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Spatio-temporal heterogeneity of actual and potential respiration in two contrasting floodplains

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Abstract

Floodplains are vital components of river ecosystems and play an important role in carbon cycling and storage at catchment and global scales. For efficient river management and conservation, it is critical to understand the functional role of spatiotemporally complex and dynamic habitat mosaics of river floodplains. Unfortunately, the fundamental understanding of mineralization and carbon flux patterns across complex floodplains is still fragmentary. In this study, respiratory potential (i.e., electron transport system activity – ETSA) was quantified seasonally across different aquatic and terrestrial habitats (wetted channels, gravel bars, islands, riparian forests and grasslands) of two Alpine floodplains differing in climate, altitude, discharge, flow alteration intensity and land use (Soča – natural flow regime, 12% grassland area; Urbach – mean annual discharge reduction by 30% due to water abstraction, 69% grassland area). *In situ* respiration (R) was measured and ETSA/R ratios calculated to examine differences in exploitation intensity of the overall respiratory capacity among floodplain habitats and seasons. ETSA and R provided potential and actual estimates, respectively, of organic matter mineralization in the different floodplain habitats. Hierarchical linear regression across habitat types showed organic matter, grain sizes <0.063 mm and water content were the most important predictors of ETSA in both floodplains, and grain sizes 2-0.063 mm and >8 mm were also highly important for the Soča floodplain. The combination of ETSA and R measurements conducted in contrasting floodplains increased our understanding of the relationships between floodplain habitat heterogeneity, organic matter mineralization and human impacts; i.e., structural-functional linkages in floodplains. These data are integral towards predicting changes in floodplain function in response to environmental alterations from increasing human pressures and environmental change.

Keywords: carbon flux, biochemical estimation of respiration, ETSA, floodplain function

Introduction

River floodplains in their natural state are complex aquatic-terrestrial ecosystems composed of diverse habitats such as active channels, pools, backwaters, gravel bars, islands and riparian forests that are strongly influenced by river flow dynamics (Junk *et al.*, 1989; Tockner and Stanford, 2002; Ward *et al.*, 2002). On a global scale, floodplains play an important role in the hydrological cycle through flood mitigation and water storage, support high biodiversity due to habitat heterogeneity, are important sinks and sources of sediment, carbon and nutrients, and function as areas of intense biogeochemical transformation (Mitsch and Gosselink, 2000; Tockner and Stanford, 2002; McClain *et al.*, 2003; Verhoeven *et al.*, 2006).

Despite these essential ecosystem functions and services, most European floodplains (up to 90%) have been degraded and are functionally extinct (Tockner and Stanford, 2002; Tockner *et al.*, 2008; 2009). In order to effectively carry out successful restoration projects or mitigate the effects of floodplain degradation, a comprehensive understanding of patterns and processes in different types of floodplains across regions and climates, and along the disturbance gradient, is urgently needed (Ward *et al.*, 2001; Tockner *et al.*, 2008; Hauer *et al.*, 2016).

A primary characteristic of natural floodplains is high spatio-temporal habitat heterogeneity (Amoros and Bornette, 2002; Tockner and Stanford, 2002; Stanford *et al.*, 2005) as reflected in the spatial and temporal variation in carbon processing (Doering *et al.*, 2011; Langhans *et al.*, 2008; 2013; Bodmer *et al.*, 2016). However, carbon processing is determined not only by its own habitat properties but by the spatial arrangement and composition of the total floodplain mosaic, which may influence the floodplain carbon transformation capacity of the entire floodplain (Tockner *et al.*, 2010; Langhans *et al.*, 2013). Thus, investigating the effects of the composition and spatial arrangement of habitats is critical towards understand the functioning of floodplain ecosystems.

Hydrology is a major driver controlling the floodplain “physical template” and, consequently, greatly influences carbon and nutrient turnover across floodplain landscapes (Poff *et al.*, 1997). Flow pulses and floods drive high habitat turnover that results in a “shifting habitat mosaic” forming various sites of different decomposition and microbial activity, including heterogeneous carbon dynamics (Stanford *et al.*, 2005; Samaritani *et al.*, 2011). During low flow, floodplain heterogeneity and microbial functioning can differ from high hydrolytic and respiratory activities in isolated pools to low activities in running waters (Foulquier *et al.*, 2014). Similarly, potential microbial respiration increases in regions of lower connectivity once they become connected during higher main river discharges (Tritthart *et al.*, 2011). Floodplain heterogeneity in carbon and nutrient flux also depends on surface-subsurface water exchange (Jones *et al.*, 1995; Doering *et al.*, 2013).

An important driver of microbial activity is the quality and quantity of organic matter, which is highly variable within floodplains partly due to distinct origins - allochthonous (litter deposition during flooding or lateral input) and autochthonous (aquatic primary production, on-site terrestrial production) sources (Junk *et al.*, 1989; Langhans *et al.*, 2013) - and partly due to distinct organic matter processing among floodplain habitats. For example, leaf decomposition is faster and more efficient in aquatic than dryland habitats (Langhans *et al.*, 2008) while respiration is higher in floodplain soils than in aquatic sediments (Doering *et al.*, 2011). Microbial activity in aquatic habitats is mostly associated with gathering carbon from small ester containing molecules such as lipids and in terrestrial compartments from complex molecules such as starch, cellulose or hemicellulose (Bodmer *et al.*, 2016).

Respiration (R), as a functional measure in nutrient cycling and organic matter degradation, has been widely used as an estimate of ecosystem function (Naegeli and Uehlinger, 1997; Hill *et al.*, 2000; Valett *et al.*, 2005; Doering *et al.*, 2011). It provides a measure of carbon

flux and has been well-studied, but rarely across riverine floodplain mosaic encompassing aquatic, semi-terrestrial and terrestrial habitats. The most commonly used determinant of aquatic heterotrophic respiration is oxygen consumption and that of soil, carbon dioxide production (e.g., Naegeli and Uehlinger, 1997; Buchmann, 2000). To estimate the amount of CO₂ produced per amount of O₂ consumed, a conversion factor – respiratory quotient (RQ) is needed as a proxy (Dilly, 2001; Williams and del Giorgio, 2005; Berggren *et al.*, 2012). Instead of direct oxygen consumption and/or carbon dioxide production measurements, the biochemical quantification of respiratory potential in floodplain soils/sediments can be used to estimate carbon turnover across aquatic-terrestrial floodplain habitats. A frequently applied biochemical method in soil and freshwater research is the measurement of respiratory electron transport system activity (ETSA) or respiratory potential (Trevors, 1984; Broberg, 1985; Mersi and Schinner, 1991; G.-Tóth *et al.*, 1994; Garcia *et al.*, 1997; Simčič and Mori, 2007; Simčič *et al.*, 2015). It measures potential respiration by detecting the activity in the dehydrogenases and cytochromes within respiratory electron transport systems that biochemically control oxygen consumption (Maldonado *et al.*, 2012). Since the electron transport system is present in both aerobic and anaerobic microbes and the tetrazolium salt used in the assay is an artificial electron acceptor (replacing O₂ or other naturally occurring acceptors), the technique estimates the total (aerobic and anaerobic) respiratory potential of the microbial community (Zimmermann, 1975; Maldonado *et al.*, 2012). Previous studies have shown that ETSA correlates highly with oxygen consumption, CO₂ production, and the amount of organic matter in soils/sediments (Trevors, 1984; Cook and Garland, 1997; Garcia *et al.*, 1997; Muri and Simčič, 2004; Simčič and Mori, 2007), and thus is a good estimate of ecosystem functioning. Further, the ratio between ETSA and R (ETSA/R ratio), both are standardized to common temperatures and units, gives information on the metabolic response of different floodplain soils/sediments exposed to different environmental conditions

relative to potential respiratory capacity. When R approaches ETSA values, the ratio comes close to 1, meaning that the system respire 'as much as possible'. Therefore, a high ETSA/R ratio indicates low exploitation of respiratory potential (Simčič *et al.*, 2015).

Heterogeneity in functional processes such as leaf decomposition, R and nutrient cycling has been examined in various floodplains, ranging from gravel-bed rivers such as the Val Roseg, Tagliamento and Urbach (Tockner *et al.*, 2002; Langhans *et al.*, 2008; Doering *et al.*, 2011; Langhans *et al.*, 2013; Bodmer *et al.*, 2016), an altered semi-arid floodplain of Rio Grande (Valett *et al.*, 2005), a restored Alpine floodplain of the Thur River (Samaritani *et al.*, 2011; Huber *et al.*, 2012) to a modified large Donau floodplain near Vienna (Tritthart *et al.*, 2011; Welti *et al.*, 2012a; b). Surprisingly, there still remains a lack of comparative studies across different floodplains. Thus, a primary aim of this study was to explore the spatiotemporal variation in ETSA across different habitat types and investigate the significance of temperature and structural features (i.e. water and organic matter contents and grain size distribution) of floodplain habitats for microbial respiratory potential within two different catchments. A secondary goal was to examine two complementary measures (i.e., respiration and respiratory potential) for evaluating the functional status of gravel-bed river floodplains. A specific objective was to examine the ratio between ETSA and R for explaining the intensity of respiratory potential exploitation within floodplain habitats.

Methods

Site description

The floodplain of the Urbach River is located near Innertkirchen in central Switzerland (Canton Bern) at 800-900 m a.s.l. (Fig. 1, Table 1). The floodplain is 3.4 km long and up to 0.6 km wide. Underlying geology consists mainly of limestone and granite. Climatic conditions are

characterized by moderate precipitation (1345 mm y^{-1}) and mean annual air temperature ranges from $7.2\text{-}10^{\circ}\text{C}$ (1960-2010). Floodplain vegetation is dominated by alder (*Alnus incana*) and different willow species (*Salix* spp.). Grassland and pasture borders the active floodplain to the west and increased from 53% to 69% during the past 70 years (Doering *et al.*, 2012). At present, only 17% of the floodplain area is overgrown by natural riparian forest. The natural discharge is driven by glacial melt water and local precipitation events (Table 1, Fig. 2a). However, the river has an altered flow regime, where average annual discharge is reduced by about 30% due to water abstraction for hydropower production about 6 km upstream of the floodplain. During the sampling period, three high flows were recorded, 2-6 times exceeding the mean annual discharge. Several levees for flood protection were installed throughout the years in the active floodplain area (Doering *et al.*, 2012). Additional inputs of organic matter to the floodplain are due to frequent avalanches off the east-side rock face in winter and early spring, and livestock (Bodmer *et al.*, 2016).

The floodplain of the Soča River is located near Bovec in northwest Slovenia at 350-370 m a.s.l. (Fig. 1, Table 1). Average annual rainfall of the area is 2386 mm and mean annual air temperature ranges between $8.4\text{-}11.4^{\circ}\text{C}$ (1960-2010). Catchment geology consists mainly of Mesozoic limestone and dolomite. The floodplain is vegetated by *Salix* spp. growing on islands and along the river margins and *Alnus* spp., *Fagus sylvatica* and *Picea abies* form mature riparian forests extending along the floodplain. Over half of the floodplain area (64%) is overgrown with mature riparian forest and only 12% is grassland and pasture. The discharge regime is pluvio-nival with spring and autumn peaks and an average annual discharge of $23.8 \text{ m}^3 \text{ s}^{-1}$ (1971-2000): $\text{min}=3.3 \text{ m}^3 \text{ s}^{-1}$, $\text{max}=554 \text{ m}^3 \text{ s}^{-1}$ (Frantar, 2007). In the Soča River, several floods >10 times higher ($>200 \text{ m}^3 \text{ s}^{-1}$) than the average annual discharge occurred during the study year (Fig. 2b). These high flows flooded gravel bars and islands but not riparian forest and grassland at the

sampling sites (N. Mori, pers. obs.). The floodplain is moderately affected by gravel extraction and most organic resources are from native floodplain vegetation and from upstream sources during spring and autumn precipitation.

Sampling protocol and field measurements

Five habitat types were identified within each floodplain, ranging from permanent aquatic (channel) to semi-aquatic (gravel bars) and predominantly terrestrial (vegetated islands, riparian forest, grassland) habitats. Habitat types were selected according to Doering *et al.* (2011, 2012), and further details can be found in those references. In the Urbach floodplain, 20 sampling sites evenly distributed throughout the floodplain were randomly selected for each habitat.

Soil/sediment samples for measurements of electron transport system activity (ETSA) were collected in spring (May), summer (August) and autumn (October/November) in 2010 ($N_{\text{total}}=300$) from the same locations as the measurements of *in situ* respiration (R) ($N_{\text{total}}=300$). In the Soča floodplain, 20 sample sites were selected for the channel and 10 for other four habitat types. Collecting of samples for ETSA ($N_{\text{total}}=180$) and measures of R in the channel ($N_{\text{total}}=60$) were done in spring, summer and autumn in 2010. In terrestrial habitats, R was measured only in summer in the Soča (August; $N_{\text{total}}=40$). Samples for ETSA were obtained from the same sediment/soil location where R was measured. At each sampling site, one sample for ETSA was collected and one R measurement was carried out.

Respiration was measured in aquatic habitats as O_2 consumption over time (Uehlinger *et al.*, 2002). Here, the surface layer of river sediments (~10 cm) was removed to avoid the presence of periphyton and to measure only heterotrophic R. This procedure was similar to terrestrial habitats where autotrophic R (scrub or trees) was excluded from respiration measures (Doering *et al.*, 2011). Sieved sediments (<8 mm) were placed into plexiglas tubes (32 cm long, 5.2 cm

diameter). During sieving, any aquatic invertebrates occurring in the samples were removed from the sediment. A subsample of this sediment, including pore water (10 g), was collected in 60 mL PVC bottles and put on dry ice (-80°C) for ETSA measurements in the laboratory. Previous measurements demonstrated negligible ETSA in the surface water of unpolluted gravel-bed rivers (Simčič and Mori, 2007) and thus does not represent significant background respiration. The respiration tubes were half-filled with sediment and then filled with water from the site and sealed with rubber stoppers. The tubes were incubated *in situ* by burying them in instream sediment at the sampling site for 4-8 hours (Uehlinger *et al.*, 2002). Temperature and oxygen concentration were measured before and after incubation using an HQ40d Dual-Input Multi-Parameter Digital Meter with a LDO temperature probe (Hach Company, Loveland, Colorado, U.S.A.) in the Urbach and a Multiline P4 meter with TetraCon 325 temperature probe and Cellox 325 oxygen probe (WTW GmbH, Weilheim, Germany) in the Soča. Following incubation, sediments were stored frozen (-20°C) and later analyzed for water content, organic matter content and grain size distribution.

For R measurements in terrestrial habitats, PVC collars (8 cm long, diameter 10.5 cm) were inserted into the soil/sediment to a depth of 5-7 cm at least 24 hours prior to measurement to minimize disturbance effects due to installation. A soil respiration chamber (LI-6400, LI-COR, Lincoln, Nebraska, U.S.A.) attached to a portable Li-6400 infrared gas analyzer (IRGA) was inserted at the top of the collar for measuring R; measurements were repeated four times for each sample and values averaged. Concurrently, soil temperature was measured at 5 cm depth using a temperature probe (Testo AG, Mönchaltorf, Switzerland). The content of each collar was collected, enclosed in PVC bags and transported to the laboratory for water content, organic matter content and grain size analysis. About 10 g of soil was collected from the same location, stored in PVC bags and immediately put on dry ice (-80°C) for ETSA measures. Particles >8 mm

were excluded from each sample to avoid metabolically inactive stones as done for aquatic samples.

Laboratory analyses

Soils/sediments collected in the field were analyzed for water content, organic matter content and grain size distribution. Water content (WC; % of initial wet mass) was determined gravimetrically, in which soil samples were weighed, dried at 105°C for 24 hours and reweighed. Organic matter content was measured as ash-free dry mass per dry mass (g AFDM kg⁻¹; 500°C for 3 hours). Soil/sediment grain size distributions were determined by sieving the ashed samples in size fractions of <0.063 mm, 0.063-2 mm, 2-4 mm, 4-8 mm and >8 mm.

Plant debris and roots were removed from the samples analyzed for ETSA. ETSA was measured using the assay originally proposed by Packard (1971) and modified by G.-Tóth (1999). Pre-weighed samples were homogenized in 4 ml of ice-cold homogenization buffer using a mortar, followed by ultrasonic homogenization (4710; Cole-Parmer, Vernon Hills, IL, USA). Homogenized samples were centrifuged (Sigma 2-K15, Sigma Laborzentrifugen GmbH, Osterode am Harz, Germany) and a 0.5 ml of supernatant (in triplicate) was incubated in 1.5 ml substrate solution with 0.5 ml 2.5 mM 2-(p-iodophenyl)-3-(p-nitrophenyl)-5-phenyl tetrazolium chloride (INT) solution for 40 min at standard temperature of 20°C. During the reaction between INT and supernatant containing cytochrome complexes from respiratory electron transport system, formazan is produced (Packard, 1971). Formazan production was determined spectrophotometrically (photoLab ® Spektral, WTW GmbH, Weilheim, Germany) from the absorbance of the sample at 490 nm against the blank.

Calculations and conversions

Based on oxygen consumption r ($\text{g O}_2 \text{ m}^{-3} \text{ h}^{-1}$) in the chamber, R per sediment volume R_v ($\mu\text{mol CO}_2 \text{ m}^{-3} \text{ s}^{-1}$) was calculated according to Doering *et al.* (2011):

$$R_v (\mu\text{mol CO}_2 \text{ m}^{-3} \text{ s}^{-1}) = r \times \frac{10^6}{32} \times \frac{1}{3600} \times \frac{V_w}{V_c} \times RQ$$

where V_w is the volume of water in a chamber (m^3), V_c is the volume of sediment (including porosity) in a chamber (m^3) and RQ is the respiratory quotient (0.85; Dilly, 2001). To estimate the area-respiration ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) for the uppermost 20 cm of channel sediments, R_v was multiplied by 0.2 m and by a factor 0.46 (Urbach) or 0.50 (Soča). This factor was determined by analyzing gravel samples and considers that the size fraction >8 mm accounted on average 46% and 50%, respectively, of the sediment volume in each river. The factors were applied to avoid overestimation of the area-respiration since larger size fractions represent substrate with low metabolic activity (Mori *et al.*, 2016).

The rate of INT reduction, measured during incubation at 20°C for 40 min, was converted to equivalents of oxygen used per dry mass in a given time interval (ETSA, $\mu\text{l O}_2 \text{ gDM}^{-1} \text{ h}^{-1}$) as described by Kenner and Ahmed (1975):

$$ETSA (\mu\text{l O}_2 \text{ gDM}^{-1} \text{ h}^{-1}) = \frac{Abs_{1\text{ cm}}^{490\text{ nm}} \times V_r \times V_h \times 60}{V_a \times DM \times t \times 1.42}$$

where $Abs_{1\text{ cm}}^{490\text{ nm}}$ is absorption of formazan, V_r total sample volume (3 mL), V_h volume of homogenization buffer (4 ml), V_a volume of homogenization buffer in the sample (0.5 ml), DM dry mass of sample, and t time of incubation (40 min). The $1.42 Abs_{1\text{ cm}}^{490\text{ nm}}$ is equal to $1 \mu\text{l O}_2$.

Area-ETSA was calculated using the determined ETSA per wet mass and the sediment amount in a surface layer of 1 m² and 20 cm depth. For this purpose, sediment samples of known volume (1-5 cm³) were weighed on an electrobalance (BP210S, Sartorius AG, Goettingen, Germany). Conversion to $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ was used to compare ETSA with R, where a conversion factor of 1 ml O₂ = 44.66 $\mu\text{mol O}_2$ (Lampert, 1984) and a respiratory quotient of 0.85 (Dilly, 2001) were applied:

$$ETSA (\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}) = ETSA (\text{ml O}_2 \text{ m}^{-2} \text{ h}^{-1}) \times \frac{1}{3600} \times 44.66 (\mu\text{mol O}_2 \text{ ml}^{-1}) \times RQ$$

In order to calculate ETSA/R ratios, the correction for temperature was carried out for both ETSA and R. The Arrhenius equation was used to convert ETSA at the incubation temperature (20°C) to that at a standardized temperature (12°C):

$$ETSA_{12^\circ\text{C}} (\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}) = ETSA_{inc} (\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}) \times e^{E_a \left(\frac{1}{T_{inc}} - \frac{1}{T_{12^\circ\text{C}}} \right) / R_u}$$

where E_a is the activation energy (a value of 15 kcal mol⁻¹) (Båmstedt, 1980) and R_u is the universal gas constant (1.985 calories per mole degree Kelvin). Incubation temperature ($T_{inc}=20^\circ\text{C}$) and standardized temperature ($T_{12^\circ\text{C}}$) were converted to Kelvin (K) to have the same units as R_u . The temperature of 12°C was chosen as this value reflects the mean soil and sediment temperature across habitats, seasons and study floodplains.

Respiration measured *in situ* in aquatic sediments and terrestrial habitats was standardized for temperature (12°C) using the following equation:

$$R_{12^{\circ}C}(\mu mol\ CO_2\ m^{-2}s^{-1}) = a \times e^{b(T-T_{12^{\circ}C})}$$

where T is the temperature measured at 5 cm soil depth (terrestrial habitat) or the temperature of the chamber water (aquatic habitat). The parameters a and b were calculated using nonlinear regression applied to R and temperature data of each individual habitat type in the Urbach floodplain. For the Soča, parameters calculated for the Tagliamento River were applied (Doering *et al.*, 2011) due to the close proximity and similar characteristics of the two floodplains.

Statistical analyses

Two-way ANOVA with habitat (five levels) and season (three levels) as independent factors was applied separately for each floodplain to test for differences in ETSA, ETSA/ R , temperature, water and organic matter content and grain size distribution. One-way ANOVA with habitat as the independent factor was carried out to test for differences in R during summer. The Tukey's HSD post hoc test was used to find out which means were significantly different from one another. Data on ETSA, R (standardized at 12°C), ETSA/ R , temperature, and water and organic matter contents were log-transformed and data on grain size distributions were arcsine square-root transformed to meet ANOVA assumptions. Variation in temperature and soil/sediment structural properties across habitat types was examined separately for the two floodplains by applying standardized principal component analysis (PCA) based on a correlation matrix where data were centered and standardized (ter Braak and Šmilauer, 2002). The PCA was run using CANOCO 4.5 (ter Braak and Šmilauer, 2002). Multilevel (hierarchical) multiple regression analysis (HLM) was performed to control for the effects of covariates (habitat type, season) and to test the effects of predictors (temperature, water content, organic matter content, grain size) on the response variable (ETSA). Prior to analysis, variables were checked for

normality by examining the normal quartile plots (Q-Q plots) and conducting Shapiro-Wilk tests. Data on grain size distribution were arcsine square-root transformed and data on ETSA were log transformed to achieve normality. The assumption of collinearity was tested by calculating VIF and tolerance and the assumption of independent errors was checked by calculating Durbin-Watson values. In order to estimate the effect of covariates, the explained proportion of variance (r^2) and significance (p) were calculated for the model with covariates only (model 1) and for the full model (model 2). Step-wise selection of variables was applied for model 2 to include only significant variables. Linear regression was applied on log-transformed data to test whether ETSA was a good predictor of soil/sediment respiration (R) in both floodplains. All statistics, except PCA, were calculated using the Statistical Package for Social Sciences (SPSS) version 18.0 for Windows (SPSS Inc, Chicago, IL, U.S.A.).

Results

Characteristics of floodplain soils and sediments

Mean temperature by habitat type ranged from $9.2 \pm 3.6^\circ\text{C}$ (channel) to $15.8 \pm 8.8^\circ\text{C}$ (gravel bar) in the Urbach and from $11.5 \pm 2.7^\circ\text{C}$ (channel) to $17.8 \pm 5.4^\circ\text{C}$ (islands) in the Soča (Table 2). Temperature was significantly affected by season (Urbach: $F_{2,300}=582.9$, $P<0.001$; Soča: $F_{2,179}=294.6$, $P<0.001$) and habitat type (Urbach: $F_{4,300}=22.6$, $P<0.001$; Soča: $F_{4,179}=51.0$, $P<0.001$) in both floodplains. In both floodplains, soil/sediment water content was significantly highest in riparian forest and grassland habitats ($>28.3\%$) and lowest in gravel-bar habitats ($<5.6\%$) (Urbach: $F_{4,300}=278.1$, $P<0.001$; Soča: $F_{4,179}=121.3$, $P<0.001$). Similarly, significantly lower organic matter content (<12.2 g AFDM kg^{-1}) was found in gravel bars and channel sediments, consisting mainly of grain sizes >4 mm (Urbach: $F_{4,300}=522.5$, $P<0.001$; Soča: $F_{4,179}=230.4$, $P<0.001$) (Table 2). High organic matter content (>71.9 g AFDM kg^{-1}) was found

in soils from islands, riparian forests and grasslands and was associated with high amounts of grain size fractions 2-0.063 mm (>55.1%). All grain sizes were significantly different among habitat types in the Urbach ($F_{4,300}>82.6$, $P<0.001$) and in the Soča floodplain ($F_{4,99}>11.7$, $P<0.001$). Water, organic matter contents, and grain sizes 8-4 and 2-0.063 mm significantly varied over season in the Soča (WC: $F_{2,179}=12.6$, $P<0.001$; OM: $F_{2,179}=16.2$, $P<0.001$; 8-4 mm: $F_{4,99}=4.6$, $P<0.05$; 2-0.063 mm: $F_{4,99}=7.7$, $P<0.01$), and grain size <0.063 mm in the Urbach floodplain ($F_{4,300}=6.7$, $P<0.01$).

The PCA explained 62.3% of the variability in the environmental data (temperature, structural variables) on the first axis and 13.5% on the second axis for the Urbach floodplain. For the Soča floodplain, 52% of the variability was explained by the first axis and 14.2% by the second axis. In both floodplains, Axis-1 was positively associated with grain sizes <0.063 mm and 2-0.063 mm and water and organic matter contents, and negatively associated with grain sizes >8 mm, 8-4 mm and 4-2 mm (Figs. 3a,b). Axis-2 was positively associated with temperature and negatively with water content in both cases. In general, there was a clear separation in structural characteristics between the channel and gravel-bar habitats and the island, riparian forest and grassland habitats in both floodplains. However, the variability in structural variables between terrestrial habitats was less prominent in the Urbach than in the Soča floodplain.

Spatiotemporal variability in ETSA

ETSA in channel sediments was lowest and similar in both floodplains (Figs. 3a, b). In the Urbach floodplain, mean ETSA was higher in gravel than in the channel and exceeded values of the Soča gravel threefold. In the Urbach floodplain, a pattern of gradual exponential increase in ETSA was observed from the permanent aquatic habitat (channel) to semi-terrestrial and

terrestrial habitats, with grasslands that are the least frequently flooded having the highest ETSA. Surprisingly, ETSA measured in samples from the Soča islands was much lower than those from the Urbach floodplain, whereas ETSA of riparian forest and grassland had comparable values.

Seasonally, mean ETSA varied least in channels and most in grassland soils at both floodplains (Fig. 4). The seasonal pattern in ETSA was inconsistent across habitats and floodplains. For example, ETSA was lowest in autumn in the island soils from Urbach, while ETSA was highest during autumn in Soča island soils. In contrast, ETSA of riparian forest soils was highest during the autumn in the Urbach floodplain and lowest during the latter season in the Soča floodplain. Significant differences between habitat types (Urbach, $F_{4,300}=232.1$, $P<0.001$; Soča, $F_{4,180}=177.4$, $P<0.001$) but not season were observed for both floodplains (Urbach, $F_{2,300}=1.1$, $P>0.05$; Soča, $F_{2,180}=1.1$, $P>0.05$). In the Urbach, significant differences were found among all habitat types except from gravel and channel habitats. In the Soča, ETSA in channel and gravel, and riparian forest and grassland, did not significantly differ. The coefficient of variation (CV) in seasonal ETSA values was lower for the Urbach (CV=130%) than for the Soča (CV=152%).

R and ETSA/R

Mean R (standardized for temperature at 12°C) in August was higher in the Urbach ($1.6 \pm 1.5 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) than in the Soča ($1.3 \pm 2.0 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) (Table 3), and differences between habitat types were significant in both floodplains (Urbach: $F_{4,100}=70.0$, $P<0.001$; Soča, $F_{4,59}=44.8$, $P<0.001$). Mean R in channel and gravel-bar habitats was much lower ($0.1\text{--}0.2 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) than in the other habitat types ($2.1\text{--}4.8 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). In the Soča, mean R and its variation was significantly highest for islands ($4.8 \pm 1.9 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), followed by riparian forests and grasslands (3.2 ± 1.8 and $3.7 \pm 0.7 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, respectively). R in the Urbach

floodplain was highest ($3.1 \pm 1.2 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) for grasslands but not significantly different from other two terrestrial habitats. The overall CV for R was lower in the Urbach (CV=94%) than in the Soča floodplain (CV=156%).

ETSA/R ratios (standardized at 12°C) were generally higher for the Urbach than for the Soča (means 4.1 and 1.3, respectively), indicating lower exploitation of respiratory potential in the former (Fig. 5). An exception was riparian forest, where ratios were comparable between the two floodplains (Urbach: 2.7 ± 1.6 , Soča: 2.6 ± 2.1). Ratios were lowest during spring, indicating the highest exploitation of respiratory potential during this season. At the floodplain scale, channel, island, riparian forest and grassland habitats from Urbach and gravel-bar, riparian forest and grassland habitats from Soča had mean ETSA/R ratios ranging from 1.0 to 3.1; ratios were significantly lower for islands of the Soča (0.4) and highest for gravel-bar habitats of the Urbach (>10) (Urbach: $F_{4,238}=16.9$, $P<0.001$; Soča, $F_{4,83}=6.0$, $P<0.001$). The regression of ETSA as an estimator of R was significant ($P<0.0001$) for both floodplains, while the predictability of the obtained models was higher for the Urbach ($R^2=0.73$) than for the Soča floodplain ($R^2=0.61$) (Fig. 6).

The relation between temperature and structural characteristics and floodplain functioning

Hierarchical linear models were significant for both floodplains (Table 4.). The results showed significant effects of water and organic matter contents, and grain size <0.063 mm on ETSA for both floodplains. Additionally, grain sizes >8 mm and 2-0.063 mm were significant predictors of ETSA for the Soča floodplain. Temperature, and grain sizes 8-4 mm and 4-2 mm did not show significant effects on ETSA. The most important predictor was organic matter as indexed by β values of 0.44 (Urbach) and 0.31 (Soča). The models indicated that a 1.0 g unit increase in organic matter content was associated with a 0.3 unit increase in ETSA for the Urbach

floodplain, and with a 0.2 unit increase in ETSA for the Soča floodplain. Significant random effects were found for habitat types for both floodplains and for season for the Soča floodplain. The habitat type and season solely explained 69% and 71% of the variability in data for the Urbach and Soča floodplains, respectively (model 1). Adding the environmental predictors improved the models to explain 78% and 83% of the variability, respectively.

Discussion

Spatio-temporal variation in ETSA

As expected, ETSA was highly variable in time and space, following the seasonal dynamics and environmental heterogeneity among habitat types of the study floodplains. In general, spatial patterns in ETSA across the two study floodplains were consistent. For instance, ETSA was lowest in coarse channel and gravel-bar sediments containing low amounts of organic matter, and was substantially higher in fine grained soils from islands, riparian forest and grassland that were rich in organic matter content. Likewise, ETSA exhibited patchy distributions within single habitat types, reflecting the variation in measured structural properties of soils/sediments (Fig. 3a, b). Similar spatial patterns of carbon flux, measured as soil/sediment R , were observed at the Tagliamento floodplain (Doering *et al.*, 2011) and Thur River (Samaritani *et al.*, 2011). ETSA in channel and gravel-bar sediments of the Soča and Urbach River was similar to other Alpine gravel-bed rivers (Table 5). Generally, ETSA reported from different freshwater and semi-terrestrial ecosystems ranged from 0.1 to 310 $\mu\text{L O}_2 \text{ g DM}^{-1} \text{ h}^{-1}$, being highest in lake sediments (39-310 $\mu\text{L O}_2 \text{ g DM}^{-1} \text{ h}^{-1}$) where high amounts of labile autochthonous organic matter are present and anaerobic processes often occur (Muri and Simčič, 2004). We identified organic matter and water content and particles $<0.063 \text{ mm}$ as significant controlling factors of ETSA in both floodplains. Additionally, particles $>8 \text{ mm}$ and $2-0.063 \text{ mm}$ were significant predictors of

ETSA for the Soča floodplain. Those results are in accordance with other studies indicating that organic matter, water content and sediment structure are important drivers of microbial metabolic activity (e.g., Romani and Sabater, 2001; Muri and Simčič, 2004; Simčič and Mori, 2007; de Vicente *et al.*, 2010; Wilson *et al.* 2011). For example, Romani and Sabater (2001) observed higher enzyme activities in fine sediments (particle size < 2 mm) in comparison to coarser substrate and explained it with higher organic matter accumulation and development of simpler biofilms with lower biomass and cell size. Though Mendoza-Lera *et al.* (2017) provided evidence that sediment surface area together with rates of advective mass transfer that includes concentration of solutes, redox partners, vertical water flux and pore water flow underlined the biofilm metabolic activity in gravel-sand rivers. Moisture is a key driver of soil microbial activity (Baldwin and Mitchell, 2000; Fierer and Schimel, 2002; Wilson *et al.*, 2011) by influencing microbe substrate availability (Stres *et al.*, 2008). Higher soil water content increases the availability of labile compounds, resulting in intense microbial growth and activity, while the presence of fine particles increases the surface to volume ratio available for biofilm growth. Additionally, the formation of soil aggregates is also important for microbial activity since it influences carbon availability (Trivedi *et al.*, 2015). For channel sediments, ETSA was shown to be much higher for fine-grained (<0.1 mm) than coarse-grained sediments due to higher surface to volume ratios and higher organic matter content of finer sediments (Simčič and Mori, 2007). This result is probably the case in this study, where floodplain soils/sediments from islands, riparian forests and grasslands had highest organic matter content, water content and fine-grained sediments and consequently highest ETSA.

ETSA increased, albeit non-significantly, for islands and grasslands of the Urbach floodplain and in gravel bars and grasslands of the Soča floodplain in summer (Fig. 4). Several studies observed an increase in ETSA during summer and explained it by a combination of higher

seasonal summer temperatures and nutrient availability (G.-Tóth *et al.*, 1994; Urbanc-Berčič and Gaberščik, 2004; de Vicente *et al.*, 2010; Germ and Simčič, 2011). This was not the case in this study, where, despite the fact that temperatures varied significantly between seasons, it was not a significant predictor for ETSA (Table 4). This pattern was similarly shown by Romaní and Sabater (2001), where ETSA did not co-vary with temperature but with organic matter quantity. Likewise, Hall *et al.* (2010) demonstrated in a series of experiments that microbial functioning is linked with complex interactions between environmental temperature and resource quality and quantity.

ETSA of different habitat types was always highest in the Urbach even though respective structural properties of soils/sediments did not differ substantially between the two floodplains (Figs. 3a, b). Large-scale drivers, most probably linked with nutrient availability could be associated with land-use differences between the two floodplains and flow alteration in the Urbach floodplain as mentioned above. In contrast to the Soča floodplain, where 64% of the land use was riparian forest, 69% of the Urbach floodplain was pasture/grassland with intense livestock grazing. Livestock increase organic matter, and N and P inputs in soils from feces and urine, resulting in increased microbial biomass, and N and P mineralization rates (Tracy and Frank, 1998; Frank *et al.*, 2000; Güsewell *et al.*, 2005; Martinsen *et al.*, 2012). These effects likely resulted in higher overall ETSA in the Urbach than the Soča floodplain (see Relexans, 1996). A similar pattern was observed when extracellular microbial enzymes, degrading different types of substrates (proteins, peptides, cellulose, etc.) were measured at the two study floodplains (Bodmer *et al.*, 2016).

In contrast to the Urbach, ETSA on Soča floodplain islands was substantially lower than for other terrestrial habitats and more similar to channel and gravel-bar sediments, while ETSA on grassland and riparian forest did not significantly differ. A possible reason for low ETSA on

islands could be due to the different hydrological patterns in the two floodplains. In the Soča, several flood events >10 times higher ($>200 \text{ m}^3 \text{ s}^{-1}$) than average annual discharge occurred during the study year (Fig. 2b), depositing large amounts of fresh sediments on the islands covering soils with established microbial communities (N. Mori, pers. obs). Small differences in ETSA between grassland and riparian forest in the Soča floodplain could be due to a lack of additional nutrient input that occurs in the Urbach floodplain due to livestock grazing (Bodmer *et al.*, 2016). Moderately higher respiratory potential in riparian forest of the Soča floodplain is likely due to higher plant biomass input. The respiratory potential was shown to be higher in habitats with higher organic matter input (Urbanc-Berčič and Gabersčik, 2003).

Higher spatial heterogeneity in ETSA among habitat types was observed in the Urbach floodplain, despite lower variation in structural heterogeneity in comparison to the Soča floodplain. This pattern reflected a stronger gradient in respiratory potential across habitat types, from the channel and islands to the grassland in the former floodplain. The primary force maintaining the distribution, connectivity, and structural and functional features of floodplain habitats was the magnitude, frequency, duration, and timing of flow events (Junk *et al.*, 1989; Poff *et al.*, 1997; Stanford *et al.*, 2005). Water abstraction at dams and disconnection of habitats by levees, as in the Urbach, narrowed the active floodplain and had severe effects on the frequency of flow and lateral extension of flood pulses that lead to habitat shifts from being hydrological- disturbance dominated to having more terrestrial-like attributes (Doering *et al.*, 2012). Additionally, in the Urbach floodplain, grasslands are used for livestock grazing, which are a source of additional nutrient input that can result in increased respiratory potential (Muri and Simčič, 2004; Bodmer *et al.*, 2016). In the Soča floodplain, frequent floods, occurring mainly in autumn but also in spring, are characteristic and support the exchange of sediment, organic matter and nutrients, and shape habitat structure (vegetation cover, soil/sediment structure, etc.)

and function (e.g., respiratory potential and respiration). Accordingly, less difference in ETSA was observed between habitats in the Soča.

Patterns of ETSA/R in floodplain soils/sediments

Spatial patterns in ETSA/R ratios at 12°C were inconsistent between the two floodplains. In the Soča floodplain, the mean ETSA/R ratio was highest for riparian forest and lowest for island soils. In the Urbach floodplain, the mean ratio was highest in gravel-bar sediments and lowest in channel sediments. Previously reported ETSA/R ratios ranged from 1.5 to 7.7 for superficial lake sediments with highest ratios for eutrophic lakes (Jones and Simon, 1979; Muri and Simčič, 2004), from 0.2 to 1.4 for hyporheic sediments (Simčič and Mori, 2007), and from 1.6 (channel) to 15 (grassland) for inundated floodplain soils/sediments (Simčič *et al.*, 2015). The low ETSA/R for Soča island soils was due to extremely high R. In terrestrial habitats, R encompasses both microbial and autotrophic, i.e. root respiration (Doering *et al.*, 2011), which may contribute to the high R in the Soča islands. Root respiration can contribute from 10% to >90% of total *in situ* soil respiration depending on vegetation type and season (Hanson *et al.*, 2000). In contrast, high ETSA/R ratios were observed in the Urbach gravel-bar habitats, where moderate ETSA and extremely low R activity (i.e., CO₂ efflux) were measured. Low R was most probably due to low water content. In the Soča gravel, ratios were lower compared to the Urbach because of low ETSA and R. The observed differences are most likely due to higher nutrient and lower water content of gravel sediments in the Urbach floodplain.

ETSA/R provides functional information on the exploitation in overall metabolic capacity, indicating how far R is from its maximum respiratory capacity (Simčič *et al.*, 2015). The ratio depends on R, which is a complex physiological process that reacts quickly to changes in environmental conditions, and ETSA, which is an enzymatic process. ETSA depends on the

concentration and characteristics of enzymes that require time to reach equilibrium after environmental change and encompass an array of metabolic pathways (from aerobic to anaerobic) (Båmstedt, 1980; Packard, 1971). The regression analysis of ETSA as a predictor of R was significant for both floodplains (Fig. 5), indicating that ETSA can be used for robust estimation of actual soil/sediment R across floodplain habitats, as suggested by Relexans (1996).

Some methodological constraints are present when calculating ETSA/R. First, a comparison of R between aquatic and terrestrial habitat types can be limited as two different methods for quantifying R must be used. In aquatic habitats, the closed chamber system is widely used to estimate sediment R (Pusch and Schwoerbel, 1994; Jones *et al.*, 1995), and the conversion of R from closed chamber to a specific stream-bed volume is complex (Naegeli and Uehlinger, 1997). Further, stream-bed R varies in relation to hydrological pathways that include vertical and lateral exchange of surface- and groundwater. In contrast, measurements of terrestrial R provide values from relatively undisturbed substratum with known surface area, and soil R is composed of soil microbial respiration (50-70% of total soil respiration) and root respiration that varies seasonally and with vegetation type, and can account for 10 to 90% of total *in situ* soil respiration (Hanson *et al.*, 2000; Buchmann, 2000). Respiratory potential is measured in the laboratory without including roots, thus giving an estimate of only microbial respiration potential. Regardless, the information on how the R/ETSA ratios vary with environmental conditions remains of fundamental importance towards understanding the adaptive links between organism physiology and their habitats (Relexans, 1996). This linkage was clearly demonstrated in an inundation study of floodplain soils and sediments by Simčič *et al.* (2015) where the intensity of exploitation in respiratory potential was suppressed (high ETSA/R ratio) immediately after short-term inundation of soils from predominantly terrestrial habitats that are less frequently flooded. In contrast, an increase in temperature caused a greater exploitation of respiratory potential (low

ETSA/R) in those habitats in comparison to aquatic habitats, suggesting the importance of environmental warming for enhancing heterogeneity of carbon fluxes across floodplains. In this study, the lower exploitation of respiratory potential (higher ETSA/R) in the Urbach floodplain reflected the higher ETSA of the Urbach soils and sediments in comparison to the Soča floodplain. Nutrient inputs due to livestock, as already suggested by Bodmer *et al.* (2016) likely stimulated respiration as well as microbial enzyme activities in the former floodplain. For ETSA, it is well known that increases occur after soil/sediment amendment (Trevors *et al.*, 1982).

Soil and sediment respiration is an important process for the turnover of dissolved and particulate organic carbon in floodplain systems and can range widely as, for example, in the Tagliamento River floodplain from 160 (floodplain ponds) to 1205 g C m⁻² year⁻¹ (islands) (Doering *et al.*, 2011). In this study, mean daily carbon turnover through R during summer varied across habitats from 0.01 to 19 g C m⁻² day⁻¹ in the Soča and from 0.01 to 5.22 g C m⁻² day⁻¹ in the Urbach floodplain. Estimated mean carbon pools in the form of AFDM (based on the assumption that ca. 58% of AFDM is C) ranged from 5.9 to 269 g C kg⁻¹ DM_{sed} for the former and from 1.9 to 88.1 g C kg⁻¹ DM_{sed} for the latter floodplain. In forested catchments, the major terrestrial inputs of carbon to rivers are large woody debris, litter inputs, inputs of fine particulate organic matter and dissolved organic carbon. The on-site litter biomass of floodplain forest was estimated to be on average 592 g C m⁻² (Robertson *et al.*, 1999). Conversely, during floods, suspended sediment originating from the tributaries, containing large amounts of particulate organic matter, is transported from the river channel to the floodplain and is estimated to be from 50-290 g C m⁻² year⁻¹ (Robertson *et al.*, 1999; Tockner *et al.*, 1999). The observed differences in the functioning of the study floodplains were the result of a mixture of distinct driving forces such as climate, flooding patterns, land use and human impact.

Conclusions

Structural properties of soils/sediments were important determinants for differences in ETSA and R within each floodplain. For example, fine-grained soils from riparian forest and grasslands contributed substantially to overall floodplain respiratory potential. Islands played an important role in carbon mineralization as well. On the other hand, gravel-bars had similar ETSA as channel sediments, which were quite low during dry periods with low R. However, gravel bars can quickly shift from a respiratory inactive compartment into an active one when rewetted, whereas floodplain forest soils turn from high respiratory activity into more inactive soils under the similar conditions (Simčič et al., 2015). Overall, this functional heterogeneity was comparable in the two study floodplains with differing land use, while showing different intensities of ETSA.

The rates of R and ETSA varied widely in the study floodplains, indicating high spatial heterogeneity in carbon fluxes within each floodplain as well as documented differences between them. Land use in concert with alterations in habitat heterogeneity can cause dramatic changes in floodplain function. Consequently, functional alterations of floodplains can lead to a disproportional shift in carbon budgets; e.g., changes in the area of the pasture/grassland with high carbon turnover rates have a much higher impact on the total carbon budget than changes in gravel habitats characterized by low turnover rates. This, in turn, would have major consequences for total carbon turnover rates at the whole floodplain scale. A shift in carbon turnover at the floodplain scale can lead to an imbalance between decomposition and net primary production with potential impacts to carbon cycling and sequestration in riverine ecosystems; i.e., affecting sources and sinks of carbon. This study provided better understanding towards predicting and evaluating changes in floodplain functioning due to environmental change (e.g., flow alterations) and human alterations, including the sustainable use and restoration of fluvial floodplains.

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Table 1. Main features of the study floodplains. Data on climate are from MeteoSchweiz and the Slovenian Environmental Agency.

	Urbach	Soča
Geographical location	46°41' N, 8°12' E	46°20' N, 13°33' E
Altitude	790 - 910 m a.s.l.	350 - 370 m a.s.l.
Length x width	3.4 x 0.6 km	5.0 x 0.6 km
Geology	Limestone and granite	Limestone and dolomite
Climate	Subalpine	Mediterranean
Mean annual air T (1960-2010)	7.2 - 10°C	8.4 – 11.4°C
Mean annual precipitation (1961-1990)	1614 mm (Guttannen, 1055 m a.s.l.)	2650 mm (Bovec, 438 m a.s.l.)
Land use	Pasture and grassland (69%), forest (17%)	Pasture and grassland (12%), forest (64%)
Discharge regime	Glacio-nival	Nivo-pluvial
Mean annual discharge	2 m ³ s ⁻¹	23.8 m ³ s ⁻¹
Nutrient concentrations in the study rivers		
NO ₃ ⁻ (mg l ⁻¹)	1.7 ± 1.1	1.3 ± 0.2
NH ₄ ⁺ (mg l ⁻¹)	0.0 ± 0.0	0.0 ± 0.0
PO ₄ ³⁻ (mg l ⁻¹)	0.0 ± 0.0	0.0 ± 0.0
N _{tot} (mg l ⁻¹)	0.6 ± 0.2	0.7 ± 0.2
P _{tot} (μg l ⁻¹)	2.9 ± 0.6	13.3 ± 4.2

Table 2. Temperature and structural characteristics of floodplain soils/sediments. C - channel; G - gravel; I -islands; RF - riparian forest; GL - grassland. AFDM - ash-free dry mass. Values are means (May, Aug, Oct/Nov) and standard deviations ($\pm$).

	Urbach					Soča				
	C	G	I	RF	GL	C	G	I	RF	GL
	<i>N</i> =60	<i>N</i> =60	<i>N</i> =60	<i>N</i> =60	<i>N</i> =60	<i>N</i> =59	<i>N</i> =30	<i>N</i> =30	<i>N</i> =30	<i>N</i> =30
Temperature (°C)	9.2 $\pm$ 3.6 ^a	15.8 $\pm$ 8.8 ^b	12.4 $\pm$ 5.7 ^c	11.7 $\pm$ 4.5 ^c	13.6 $\pm$ 6.2 ^{b,c}	11.5 $\pm$ 2.7 ^a	15.9 $\pm$ 5.3 ^b	17.8 $\pm$ 5.4 ^c	15.0 $\pm$ 4.1 ^b	15.9 $\pm$ 5.0 ^b
Water content (%)	9.8 $\pm$ 0.5 ^a	2.3 $\pm$ 2.2 ^b	21.6 $\pm$ 13.1 ^c	31.8 $\pm$ 12.4 ^d	35.5 $\pm$ 9.9 ^d	9.7 $\pm$ 1.0 ^a	5.6 $\pm$ 3.2 ^b	13.3 $\pm$ 7.2 ^a	34.9 $\pm$ 13 ^c	28.3 $\pm$ 8.8 ^c
OM _{tot} (g AFDM kg ⁻¹)	3.4 $\pm$ 1.0 ^a	4.2 $\pm$ 2.3 ^a	71.9 $\pm$ 71.6 ^b	141.3 $\pm$ 88.4 ^c	151.8 $\pm$ 77.6 ^c	10.3 $\pm$ 3.6 ^a	12.1 $\pm$ 6.9 ^a	382.6 $\pm$ 283 ^b	464.8 $\pm$ 322 ^b	239.7 $\pm$ 97.1 ^b
Grain size distribution										
>8 mm (%)	54.4 ^{+a}	54.4 $\pm$ 21.1 ^a	9.3 $\pm$ 15.4 ^b	6.3 $\pm$ 13.2 ^b	8.6 $\pm$ 15.5 ^b	32.8 ^{+a}	32.8 $\pm$ 19.6 ^a	0 ^b	4.3 $\pm$ 8.0 ^c	10.4 $\pm$ 11.9 ^d
8-4 mm (%)	17.9 $\pm$ 4.7 ^a	11.5 $\pm$ 4.9 ^b	4.0 $\pm$ 7.0 ^c	2.4 $\pm$ 3.9 ^c	2.3 $\pm$ 2.4 ^c	25.6 $\pm$ 13.5 ^a	22.7 $\pm$ 4.7 ^a	0.1 $\pm$ 0.2 ^b	2.3 $\pm$ 3.2 ^b	12.4 $\pm$ 10.6 ^c
4-2 mm (%)	13.7 $\pm$ 2.0 ^a	8.5 $\pm$ 5.0 ^b	3.8 $\pm$ 3.9 ^c	2.9 $\pm$ 4.9 ^c	3.1 $\pm$ 3.4 ^c	16.2 $\pm$ 7.5 ^a	16.6 $\pm$ 7.2 ^a	1 $\pm$ 1.5 ^b	6.7 $\pm$ 15.6 ^c	18.4 $\pm$ 13.5 ^d
2-0.063 mm (%)	13.9 $\pm$ 4.9 ^a	25.1 $\pm$ 17.4 ^b	80.6 $\pm$ 21.3 ^c	86.3 $\pm$ 13.1 ^c	83.4 $\pm$ 17.6 ^c	25.2 $\pm$ 15.0 ^a	27.4 $\pm$ 12.3 ^a	90.9 $\pm$ 8.0 ^b	68.5 $\pm$ 14.8 ^{b,c}	55.1 $\pm$ 20.5 ^c
<0.063 mm (%)	0.1 $\pm$ 0.1 ^a	0.4 $\pm$ 0.4 ^b	2.4 $\pm$ 2.0 ^c	2.1 $\pm$ 1.7 ^c	2.6 $\pm$ 1.6 ^c	0.1 $\pm$ 0.3 ^a	0.4 $\pm$ 0.2 ^a	8.0 $\pm$ 8.4 ^b	18.2 $\pm$ 14.8 ^c	3.7 $\pm$ 4.8 ^d

+Estimate based on the grain size distribution of gravel habitats.

^{a,b,c,d,e}, significant differences between habitats, $p < 0.05$

Significant differences ($p < 0.05$) between seasons were in temperature for both floodplains, in grain size (<0.063 mm) for the Urbach, and in the water and organic matter contents for the Soča floodplain.

Table 3. Respiration ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) standardized at 12°C in individual habitat types measured by the flux chamber method (terrestrial habitats) and closed chamber method (aquatic habitat) in the two floodplains in August 2010.

	Urbach (N=100)			Soča (N=60)		
	mean	SD	CV	mean	SD	CV
Channel	0.17 ^a	± 0.10	62	0.13 ^a	± 0.28	213
Gravel	0.01 ^a	± 0.03	521	0.07 ^a	± 0.14	200
Islands	2.09 ^b	± 1.01	48	4.76 ^b	± 1.87	39
Riparian forest	2.52 ^b	± 0.81	32	3.22 ^c	± 1.80	56
Grassland	3.14 ^b	± 1.20	38	3.69 ^{b,c}	± 0.71	19
overall	1.58	± 1.49	94	1.26	± 1.97	156

^{a,b,c} significant differences between habitats, $P<0.001$

Table 4. Results of hierarchical multiple regression analysis (HLM) with respiratory potential as response variable. The effects of covariates (habitat types, season) and the effects of predictors (temperature, water content, organic matter content, grain size) were tested on the response variable.

	coefficient	SE	β	p
Urbach floodplain (N=300)				
(Constant)	-0.21	0.049		<0.001
Habitat type	0.10	0.020	0.28	<0.001
Season	-0.00	0.016	-0.01	0.86
OM _{tot}	0.31	0.057	0.44	<0.001
<0.063 mm	0.48	0.146	0.14	<0.01
Water content	0.12	0.055	0.11	<0.05
Soča floodplain (N=179)				
(Constant)	-0.72	0.13		<0.001
Habitat type	0.15	0.02	0.47	<0.001
Season	-0.07	0.02	-0.12	<0.001
<0.063 mm	0.34	0.06	0.26	<0.001
OM _{tot}	0.19	0.05	0.31	<0.001
> 8 mm	0.24	0.06	0.30	<0.001
2-0.063 mm	0.12	0.04	0.17	<0.01
Water content	0.18	0.08	0.12	<0.05
Urbach: Model 1: $R^2=0.692$, $p<0.001$; Model 2: $R^2=0.779$, $p<0.001$				
Soča: Model 1: $R^2=0.713$, $p<0.001$; Model 2: $R^2=0.831$, $p<0.05$				

Table 5. Respiratory potential (ETSA) in different soils and freshwater sediments from various studies applying the same laboratory procedure.

Type of sample	Depth (cm)	ETSA ($\mu\text{l O}_2\text{gDM}^{-1}\text{h}^{-1}$)	ETSA ($\mu\text{l O}_2\text{gWM}^{-1}\text{h}^{-1}$)	T _{inc} (°C)	Source
Aquatic sediments (rivers)					
Soča River, Slovenia	0-20	0.09 ± 0.09	0.08 ± 0.07	20	This study
Urbach River, Switzerland	0-20	0.15 ± 0.13	0.13 ± 0.11	20	This study
Bača River, Slovenia	30-60	-	0.23 ± 0.17	20	Mori <i>et al.</i> (2011)
Sava River, Slovenia	30-90	0.27 ± 0.10	0.21 ± 0.08	20	Mori <i>et al.</i> (2012)
Gravel					
Soča River, Slovenia	0-10	0.10 ± 0.10	0.10 ± 0.10	20	This study
Bača River, Slovenia	60-90	-	0.19 ± 0.09	20	Mori <i>et al.</i> (2011)
Sava River, Slovenia	240-270	0.37 ± 0.44	0.29 ± 0.35	20	Mori <i>et al.</i> (2012)
Urbach River, Switzerland	0-10	0.39 ± 0.49	0.37 ± 0.44	20	This study
Floodplain islands					
Soča River, Slovenia	0-10	2.63 ± 2.05	2.20 ± 1.67	20	This study
Urbach River, Switzerland	0-10	5.79 ± 6.33	4.26 ± 3.99	20	This study
Riparian forest					
Urbach River, Switzerland	0-10	8.34 ± 6.58	5.87 ± 4.04	20	This study
Soča River, Slovenia	0-10	10.37 ± 5.82	6.44 ± 3.01	20	This study
Floodplain grasslands					
Soča River, Slovenia	0-10	6.66 ± 4.30	4.76 ± 3.04	20	This study
Urbach River, Switzerland	0-10	11.29 ± 6.83	7.89 ± 4.06	20	This study
Wetlands					
terrestrial reed stands, Lake Cerknica, Slovenia	30	53.38 ± 44.81	-	20	Urbanc-Berčič and Gaberščik (2003)
Aquatic sediments (lakes)					
Lake Bohinj, Slovenia	0-10	39.30 ± 19	-	20	Germ and Simčič (2011)
Lake Ledvica, Slovenia	0-5	75	-	20	Muri and Simčič (2004)
Lake Kriško, Slovenia	0.5	165	-	20	Muri and Simčič (2004)
Lake Planina, Slovenia	0-5	275	-	20	Muri and Simčič (2004)
Lake Bled, Slovenia	0-5	310	-	20	Muri and Simčič (2004)

T_{inc} – temperature of incubation during ETSA analysis; DW – dry weight (24 h, 105°C); WW – wet weight. * There are other studies measuring INT reduction activity in soils, but the methodology is different and the results are not comparable with the results above.

Fig. 1. Aerial views of the Urbach River floodplain in 2007 (upperleft) and the Soča River floodplain in 2006 (below). The corresponding map of the Alpine Region indicates the locations of the floodplains. Source: Surveying and Mapping Authority of the Republic of Slovenia and Bundesamt für Landestopografie, Switzerland.

173x189mm (600 x 600 DPI)

Fig. 2. Mean daily discharge of the Urbach (a) and Soča (a) Rivers in 2010. Asterisks indicate the sampling dates and dotted line the mean annual discharge.

191x226mm (600 x 600 DPI)

Fig. 3. The relationship between PCA axis-1 scores on structural characteristics of soils/ sediments and respiratory potential for the Urbach (a) and Soča (b) floodplains. Symbols are mean values of scores and error bars are standard deviations.

209x296mm (600 x 600 DPI)

Fig. 4. Box plots of respiratory potential measured at 20°C in soils/sediments collected over three seasons from five habitats in the Urbach and Soča floodplains. Empty circles (o) indicate outliers and the lines are means. N=20 for each box plot for the Urbach habitats and the Soča channel and N=10 for the Soča gravel, islands and two other terrestrial habitats. a,b,c,d significant differences between habitats, p<0.05.

109x62mm (600 x 600 DPI)

Fig. 5. Box plots for ETSA/R ratios across habitats and the two floodplains standardized at 12°C. Empty circles (o) indicate outliers and the lines in the boxes are means. Respiratory potential was recalculated to $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ prior to standardization, RQ of 0.85 was applied. * For Urbach gravel habitats the mean ETSA/R was 73 and maximum 178 for autumn sampling. a,b significant differences between habitats, $p < 0.05$.

104x56mm (600 x 600 DPI)

Fig. 6. The relationship between respiratory potential (ETSA) and respiration (R) (both standardized for temperature of 12°C) across all habitats for the Urbach and Soča floodplains.

108x78mm (600 x 600 DPI)