

The key role of increased fine sediment loading in shaping macroinvertebrate communities in a Eurasian steppe river (Kharaa River, Mongolia) under multiple stressor

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Keywords: steppe rivers, community metrics, anthropogenic impact, river bank erosion, continental climate

Abstract

Aquatic communities across the Eurasian steppe belt are facing increased anthropogenic pressures that result from rapid population growth and catchment wide land-use changes. The particular variety, intensity, overlay and legacy of these impacts provide a unique setting to investigate ecological responses of multiple stressors. We studied macroinvertebrate communities along the Kharaa River in Mongolia, which displayed a distinct, downstream directed gradient of nutrient enrichment, disturbed bank morphology, reduced riparian vegetation, elevated turbidity and increased fine sediment intrusion into the hyporheic zone. Under these impacted conditions (TP 0.02 – 0.09 mg l⁻¹, TN 0.33 – 0.96 mg l⁻¹, FNU 0.62 – 5.43) population densities and biomass of macroinvertebrates were high (5293 ± 409 individuals m⁻² and 2631 ± 153 mg dry weight m⁻²) and stable. In contrast, macroinvertebrate community structure showed significant negative linear relationships (Pearson's *r*) for taxa richness (*r* = -0.79), Shannon Index of Diversity (*r* = -0.85), Evenness (*r* = -0.81), relative abundance of EPT individuals (*r* = -0.88) and relative biomass of hard substrate colonisers. At the same time, relative biomass of Chironomidae and Oligochaeta (*r* = 0.76) was positively correlated to mean turbidity values. Our results indicate a key impact of suspended fine sediment loads on macroinvertebrate community structure and to a lesser extent on habitat complexity at low rates of hyporheic fine sediment intrusion (mean values 0.9 - 1.6 g DW l⁻¹d⁻¹) in the Kharaa River. Hence, the implementation of effective regional management strategies aiming at to reduce erosion processes to ecologically tolerable levels deserves high priority.

Introduction

Historically, Mongolia's low population density and the traditional nomadic lifestyle have caused only minimal impacts on the country's pristine landscape. However, over the last few decades, rapid economic development has resulted in significant population growth and urbanisation, which has subsequently led to the widespread expansion of agriculture and large increases in livestock densities (Maasri and Gelhaus 2010, Priess et al. 2011, Demeusy 2012, Karthe et al. 2014, Karthe et al. 2015a, Malsy et al. 2016). However, the conversion from natural steppe grasslands and riparian river corridors into crop farmland has elevated the risk of top soil erosion, depending on the type of agricultural practice (Valentin et al. 2008, Priess et al. 2015). Larger herds, with their unrestricted access to rivers and riparian vegetation have caused extensive river bank and channel erosion (Hayford and Gelhaus 2010, Hartwig and Borchardt 2014). Both processes have a high potential to increase the fine sediment loads in adjacent streams and rivers, which has resulted in an impairment of aquatic biota and ecosystem functioning. The Kharaa River basin is the second most densely

populated catchment in Mongolia (9.4 inhabitants m⁻², Gerelchuluun et al. 2012), making it particularly vulnerable to overexploitation. Since the year 2000, livestock numbers in the Kharaa River basin have approximately doubled (Priess et al. 2015), with estimations of 1.5 million heads at present (Hofmann et al. 2016). Most grazing is concentrated in the riparian and floodplain zones (Hartwig et al. 2016) but has recently expanded to steeper slopes, which possess a higher erosion risk (Priess et al. 2015).

In catchments that are dominated by agriculture and livestock grazing, the aquatic community has to cope with multiple pressures that impact their habitat quality (Dudgeon 2010, Wagenhoff et al. 2012, Matthaei and Lange 2016), with the main stressors being nutrient enrichment, elevated fine sediments and water abstraction for irrigation (Matthaei et al. 2010). Although experimental approaches are able to disentangle the effects that are mediated by different stressors or their interactions (e.g. Townsend et al. 2008, Wagenhoff et al. 2012, Magbanua et al. 2013, Elbrecht et al. 2016), in natural systems, the variety of stressor impacts and their interactions often result in difficulties in their identification (Wagenhoff et al. 2011). Furthermore, as described by Murphy et al. (2015) fine sediment input is also a natural process which follows the longitudinal gradient along the river continuum (Vannote et al. 1980) and thus, assessing the effect of additional (anthropogenic) fine sediment pollution is challenging. In developed, industrialised countries, rivers are often channelized or structurally impaired for multiple usages (Gergel et al. 2002, Allan 2004), which can have the potential to mask or interact with other stressor impacts (Horsák et al. 2009). The conditions in the middle reaches of the Kharaa River basin, where the river channel typically follows its natural hydro-morphological dynamics, is characterised by a relatively low population density, large numbers of un-fenced multispecies herds, and extensive agricultural areas with low fertiliser application (Hofmann et al. 2016). A longitudinal gradient of human induced impacts has been identified in the region, thus making it an appropriate study site for investigating the potential effects of these activities on the resident aquatic macroinvertebrate fauna.

The increased fine sediment input from both point and non-point sources are known to have a multitude of consequences on macroinvertebrate communities (Jones et al. 2012). This fine sediment can directly impact on habitat quality and ultimately result in significant changes in the community composition (Larsen et al. 2009). Different case studies focusing on the impacts of fine sediment input caused by mining or construction activities have also reported a decrease in macroinvertebrate abundances and taxa richness (Cline et al. 1982, Wagener and LaPerriere 1985, Quinn et al. 1992a, Milner and Piorkowski 2004). Similar land-use mediated influences on macroinvertebrate communities have also been reported in New Zealand rivers by Quinn et al. (1997), where pasture dominated sites characterised by increased fine sediment loads were compared to native forested sites. The results of this study indicated increased total density while density of Ephemeroptera, Plecoptera and Trichoptera (EPT) and the quantitative macroinvertebrate community index was decreased, which has highlighted a loss in habitat diversity and/or quality for macroinvertebrates due to organic enrichment. Other studies aiming to identify the impacts of catchment urbanisation on macroinvertebrate assemblages have reported increased nutrients, electrical conductivity and turbidity, which in turn negatively impact on biotic indices such as taxa and EPT richness (Roy et al. 2003). Additionally, Burdon et al. (2013) reported a strong negative response in the relative EPT abundance to increased deposited inorganic fine sediment resulting from reduced habitat availability, where they derived a critical threshold of 13-20 % for surficial sediments. While, Shearer and Young (2011) observed that pastured sites had a decreased macroinvertebrate community index due to saprobic pollution, compared to sites in native forest areas. However, on the contrary, macroinvertebrate community metrics from headwater streams in the United States did not differ (except percentage of clingers) between low, medium and high sedimentation categories caused by historical timber harvest activities (Longing et al. 2010).

Therefore, the aims of the present study were to determine (i) whether macroinvertebrate structural and functional metrics would indicate stress on the resident macroinvertebrate communities living in the middle reaches of the Kharaa River; (ii) is there evidence that this pressure is a result of a single environmental stressor; (iii) is this related to fine sediment (organic and/or inorganic particles) migration and deposition into the upper sediment layers. As a consequence, important ecosystem functioning may have also been impacted and thus specific river management recommendations are urgently needed to address these issues in a holistic approach by incorporating them into a River Basin Management Plan within the framework of Integrated Water Resource Management (IWRM) in the Kharaa River basin in the near future (Karthé et al. 2015b).

Materials and Methods

Study site

The Kharaa River basin is situated in northern Mongolia, approximately 60 km north of the capital Ulaanbaatar (Fig. 1). The Kharaa River is a fourth order stream, which originates in the western Khentii Mountains (> 2,600 m a.s.l.) and flows in a north-westerly direction and into the Orkhon River (654 m a.s.l.). The size of the basin is approximately 15 000 km², and the length of the main river channel is 362 km. The annual average air temperature in the basin is -0.4 °C (Törnros and Menzel 2010). Between June 2009 and May 2010 the mean water temperature in the middle regions was 5.3 ± 1.1 °C (± SD; five sites; 30 min interval; EBI 85-A, Ebro Electronic GmbH & Co. KG, Ingolstadt, Germany). The long-term annual discharge (1990-2008) near to the confluence with the Orkhon River was approximately 12 m³ s⁻¹. As the river is usually frozen from November to March each year there is minimal discharge during these winter months, aquatic communities must endure harsh climatic conditions as a consequence (Avlyush et al. 2013, Karthe et al. 2015a). For a further detailed description of the catchment refer to Hofmann et al. (2011, 2015, 2016). The middle regions of the Kharaa River main channel are characterised by a longitudinal gradient in land-use intensity mainly caused by the geomorphological structure of the floodplain but also by the occurrence of larger settlements (Hartwig et al. 2016). In the upper part the valley is relatively narrow with small villages, sparse nomadic camps and moderately intense livestock grazing. Upstream of the town of Zuunkharaa, the river valley opens into a wider floodplain where agricultural activities increase including widespread grain and vegetable production around the townships. Dispersed nomadic families also reside here with increased herd sizes of mixed livestock species of mostly, sheep, goats, cattle and horses.

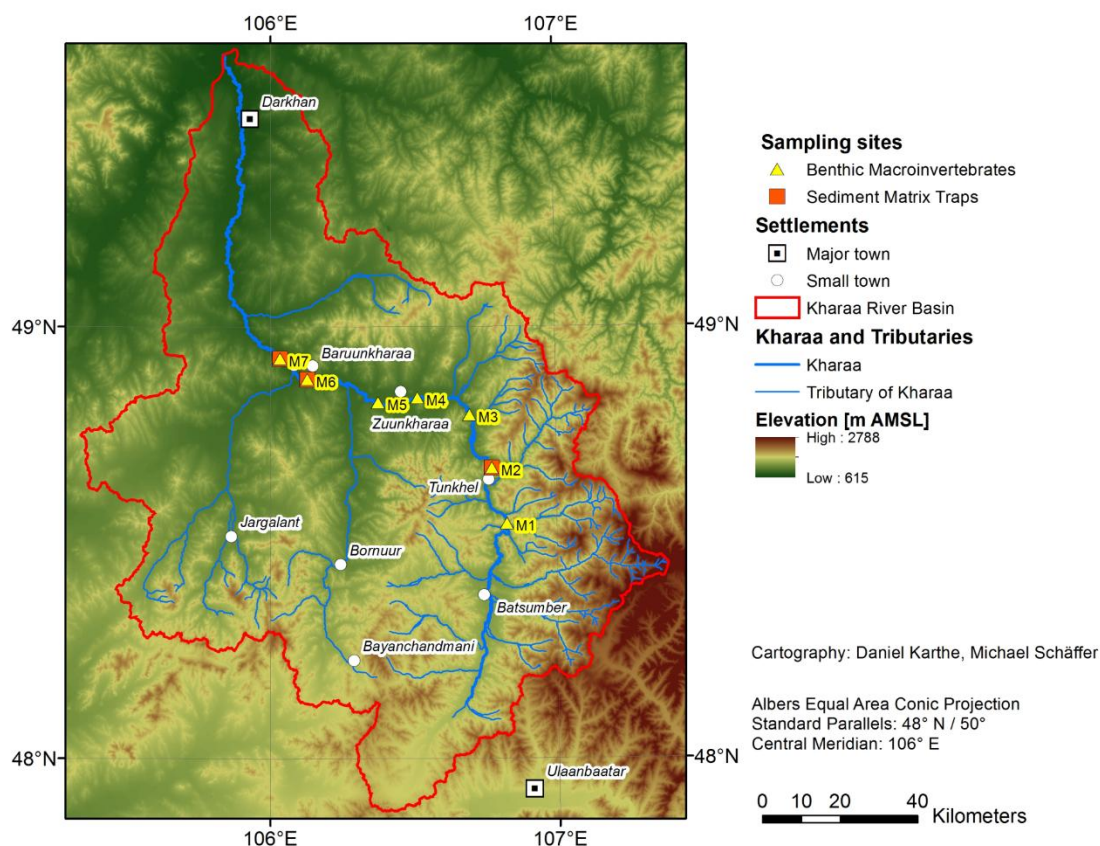


Fig. 1 Map of the Kharaa River basin. The location of the sampling sites for the macroinvertebrate communities (yellow triangles) and fine sediment infiltration rate (red squares) are displayed

Field sampling

Between September 2006 and May 2010 macroinvertebrate samples were collected from seven sites along the Kharaa River mid region (M1 - M7; Fig. 1). To cover annual variability, yearly spring and

autumn samples were taken, except site *M2* (only in 2009 and spring 2010), site *M5* (only in autumn 2006 and 2008 and spring 2007) and site *M7* (not in autumn 2007 and spring 2008). In order to increase ecological meaningfulness, further samples, were taken during the ice-free period between April and October in 2007, 2008 and 2009, at sites *M1*, *M3* and *M6*. A multi-habitat sampling approach (Haase et al. 2004) was used. Kick nets with an open frame of 25 x 25 cm (sample area 0.0625 m²) and 500 µm aperture were used. Benthic substrates were visually mapped and macroinvertebrate sampled, according to their spatial percental occurrence, in order to cover all existing instream microhabitats (20 sample units in total and 1.25 m² respectively). This quantitative sampling approach was assumed to best reflect the local macroinvertebrate community composition, while comparability was ensured. Sample units were combined, preserved with 96 % ethanol, and transported to the laboratory for analysis. In order to quantify the fine sediment load that has infiltrated the upper layer of the river substrate, sediment matrix traps were installed for the period May to September 2009 (summer) and between September 2009 and May 2010 (winter). Three sites were chosen, one in the upper middle region (Site *M2*), and two in the lower middle region (Site *M6* and *M7*, Fig. 1). The traps were composed of two cylindrical baskets (diameter 15 cm and 20 cm, height 22 cm) made of stainless steel mesh material (aperture 5 mm) after Sear (1993) and Seydell et al. (2009). The sediment matrix consisted of particles removed on-site, with a grain size between 25 µm and 63 µm, which did not have a detectable biofilm layer. Three replicates were installed per site in hydraulically comparable locations of riffle or glide topographies. Riffles or glides in gravel-bed rivers are naturally well connected with surface water flow, and therefore have been assumed to best reflect sediment dynamics while displaying the strongest effect size. To minimise the interactions between the traps while covering natural hydraulic variabilities, a side by side arrangement perpendicular to the river current was chosen. As both vertical and horizontal particle intrusion into the sediment matrix occurred at the sample locations, not only was the sediment migration via surface water column captured but also surrounding sediment coming from pore water. In this way the results include the net fine sediment intrusion over a specific time period from recently mobilised particles (vertical path) and historically, in interstices deposited particles (horizontal path) from floodplain or catchment erosional processes as well as in-stream processes. This methodology was selected, instead of continuous turbidity measurements, because it allowed for the time-integrating in situ estimation of the fine sediment net intrusion in the benthic zone, and also provides an indication of the local sediment history.

Additional environmental data was acquired to describe the characteristics of the sampling sites (Table 1). During the macroinvertebrate sampling, physical-chemical parameters including water temperature, pH, oxygen, electric conductivity (EC) and turbidity were measured on-site using MULTI[®] 350i and TURB[®] 430 IR (WTW, Weilheim, Germany). Due to the strong circadian dependency of the first three parameters and the methodologically induced differences in measuring times during the day, only EC and turbidity were included into the analyses. Mean turbidity values (\pm SE) were calculated for each sampling site depending on sampling effort (range: 3 \leq n \leq 8). For plausibility reasons, these measurements were related to the total environmental turbidity gradient of the study area. For this purpose continuous turbidity measurements (15 minutes interval) from two monitoring stations in the Kharaa River main channel were taken between June 7th and July 17th 2012 (41 day period), covering both low and high discharge periods due to the beginning of the summer rainfall period (Karthé et al. 2014, Suppl. Fig. 1b). The monitoring stations were located 45 km upstream from the sampling site *M1* (GPS: N 48.41322°; E 106.93521°) and close to sampling site *M7* (1.36 km upstream; GPS: N 48.91165°; E 106.075033°). Daily mean turbidity values were calculated based on continuous interval data and were plotted cumulatively. Median values were used as estimates for the total environmental turbidity gradient of the study reach. River bottom substrate composition was mapped during macroinvertebrate sampling procedures at each site. The 50 % cumulative percentile grain size value (D₅₀) and the grain uniformity coefficient D₆₀/D₁₀ (Vukovic and Soro 1992) were estimated by fitting Weibull distributions (implemented in R package 'stats', R Development Core Team) to the river bottom substrate data in order to characterise substrate composition and to identify colmation effects. Furthermore, hydro-morphological data from Berner (2007) was supplemented with personal observations in terms of mean river width, mean water depth, bank erosion intensity and bank vegetation coverage to estimate the overall bank erosion risk. River banks were mapped along a 2 km stretch per site. Mean bottom shear stress (τ) was estimated by using FST hemisphere data (Statzner and Müller 1989) from Berner (2007). Mean total nitrogen and mean total phosphorus were calculated from surface water samples for each site (2 \leq n \leq 7) to estimate the nutrient status (MoMo consortium, R. Ibsch unpublished data). To estimate the anthropogenic pressures, classified SPOT and Landsat TM data for land-use and land coverage (Schweitzer 2012, Priess et al. 2015) were used and adapted to the sampling site's sub-catchments (Suppl. Table 1).

Sample and data processing

The benthic invertebrates were identified to the lowest possible taxonomic level, counted and the total body length was measured under a stereomicroscope (precision 0.1 mm). Taxa in high abundances were length measured in meaningful aliquots resulting in a measuring ratio of 36 % of all individuals. The invertebrate biomass was estimated using length-mass relationships (Meyer 1989, Burgherr and Meyer 1997, Benke et al. 1999, own unpublished data). Furthermore functional (feeding, habitat and locomotion types), structural, and diversity macroinvertebrate community metrics have been derived from the taxonomic data. For the determination of the fine sediment impact on macroinvertebrate communities, a set of nine metrics were selected: taxa richness (number of taxa), Shannon index of diversity (H , Shannon and Weaver 1949), Evenness (E , Magurran 1988), relative density of EPT individuals (Density % EPT), total benthic density (individuals m^{-2}), density of Chironomidae (Chiro Density; chironomid individuals m^{-2}), relative biomass of Chironomidae and Oligochaeta (Biomass % Chiro/Oligo; chironomid and oligochaete biomass relative to total biomass), relative biomass of fine substrate (sand and mud) colonisers (Biomass % FS Coloniser) and relative biomass of hard substrate (coarse pebbles to boulders) colonisers (Biomass % HS Coloniser).

After recovery of the sediment matrix traps, the samples were transported to the Central Geological Laboratory in Ulaanbaatar for analysis. The samples were dried (105°C, 24 h) and the grain size fractions smaller than 250 μm were unified and defined as fine sediment in the context of this study. The net rate of fine sediment intrusion (NIR_{fs}) was calculated using the following formula:

$$NIR_{fs} [g L^{-1} d^{-1}] = \frac{m_{fs} [g]}{V_{trap} [L] \cdot t_{inc} [d]}$$

with m_{fs} being the mass of fine sediment with grain sizes smaller than 250 μm in grams, V_{trap} being the volume of the inner basket of the trap in litres and t_{inc} being the incubation time in days. To estimate the organic portion of this fine sediment fraction particulate organic carbon (POC) and particulate nitrogen (PN) were measured using a carbon/nitrogen/sulphur analyser (vario EL, Elementar Analysensysteme GmbH, Germany) according to the method described by Hartwig and Borchardt (2014).

Statistical analyses

Nonmetric multi-dimensional scaling (NMDS) using Bray-Curtis dissimilarity was performed in order to visualise taxonomic data. The data set was standardised using Wisconsin standardisation and was fourth-root transformed (Faith et al. 1987, Legendre and Gallagher 2001). Significant environmental factors were identified using environmental fitting (10^6 permutations; R package 'vegan', Oksanen et al. 2017). Macroinvertebrate community metrics have been used afterwards in order to identify fine sediment related differences between the sampling sites. The calculated metrics were tested in order to determine the difference between sampling sites by applying an rmANOVA and a Least Significant Difference test (LSD) with Bonferroni adjustment of p -values. Prerequisites for statistics were tested using Fligner-Killeen test and Shapiro-Wilk test to determine the data's homogeneity of variance and normal distribution. Data transformations were identified by the boxcox method (Box and Cox 1964) and calculated as follows: relative density of EPT individuals: $y' = y^{0.87}$; relative biomass of hard substrate coloniser: $y' = y^{0.5}$; relative biomass of fine substrate coloniser and relative biomass of Chironomidae and Oligochaeta: $y' = y^{0.3}$; total density and density of Chironomidae: $y' = y^{0.22}$.

Linear regression analyses (Pearson's r) were performed between macroinvertebrate metric means and mean of turbidity measures at each site. Although linear models may suffer from some weaknesses in explaining the relationships between fine sediment pollution and biotic response variables they have been applied due to their robustness.

Differences between the net rate of fine sediment intrusion and the fine sediment organic matter content (POC, PN) of the sites were tested with a one-way ANOVA and a multiple comparison test (Tukey's HSD) for both incubation periods, during summer and winter. All graphics and statistical analyses were computed by using open source R (R Development Core Team 2010, Version 2.11.1).

Results

Macroinvertebrate community metrics

The macroinvertebrate communities examined in the middle region of the Kharaa River were characterised by high total densities (5293 ± 409 individuals m^{-2} , $n = 70$) and total biomasses (2631 ± 153 mg dry weight m^{-2} , $n = 70$, both mean \pm SE). The comparison of the macroinvertebrate communities using structural and functional metrics indicated changes in community composition, biodiversity and habitat complexity from upstream (M1) to downstream (M7) sites (Fig. 2, Suppl. Table 1).

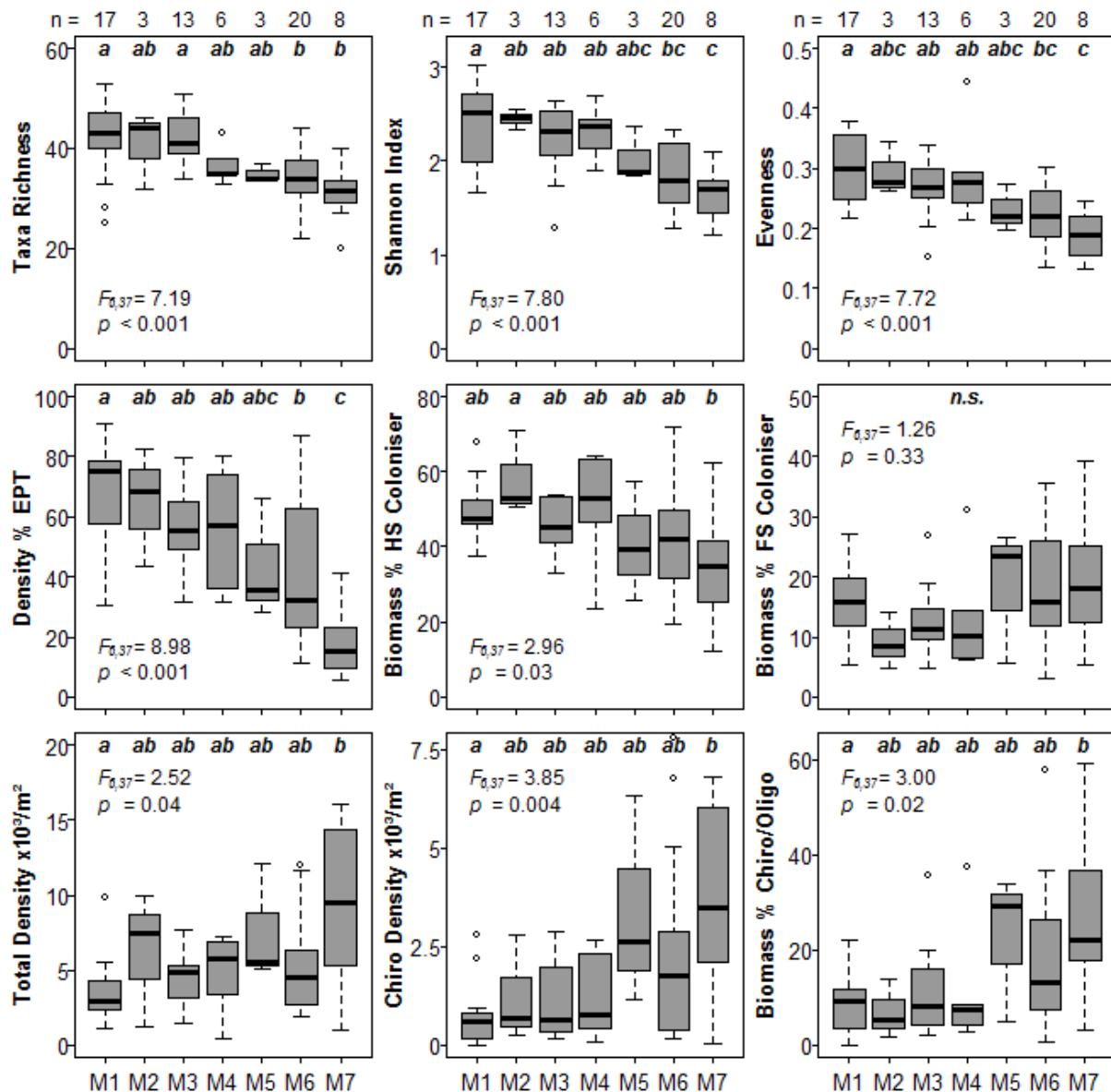


Fig. 2 Boxplot (median, 25/75 percentile, 1.5 x interpercentile range, outliers) of macroinvertebrate metrics of the sites M1 to M7 in the middle Kharaa River along a longitudinal gradient; significant differences between sites grouped by letters 'abc'; 'n.s.' - non-significant (LSD test with *Bonferroni* correction), sample number (n) is indicated above the plots; results from rmANOVA for differences between the sites are given in each plot

Table 1 Environmental characteristics (mean \pm SE, n in brackets) of the sites in the middle region of the Kharaa River from upstream (*M1*) to downstream (*M7*).
TN - Total nitrogen, TP - Total phosphorus

Site		<i>M1</i>	<i>M2</i>	<i>M3</i>	<i>M4</i>	<i>M5</i>	<i>M6</i>	<i>M7</i>
GPS location	N	48.54406°	48.67167°	48.80335°	48.83460°	48.82686°	48.87986°	48.91589°
	E	106.82719°	106.77667°	106.82719°	106.50909°	106.37836°	106.12990°	106.0604°
Outlet distance (km)		296.7	276.6	252.2	227.3	213.9	181.1	170.2
Elevation (m)		1048	944	915	865	840	804	787
River width (m)		16.8 \pm 0.7 (10)	21.7 \pm 1.1 (10)	25.3 \pm 1.4 (10)	19.7 \pm 0.7 (10)	30.8 \pm 0.6 (10)	25.9 \pm 1.0 (10)	24.5 \pm 1.8 (10)
River depth (m)		0.30 \pm 0.03 (58)	0.30 \pm 0.02 (68)	0.30 \pm 0.02 (78)	0.32 \pm 0.03 (67)	0.33 \pm 0.02 (93)	0.43 \pm 0.03 (66)	0.35 \pm 0.02 (74)
Dominant benthic substrates ^a		blocks and boulders	blocks and boulders	boulders and cobbles	boulders and cobbles	cobbles and coarse pebbles	cobbles and coarse pebbles	cobbles and coarse pebbles
Fine substrates cover < 2 mm (%)		8.7 \pm 1.6 (7)	9.5 \pm 3.8 (3)	12.3 \pm 1.3 (8)	9.7 \pm 1.1 (6)	11.8 \pm 0.0 (3)	11.3 \pm 3.0 (8)	16.7 \pm 2.2 (7)
D ₅₀ (mm) ^b		198.8	192.7	116.2	61.4	34.0	32.1	24.5
D ₆₀ / D ₁₀ ^c		2.3	3.8	7.4	3.4	6.5	5.5	5.1
Shear stress ^d (N m ⁻²)		4.91	3.86	2.81	2.53	2.10	4.28	4.93
Wooden riparian vegetation		41 %	52 %	21 %	21 %	0 %	26 %	0 %
River bank damage ^e		10 %	19 %	12 %	17 %	91 %	69 %	91 %
Turbidity (FNU)		1.94 \pm 1.0 (7)	0.62 \pm 0.2 (3)	1.22 \pm 0.4 (8)	1.55 \pm 0.6 (6)	1.74 \pm 0.8 (4)	2.68 \pm 1.5 (7)	5.43 \pm 1.6 (7)
Conductivity (μ S cm ⁻¹)		176 \pm 23 (7)	180 \pm 31 (3)	203 \pm 15 (10)	210 \pm 17 (8)	223 \pm 16 (6)	287 \pm 14 (11)	322 \pm 19 (10)
TN (mg L ⁻¹)		0.50 \pm 0.05 (4)	0.46 \pm 0.05 (2)	0.38 \pm 0.1 (6)	0.49 \pm 0.07 (6)	0.48 \pm 0.07 (5)	0.33 \pm 0.04 (7)	0.96 \pm 0.18 (6)
TP (mg L ⁻¹)		0.03 \pm 0.01 (4)	0.02 \pm 0.003 (2)	0.02 \pm 0.003 (6)	0.02 \pm 0.002 (6)	0.02 \pm 0.001 (5)	0.03 \pm 0.002 (7)	0.09 \pm 0.03 (6)

^aRiver bottom substrate was characterised using Wentworth (1922) scale.

^bGrain size where 50 % of the substrate grains are smaller.

^cGrain uniformity coefficient (Vukovic and Soro 1992).

^dData source: Berner 2007, average weighted per micro-habitat occurrence.

^eRiver bank damage was defined as broken banks due to trampling livestock and/or direct anthropogenic influence, e.g. nearby roads or river crossings.

These changes were characterised by significantly decreased taxa richness, Shannon diversity, Evenness, the relative density of EPT individuals and the relative biomass of hard substrate colonisers. In contrast, total densities, densities of chironomids and the relative biomass of chironomids and oligochaetes have been significantly increased at site *M7* compared to *M1*. The relative biomass of fine substrate colonisers did not show significant differences between the seven sites. Most of the metrics followed linear trends in a longitudinal direction resulting in significantly increased or decreased values at site *M7*. This suggested a gradient in the quality of environmental parameters for the macroinvertebrate communities along the river region, although the inter-annual and inter-seasonal variation was particularly high, as indicated by the results of the rmANOVA (Suppl. Table 2).

Macroinvertebrate community composition related to environmental factors

The environmental data from sites *M1* to *M7* displayed multiple longitudinal changes along the middle region of the Kharaa River (Table 1, Suppl. Table 2). Along natural gradients representing the river continuum, namely elevation, distance to outlet, mean river width or benthic substrate dominant grain size (D_{50} value), factors indicating more intense human activities also appeared to be aligned. Impairment of riparian wooden vegetation coincided with increased bank damage, mean turbidity, mean electric conductivity, wheat production, and fallow land, the latter two both indicating increasing large scale agriculture, from an upstream to downstream direction.

As the NMDS displayed, the taxonomic composition of the sampling sites represented a longitudinal gradient along the river continuum as related to the factors mentioned above and grouped in sub-region clusters (Fig. 3a). Furthermore, most other (anthropogenic) factors considered, were found to be either positively or negatively significant along this gradient (Suppl. Table 3). Mean turbidity, mean electrical conductivity, bank damage, and substrate D_{60}/D_{10} ratio were orientated in a downstream direction in accordance with mean river width and, to a lesser extent, mean river depth, further suggesting an increased soil and fine sediment input or in-stream migration respectively in the downstream part of the Kharaa River middle region (Fig. 3b). On the contrary, wooden riparian vegetation did decrease in a downstream direction, culminating in its complete disappearance at site *M5* and *M7*, and resulting in higher proportions co-occurring with higher elevation, outlet distance and benthic substrate grain size (Fig. 3b, Table 1). In comparison to the analysis of the land-use and land-coverage data using environmental fitting, the results indicated that mixed forest and potato cultivation (small scale agriculture) were more related to the upstream sub-regions than wheat cultivation, fallow, settlements and floodplain vegetation, which increased in a downstream direction (Fig. 3c, Suppl. Table 2). Apart from these longitudinal oriented gradients, nutrient parameters such as total nitrogen and total phosphorus as well as the percentage of fine river bottom substrate, followed a different orientation indicating a specific importance of these factors at the most downstream site *M7*. Even though there was indication for increased fine sediment fractions at the most downstream sampling site, a quantitative statement regarding the composition of the fine particle matrix in between the dominate grain size was not possible based on the applied mapping approach.

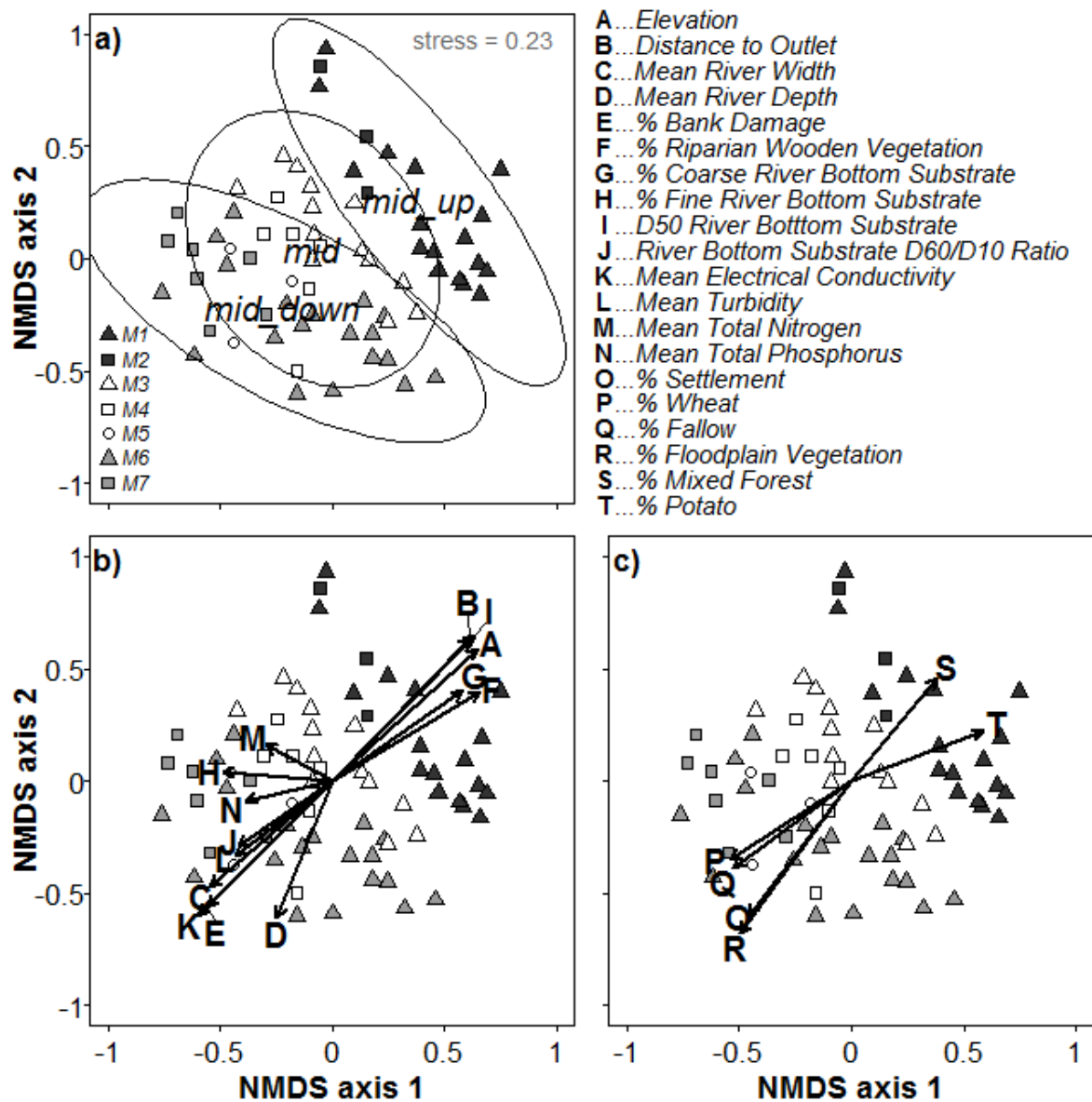


Fig. 3 Non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarities between macroinvertebrate taxonomic composition from the seven sampling sites (M1-M7, legend see plot a) in the Kharaa middle region with a) 95% confidence intervals (ellipsoids) of sub-regions middle upstream (mid_up), middle (mid) and middle downstream (mid_down), b) in relation to environmental and hydro-morphological variables and c) in relation to classified land cover data derived from remote sensing variables (arrows; only significant [$p < 0.05$] were added to the NMDS plot and labelled with capitalised Arabic characters; description is given in the figure)

The regression analyses between the mean of each macroinvertebrate metric and the mean turbidity values at each site of the Kharaa River middle reaches resulted in negative linear relationships for taxa richness ($r = -0.79$, $p = 0.036$, $R^2 = 0.54$), Shannon Index of Diversity ($r = -0.85$, $p = 0.016$, $R^2 = 0.67$), Evenness ($r = -0.81$, $p = 0.028$, $R^2 = 0.58$), relative abundance of EPT individuals ($r = -0.88$, $p < 0.01$, $R^2 = 0.74$) and relative biomass of hard substrate colonisers ($r = -0.82$, $p = 0.03$, $R^2 = 0.57$). Relative biomass of Chironomidae and Oligochaeta ($r = 0.76$, $p = 0.049$, $R^2 = 0.49$) was positively correlated to mean turbidity values. The other metrics also displayed positive relationships to mean turbidity, although linear regression was not statistically significant (relative biomass of fine substrate colonisers: $r = 0.73$, $p = 0.06$, $R^2 = 0.45$; total density: $r = 0.63$, $p = 0.08$, $R^2 = 0.38$; density of Chironomidae: $r = 0.65$, $p = 0.11$, $R^2 = 0.31$). These results indicated an impact of suspended fine sediments on the macroinvertebrate community structure and to a lesser extent on habitat complexity by shifting from EPT dominance to increased proportions of fine sediment colonisers, like Chironomidae and Oligochaeta, and associated with a loss in biodiversity.

The range of turbidity measurements from the macroinvertebrate sampling campaigns (0.69 – 5.43 FNU) were approximately three times lower upstream and six times lower downstream of the study reach compared to the estimated total environmental turbidity gradient from continuous measurements (median: 2.4 FNU upstream, 34.6 FNU downstream, Suppl. Fig. 1a). These measurements covered both, low and high flow conditions (Suppl. Fig. 1b). It became obvious that macroinvertebrate samples and thus, also turbidity measurements were taken from rarely occurring conditions (15 % of the observations) at the lower range of the environmental turbidity gradient.

Fine sediment intrusion

The analysis of fine sediments (< 250 μm) at the three sites in the middle region of the Kharaa River, during both the summer and winter periods, indicated an increased fine sediment net intrusion into the upper layers of the river bed at the most downstream site *M7* compared to the upstream site *M2* (summer: $F_{2,6} = 38.73$, $p < 0.001$; winter: $F_{2,6} = 5.93$, $p = 0.038$). During the summer period the mean net intrusion rate (NIR_{fs}) indicated an increased deposition of fine sediments at site *M7* by close to five times compared to site *M2*, and still more than three times compared to site *M6* (Fig. 4a). During the winter period, deposition of fine sediments was lower and increased by four times at site *M7* compared to site *M2* and close to two times compared to site *M6* (Fig. 4b). The NIR_{fs} measurements over the winter period corresponded very well to the mean of the turbidity measurements during the field expeditions and the macroinvertebrate samplings ($r = 0.999$, $p = 0.03$, Fig. 4b and c). This was not the case during the summer period ($p = 0.2$) where fine sediment deposition into the interstitial space on the river substrate at site *M7* was further increased by other factors explainable by the intermittent turbidity measurements (Fig. 4a and c). While the amount of infiltrated fine sediments at the three sites followed a clear longitudinal pattern, the estimation of their organic portions did not. Although no differences in the contents of PN ($F = 0.41$, $p = 0.7$) or POC ($F = 1.33$, $p = 0.3$) occurred between the sites during the summer period (Fig. 4d), the POC content was slightly increased at site *M2* compared to both downstream sites (*M6*, *M7*) during the winter period ($F = 18.6$, $p = 0.003$), whereas the PN content was not ($F = 4.62$, $p = 0.06$, Fig. 4e).

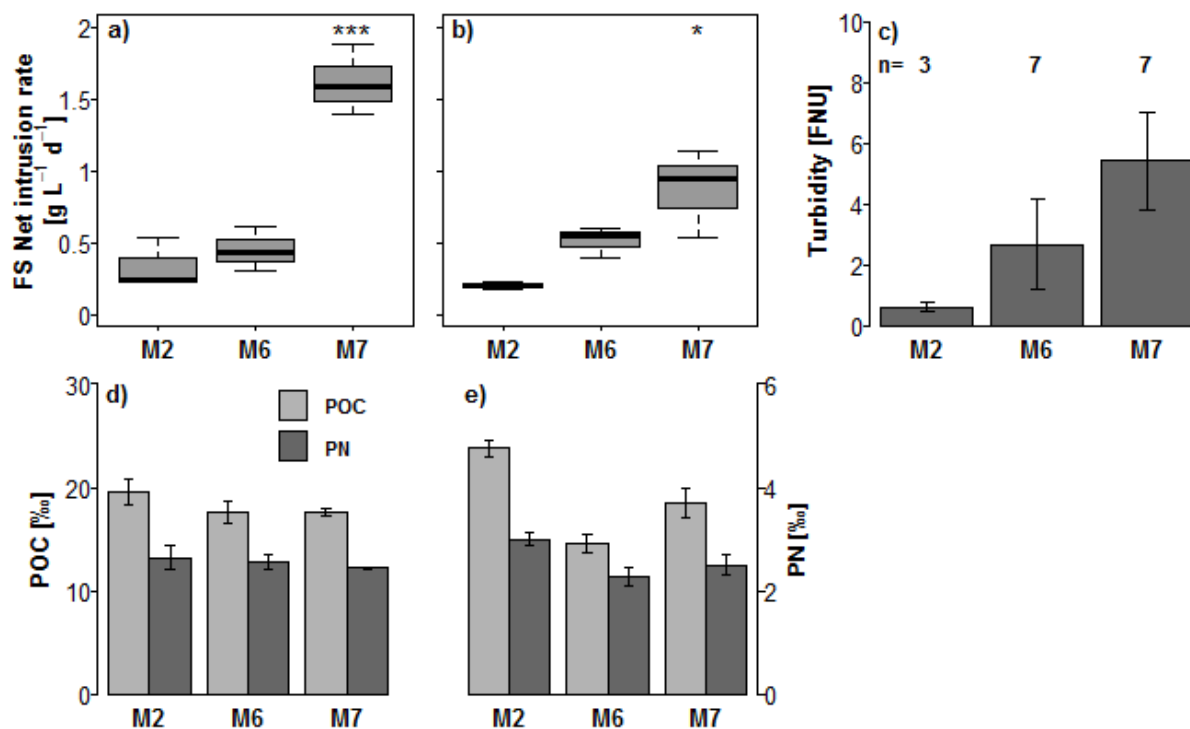


Fig. 4 Fine sediment net intrusion rate at the three sites in the middle region of the Kharaa River during a) the vegetation period from May to September 2009 and b) the winter from September 2009 to May 2010 in comparison to c) turbidity measurements, and d) and e) the fine sediment portions of particulate organic carbon (POC) and particulate nitrogen (PN) for both incubation periods, respectively. Boxes are indicating median, 25/75 quartile, minimum and maximum (whiskers), significant differences marked with asterisks (one-way ANOVA); bars are indicating means \pm SE

Discussion

General changes of community metrics along the sampling gradient

The macroinvertebrate community along the Kharaa River middle region showed a substantial deficit in the structure, diversity and to a lesser extent habitat complexity at the most downstream site (*M7*) of the study reach. The community metrics indicated a shift from EPT and hard substrate coloniser dominance to increased proportions of fine substrate colonisers, and thus increased fine sediment pollution at this site. However, the increasing trend in relative biomass of fine substrate colonisers was not statistically significant, even if biomass proportions of chironomids and oligochaetes (both closely related to fine sediment habitats) were significantly increased. It is assumed that the higher individual biomass of other fine substrate colonising taxa, especially those larger in body size, compared to chironomids and oligochaetes, was most likely the reason for the missing overall fine sediment coloniser's biomass effect. Larvae of larger insect taxa characterised by fine substrate preferences (esp. psammophilous Ephemeroptera, i.e. *Ephemera orientalis*) occurred in higher abundances also at the upstream sites of the Kharaa River middle region and may have masked such potentially longitudinal effects resulting from the increasing chironomid and oligochaete densities. Following the decreasing elevation gradient along the natural continuum of a river, which also implies decreasing sediment transport energy, natural changes in benthic substrate composition can be observed. Considering these changes, shrinking proportions of hard substrate colonisers and increasing proportions of fine substrate colonisers is expected. However, even if such natural longitudinal changes in hydro-morphological aspects can to a certain extent explain the observed macroinvertebrate colonisation pattern, it is very unlikely that this was the main environmental factor causing the situation in the downstream study region, as there is a relatively small distance (10 km) between the two sites (*M6* and *M7*), and their hydraulic conditions are also similar (Hartwig and Borchardt 2014).

Relevance of natural changes in environmental factors for explaining the gradient

In spite of the evidence that the macroinvertebrate community was influenced by environmental stressors, the taxonomic composition and metrics of the macroinvertebrate communities in relation to the environmental data revealed a clear longitudinal gradient following the natural river continuum elucidated by morphologic and geographic environmental factors (Vannote et al. 1980). This was expected, caused by the longitudinal design of the present study, but, it has to be considered that the study reach was within a single biocoenotic region (Berner 2007) and not extended to the whole catchment, which ensured better comparability between sampling sites. Furthermore, also other factors related to fine sediment pollution were aligned to this natural gradient. The relative occurrence of wooden riparian bank vegetation decreased from upstream to downstream, whereas the frequency of disturbed bank morphology increased. This coincided with an increase in electrical conductivity, in turbidity as well as in the grain uniformity coefficient (D_{60}/D_{10} ratio), indicating increased fine sediment migration and deposition, and is in accordance with bank stabilising and sediment retaining functions of riparian vegetation buffer stripes (Tal et al. 2004). In addition, the relative occurrence of fine river bottom substrates displayed a special relevance at the most downstream site (*M7*), and thus supported the hypothesis of fine sediment pollution at this site. A further reason for the observed fine sediment effect at site *M7* compared to the other sites could be the influence of the tributary *Zagdalin Gol* flowing into the Kharaa River approximately 2.5 km upstream from the *M7* site. The *Zagdalin Gol* is known to regularly transport high loads of fine sediments into the Kharaa River main channel, especially during high discharge events (Hartwig et al. 2012, Karthe et al. 2014, Theuring et al. 2015). This additional sediment load over a long period may have resulted in exceeding the ecological tolerance of many invertebrate species and subsequently lowered the habitat suitability, thus indicating an initial fine sediment accumulation threshold (Kaller and Hartman 2004) for altering macroinvertebrate communities. In comparison to the results from Burdon et al. (2013), the benthic substrate composition at this most downstream sampling site (16.7 ± 2.2 %; macroinvertebrate's microhabitat mapping data) was within the threshold range of 13-20 % surficial sediment < 2 mm, while at all other sites it remained below this threshold. In agreement with Burdon et al. (2013), strong influences on EPT taxa were also detected in the present study with further evidence for this threshold can be derived.

Effects of fine sediment on benthic macroinvertebrates

Macroinvertebrate communities of river ecosystems have shown diverse stressor responses to fine sediment pollution in both direct and/or indirect ways (Wood and Armitage 1997, Jones et al. 2012). Responses were ranging from increased drift (e.g. Culp et al. 1986, Matthaei et al. 2006, Larsen and Ormerod 2010a), and reduced trait diversity (Larsen and Ormerod 2010b) to reduced taxa richness and/or density (e.g. Quinn et al. 1992b, Kaller and Hartman 2004, Milner and Piorkowski 2004, Wantzen 2006, Yule et al. 2010). In particular, EPT organisms were often reported to be sensitive to increased fine sediment loads in rivers (Angradi 1999, Mebane 2001, Freeman and Schorr 2004, Larsen et al. 2009, Bryce et al. 2010, Burdon et al. 2013, Bertaso et al. 2015). This again is in agreement with the current results showing the relative density of EPT individuals as the most sensitive metric to increased fine sediment pollution. Moreover, due to their widespread crawling locomotory type, the habitat preferences of EPT species are mostly closely related to lithal (stony or rocky) or phytal (mosses, macrophytes or submerged parts of terrestrial plants) substrates. The deposition of higher loads of fine sediment can alter the suitability of habitats for EPT colonisation, due to the increased substrate instability, which can create a higher risk of being displaced by accidental (catastrophic) drift for the individuals present. Furthermore, food availability or quality may be lowered, especially for grazing and passive filtering feeding species, which ultimately results in lower individual fitness. Furthermore, a large portion of the reduction in the overall taxa richness at M7 can be traceable to a reduction in EPT taxa richness, as both metrics were highly correlated to each other ($R^2 = 0.83$, $p < 0.001$, $n = 76$). This sensitivity of EPT species to fine sediment pollution can be attributed to the high proportion of stenoecious species, which have high requirements for habitat quality. Wood and Armitage (1997) identified (1) benthic habitat suitability due to substrate composition alterations, (2) increased drift resulting from (fine) sediment deposition or substrate instability, (3) affected respiration or low oxygen concentrations due to fine sediment deposition, and (4) impaired feeding activity, as the four different effects on benthic invertebrates from (increased) fine sediment suspension and deposition. Although we cannot quantify the individual effect of these four mechanisms from the data, all four can be expected to play a role in shaping the macroinvertebrate communities in the Kharaa River middle region. Considering the harsh climatic conditions in Mongolia, particularly during the long and cold winters, when rivers are covered by ice partly down to the sediment surface (Batima et al. 2004, Avlyush et al. 2013), mechanisms (1) and (3) appear to be highly relevant for the survival of macroinvertebrate organisms. The hyporheic interstitial zones in gravel-bed rivers provides refuges not only during the ice cover period, but also during floods when the risk of catastrophic drift increases correspondingly to the shear stress in benthic habitats (Stubbington 2012). The increased deposition of fine sediments can either directly impair the vital function of this hyporheic compartment by physical clogging, or indirectly, by lowering the oxygen availability, which ultimately results in decreased habitat quality for benthic macroinvertebrates. Both processes have been detected at site M7 in the study of Hartwig and Borchardt (2014) and therefore can be assumed to be the major factors influencing the habitat quality and therefore the macroinvertebrate community composition at this site. This was evident by due to the shift from EPT dominance to chironomids' and oligochaetes' dominance.

Sediment alterations by fine sediment intrusion - seasonal and methodical discussion

The increased net intrusion rate of fine sediment ($< 250 \mu\text{m}$) at the sampling site (M7) supported the hypothesis of increased fine sediment pollution in these reaches of the Kharaa River. This increase was higher over the summer (vegetation) period when 70 % of the precipitation occurs compared to the winter period when rivers are covered by ice for several months (Avlyush et al. 2013, Karthe et al. 2015b). Flood and storm events were reported to be major causes for sediment mobilisation and re-mobilisation processes in Mongolia (Chalov et al. 2015, Pietron et al. 2015) and therefore can explain the stronger increase of fine sediments during this period. As the chemical analyses of the fine sediment fraction indicated, organic particles did not reflect the fine sediment gradient. This suggested that they were less important in explaining the macroinvertebrate community pattern. The higher density of wooden riparian vegetation upstream in the study region could have led to the assumption of also higher organic matter due to leaf litter input. However, this was not the case during the summer and only tended to occur during the winter sampling period, where POC was slightly increased at the upstream site. Higher rates in nutrient turnover during the hot summer conditions could explain this difference, but this cannot be stated from the data and therefore, has to remain speculative. Although other studies mostly focused on an upper grain size limit of 2 mm (e.g. Von Bertrab et al. 2012, Burdon et al. 2013, Jones et al. 2015) it appeared to be meaningful to focus on a smaller grain size limit in the Kharaa River middle region. Sand (0.125 to 2 mm, Wentworth 1922) was a considerable

natural component of riverine sediments along the studied region (Hartwig and Borchardt 2014) and therefore, particles < 250 µm were expected to be more ecologically relevant in terms of potential clogging of habitats for resident macroinvertebrate organisms. Due to the long incubation period of several months and to enable both, vertical and horizontal intrusions the sediment matrix trap method allows for time integrating analysis. Thus, the NIR_{fs} values from the one-year incubation period in this study can be expected to be representative for the situation in the Kharaa River study reach in the past. This was a specific attempt to not only cover current river bed erosion/deposition processes but also more historical processes that likely influenced benthic habitats, which is responsible for shaping the contemporary macroinvertebrate community composition. It cannot be excluded that horizontal intrusion processes exceeded or overlaid vertical ones, and the sediment matrix traps used in the current study acted as a fine particle sink for the surrounding sediment. Therefore, the values from this study are likely overestimated considering only vertical intrusion, but are comparable to other studies using similar methodologies (Seydell et al. 2009). However, it has to be considered that long-term discharge and sediment loads were decreasing in the region (Potemkina 2011, Chalov et al. 2015), which may influence management decisions in the future.

Effects of anthropogenic stressors on fine sediment pollution

Further support for the fine sediment impairment in the downstream reaches of the Kharaa River middle region can be derived from the results of Hartwig and Borchardt (2014), where total suspended solids (TSS) and physical clogging of the hyporheic zone had significantly increased at the most downstream site (M7 in the present study). As described by Schweitzer and Priess (2009), Hofmann et al. (2011) and Priess et al. (2011, 2015) land-use type and land-use intensity along the Kharaa River middle region were largely determined by the geographical characteristics of the riparian and flood plain areas in terms of providing suitable spatial capacity for increased population, agriculture and animal husbandry. The narrower upstream valley allows only a limited population density and minimal agricultural activities and thus was mostly characterised by moderate grazing levels. In contrast, the wider flood plain downstream provides suitable farmland for crop production and grassland areas for a larger number of livestock and urban settlements, and thus were characterised by higher grazing pressure and erosion risk. These patterns were reflected in the results of the multivariate analysis where hydro-morphological deficits, such as river bank damage and a progressive decline of the larger riparian vegetation such as bushes and trees were aligned in an upstream-downstream direction in concordance with an increasing area of large-scale agriculture, human settlements and floodplain vegetation as related to wider valley morphologies. The negative impacts of livestock on river bank stability and macroinvertebrate communities are well reported (e.g. Quinn et al. 1992a, Raymond and Vondracek 2011). Thus, considering that livestock is allowed to graze un-restrained in Mongolia it is very likely that the observed hydro-morphological deficits were caused by the constant feeding activity adjacent to the river channel. Therefore, the direct impact of livestock trampling river bank soil, along with the indirect impact by overgrazing the riparian vegetation (pers. observations), both have severely impaired the river bank stability in the region (Hartwig et al. 2016). An increased load of fine sediment entering the river course is an obvious consequence of this river bank deterioration (Theuring et al. 2013). Increased turbidity values suggested that this process occurred especially in the downstream part of the investigation area, however, it must be recognised that these occasional turbidity measurements taken in parallel with the macroinvertebrate sampling, cannot fully reflect the complete range of environmental factors that shape the macroinvertebrate community in the Kharaa River. Special consideration should be given to the fact that macroinvertebrate samples were only sampled during wadeable low- and mid-flow conditions, when the river was characterised by lower turbidity. In contrast, most sediment mobilisation and re-mobilisation primarily occurs during short high-flow events (Chalov et al. 2015, Pietroń et al. 2015). Although, as indicated by the relationships between macroinvertebrate community metrics and the mean turbidity values, it can be assumed that these measurements are reflected in the environmental gradient, albeit on a lower level.

Effects of nutrients and EC on benthic macroinvertebrates

Increasing nutrient concentrations were reported along the Kharaa River with maximum values measured at the Kharaa-Orkhon confluence (total nitrogen and total phosphorus; Hofmann et al. 2011). Eutrophic conditions due to increased nutrient input induce high respiratory rates and oxygen demands. This can potentially result in a macroinvertebrate colonisation pattern similar to the pattern observed during the current investigations. However, despite slightly increased nutrient concentrations in the Kharaa mid region, Hartwig and Borchardt (2014) measured decreasing periphyton biomass

and gross primary production with community respiration remaining comparable in the downstream site (M7) compared to the next upstream site (M6). This was attributed to light limitations caused by high loads of total suspended solids and altered habitat availability due to increased fine particle deposition on the benthic substrate. Furthermore, the measured total nitrogen and total phosphorus concentrations were consistently low and therefore the ecological consequences can be assumed to be less relevant. Thus, the share of saprobically caused alterations in the macroinvertebrate community pattern can be expected to be minimal. This was supported by the fact that larger stoneflies (*Agnetina* sp., Perlidae), or different species of Perlodidae (*Isoperla* spp., *Skwala* sp., *Diura* sp.) and Chloroperlidae (*Triznaka* sp.) as well as mayflies of the genus *Epeorus* (*E. (Belovius) pellucidus*), which generally showed very small saprobic tolerances (Rosenberg and Resh 1993) have been sampled from all sites (including M7) of the study area, at least at low densities. While other studies have reported EC as being closely related to biological degradation (Vander Laan 2013), in the present study, it was also closely related to the longitudinal gradient, the mean turbidity and the bank damage. Although, separating the possible effects of EC on macroinvertebrate communities from the effects of fine sediment was not possible during the current research, soil intrusion from bank erosion could be identified as the main source of the EC gradient, due to very low fertiliser use in the local agriculture (Hofmann et al. 2015) and due to also low population density in the region (Hofmann et al. 2011). Furthermore, the ecological consequences of this relatively small EC gradient ($\Delta EC_{\text{mean}} = 146 \mu\text{S cm}^{-1}$), which occurs on a relatively low level ($EC_{\text{max}} = 383 \mu\text{S cm}^{-1}$) can be assumed to have little effect in relation to the more severe habitat impairing effects of increased fine sediment intrusion. This conclusion is supported by the results of another study which focused on the ecological consequences of EC on macroinvertebrates (Kefford 1998).

Conclusion

Although it cannot be excluded completely that other natural and/or anthropogenic environmental factors could have been causal in shaping the macroinvertebrate community pattern in the Kharaa River middle region, from the current results it is evident that the increased fine sediment pollution was one of the most important driving factors. This is especially true in the lower parts of the Kharaa River middle region, which ultimately supports our original hypothesis that stated the macroinvertebrate communities were impaired by fine sediment pollution. These main sources of fine sediments in the Kharaa River basin, as identified using sediment isotope fingerprinting, have been determined to be river bank erosion and to a lesser extend upland erosion processes (Theuring et al. 2013). Therefore the urgent need for the implementation of river bank stabilising and livestock managing measures, as well as further fine sediment related monitoring along the course of the Kharaa River middle region is unquestionable. These management recommendations and threshold values for ecologically critical fine sediment loadings are likely transferable and essential in order to mitigate the adverse impacts on the aquatic environment in other intensively grazed regions and basins of the Eurasian steppe belt.

Acknowledgements

We sincere thank M. Hartwig, P. Theuring, Ts. Batchuluun, N. Natsagnyam and several students, namely U. Frömmel, A. Rother, S. Nergui, A. Otgonchimeg, Kh. Undarmaa, B. Erdenezul, Ch. Batsaikhan, Kh. Chantuu, and E. Zoljargal for field and laboratory assistance in Germany and Mongolia, R. Ibisch for fruitful discussions, D. Karthe for creating the catchment map and A. Kaus and A. Terwei for proofreading the manuscript. This study was part within the research project “Integrated Water Resource Management in Central Asia: Model region Mongolia” (MoMo) funded by the German Ministry of Education and Research (BMBF Grant 0033L003A). Additionally, S. Avlyush was supported by the German Academic Exchange Program-DAAD (A/07/99089).

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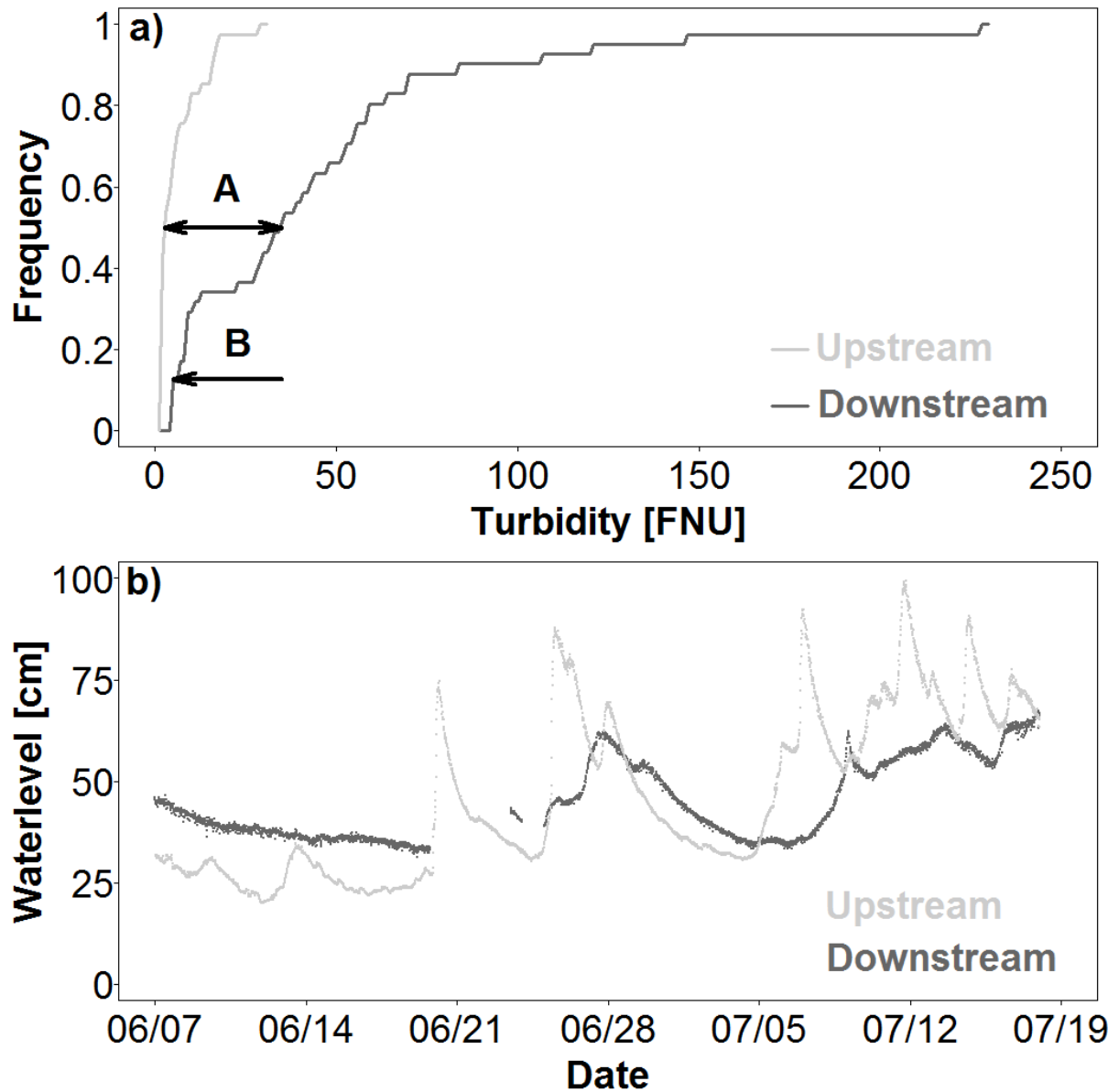
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Supplement Fig. 1 a) Cumulative frequency plot of daily mean turbidity values from two continuously measuring stations (15 min interval) in the Kharaa River main channel from June 7th to July 17th 2012; Upstream - about 45 km upstream of sampling site *M1*, Downstream - close to sampling site *M7*. The difference between the two station's median values (arrow A) estimating the environmental turbidity gradient and the frequency of the mean turbidity values from the sampling campaigns (arrow B) are indicated; b) water level data from the two monitoring stations in the Kharaa catchment from the same 41 day period.

Supplement Table 1 Relative land coverage per sampling site's sub-catchment area in the Kharaa middle region.

Land coverage (%)*	<i>M1</i>	<i>M2</i>	<i>M3</i>	<i>M4</i>	<i>M5</i>	<i>M6</i>	<i>M7</i>
Settlement	0.09	0.09	0.09	0.08	0.38	0.33	0.30
Wheat	0.83	0.72	0.62	0.92	1.20	1.90	4.40
Fallow	0.75	0.65	0.56	0.62	1.15	1.60	3.30
Potato	0.46	0.40	0.34	0.30	0.39	0.39	0.34
Grassland	53.5	50.1	46.9	46.3	48.3	54.3	56.9
Floodplain vegetation	1.95	1.87	2.10	2.60	2.80	2.80	2.50
Mixed forest	30.0	30.9	33.2	32.2	29.4	24.9	21.1
Needle leaf forest	12.4	15.3	16.3	17.0	16.4	13.8	11.3

*Land coverage classification of SPOT and Landsat TM data from Schweitzer (2012), applied to sampling site's sub-catchments.

Supplement Table 2 Results of the rmANOVA for macroinvertebrate community metrics from the seven sites of the middle Kharaa River; *Pr* values < 0.05 indicating significant differences are given in bold numbers. Only significant interactions are included.

<i>Within</i>	<i>Df</i>	<i>Sum Sq</i>	<i>Mean Sq</i>	<i>F value</i>	<i>Pr (>F)</i>
Taxa richness					
<i>Site</i>	6	1180.6	196.8	7.19	<0.001
<i>Year</i>	1	533.8	533.8	19.51	<0.001
<i>Season</i>	2	185.5	92.7	3.39	0.04
<i>Residuals</i>	37	1012.6	27.4		
Shannon diversity					
<i>Site</i>	6	5.54	0.92	7.80	<0.001
<i>Year</i>	1	0.16	0.16	1.32	0.26
<i>Season</i>	2	2.02	1.01	8.53	<0.001
<i>Residuals</i>	37	4.38	0.12		
Evenness					
<i>Site</i>	6	0.110	0.018	7.72	<0.001
<i>Year</i>	1	0.001	0.001	0.25	0.62
<i>Season</i>	2	0.047	0.024	9.95	<0.001
<i>Residuals</i>	37	0.088	0.002		
Relative EPT density					
<i>Site</i>	6	1.62	0.27	8.98	<0.001
<i>Year</i>	1	0.12	0.12	3.85	0.06
<i>Season</i>	2	0.46	0.23	7.58	0.002
<i>Residuals</i>	37	1.11	0.03		
Relative hard substrate coloniser's biomass					
<i>Site</i>	6	0.22	0.037	2.96	0.03
<i>Year</i>	1	0.01	0.009	0.75	0.41
<i>Season</i>	2	0.03	0.015	1.20	0.31
<i>Residuals</i>	37	0.46	0.012		
Relative fine substrate coloniser's biomass					
<i>Site</i>	6	0.06	0.010	1.26	0.33
<i>Year</i>	1	0.01	0.007	0.84	0.37
<i>Season</i>	2	0.03	0.013	1.62	0.21
<i>Residuals</i>	37	0.31	0.008		
Total density					
<i>Site</i>	6	10.30	1.72	2.52	0.04
<i>Year</i>	1	0.47	0.47	0.70	0.41
<i>Season</i>	2	3.37	1.69	2.47	0.1
<i>Year:Season</i>	2	7.63	3.82	5.60	0.007
<i>Residuals</i>	37	25.21	0.68		
Chironomid density					
<i>Site</i>	6	27.80	4.63	3.85	0.004
<i>Year</i>	1	2.42	2.42	2.01	0.17
<i>Season</i>	2	16.31	8.15	6.77	0.003
<i>Residuals</i>	37	44.57	1.20		
Relative biomass of Chironomidae and Oligochaeta					
<i>Site</i>	6	0.34	0.057	3.00	0.02
<i>Year</i>	1	0.00	0.002	0.10	0.75
<i>Season</i>	2	0.11	0.053	2.83	0.07
<i>Residuals</i>	37	0.70	0.019		

Supplement Table 3 Environmental factors used for environmental fitting to the NMDS and results after 10⁶ permutations. Significant factors are indicated by *p*-values < 0.05.

Factor	NMDS Axis 1	NMDS Axis 2	<i>R</i>²	<i>p</i>-value
Elevation	0.75	0.66	0.78	<0.001
Distance to Outlet	0.70	0.71	0.78	<0.001
Mean River Width	-0.75	-0.66	0.51	<0.001
Mean River Depth	-0.36	-0.93	0.43	<0.001
Mean benthic shear stress (τ)	1.00	0.06	0.06	0.15
% Coarse River Bottom Substrate	0.84	0.55	0.51	<0.001
% Fine River Bottom Substrate	-0.99	0.10	0.25	<0.001
D ₅₀ River Bottom Substrate	0.71	0.71	0.82	<0.001
River Bottom Substrate D ₆₀ /D ₁₀ Ratio	-0.82	-0.57	0.26	<0.001
Mean Turbidity	-0.79	-0.62	0.30	<0.001
Mean Electrical Conductivity (EC)	-0.70	-0.71	0.73	<0.001
Mean Total Nitrogen (TN)	-0.88	0.46	0.11	0.020
Mean Total Phosphorus (TP)	-0.98	-0.22	0.16	0.002
% Damaged Banks	-0.70	-0.71	0.63	<0.001
% Riparian Wooden Vegetation	0.86	0.50	0.59	<0.001
% Settlement	-0.60	-0.80	0.58	<0.001
% Wheat	-0.84	-0.55	0.41	<0.001
% Fallow	-0.80	-0.60	0.42	<0.001
% Grassland	-0.10	-0.99	0.05	0.20
% Floodplain Vegetation	-0.58	-0.81	0.71	<0.001
% Mixed Forest	0.64	0.77	0.35	<0.001
% Needle Forest	-0.99	0.15	0.02	0.57
% Potato	0.94	0.33	0.41	<0.001