernfeind and Humpesch 2001; Graf and Kovacs 2002; Jäch et al. 2005; Buffagni et al. 2016).

Our results emphasize that not only the presence of LW is of importance. The suitability as a habitat significantly depends on the state of decay. That relates to two important, interrelated aspects, specifically the residence time of logs in stream channels and the species of wood. While residence time and the state of decay are clearly connected, species of wood may be decisive as well. Besides possible colonization preferences for certain wood species, differing degradation rates (Spänhoff and Meyer 2004) and thus variations of the required residence time in rivers add another scale to the research topic. These findings are of particular importance considering management actions like the large-scale removal of instream LW, which deprived rivers from an essential structural element and habitat and significant changes of riparian vegetation communities (Hering et al. 2000; Hohensinner et al. 2013). Given these initial insights on the effect of wood quality on benthic invertebrate colonization patterns further research incorporating also the species of wood becomes of particular interest. Wood species-specific properties (e.g., firmness, structure, texture, stability, chemical composition) and subsequent varying degradation and habitat characteristics will be investigated in a follow-up research.

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Annex

See Tables 5, 6 and 7.

Table 5 Overview of decay categories; decay class: decay category according to Robinson and Beschta (1990)

Decay class	Bark	Twigs	Surface texture	Shape	Wood color	State
1	Intact	Present	Intact/firm	Round	Original	n
2	Intact	Absent	Intact/firm	Round	Original	n
3	Trace	Absent	Smooth to some surface abrasion	Round	Original to darkening	n
4	Absent	Absent	Abrasion to some holes and openings	Round to oval	Dark	d
5	Absent	Absent	Vesicular with many holes and openings	Irregular	Dark	d

n not decayed, *d* decayed

Table 6 Overview of decay categories; decay class: decay category according to Grette (1985)

Decay class	Bark	Limbs	Surface texture	Center	State
1	Intact	Present	Firm	Solid	n
2	Intact	Absent	Firm	Solid	n
3	Loose or absent	Absent	Firm	Solid	n
4	Absent	Absent	Slightly rottend	Solid	n
5	Absent	Absent	Extensively rottend	Solid	d
6	Absent	Absent	Completely rottend	Solid	d
7	Absent	Absent	Completely rottend	Rotted	d

N not decayed, *d* decayed

Table 7 Taxalist of all taxa found at all four sites; “c”—concrete bars, “f”—fresh logs, “r”—rotten logs

Order	Family	Taxon	c	f	r
Turbellaria	Turbellaria	Turbellaria Gen.sp.	*	*	*
Gastropoda	Hydrobiidae	*Potamopyrgus antipodarum* (J.E. Gray, 1843)	–	*	–
Oligochaeta	Oligochaeta	Oligochaeta Gen.sp.	*	*	*
Amphipoda	Corophiidae	*Corophium* sp.	–	*	–
	Gammaridae	*Gammarus fossarum* Koch, 1835	*	*	*
Hydrachnidia	Hydrachnidia	*Hydrachnidia* Gen.sp.	*	*	*
Ephemeroptera	Baetidae	*Baetis* sp.	*	*	*
	Caenidae	*Caenis* sp.	–	*	–
	Ephemerellidae	*Ephemerella ignita* (Poda, 1761)	*	*	*
		Ephemerella mucronata (Bengtsson, 1909)	*	*	*
		Ephemerella notata Eaton, 1887	*	*	*
		Ephemerella sp.	*	*	*
	Ephemeridae	*Ephemera danica* Müller, 1764	–	–	*
	Heptageniidae	*Ecdyonurus* sp.	*	*	*
		Electrogena sp.	–	*	–
		Epeorus alpicola (Eaton, 1871)	*	–	–
		Epeorus assimilis (Eaton, 1871)	*	*	*
		Heptagenia coerulans Rostock, 1877	–	–	*
		Heptagenia flava Rostock, 1877	*	*	*
		Heptagenia longicauda (Stephens, 1836)	*	*	*
		Heptagenia sp.	*	*	*
		Heptagenia sulphurea (Müller, 1776)	*	*	*
		Heptageniidae Gen.sp.	*	*	*
		Rhithrogena sp.	*	*	*
	Leptophlebiidae	*Habroleptoides* sp.	–	–	*
		Habroleptoides confusa Sartori & Jacob, 1986	–	–	*
		Habrophlebia sp.	–	*	*
		Paraleptophlebia sp.	–	*	*
	Oligoneuriidae	*Oligoneuriella rhenana* (Imhoff, 1852)	*	*	*
	Potamanthidae	*Pothamantus luteus* (Linnaeus, 1767)	*	*	–
Odonata	Calopterygidae	*Calopteryx* sp.	–	*	–
	Gomphidae	*Gomphus vulgatissimus* (Linnaeus, 1758)	*	*	–
		Onychogomphus sp.	*	*	–
		Ophiogomphus cecilia (Geoffroy In Fourcroy, 1785)	–	–	*
	Platycnemididae	*Platycnemis pennipes* (Pallas, 1771)	–	*	–
Plecoptera	Chloroperlidae	*Chloroperla* sp.	–	*	–
		Siphonoperla sp.	*	*	*
	Leuctridae	*Leuctra* sp.	*	*	*
	Nemouridae	*Amphinemura* sp.	*	*	*
		Nemoura/Nemurella sp.	*	*	*
		Protonemura sp.	*	*	*
	Perlidae	*Agnetina elegantula* (Klapalek, 1905)	–	*	*
		Dinocras sp.	*	*	*
		Perla sp.	*	*	*
		Perlidae Gen.sp.	–	*	*

Table 7 continued

Order	Family	Taxon	c	f	r
	Perlodidae	*Isoperla* sp.	*	*	*
		Perlodes sp.	*	*	*
	Taeniopterygidae	*Brachyptera risi* (Morton, 1896)	*	*	*
		Brachyptera seticornis (Klapalek, 1902)	*	*	*
		Brachyptera sp.	*	*	*
		Rhabdiopteryx navicula Theischinger, 1974	–	–	*
Heteroptera	Aphelocheiridae	*Aphelocheirus aestiv*alis (Fabricius, 1803)	*	–	*
	Corixidae	Corixidae Gen.sp.	*	–	–
Coleoptera	Dryopidae	*Pomatinus* sp.	–	–	*
	Dytiscidae	Dytiscidae Gen.sp.	–	–	*
	Elmidae	Elmidae Gen.sp.	–	–	*
		Elmis sp.	*	*	*
		Esolus sp.	–	*	*
		Limnius sp.	*	*	*
		Macronychus quadrituberculatus Müller, 1806	–	*	*
	Gyrinidae	*Orectochilus villosus* (Müller, 1776)	–	*	*
	Helophoridae	*Helophorus* sp.	–	*	*
	Hydraenidae	*Hydraena* sp.	*	*	*
Trichoptera	Brachycentridae	*Brachycentrus subnubilus* Curtis, 1834	*	*	*
	Glossosomatidae	*Glossosoma conformis* Neboiss, 1963	*	–	*
		Glossosoma sp.	*	–	–
	Goeridae	*Goera pilosa* (Fabricius, 1775)	–	–	*
		Goeridae sp.	*	*	–
		Silo pallipes (Fabricius, 1781)	*	*	–
	Hydropsychidae	*Cheumatopsyche lepida* (Pictet, 1834)	*	–	*
		Hydropsyche bulbifera Mclachlan, 1878	–	*	–
		Hydropsyche dinarica Marinkovic, 1979	–	*	*
		Hydropsyche instabilis (Curtis, 1834)	*	*	*
		Hydropsyche pellucidula (Curtis, 1834)	*	*	*
		Hydropsyche siltalai Döhler, 1963	–	*	*
		Hydropsyche sp.	*	*	*
	Hydroptilidae	*Hydroptila* sp.	–	*	–
		Ithytrichia lamellaris Eaton, 1873	*	*	*
	Lepidostomatidae	*Lepidostoma basale* (Kolenati, 1848)	*	*	*
	Leptoceridae	*Ceraclea dissimilis* (Stephens, 1836)	–	–	*
		Leptoceridae Gen.sp.	–	*	*
		Ylodes simulans (Tjeder, 1929)	–	–	*
	Limnephilidae	*Allogamus auricollis* (Pictet, 1834)	*	*	*
		Anabolia furcata Brauer, 1857	–	*	*
		Chaetopteryx fusca Brauer, 1857	–	*	*
		Chaetopteryx sp.	–	*	*
		Halesus sp.	*	*	*
		Limnephilidae Gen.sp.	*	*	*
		Melampophylax melampus (McLachlan, 1867)	–	–	*
		Potamophylax cingulatus (Stephens, 1837)	*	*	*

Table 7 continued

Order	Family	Taxon	c	f	r
		Potamophylax rotundipennis (Brauer, 1857)	*	*	*
	Odontoceridae	*Odontocerum albicorne* (Scopoli, 1763)	*	*	*
	Polycentropodidae	*Cyrnus trimaculatus* (Curtis, 1834)	–	*	–
	Polycetropodidae	*Polycentropus flavomaculatus* (Pictet, 1834)	–	–	*
	Psychomyiidae	*Lype phaeopa* (Stephens, 1936)	–	–	*
		Psychomyia pusilla (Fabricius, 1781)	–	*	*
	Rhyacophilidae	*Rhyacophila* s.str.sp.	*	*	*
		Rhyacophila tristis Pictet, 1834	–	*	–
	Sericostomatidae	*Sericostoma* sp.	*	*	*
Diptera	Athericidae	*Ibisia marginata* (Fabricius, 1781)	*	*	*
	Ceratopogonidae	Bezzia-Gruppe sp.	–	*	–
	Chironomidae	Chironomidae Gen.sp.	*	*	*
	Empididae	Empididae Gen.sp.	–	*	*
	Limoniidae	*Antocha sp.*	*	*	–
		Hexatoma sp.	*	*	*
	Limoniidae/ Pediciidae	Limoniidae Gen.sp.	–	*	*
	Pediciidae	*Dicranota* sp.	*	*	*
	Psychodidae	Psychodidae Gen.sp.	–	–	*
	Simuliidae	*Prosimulium* sp.	–	*	–
		Simulium sp.	*	*	*
	Tipulidae	Tipulidae Gen.sp.	–	–	*

*Present, – absent

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