

Spatiotemporal heterogeneity of soil and sediment respiration in a river-floodplain mosaic (Tagliamento, NE Italy)

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SUMMARY

1. In their natural state, river floodplains are composed of a complex mosaic of contrasting aquatic and terrestrial habitats. These habitats are expected to differ widely in their properties and corresponding ecological processes, although empirical data on their capacity to produce, store and transform organic matter and nutrients are limited.
2. The objectives of this study were (i) to quantify the spatiotemporal variation of respiration, a dominant carbon flux in ecosystems, in a complex river floodplain, (ii) to identify the environmental drivers of respiration within and among floodplain habitat types and (iii) to calculate whole-floodplain respiration and to put these values into a global ecosystem context.
3. We measured soil and sediment respiration (sum of root and heterotrophic respiration; SR) throughout an annual cycle in two aquatic (pond and channel) and four terrestrial (gravel, large wood, vegetated island and riparian forest) floodplain habitat types in the island-braided section of the near-natural Tagliamento River (NE Italy).
4. Floodplain habitat types differed greatly in substratum composition (soil to coarse gravel), organic matter content (0.63 to 4.1% ash-free dry mass) and temperature (seasonal range per habitat type: 8.6 to 33.1 °C). Average annual SR ranged from 0.54 ± 1.56 (exposed gravel) to $3.94 \pm 3.72 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (vegetated islands) indicating distinct variation in respiration within and among habitat types. Temperature was the most important predictor of SR. However, the Q_{10} value ranged from 1.62 (channel habitat) to 4.57 (riparian forest), demonstrating major differences in habitat-specific temperature sensitivity in SR.
5. Total annual SR in individual floodplain habitats ranged from 160 (ponds) to 1205 g C m^{-2} (vegetated islands) and spanned almost the entire range of global ecosystem respiration, from deserts to tropical forests.

Keywords: aquatic–terrestrial metabolism, ecosystem process, environmental heterogeneity, floodplain

Introduction

River floodplains, i.e. the active tract and fringing riparian zone along rivers, can be portrayed as a complex mosaic of contrasting aquatic and terrestrial

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habitats. This spatially and temporally complex habitat mosaic varies widely in habitat properties, such as habitat composition (e.g. different soil and sediment types), temperature patterns, hydrological conditions (e.g. water content) and in terms of ecosystem processes (e.g. respiration). Thus, floodplains may serve as a model to study the effect of habitat properties on ecosystem processes in aquatic, semi-aquatic and terrestrial habitats (Naiman, Décamps & McClain, 2005; Ward *et al.*, 2002; Tockner, Lorang & Stanford, 2010; Fig. 1). For example, exposed gravel is considered as a harsh environment exhibiting extreme temperature variation, high water stress and low productivity (Tockner *et al.*, 2006), whereas riparian forests provide benign environmental conditions and are rich in resources that sustain high productivity (Tockner & Stanford, 2002). Vegetated islands and riparian forests provide large amounts of bioavailable organic carbon to aquatic habitats, where it is either processed *in situ* or exported downstream (Cuffney, 1988; Junk, Bayley & Sparks, 1989; Langhans *et al.*, 2006, 2008). However, most ecosystem studies have focussed on either aquatic (Pusch & Schwoerbel, 1994; Naegeli & Uehlinger, 1997; del Giorgio & Williams, 2005; Ingendahl *et al.*, 2009) or terrestrial (Davidson, Belk & Boone, 1998; Buchmann, 2000; Euskirchen *et al.*, 2003; Ball *et al.*, 2009) habitat types. A key challenge in ecosystem research is to understand the influence of habitat properties on processes. Therefore, we need to study the combined effects of the composition, spatial configuration and dynamics of both aquatic and terrestrial habitat types on ecosystem processes.

In this study, we focussed on the effect of habitat properties on sediment and soil respiration in aquatic and terrestrial river-floodplain habitats. Respiration is a central ecosystem process that regulates organic matter decomposition, detrital storage, nutrient cycling and flux of CO₂ to the atmosphere (Andrews & Schlesinger, 2001). Therefore, respiration can be used as an indicator of ecosystem integrity (Van Voris *et al.*, 1980; Uehlinger & Naegli, 1998; Euskirchen *et al.*, 2003). Generally, respiration increases exponentially with temperature and is often limited by deficits in soil moisture and substratum availability (Buchmann, 2000; Euskirchen *et al.*, 2003; Tang *et al.*, 2006). Thus, even marginal changes in temperature, water availability or quantity and quality of organic matter probably alter aquatic and turnover rates of terrestrial carbon (Schimel *et al.*, 1994; Jones, 1995; Randerson

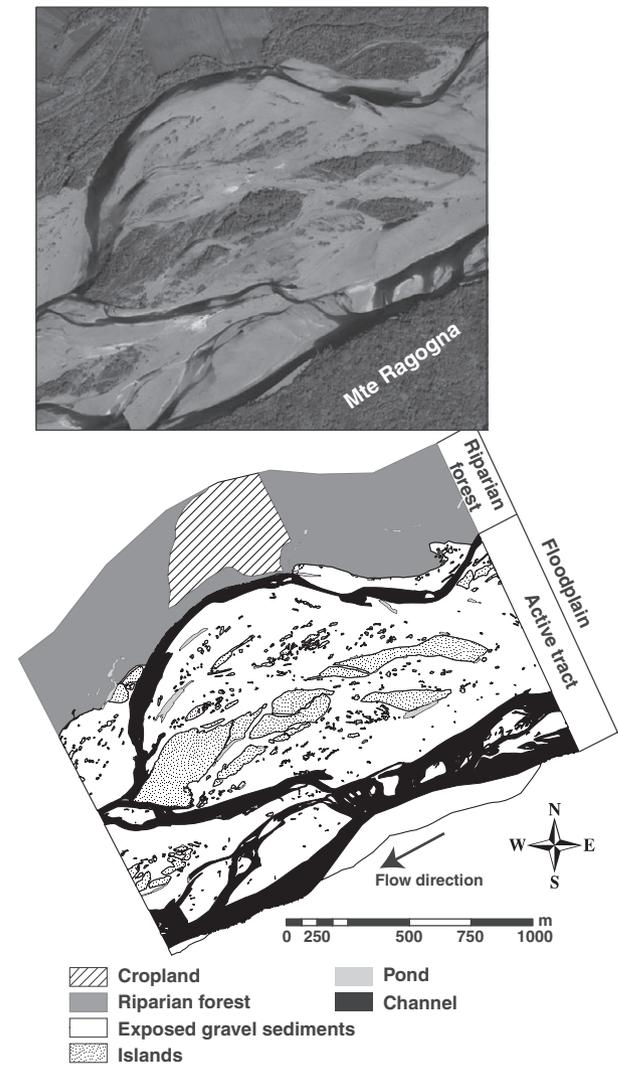


Fig. 1 Aerial photograph (May 2005) of the main study area (upper panel) and detailed map of the study area showing the spatial distribution of individual habitat types (lower panel). Large wood accumulations are too small to be shown on the map. All habitats were delineated by an intensive field survey in February 2005 at low discharge using a dGPS.

et al., 1996; Davidson *et al.*, 2000; Xu & Qi, 2001; Li, Xu & Zou, 2006; McIntyre *et al.*, 2009).

To gain a better understanding of the factors governing soil respiration in a spatially complex and temporally dynamic ecosystem, we conducted intensive field studies in the island-braided section of one of the last remaining near-natural river corridor in Central Europe (Tagliamento River, NE Italy). The Tagliamento offers insights into the structural and functional complexity that probably characterised most Alpine rivers before river engineering and

hydrological power production affected river morphology, sediment balance and hydrology. We measured soil temperature, soil water content, grain size distribution, organic matter content and soil and sediment CO₂ efflux in two aquatic and four terrestrial habitat types over an annual cycle. The main goals of the study were to (i) quantify the spatiotemporal variability of soil and sediment respiration (i.e. CO₂ flux as the sum of root and heterotrophic respiration; SR) of the dominant aquatic and terrestrial habitat types, (ii) identify the main potential environmental drivers of SR and (iii) quantify total annual SR at the entire floodplain scale and to compare SR with respiration reported from various ecosystem types globally.

Methods

Study site

This study was conducted from January to October 2005 in the island-braided section of the seventh-order Tagliamento River in north-eastern Italy (46° N, 12°30' E). The Tagliamento (catchment area: 2580 km²) originates at 1000 m a.s.l. in the southern fringe of the European Alps and flows almost unimpeded by dams for 172 km to the Adriatic Sea.

The main study area was a 116-ha island-braided floodplain complex (river km 79.8–80.8; 135 m a.s.l.) where maximum annual water level fluctuations were about 2 m (Tockner *et al.*, 2003). This reach contains a spatially complex and temporally dynamic habitat mosaic dominated by extensive areas of exposed riverine sediments (Petts *et al.*, 2000; Van der Nat *et al.*, 2003) (Fig. 1). The 800-m-wide active tract of the floodplain encloses numerous islands. The north-western border of the active tract is fringed by a ribbon of intact riparian forest, with black poplar (*Populus nigra* L.) and five willow (*Salix* spp.) species as the dominant tree species (Karrenberg *et al.*, 2003). The steep hillslope forest of Monte Ragogna fringes the south-eastern border of the floodplain (Fig. 1). Soil types of the riparian forest and vegetated islands are classified as Eutrochrept fluvisols.

At base flow (about 20 m³ s⁻¹), the floodplain is composed of a complex mosaic of exposed gravel habitats (60.3 ha, 51.8% of total area), vegetated islands (10.4 ha, 8.9%), large wood accumulations (0.4 ha, 0.4%), the channel network (18.2 ha, 15.6%),

numerous ponds (0.6 ha, 0.6%) and the riparian forest (26.5 ha, 22.8%) (Table 1). The river has a flashy flow regime ($Q_{80} = 72 \text{ m}^3 \text{ s}^{-1}$; Ward *et al.*, 1999) with frequent and short flow and flood pulses (Tockner, Malard & Ward, 2000) throughout the year (Arscott *et al.*, 2002). Detailed information on the Tagliamento catchment and the main study area has been published by Ward *et al.* (1999), Gurnell *et al.* (2001), Tockner *et al.* (2003), Bertoldi *et al.* (2009) and Tonolla *et al.* (2010).

Characterisation of habitat patches

Two aquatic (channels and ponds) and four predominantly terrestrial (riparian forest, vegetated islands, large wood accumulations and exposed gravel) habitat types (Fig. 1; Table 1) were analysed for grain size distribution, water content and organic matter content (four times over the annual cycle). The number of sampling sites was allocated according to the relative areal contribution of each individual habitat type to

Table 1 Characterisation of the terrestrial and aquatic habitat types sampled in this study. LWA = Large wood accumulation. Apart from riparian forests, all habitats are located within the active tract of the floodplain

Habitat type	Characteristics
Channels	Permanent lotic primary and secondary channels composed of coarse permeable gravel sediments and typically fringed by gravel bars
Ponds	Permanent parafluvial ponds, often located adjacent to islands and large wood accumulations, composed of coarse permeable gravel sediments
Riparian forest	Predominantly forested terrestrial* habitat type, fringing the active tract of the floodplain and characterised by developed soil (Eutrochrept fluvisol). The vegetation is mainly composed of black poplar (<i>Populus nigra</i>) and different willow (<i>Salix</i> spp.) species
Islands	Predominantly terrestrial* habitat type, mainly colonised by <i>Populus nigra</i> and different willow species and characterised by sandy substrata and developed soil (Eutrochrept fluvisol).
LWA	Predominantly terrestrial* accumulations of large wood trapping mainly fine sediments and organic matter
Gravel	Predominantly terrestrial* areas characterised by bare or sparsely vegetated gravel deposits

*These habitats become aquatic habitats during floods only.

the whole-floodplain area. Samples were taken randomly but evenly distributed along the riparian forest strip on the north-western part of the floodplain, along the main and site channel and in the exposed gravel. Individual vegetated islands, large wood accumulations and ponds were subject to sampling within the whole active tract. The water content in terrestrial soils and sediments was always below maximum water-holding capacity. The aquatic sites were characterised by coarse and permeable gravel deposits (Table 2). Therefore, anaerobic conditions are expected to be absent in this floodplain system. Soil (riparian forest, vegetated islands) and sediment (large wood accumulations, channels, ponds and exposed gravel) water content (% of dry soil and sediment) was determined gravimetrically 3–12 h after sample collection. Samples were weighed, dried at 105 °C for 24 h and reweighed. Gravimetric water content (WC; % of dry sediment) of aquatic sediments was calculated according to eqn 1.

$$WC = \frac{P \times V_{\text{tot}} \times \rho}{S + P \times V_{\text{tot}} \times \rho} \times 100 \quad (1)$$

where P is porosity, V_{tot} is sediment volume in cm^3 , S is dry sediment weight, and ρ is water density. Porosity was assumed to be 0.2 (Eglin, 1990; Jussel, 1992) and water density 1 g cm^{-3} (Eglin, 1990).

To measure the maximum water-holding capacity (WHC; % of dry soil and sediment), five random

samples per habitat type were dried at 105 °C, weighed, saturated with deionised water for 24 h, drained for 24 h and weighed again. Organic matter content of dry samples was measured as ash-free dry mass (AFDM; ashed at 500 °C for 3 h) per kg dry soil or sediment. Ashed sediments were sieved to separate grain size fractions <0.063 mm, 0.063–2 mm, 2–4 mm, 4–8 mm and >8 mm.

Temperature was continuously recorded in terrestrial and aquatic habitat types. Five temperature loggers (DS1921G, Dallas Semiconductor, Dallas, U.S.A.) were deployed in each terrestrial habitat type at a depth of 5 cm. Five loggers (TR MINILOG, VEMCO, Nova Scotia, Canada and PDLR70; Ecotech, Germany) were also deployed at the sediment surface of each aquatic habitat.

Measurement of SR in terrestrial habitats

Soil and sediment respiration (i.e. sum of root and heterotrophic respiration; SR) was measured as positive CO_2 flux per $\text{m}^{-2} \text{ s}^{-1}$ in January, April, July and October 2005 using a soil respiration chamber (Li 6400, LiCor, Lincoln, Nebraska, U.S.A.) attached to a portable Li-6400 infrared gas analyser (IRGA). PVC collars of known volume (8 cm long, 10.5 cm inside diameter) were inserted into the soil evenly distributed along the north-western contiguous riparian forest stretch ($n = 16$ collars per date), in the soils of

Table 2 Characterisation of terrestrial and aquatic habitat types. Average and standard deviation of pooled data from four seasons. Temperature includes spot measurements (°C), water content is expressed as % of dry sediments, water content as % of the water-holding capacity, organic matter (OM) content of two size fractions and total organic matter content per mass of sediment as g AFDM kg^{-1} . Grain size classes are expressed in % of the sum of all size fractions

Habitat	Riparian forest $n = 63$	Island $n = 114$	LWA $n = 52$	Gravel $n = 322$	Channel $n = 100$	Pond $n = 53$
Temperature (°C)	12.9 ± 7.4	14.2 ± 8.9	14.9 ± 9.8	16.8 ± 11.7	12.9 ± 4.6	13.5 ± 6.2
Water content (%)	25.7 ± 10.3	15.2 ± 10.5	15.7 ± 10.8	3.7 ± 8.7	9.4 ± 0.8*	9.8 ± 1.4*
% of water-holding capacity	57.7 ± 22.7	36.6 ± 24.2	55.8 ± 29.8	41.1 ± 31.3	100 ± 0	100 ± 0
OM >2 mm (g AFDM kg^{-1})	8.3 ± 6.0	5.4 ± 5.7	3.7 ± 4.9	3.3 ± 2.2	3.6 ± 1.3	2.3 ± 1.6
OM <2 mm (g AFDM kg^{-1})	32.6 ± 12.4	17.9 ± 12.4	15.5 ± 13.0	3.0 ± 2.7	2.8 ± 1.3	3.7 ± 2.3
Total OM (g AFDM kg^{-1})	40.9 ± 15.64	23.3 ± 16.4	19.2 ± 17.2	6.5 ± 2.9	6.3 ± 1.3	6.6 ± 1.9
Grain size distribution						
>8 mm (%)	0.04 ± 0.07	0.06 ± 0.2	3.4 ± 9.2	46.1 ± 26.7	46.1 [†]	46.1 [†]
8–4 mm (%)	0.06 ± 1.4	0.04 ± 0.1	1.8 ± 3.2	8.6 ± 5.6	20.1 ± 7.0	16.0 ± 8.6
4–2 mm (%)	0.8 ± 1.3	0.5 ± 0.7	1.6 ± 2.0	5.1 ± 4.0	11.7 ± 3.3	8.1 ± 4.4
2–0.063 mm (%)	80.1 ± 17.2	87.4 ± 15.3	86.2 ± 13.2	39.2 ± 31.9	21.8 ± 8.4	29.4 ± 12.2
<0.063 mm (%)	19.0 ± 17.5	12.0 ± 15.4	7.0 ± 5.2	1.0 ± 1.9	0.3 ± 0.3	0.5 ± 0.4

AFDM, ash-free dry mass; LWA, large wood accumulation; n , number of samples in each habitat.

*Values calculated for permanent aquatic sediments.

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

eight distinct vegetated islands ($n = 29$), in the trapped sediments of 13 individual large wood accumulations ($n = 13$) and in the sediments of the exposed gravel sediment matrix ($n = 81$). To avoid effects of prior sampling disturbance, sites were located slightly offset from previous sampling sites but within 1 m; the exact position of each randomly chosen sampling location was determined using a differential global positioning system (dGPS; accuracy <0.5 m). Collars were inserted to a sediment/soil depth of 5–7 cm. According to Norman *et al.* (1997), the insertion of a collar may result in initially high CO₂ fluxes that stabilise after 10–30 min. To minimise this effect, collars were installed at least 24 h prior to measurement (Buchmann, 2000). The soil chamber was set on top of the collar to measure the undisturbed CO₂ flux. The IRGA measurement was repeated four times per date and collar, and values were averaged. To estimate diel variation in CO₂ fluxes, five additional collars were exposed at each habitat type and measured three to four times from 7 am to 8 pm. Temperature was measured at 5-cm sediment depth next to the collar. After each measurement, the soil enclosed by each collar was collected, stored in sealed PVC bags and transported to the laboratory for water, organic matter content and grain size analysis.

Measurement of SR in aquatic habitats

Respiration of aerobic aquatic sediments was measured as the change in O₂ concentration over time in plexiglas tubes (5.2 cm diameter, 32 cm long) sealed with rubber stoppers (Uehlinger, Naegeli & Fisher, 2002). Surface autotrophs (exclusively epilithic algae) were excluded. This measure corresponds to the respiration measurements in terrestrial habitats that did not include the respiration of trees or shrubs. Sediment samples evenly distributed in the main and side channel ($n = 25$ sampling sites per date) and in 14 individual ponds ($n = 14$) were collected from 0 to 20 cm depth. Prior to sampling, the surface layer, typically covered with epilithic algae, was removed. Respiration tubes were filled with pre-sieved sediments (≤ 8 mm), filled to the top with surface water from the sampling site and subsequently incubated *in situ*, i. e. tubes were buried in surface sediments at the sampling site for about 4 h (Uehlinger *et al.*, 2002). Sediment particles >8 mm were excluded because the

random presence or absence of a few pebbles, representing a relatively large inactive metabolic volume in the relatively small chambers, result in high variability of oxygen consumption within habitats. Oxygen concentration and temperature were measured with a portable oxygen metre (Oxi 340/bset, WTW, Weilheim, Germany) at the beginning and end of the incubation period. After incubation, sediments were stored frozen and later analysed for organic matter content and grain size distribution.

Calculation of SR from sediment tube measurements

Based on the oxygen consumption in the chamber water r ($\text{g O}_2 \text{ m}^{-3} \text{ h}^{-1}$), we first calculated the respiration per sediment volume R_v ($\mu\text{mol CO}_2 \text{ m}^{-3} \text{ s}^{-1}$) according to eqn 2:

$$R_v = r \times \frac{10^6}{32} \times \frac{1}{3600} \times \frac{V_w}{V_c} \times RQ \quad (2)$$

V_w is the volume of water in a chamber (m^3), V_c the volume of sediment (including porosity) filled into a chamber (m^3), and RQ is respiratory quotient (0.85; Dilly, 2001). The porosity of exposed gravel, channel and pond sediments was assumed to be 20% (Eglin, 1990; Jussel, 1992). To get an estimate of areal respiration R ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) for the uppermost cm of pond or channel sediments, we multiplied R_v by 0.2 m and by 0.54. The factor 0.54 considers that size fraction >8 mm accounted on average for 54% of the sediment volume (this percentage was determined by analysing 322 gravel samples collected at 81 sites).

Temperature dependence of SR

We described the temperature dependence of respiration as (3):

$$y = a * \exp^{(b*T)}, \quad (3)$$

where T is the sediment temperature ($^{\circ}\text{C}$) at 5 cm depth (terrestrial habitats) or the temperature of the chamber water. The model parameters a and b were identified using nonlinear regression applied to respiration and temperature data of each individual habitat type over the course of the study.

Residual analyses were performed to test for correlations between residuals of the temperature model and soil and sediment water content, organic matter content and individual grain size fractions.

Q_{10} values were calculated according to eqn 4 (Buchmann, 2000):

$$Q_{10} = \exp^{10 \cdot b} \quad (4)$$

Respiration at reference temperature (T_r) 12 °C was calculated according eqn 5:

$$R(T_r) = \exp^{b \cdot (T - T_r)} \quad (5)$$

Annual soil and sediment CO_2 flux

The total annual SR for the individual habitat types, as well as for the entire floodplain system, was calculated based on the exponential equations derived from empirical field data (Table 5). Temperature data were taken from average daily logger data. The areal extent of each habitat type was used to scale up the results to the entire floodplain system and was extracted from a geographic information system (GIS) layer based on a dGPS mapping survey in 2005 (Fig. 1).

Statistical analyses

A factorial design was used with habitat type (six levels) and season (four levels) as factors and respiration as the dependent variable. The number of replicates of each habitat type was partly determined by its coverage and distribution within the floodplain section (i.e. by a single contiguous forest stretch or gravel matrix, and a limited number of islands and channels). Since subsequent seasonal measurements were placed next to the prior sampling sites, two-way ANOVA with *a posteriori* tests (Bonferoni *post hoc*) was applied to separate means. Data were log-transformed, if necessary, to meet the assumptions of normality (Sokal & Rohlf, 1995). Spearman rank correlation was applied to describe the relationships between habitat variables and within-habitat respiration. Regression analysis was carried out to predict soil respiration from diel and seasonal temperature variation. All statistics were calculated using Statistica 6.0 (Statsoft Inc., Tulsa, Oklahoma, U.S.A.).

Results

Environmental characterisation of habitat types

Each habitat type exhibited distinct seasonal and diel temperature patterns (Fig. 2). The seasonal varia-

tion in daily mean temperature ranged from 8.6 °C (channel) to 33.1 °C (exposed gravel). The diel amplitude, averaged over the annual cycle, ranged between 2.7 °C (channel) and 9.7 °C (exposed gravel) (Fig. 2). The total annual degree days (sum of average daily temperature) ranged from 4017 (riparian forest) to 4560 (exposed gravel).

Particles >8 mm prevailed in exposed gravel sediments and in aquatic habitats (>46%), whereas the grain size fraction 2–0.063 mm dominated other types of terrestrial habitats (>39.2%). Average gravimetric water content ranged from 3.7% (exposed gravel sediments) to 25.7% (riparian forest). The average WC, expressed as % of WHC, was lowest in vegetated islands (36.6%) and highest in the riparian forest (57.7%). In the terrestrial habitats, the total organic matter per mass of sediment (TOM; g AFDM kg^{-1}) ranged from 6.5 g (0.65%) in exposed gravel sediments to 40.9 g (4.1%) in the riparian forest, with the grain size fraction <2 mm as the dominant organic matter (OM) fraction. The OM content in aquatic habitats was similar to the content in exposed gravel sediments (Table 2).

Spatiotemporal variation of SR

Average annual SR ($\mu\text{mol } CO_2 \text{ m}^{-2} \text{ s}^{-1}$) per habitat type ranged from $0.54 \pm 1.56 \mu\text{mol}$ (exposed gravel sediment) to $3.94 \pm 3.72 \mu\text{mol}$ (vegetated island). In particular, exposed gravel sediments revealed a patchy spatial distribution in SR indicated by high standard deviations. Seasonally, average SR varied from 0.04 (January) to $1.29 \mu\text{mol } CO_2 \text{ m}^{-2} \text{ s}^{-1}$ (July) in exposed gravel sediments and from 0.86 (January) to $8.22 \mu\text{mol } CO_2 \text{ m}^{-2} \text{ s}^{-1}$ (July) in vegetated islands. Seasonal variation in SR was relatively low in aquatic habitats (Table 3). SR differed significantly among habitat types (d.f. = 5; $F = 169.58$; $P < 0.001$), although SR in the riparian forest and vegetated islands was not significantly different (Bonferoni *post hoc*; $P > 0.05$). SR varied significantly with time (season) (d.f. = 3; $F = 121.06$; $P < 0.001$) and there was a significant interaction between time and habitat type (d.f. = 15; $F = 10.31$; $P < 0.001$).

Temperature-corrected average annual SR (reference temperature: 12 °C, eqn 5, $\mu\text{mol } CO_2 \text{ m}^{-2} \text{ s}^{-1}$) ranged from $0.21 \pm 0.50 \mu\text{mol}$ (exposed gravel) to $2.66 \pm 2.04 \mu\text{mol}$ (riparian forest). Average seasonal SR varied in exposed gravel sediments from $0.07 \mu\text{mol}$

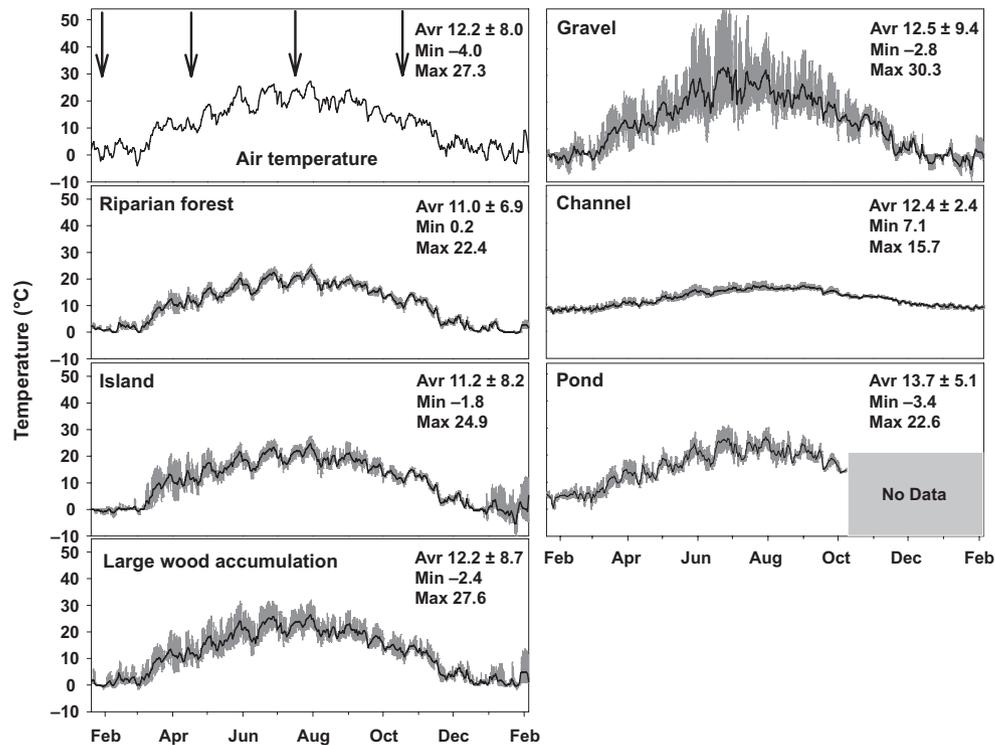


Fig. 2 Average daily air temperature measured 10 km south-east from the study site (Fagagna; 46°1004'N, 13°0903'E) and average, minimum and maximum daily temperature retrieved from loggers including summarising statistics (average \pm SD, minimum and maximum of annual daily mean temperature in $^{\circ}$ C) in the six aquatic and terrestrial habitat types from January 2005 to February 2006 (arrows indicate seasonal sampling dates; see text for further information on sampling sites).

Table 3 Seasonal soil and sediment respiration ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) in aquatic and terrestrial habitats (average $\bar{X} \pm \text{SD}$)

Month	Riparian forest <i>n</i> = 63		Islands <i>n</i> = 114		LWA <i>n</i> = 52		Gravel <i>n</i> = 322		Channels <i>n</i> = 100		Pond <i>n</i> = 53	
	$\bar{X} \pm \text{SD}$	CV	$\bar{X} \pm \text{SD}$	CV	$\bar{X} \pm \text{SD}$	CV	$\bar{X} \pm \text{SD}$	CV	$\bar{X} \pm \text{SD}$	CV	$\bar{X} \pm \text{SD}$	CV
January	0.97 \pm 0.51	53	0.86 \pm 1.14	133	0.37 \pm 0.54	146	0.04 \pm 0.24	573	0.57 \pm 0.32	56	0.23 \pm 0.19	83
April	3.10 \pm 0.96	31	3.13 \pm 1.35	43	1.50 \pm 0.85	57	0.52 \pm 0.82	158	1.00 \pm 0.59	59	0.47 \pm 0.28	60
July	7.44 \pm 2.04	27	8.22 \pm 3.79	46	5.51 \pm 2.34	42	1.29 \pm 2.65	206	1.03 \pm 0.54	52	1.09 \pm 0.46	42
October	2.67 \pm 1.36	51	3.38 \pm 3.17	94	1.46 \pm 1.26	86	0.30 \pm 0.58	194	0.62 \pm 0.5	81	0.62 \pm 0.37	60

LWA, large wood accumulation; CV, coefficient of variation.

(January) to 0.38 μmol (July) and in the riparian forest from 1.64 μmol (April) to 5.01 μmol (January). In terrestrial habitats, temperature-corrected SR peaked in July, except in the riparian forest, and was most variable in January. In aquatic habitats, temperature-corrected SR remained fairly constant throughout the year (Fig. 3). Temperature-corrected average annual SR ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) per kg OM ranged from 408.5 \pm 835.4 (Islands) to 65.3 \pm 221.3 (Gravel). The differences between habitats were significant (d.f. = 5; $F = 171.51$; $P < 0.001$) but an *a posteriori* test indicated

significant differences between gravel and all other habitats only (Bonferroni *post hoc*; $P < 0.001$). Seasonal differences in temperature-corrected SR per kg OM were significant (d.f. = 3; $F = 7.88$; $P < 0.001$) but mainly because of high values in riparian forest, islands and LWA habitats in January (Bonferroni *post hoc*; $P < 0.001$). The calculated Q_{10} values ranged from 1.62 (channel habitats) to 4.57 (riparian forest) (Table 5).

Within habitat types, average spatial variation in SR, expressed as the coefficient of variation (CV), was lowest in the riparian forest (CV = 41%) and highest

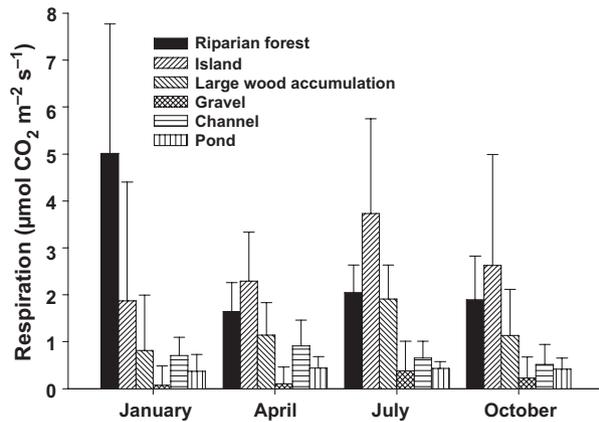


Fig. 3 Total soil and sediment respiration (average \pm SD) in individual habitat types standardised at 12 °C. $N = 52$ –322 per habitat type (see Table 3).

in exposed gravel sediments (282%). The within-habitat spatial variation decreased with increasing temperature and was therefore lowest in July (Table 3). The diel variation in SR was highest in July and ranged between 0.99 (vegetated island) and 1.63 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (large wood accumulation). The diel amplitude in SR was significantly related to the diel variation in temperature ($r^2 \geq 0.82$; $P < 0.001$).

Potential drivers of SR

Although significant correlations were observed for several within-habitat variables (e.g. WC, WHC and

OM content) and SR, we found the strongest correlations between temperature and SR ($0.32 < r < 0.85$), except for the channel habitat type (Table 4). The relationship between temperature and SR was best described by an exponential equation. Temperature explained between 38 and 72% of the SR variation, except for exposed gravel and channel habitats ($R^2 = 0.05$ and 0.11, respectively); although all models were highly significant ($P < 0.0001$) (Table 5). Residual analysis confirmed temperature as the dominant variable explaining respiration within individual habitat types.

Annual soil and sediment CO_2 flux

The habitat-specific annual SR (February 2005 to January 2006) ranged from 160 (ponds and exposed gravel sediments) to 1205 $\text{g C m}^{-2} \text{ year}^{-1}$ (islands), thereby spanning almost the entire range of respiration reported from various ecosystem types worldwide (Tables 6 & 7). Total annual SR (area-weighted mean) for the entire 116-ha island-braided floodplain was calculated as 467 $\text{g C m}^{-2} \text{ year}^{-1}$, corresponding to a total carbon efflux of 544 tC. The riparian forest (23% of floodplain area) and island (9% of floodplain area) contributed disproportionately to total annual floodplain respiration (47 and 23%, respectively), while the relative contribution of exposed gravel sediments was low (18%) compared to its areal extent (51% to total area; Table 6).

Table 4 Spearman rank correlations of total soil and sediment respiration ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and different habitat variables (pooled data from four seasons). Significant correlations ($P \leq 0.05$) are highlighted in bold

Independent variable	Riparian forest $n = 63$		Islands $n = 114$		LWA $n = 52$		Gravel $n = 322$		Channels $n = 100$		Ponds $n = 53$	
	r	P	r	P	r	P	r	P	r	P	r	P
Temperature (°C)	0.85	<0.001	0.72	<0.001	0.73	<0.001	0.35	<0.001	0.32	<0.001	0.73	<0.001
Water content (%)	-0.37	0.002	-0.22	0.018	-0.28	0.046	0.17	0.002	-0.19	0.099	-0.18	0.278
% of water-holding capacity	-0.37	0.002	-0.22	0.018	-0.28	0.046	0.17	0.002	-	-	-	-
OM >2 mm (g kg^{-1} sediment)	0.27	0.036	0.10	0.273	0.12	0.194	0.22	0.148	0.27	0.001	0.14	0.394
OM <2 mm (g kg^{-1} sediment)	0.27	0.030	0.10	0.286	0.18	0.391	0.08	<0.001	0.13	0.210	0.19	0.175
Total OM (g kg^{-1} sediment)	0.24	0.054	0.10	0.301	0.17	0.224	0.21	<0.001	-0.02	0.830	-0.08	0.555
Grain size >8 mm (%)	-0.43	<0.001	-0.33	<0.001	0.19	0.169	-0.19	0.001	-	-	-	-
Grain size 8–4 mm (%)	-0.58	<0.001	-0.42	<0.001	0.18	0.190	-0.19	0.001	-0.03	0.742	-0.00	0.990
Grain size 4–2 mm (%)	-0.22	0.077	0.02	0.866	0.15	0.297	-0.19	0.001	-0.27	0.006	0.01	0.945
Grain size 2–0.063 mm (%)	-0.67	<0.001	-0.32	<0.001	-0.32	0.020	0.18	0.001	0.15	0.132	-0.02	0.868
Grain size <0.063 mm (%)	0.69	<0.001	0.33	<0.001	0.44	0.001	0.23	<0.001	0.46	<0.001	0.32	0.018

OM, organic matter; LWA, large wood accumulation.

Table 5 Regression models between total respiration ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and sediment (s; 5 cm depth) and water (w) temperatures calculated for six habitat types. LWA = Large wood accumulation. SE = Standard error. Q_{10} = Temperature sensitivity. n = number of replicates

Habitat	Model	Parameter	SE	Q_{10}	n	R^2	P
Riparian forest	$R = a \cdot \exp(b \cdot Ts)$	$a = 0.305$ $b = 0.152$	0.094 0.016	4.57	63	0.72	<0.0001
Island	$R = a \cdot \exp(b \cdot Ts)$	$a = 1.292$ $b = 0.068$	0.287 0.010	1.97	114	0.38	<0.0001
LWA	$R = a \cdot \exp(b \cdot Ts)$	$a = 0.394$ $b = 0.093$	0.116 0.011	2.53	52	0.67	<0.0001
Gravel	$R = a \cdot \exp(b \cdot Ts)$	$a = 0.165$ $b = 0.056$	0.086 0.018	1.75	322	0.05	<0.0001
Channel	$R = a \cdot \exp(b \cdot Tw)$	$a = 0.423$ $b = 0.048$	0.089 0.014	1.62	100	0.11	<0.0001
Pond	$R = a \cdot \exp(b \cdot Tw)$	$a = 0.168$ $b = 0.085$	0.034 0.010	2.34	53	0.59	<0.0001

Table 6 Extend and respiration activity of individual habitat types. Area (m^2), area (%), respiration (tC year^{-1}), respiration ($\text{g C m}^{-2} \text{ year}^{-1}$), respiration (%). LWA = Large wood accumulation

Habitat	Area (ha)	Area (%)	Respiration (tC year^{-1})	Respiration ($\text{g C m}^{-2} \text{ year}^{-1}$)	Respiration (%)
Riparian forest	26.5	22.8	260	982	47.8
Island	10.4	8.9	126	1206	23.1
LWA	0.4	0.4	3	624	0.5
Channel	18.2	15.6	53	292	9.7
Pond	0.6	0.6	1	160	0.2
Gravel	60.3	51.8	102	168	18.7
Total floodplain	116.4	100.0	544	467	100.0

Discussion

Soil and sediment respiration (SR) represents an important carbon flux and thus is a well-studied process in both permanent aquatic and terrestrial ecosystems (del Giorgio & Williams, 2005; Luo & Zhou, 2006). However, very limited information is available from morphologically complex and temporally dynamic ecosystems such as river floodplains (but see Valett *et al.*, 2005). The floodplain of the Tagliamento River, a model ecosystem of European importance, provides an excellent framework to study the effect of habitat properties on functional processes across different habitat types over various temporal scales. Our study clearly demonstrated that SR was highly variable in space and time, reflecting the seasonal dynamics and the spatial heterogeneity of the complex floodplain mosaic. We identified temperature as the main factor controlling SR within the various habitat types, although the individual habitat types differed considerably in their sensitivity to temperature.

Spatiotemporal variation of SR

Average SR differed among habitat types by an order-of-magnitude (Fig. 3) and high standard devi-

ations revealed a patchy distribution of respiration activity, especially for the exposed gravel sediments (Table 3). The riparian forest and, in particular, vegetated islands exhibited a high SR, as high as SR reported for tropical forests (Table 7). The availability of large pools of organic matter and the contribution of root respiration to total SR probably explained these high values. Microbial activity depends on the availability of labile fractions of OM derived from fresh litter input and *in situ* primary production (Schimel *et al.*, 1994; Janssens *et al.*, 2001). In the Tagliamento, islands are young (maximum age 20 years) and highly productive floodplain habitats (Langhans *et al.*, 2006, 2008). High input and storage rates of bioavailable OM are expected to favour heterotrophic SR on vegetated islands. Our results underpin the potential role of vegetated islands as 'hot spots' for ecosystem processes (this study; Langhans *et al.*, 2006, 2008) as well as for biodiversity (Gurnell *et al.*, 2001; Tockner *et al.*, 2006). Islands exhibit a high perimeter to area ratio and are expected to be linked with adjacent habitats that are less productive and diverse. At the same time, islands are among the first habitats that disappear as a consequence of flow and channel regulation (Gurnell *et al.*, 2001). Therefore, they can be used as sensitive

Table 7 Annual respiration (average \pm SD; g C m⁻² year⁻¹) for global terrestrial and aquatic ecosystem types (Bond-Lamberty and Thomson, 2010; Raich and Schlesinger, 1992; Uehlinger, 1993), compared to aquatic and terrestrial annual respiration in different floodplain habitat types of this study (in bold; *: number of measurements as shown in Table 3)

Global soil ecosystems and floodplain habitat types	Respiration (g C m ⁻² year ⁻¹)	<i>n</i>
Arctic desert	1 \pm 0	1
Tundra	60 \pm 20	11
Northern bogs and mires	94 \pm 55	12
Arctic wetland	105 \pm 0	1
Arctic shrubland	116 \pm 113	15
Boreal grassland	125 \pm 94	2
Ponds	160	*
Gravel	168	*
Temperate savanna	181 \pm 0	1
Temperate desert	243 \pm 263	21
Boreal wetland	271 \pm 159	64
Boreal agriculture	280 \pm 243	4
Channels	292	*
Mediterranean savanna	439 \pm 85	3
Temperate shrubland	448 \pm 289	14
Boreal forest	448 \pm 218	137
Temperate wetland	479 \pm 390	34
Tropical wetland	500 \pm 262	2
Subtropical agriculture	505 \pm 186	12
Large wood accumulations	624	*
Temperate agriculture	650 \pm 362	159
Mediterranean agriculture	702 \pm 0	1
Subtropical grassland	721 \pm 311	3
Mediterranean grassland	746 \pm 480	20
Temperate streams	769 \pm 316	13
Temperate forest	781 \pm 429	1020
Subtropical forest	806 \pm 434	35
Desert streams	807 \pm 668	9
Temperate grassland	827 \pm 512	215
Mediterranean forest	951 \pm 413	41
Riparian forest	982	*
Islands	1205	*
Tropical forest	1284 \pm 605	227
Tropical grassland	1326 \pm 895	23
Tropical savanna	1437 \pm 520	13
Tropical agriculture	1525 \pm 657	23

indicators for assessing the integrity of floodplain ecosystems.

In this study, we focussed solely on sediment respiration – definitively an important ecosystem process – and how this process is related to habitat-specific properties. However, these results cannot be simply translated to other ecosystem processes. Langhans *et al.* (2008), for example, studied the decomposition of leaves, another important process in the carbon cycle, in the same habitat types along the

Tagliamento. In contrast to SR, decomposition was an order-of-magnitude higher in aquatic than in terrestrial habitats. Hence, a key challenge for future research is to study several ecosystems processes concurrently and to investigate how these processes are interdependent.

Potential drivers of SR

Within habitat types, SR exhibited distinct diel and seasonal patterns and was strongly correlated with temperature. Temperature has been identified as one of the most important predictors for SR (Gansert, 1994; Burton *et al.*, 1998; Buchmann, 2000). The average Q_{10} value in the Tagliamento floodplain was similar to other terrestrial ecosystems (Davidson *et al.*, 1998; Buchmann, 2000; Raubuch *et al.*, 2002; Chivers *et al.*, 2009), although differences among habitat types were distinct (1.62–4.57; Tables 4 & 5). SR represented the sum of autotrophic (root) and heterotrophic respiration, for which the Q_{10} can be quite different (Buchmann *et al.*, 1997; Boone *et al.*, 1998). In most habitats, the temperature-corrected (standardised at 12 °C) seasonal trend in SR reflected the potential influence of root respiration, with higher respiration during the growing season (Fig. 3; Buchmann, 2000; Hanson *et al.*, 2000). In the riparian forest, however, the standardised respiration peaked in January, and not in July, like in the other floodplain habitats investigated. To our knowledge, the lack of seasonality in forest soil respiration is not supported by other studies. We cannot rule out that the temperature dependence function (eqn 3) may fail to estimate the potential respiration of a soil community at 12 °C if the calculation is based on respiration measured around freezing point or that differences in organic matter quality may account for the higher respiration. However, we lack information to support or reject these assumptions.

Frequent flood disturbance (Jones, Fisher & Grimm, 1995; Uehlinger, 2000, 2006) and high-temperature amplitudes that can affect abundance, physiology and composition of microbial communities (Lloyd & Taylor, 1994; Palmer Winkler, Cherry & Schlesinger, 1996; Rinklebe & Langer, 2006) might explain the minor temperature dependence of SR in channel habitats and exposed gravel sediments (Table 5). Periods of heterotrophic activity do not necessarily coincide with periods of autotrophic

activity (Acuña *et al.*, 2004). It is the interplay between these processes that determine the seasonality of SR, and hence, differences among habitat types.

In addition to temperature, moisture (Davidson *et al.*, 2000; Xu & Qi, 2001; Li *et al.*, 2006; McIntyre *et al.*, 2009) and OM content (Schimel *et al.*, 1994; Randerson *et al.*, 1996) are known to influence SR. For example, Carlyle & BaThan (1988) found a significant correlation between SR and moisture when water content dropped below 12.5%. Amalfitano *et al.* (2008) found that a water content of ~20% (% of max. WHC; grain size <2 mm) was the critical threshold for bacterial carbon production (BCP). Below this value, BCP ceased, although a considerable proportion of bacteria remained alive. In our floodplain system, water content was always well above this critical threshold level (Table 2). Although OM and water content did not explain within-habitat variation of SR, OM content was closely linked to differences in SR among habitat types. Factors such as OM quality, water availability and root density, which were not assessed in the present study but are known to be highly variable in space (Buchmann, 2000), may contribute to the observed within-habitat variability of SR.

Flooding influences soil and sediment respiration. However, the impact of flooding could not be assessed because there were no major floods during our investigation and small flood pulses did not affect the terrestrial sampling sites. Most rewetting studies in permanent terrestrial habitats (e.g. Orchard & Cook, 1983; Carlyle & BaThan, 1988; Fierer & Schimel, 2002; Fischer, 2009) resulted in increased SR, whereas flooding (WC > WHC) often causes a decrease in SR (Gutiñas *et al.*, 2009; McIntyre *et al.*, 2009). In contrast, Valett *et al.* (2005) found a >200-fold increase in soil respiration after a few days of inundation in an experimentally flooded floodplain forest of the Middle Rio Grande. In the Tagliamento floodplain, flow pulses that inundated up to 20% of the active tract lasted on average <6 days, and floods that affected 80% of the active tract lasted on average <1.5 days (Van der Nat *et al.*, 2002). Furthermore, at base flow conditions, most of the floodplain consists of exposed gravel sediments (~53%) and permanent aquatic habitats (~16%), which exhibited lowest SR. Therefore, the effect of flooding on annual SR is probably low.

Annual soil and sediment CO₂ flux

Total mean annual SR (area-weighted mean) for the entire island-braided floodplain was calculated as 467 g C m⁻² year⁻¹ and is similar to the mean annual respiration reported for temperate wetlands (Table 7). However, this mean value does not take into consideration the high spatial complexity in SR within and among the various habitat types in the Tagliamento floodplain. Habitat-specific efflux of CO₂ from soils and sediments spanned almost the entire range reported from aquatic and terrestrial ecosystems globally. While exposed gravel sediments and pond habitats exhibited CO₂ fluxes similar to Arctic and desert ecosystems, fluxes from vegetated islands were as high as in tropical forests (Table 7). Hence, in the natural floodplain mosaic of the Tagliamento River, 'desert-like' habitats are located in close proximity to 'rainforest-like' habitats. The abrupt change in respiratory carbon fluxes at the interface between vegetated (islands and riparian forest) and unvegetated habitat types (exposed gravel sediments and aquatic habitats) indicates not only fundamental differences in C sources and C cycling within these contrasting habitat types but also limited transfer of C across habitat boundaries. The direct input of litter to the active tract is restricted to the immediate interface between vegetated islands, the riparian forest and the active tract (Langhans, 2006).

Methodological aspects in assessing SR

Unfortunately, it was not possible to apply the same methods for quantifying SR in aquatic and terrestrial habitat types. This difference constrained to some extent comparability between aquatic and terrestrial habitat types. The assessment of terrestrial respiration provided area-specific values, and sediment or soil patches remained relatively undisturbed during sampling. In aquatic systems, enclosures are a common method used to quantify SR (Pusch & Schwoerbel, 1994; Jones, 1995; Jones *et al.*, 1995; Naegeli *et al.*, 1995). Enclosures create an artificial sediment structure that may disrupt the enclosed microbial communities (Uehlinger & Brock, 1991; Naegeli *et al.*, 1995). Moreover, the conversion of SR from chamber to area-related values required information about the change in SR with sediment depth, a difficult task in aquatic environments (Naegeli & Uehlinger, 1997).

Open-system methods (Odum, 1956) can circumvent such methodological constraints. In braided systems, however, the divergence and convergence of channels around bars and islands and the intense vertical exchange of surface and ground waters prevented determination of reliable oxygen balances. By integrating the measured aquatic respiration over a depth of 20 cm, we probably underestimated aquatic sediment respiration.

In terrestrial habitats, SR measurements using IRGA probably integrated the SR in the uppermost 20–40 cm of soil and sediment layers (Luo & Zhou, 2006). Furthermore, respiration included different functional compartments. In aquatic habitats, respiration included only the contribution of the hyporheic zone. In gravel deposits and large accumulations of wood, where an autotrophic compartment was almost completely missing, SR presumably represented microbial respiration. However, in islands and riparian forest, SR encompassed both microbial and autotrophic, i.e. root respiration. Root/rhizosphere respiration can account for as little as 10% to more than 90% of total *in situ* soil respiration depending on vegetation type and season and is usually highest during the growing seasons (Hanson *et al.*, 2000). Further, heterotrophic abundance, composition and activity of fungi and bacteria is habitat specific (e.g. type of soil and sediment) and depends on seasonal variations in habitat properties (Battin *et al.*, 2004; Rinklebe & Langer, 2006). Although respective seasonal investigations into floodplain soils and sediments are lacking, it can be assumed that seasonal contribution of heterotrophic organisms to SR varies differently in individual habitat types throughout the year. Despite these methodological shortcomings, our study provides a first estimate of the spatiotemporal heterogeneity of SR in a highly complex and dynamic river landscape.

In conclusion, we found a tight link between habitat properties and soil and sediment respiration across the aquatic–terrestrial environment. SR differed by an order-of-magnitude among habitat types, with temperature being the most important variable determining SR. Hence, even small changes in the relative proportion of individual habitat types and temperature can substantially alter whole-floodplain efflux of CO₂. This is important in the context of river modification and changing climate. Channelisation and flow regulation decrease habitat complexity

in floodplain systems, with severe consequences for the spatial variation in SR. For example, vegetated islands are among the first landscape elements that disappear as a consequence of flow regulation and channel modification (Gurnell *et al.*, 2001). The clearance of all vegetated islands (9% of total area; 23% of total floodplain SR), as was the case during World Wars I and II, would lead to a massive decrease in the overall floodplain SR. On the other hand, a lack of hydrological dynamics could lead to an extension of the relative proportion of the floodplain forest (23% of total area; 48% of total floodplain SR) with a subsequent increase in SR (Table 6). Global warming will increase aquatic and terrestrial soil and sediment temperature and therefore SR. As a consequence, decomposition and mineralisation can exceed net primary production and deposition leading to a decrease in soil and sediment organic matter content (Kirschbaum, 1995; Gudas *et al.*, 2010), and therefore, decrease process heterogeneity and probably carbon cycling in floodplain systems.

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