Patchiness of River–Groundwater Interactions within Two Floodplain Landscapes and Diversity of Aquatic Invertebrate Communities

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ABSTRACT

In fluvial systems, the interactions between rivers and groundwater significantly affect various ecological structures (for example, riparian vegetation) and functions. To examine the effects of hydrological exchange between groundwater and surface water on the distribution of aquatic invertebrates within a riverine landscape, we investigated the main stem, tributaries, and various surface and sub-surface waters of two floodplains of a southern Alpine river (Brenno, Switzerland) in terms of their physicochemical, hydraulic, substratum, and faunal characteristics. The origins of the water were investigated by analyzing geomorphic settings and physicochemical variables. The two floodplains had different hydrological regimes. The middle floodplain was dominated by lateral inputs and exfiltration of hillslope groundwater from two different subcatchments. Bank filtration of river water sustained sub-surface water only close to the channel. The aquatic habitats of the middle floodplain formed a rather homogeneous group with high taxon richness and intrahabitat diversities. These aquatic habitats resembled mountain springbrooks in their physicochemical characteristics and faunal compositions. In the lower floodplain, the exchange between river water and groundwater was more extensive. The aquatic floodplain habitats of the lower floodplain

were fed mainly by deep and shallow alluvial groundwater, hyporheic exfiltration, and partly by surface water. In contrast to aquatic habitats of the middle floodplain, habitats of the lower floodplain showed a low intrahabitat and a high interhabitat diversity in terms of both substrate characteristics and faunal compositions. For both floodplains, ordination analyses showed a high concordance between the structure of the invertebrate community and the characteristics of the environmental habitat, including chemical, geomorphic, and hydraulic variables. Ordinations grouped aquatic habitats according to the origins of the waters. Taxon richness was related to local structural diversity, but species turnover was related to differential vertical and lateral connectivity. Exfiltration of groundwaters provided aquatic floodplain habitats for several specialized species. The results of this study show the significance of the river–groundwater connectivity for the creation of the habitat mosaic that sustains biodiversity in floodplains and thus have important implications for managing the ecological integrity of floodplains.

Key words: ecology; river; floodplain; hydrogeology; geomorphology; biodiversity; habitat diversity; benthos.

INTRODUCTION

Patchiness, seen as spatial variation of some factor, is a characteristic feature of ecological systems; it is fundamental for metabolism, population dynamics,

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and community organization (Levin 1992). Patchiness can be continuous or discrete, and patches can vary in size, shape, intensity, spatial configuration, and interconnectedness (Cooper and others 1997). Traditionally, patch theory and dynamics are focused on micro- and mesoscales, whereas heterogeneity is focused largely at mesoscales and landscape ecology looks at the meso- and macroscale (Wiens 1997). However, the appropriate metric scales of these approaches to patchiness depend on the nature of the ecological system under study (Kotliar and Wiens 1990). For example, a holistic view of a river in its fluvial valley (Hynes 1975) would consider river–floodplain systems in a landscape context (Ward and others 1999).

Patchiness in fluvial systems develops through interactive pathways along all three spatial dimensions (Ward 1989). The patches in any fluvial landscape are linked by hydrological connectivity. Flooding is generally assumed to be the lateral pathway and the determinant for organisms in river–floodplain systems (Junk and others 1989). However, flooding may not necessarily be the key factor in, for example, riverine food web structure (Thorpe and others 1998) and the productivity of floodplain vegetation (Spink and others 1998). Vertical interaction between rivers and groundwater is important for the structure and function of stream and floodplain ecosystems. This interaction has received little attention and is rarely emphasized (Hynes 1983; Amoros and others 1987; Boulton 1993; Brunke and Gonser 1997; Ward and others 1998). The infiltration of surface water to groundwater, its flow through the alluvial aquifer and mixing with groundwater of other origin or age, and the exfiltration of subsurface water to rivers with different properties may exert various controls within river–floodplain systems. Stanford and Ward (1993) introduced the hyporheic corridor concept, in which the vertical dimension incorporates a lateral component due to exfiltrating groundwater, which feeds alluvial springbrooks and other floodplain water bodies. In general, floodplain groundwaters are composed of baseflow components that move broadly perpendicular to the river and of underflow components that move parallel to the river (Larkin and Sharp 1992).

The role of subsurface transformations of nitrogen and other nutrients in river–floodplain systems has been appreciated for some time (Chauvet and Decamps 1989; Dahm and others 1988). Furthermore, groundwater circulation patterns are thought to be responsible for the spread of pollutants across floodplains (Tremolieres and others 1997). However, we are only beginning to appreciate the intri-

cate flowpaths of different waters and their interactions, which create a network that influences water retention, nutrient dynamics, and biological diversity on a landscape scale (Stanford and others 1994; Pusch and others 1998; Brunke and Gonser 1999).

On floodplains, the properties of aquatic habitats are on one hand, influenced by the degree of lateral connectivity with the river—that is, the frequency and duration of flooding and the intensity of scour and fill (Amoros and Roux 1988; Ward and Stanford 1995). On the other hand, many of these habitats are vertically connected to the groundwater most of the time (Amoros and others 1987; Brunke and Gonser 1997; Malard and others 2000). The interplay between lateral and vertical connectivity may result in specific plant and faunal communities in floodplain water bodies (Castella and others 1984; Foeckler and others 1994; Marmonier and others 1992; Bornette and others 1998).

The objective of this study was to analyze mesoscale patchiness in floodplains based on river–groundwater interaction and to scale the results to patchiness on the landscape level. We focused on the patchiness of surface water–groundwater exchange patterns in two floodplains. Because of the complexity of subsurface flow, most research has been conducted along simple transects (Burt and Haycock 1996). Here we present an analysis of the spatial mosaic of aquatic habitats against the intricate background of mainly invisible river–groundwater interactions during low-flow conditions. We concentrated on the origins of exfiltrating groundwaters and the significance this has for the diversity of aquatic floodplain habitats and aquatic invertebrates. The surface habitat patches we studied were discrete and clearly defined by the aquatic–terrestrial boundary and their location within areas subjected to riverine flooding. Specifically, we address the following questions: (a) Do various floodplain water bodies depend on exfiltration of different ground waters? (b) Are structural intra- and interhabitat diversities of aquatic floodplain habitats related to groundwater exfiltration? (c) Do various origins of groundwaters play a role in the faunal intra- and interhabitat diversity of aquatic floodplain habitats?

METHODS

Study Area

The study was conducted in two floodplains of the Brenno River in the Valle di Blenio, which is a part of the Ticino River drainage basin in the southern

Figure 1. Catchment of the Brenno River, southern Switzerland, with middle and lower floodplains.

Alps of Switzerland (Figure 1). The Brenno is a fifth-order gravel bed river that drains 409 km² from altitudes ranging between 209 and 3400 m a.s.l. (mean altitude, 1820). The Brenno's catchment contains three floodplains, of which the middle and lower floodplain were included in the study because they contain several surface water body types (Brunke 2002). The spatial distribution of water bodies and the types of vegetation in both floodplains were mapped using aerial photographs and ground-truthing. The two floodplains have different gradients, valley widths, locations within the geological basin, and influences of tributaries from lateral slopes. In the sense of Nanson and Croke (1992), the middle floodplain can be considered to be "high-energy noncohesive," whereas the lower floodplain is "medium-energy noncohesive."

The middle floodplain is located between 530 and 630 m a.s.l.; it has an average gradient of 3.1% and covers an area of 18.6×10^5 m². It extends along the river in a narrow corridor consisting of softwood forest and poorly vegetated dry areas. The floodplain sediments (gravel and coarse sand) generally have a high hydraulic conductivity of 10^{-5} – 10^{-3} m s⁻¹.

The Brenno has been straightened and its banks reinforced to the point where it is directly upstream of the lower floodplain. The lower floodplain is located between 360 and 390 m a.s.l.; it has an average gradient of 0.8% and covers an area of 14×10^5 m². A major tributary, the Lesgiuna, enters at

the east side of the lower floodplain (Figure 1). Old softwood forest dominates the vegetation at the west side of the floodplain and upstream of the confluence. The other sides of the floodplain are influenced by the Lesgiuna; they are composed of younger softwood and are bare or partially vegetated by pioneer communities, depending on the sediment transport and the distance to the groundwater table.

Data Collection

At the scale of 10–100 m, 11 distinct surface water bodies were selected for detailed investigations—namely, the main stem of the Brenno River, the Lesgiuna River, three water bodies in the middle floodplain (meadow springbrook, aggradated springbrook, forest springbrook), and six water bodies in the lower floodplain (hyporheic-fed channels, pasture springbrook, forest springbrook, terrace springbrook, levee springbrook, ponds). The aggradated springbrook emerges on an aggradated gravel bar that was deposited on the floodplain during an extreme flood in 1987 (G. Carraro personal communication). Aggradated areas were produced from sedimentation on the floodplain at periods of high flows. Levees are channel-side ridges produced by accretion when overbank flows first pass out onto the floodplain. Terraces are raised banks of sediment with sloping sides and a flat top and are produced by down-cutting of the river into fluvoglacial sediments.

The following physical and chemical variables were measured according to standard analysis protocols (DEW 1985) for a chemical discrimination of the type of surface water and groundwater: water levels, water temperature, sodium (Na^+), potassium (K^+), magnesium (Mg^{2+}), calcium (Ca^{2+}), chloride (Cl^-), sulphate (SO_4^{2-}), nitrate (NO_3^-), alkalinity, specific conductance, and pH. Groundwater was sampled from 25 steel piezometers (internal diameter = 5 cm), of which 18 were inserted to sediment depths of 90 and 140 cm at sites selected following mapping. Seven deeper wells existed in sediment depths ranging between 2 and 7.5 m. Surface waters were collected from 18 sites at mesohabitats and minor rivulets. Water sampling was conducted in July and October 1999. Groundwater was collected by pumping with a submersible electric pump (Whale Water Systems GP9955 Superlinie 991, 12V D.C., 9.8 L/min; Munster Simms, Bangor, N. Ireland, UK).

For characterization of the environmental habitat diversity of water bodies, the following variables were measured: temperature, pH (678 EP/KF Processor; Metrohm, Herisau, Gossau, Switzerland), specific conductance (LF91; WTW, Weilheim, Germany), dissolved oxygen (Oxi 323-B; WTW), water depth, and flow velocity at 60% water depth (Mini-Air2; Schiltknecht, Switzerland), coverage by trees on an estimated percentage scale, and bottom substratum. The substratum composition was measured as percentage cover of the bottom of the water bodies according to the following nine categories: boulders (more than 200 mm), cobbles (200–63 mm), gravel (63–2 mm), sand (2–0.063 mm), silt and clay (less than 0.063 mm), submerged moss, filamentous algae, submerged macrophytes, and coarse woody debris larger than 10 mm (CWD). Sediment grain sizes were measured with sieves (Retsch, Haan, Germany) and a SediGraph 5100 (Micromeritics, Norcross GA, USA). The variables were measured at 10 sites for each water body.

The recurrence interval of flooding was assessed on a categorical scale by analyzing the discharge regime of the Brenno in the period from 1904 to 1996 (Brunke 2002). The aquatic fauna of floodplain water bodies was collected on four sampling dates between June and November 1998 by using a hand net (mesh size, 300 μm) according to the methods of Richardot-Coulet and others (1987) and Castella and others (1991). The different types of substratum were sampled randomly according to their cover percentage. The fauna associated with CWD and aquatic vegetation (placed in white dishes) was sorted in the field. Sediment was dis-

lodged by hand (sampled area, 0.04 m^2), and samples were preserved in ethanol and washed through sieves (2000 μm , 300 μm) in the laboratory. The fauna was hand-sorted, counted, preserved in 70% ethyl alcohol, and classified to the species level (except for Chironomidae and Oligochaeta) under $\times 12$ magnification.

Data Analysis

Principal component analyses (PCA) were conducted for an ordination of (a) physicochemical properties of waters to discriminate groups of surface and groundwaters in both floodplains, (b) environmental habitat variables, and (c) faunal community structure gradients according to Jongman and others (1995). The application of principal component analyses on data was checked by the guidelines listed by Legendre and Legendre (1998) and revised by the interpretability of ordination plots via individual analyses of variables. Nonmetric multidimensional scaling (NMDS) was not suitable for the analyses because the focus was on the comparison between variables and sites; therefore, two ordination diagrams (loadings and scores) per analysis were needed. The expression of the dissimilarity between sites or variables—the strength of NMDS—was of minor importance. A PCA for examining the faunal community was preferred over a correspondence analysis because rare species were included, but this should not have an unduly large influence on the analysis (Legendre and Gallagher 2001). Analysis of the data sets using detrended correspondence analysis showed that gradients displayed on factorial axes ranged between 1.3 and 4.0 SDs. The advantage of PCA is not outweighed until ordination lengths are more than 4.0 SDs (Jongman and others 1995). Comparisons between scores of the faunal PCA axes 1 to 4 and environmental habitat variables were made by Spearman correlations. The flow velocity preferences of taxa were allotted according to Colling and Schmedtje (1996).

A coinertia analysis was performed to relate both ordination results obtained by environmental habitat variables and by faunal data (Dolédéc and Chesnel 1994). The costructure between environmental variables and fauna is illustrated by a plot of scores from both ordinations; the corresponding site scores are linked by an arrow. The length of the arrow is a measure of the strength of the costructure; the shorter the distance, the better the concordance between the two structures. The significance of the coinertia analysis was tested by a Monte Carlo permutation test with 1000 simulations. Environmental variables were standardized, and faunal data

Figure 2. Principal component analysis plots of physicochemical variables of the middle floodplain waters. (a) Ordination diagram of physicochemical variables. (b) Ordination diagram of factorial scores of sites. Filled and open dots indicate the sites measured in July and October 1999, respectively. Circles identify the centroid of the groups of waters. Percentages in parentheses along the axes are the amount of variation explained by the principal component.

were presence/absence-scaled prior to analyses (Jackson 1993; Cellot and others 1994). Because of the various types of aquatic habitats and substratum categories investigated, abundances were not included in the interhabitat analyses. Ordination statistics were calculated with ADE-4 (Thioulouse and others 1997).

Substratum diversity is a decisive feature of invertebrate habitats (Erman and Erman 1984; Minshall 1984). The following three indices were calculated to assess the substratum diversity of aquatic habitats: (a) The structural *intra*habitat diversity of water bodies was calculated using the Shannon index H' for percentage cover of the substratum (Cellot and others 1994; Burnett and others 1998). (b) The *intra*habitat dominance of the substratum was calculated as the deviation from evenness (Marston and others 1995). (c) The structural *inter*habitat diversity was calculated using the Euclidian distance between substratum percentages of the floodplain habitats (Cellot and others 1994). The structural interhabitat diversity (or the contrast *sensu* Li and Reynolds 1995) of, for example, the lower floodplain or the entire region (that is, all rivers and floodplain habitats) represents the degree of structural heterogeneity between habitats and is a measure of structural beta diversity.

Taxon richness per habitat (for example, a springbrook) and for combined habitats (for example, all springbrooks of a floodplain) served as measures for alpha and gamma diversity, respectively. Spearman correlations were used to reveal strength of relationship between alpha diversity and intra-habitat structural diversity. Faunal beta diversity was cal-

culated by using Jaccard's species identity (Magurran 1988). A low Jaccard index indicates a high faunal beta diversity. For detailed explanations on the characterization of biodiversity, see Bisby (1995).

RESULTS

Physicochemical Discrimination of Waters

For the middle floodplain, the first two factors of the PCA of physicochemical variables account for 74.3% of the total variability. The concentrations of major cations, sulphate, and Cl were highly correlated, which was depicted by factor 1 (Figure 2a). Nitrate, alkalinity, and pH were correlated, but they had no correlations to the former group of ions. The concentrations of solutes tended to be lower in October than in July (Figure 2b). The PCA revealed the following four chemical groups of waters: (a) Brenno surface waters that were characterized by a high ratio of Ca^{2+} to Mg^{2+} and subsurface waters that were characterized by high concentrations of ions except nitrate; (b) surface waters of hillslope tributaries that were characterized by high pH and low alkalinity and low nitrate concentrations; (c) springbrooks and subsurface waters that were located at the margin of the floodplain and in the softwood forest and were characterized by low pH and high alkalinity and nitrate concentrations; and (d) aggradated bar springbrooks in the upstream section of the middle floodplain that had a high magnesium concentration (Figure 2a and b) and the highest specific conductance (Table 1). The high Mg con-

Table 1. Means and Coefficients of Variations (CV) of Environmental Variables in the Brenno, the Lesgiuna, and the Aquatic Floodplain Habitats of the Middle Floodplain (MF) and the Lower Floodplain (LF) of the Brenno

Habitat	Floodplain	Flooding Frequency	Flow Velocity (m/s)		Water Depth (cm)		Dissolved Oxygen (mg/L)		Specific Conductance (μ S/cm)		pH		Temperature ($^{\circ}$ C)	
			Mean	CV	Mean	CV	Mean	CV	Mean	CV	Mean	CV	Mean	CV
Brenno	MF, LF	—	50.2	52	17.8	27	10.6	11	486	16	8.4	13.3	32.5	
Lesgiuna	LF	—	41.5	70	14.5	17	11.4	4	51	16	8	13.9	44.9	
Aggradated springbrook	MF	10–20 y	17.9	85	13.5	30	7.7	10	605	13	7.7	10.4	3.2	
Forest springbrook	MF	10–20 y	21.2	68	22.1	30	9.5	7	324	8	7.95	11.1	7.3	
Meadow springbrook	MF	10–20 y	23.0	53	5.4	31	7.3	7	306	7	7.6	11.6	4.4	
Hyporheic fed-channels	LF	≤ 1 y	10.5	69	10.3	87	8.7	11	83	19	8.9	13.6	32.4	
Forest springbrook	LF	1–5 y	1.9	95	21.3	47	6.3	9	466	4.4	7.5	10.9	1.0	
Levee springbrook	LF	1–5 y	3.8	95	31.9	47	—	—	417	1	—	11.1	0.6	
Pasture springbrook	LF	1–5 y	12.0	85	13.5	51	9.6	21	239	73	8.1	14.2	38.8	
Terrace springbrook	LF	< 1 y	7.6	76	15.7	64	3.6	27	227	12	7.8	9.8	30.9	
Ponds	LF	< 1 y	0		51.2	44	3.0	41	300	30	7.4	10.8	59.3	

n = 10, except for pH which was measured once.

Flooding frequency indicates the recurrence interval of flooding in years (y).

Figure 3. Principal component analysis plots of physicochemical variables of the lower floodplain waters. (a) Ordination diagram of physicochemical variables. (b) Ordination diagram of factorial scores of sites. Filled and open dots indicate the sites measured in July and October 1999, respectively. Circles identify the centroid of the groups of waters. Percentages in parentheses along the axes are the amount of variation explained by the principal component.

tent indicates that these waters originated from a subcatchment with a high dolomite component.

Four samples showed inconsistencies in their chemical composition relative to other samples at their location within the middle floodplain (Figure 2b). One subsurface water from a piezometer located closely to the Brenno was chemically related to group (c). The opposite was the case for one forest springbrook. Another forest springbrook was more similar to the aggradated bar springbrooks, one of which was chemically related to Brenno riparian subsurface waters. These inconsistencies contribute to a chemically complex landscape. They also indicate that single interstitial flowpaths could pass groundwater subcatchments, or alternatively, that some areas are sporadically recharged—for example, during floods.

The installation of piezometers and existing gravel outcrops showed that the small hillslope tributaries of the middle floodplain were disconnected from groundwater in the floodplain by vertical distances of up to 4 m. Fine-grained sediments colmated the channel sediments. A grain-size analysis of the sediment revealed the presence of large volumes of particles smaller than 30 μm , which are decisive for colmation of the river bed (Brunke 1999). The sediments 15 cm below the stream's bottom were only partially water-saturated.

For the lower floodplain, the first two factors of the PCA of physicochemical variables (Figure 3a)

accounted for 73% of the total variability. The only apparent correlations were between nitrate, Na^+ and Cl^- . In contrast to the middle floodplain, there was no correlation between this group of ions and Ca^{2+} and K^+ . The PCA revealed that there were four chemical groups of waters (Figure 3b): (a) Brenno surface and subsurface waters that were characterized by high concentrations of Mg and sulphate; (b) the pasture springbrook, which originates in meadows at the margin of the floodplain is characterized by high loads of nitrate, Na^+ and Cl^- ; (c) surface waters of the major tributary, the Lesgiuna, and subsurface waters located in between the ponds and the terrace springbrook. These waters showed low concentrations of Mg^{2+} and Ca^{2+} and had high sulphate- Mg^{2+} and Ca^{2+} - Mg^{2+} ratios. Lesgiuna waters have a very low specific conductance of 50–60 $\mu\text{S}/\text{cm}$ because the Lesgiuna catchment is located entirely in crystalline rock; (d) a heterogeneous group of ponds and exfiltration sites located close to the Lesgiuna and Brenno rivers. These waters were characterized by high alkalinity and K content. The water was anoxic and exfiltrated at many minor sites and directly at a higher volume in a terrace where it fed the terrace springbrook and the ponds. These habitats had low concentrations of dissolved oxygen (DO) (Table 1). All other springbrooks had intermediate to high DO, but these concentrations were lower than those of the Brenno and Lesgiuna rivers.

Figure 4. Ordination diagrams of principal component analyses of environmental habitat variables (a) and aquatic fauna (b). Correlation arrows were removed to improve the clarity of the faunal ordination diagram. Percentages in parentheses along the axes are the amount of variation explained by the principal component. DO, dissolved oxygen.

Three samples showed inconsistencies in their chemical composition relative to other samples at their location within the lower floodplain (Figure 3b). Subsurface water taken in October from one piezometer located upstream of the confluence was fed by Lesgiuna water (group c) instead of Brenno water (group a). Two exfiltration sites located closely downstream of the Lesgiuna (group c) were fed by Lesgiuna water (group c) in July and by Brenno water (group a) in October and contributed to the waters of group d.

Environmental Conditions of Aquatic Habitats

The first two factors of the PCA of environmental habitat variables characterizing riverine and floodplain water bodies in both floodplains accounted for 57% of the total variability (Figure 4a). Factor 1 depicted a gradient of increasing hydraulic influence on environmental conditions. High-flow velocities and dissolved oxygen contents and coarse bottom substrate were inversely correlated to fine sediment and the occurrence of submerged macrophytes. Factor 2 depicted the influence of the adjacent land on habitat conditions. The occurrence of boulders, moss, and CWD and a high specific conductance were inversely correlated to the variability of water temperature, depth, dissolved oxygen content, and the occurrence of filamentous algae. A dense coverage by the forest canopy was inversely correlated with high water temperature and pH. A further inverse correlation was seen between the occurrence of moss and gravel and water depth.

Flow velocity was highest in the Brenno and Lesgiuna rivers; the springbrooks of the middle floodplain were clearly more lotic than those of the lower floodplain (Table 1). The temperature variability was very low in springbrooks (mean temperature, about 10–11°C; Table 1), with the exception

of the terrace springbrook. All were dominated by the exfiltration of groundwater. The higher temperature variability in the terrace springbrook was a result of the seasonal air temperature fluctuations and direct solar radiation due to its origin from shallow groundwater. Temperature variability was most pronounced in the ponds and was also obvious for the Brenno, the Lesgiuna, and the pasture springbrook, the latter had already traveled about 1 km through open land before entering the floodplain.

The springbrooks of the middle floodplain had the lowest connectivity with the Brenno River because they were located behind ridges and levees (forest springbrook), at the margin of the floodplain (meadow springbrook), and on elevated sediment sheets (aggradated springbrook). In contrast, the water bodies of the lower floodplain showed a higher degree of connectivity to the Brenno and Lesgiuna rivers. The hyporheic-fed channels form parts of the riverine channels during mean flows, and they can be considered to be intermittently-connected in the sense of Tockner and others (1997). The ponds and the terrace springbrook were flooded at least once a year, whereas the levee and pasture springbrooks were more isolated by levees and ridges. The sediment and geomorphic forms revealed that the ponds, the terrace springbrook, and the hyporeic-fed channels experienced erosive flooding, whereas thick sandy depositions in the levee springbrook indicated alternating erosion and deposition during floods.

Patchiness and Gradients in Aquatic Invertebrate Assemblages

The first two factors of the PCA of the aquatic fauna accounted for 43.8% of the total variability (Figure 4b). The scores of factor 1 correlated significantly with mean and range of flow velocity, coarse-

Table 2. Spearman Correlation Coefficients between Scores of Faunal PCA Axes 1 to 4 and Environmental Variables

Environmental Variable	Factor 1 (25.9%)	Factor 2 (17.9%)	Factor 3 (12.3%)	Factor 4 (11.1%)
Flooding frequency	—	−0.63 ^b	0.57	−0.66 ^b
Coverage	−0.34	0.57	—	—
Boulders	0.77 ^a	0.23	0.24	−0.14
Stones	0.61 ^b	−0.44	—	−0.17
Gravel	0.58	−0.1	—	—
Sand	−0.11	0.13	0.25	−0.45
Mud	−0.67 ^b	0.33	—	0.48
Moss	0.67 ^b	—	0.46	−0.27
Algae	0.22	−0.67 ^b	0.63 ^b	−0.11
Macrophytes	−0.43	0.43	0.3	—
CPOM	−0.19	0.69 ^b	−0.23	—
Flow velocity (mean)	0.80 ^a	−0.26	0.12	−0.16
Flow velocity (range)	0.83 ^a	−0.27	—	−0.2
Water depth (range)	−0.66	—	0.25	—
Water depth (mean)	−0.31	—	0.57	—
Dissolved oxygen (mean)	0.58	−0.52	−0.24	−0.18
Dissolved oxygen (range)	−0.10	−0.40	0.34	0.26
Specific conductance	0.33	0.31	−0.16	−0.11
pH	0.47	−0.64 ^b	—	−0.33
Temperature (mean)	0.25	−0.54	−0.36	—
Temperature (range)	−0.21	−0.46	0.34	0.25

PCA, principal component analyses

Percentages refer to the proportion of variance in faunal data explained by the principal component.

—indicates that correlation was zero.

^a $P < 0.01$

^b $P < 0.05$

grained inorganic particles, and dissolved oxygen; inverse correlations were found for water depth and mud (Table 2). Factor 1 depicted a composite gradient of hydraulics and coarse sediment and was therefore similar to factor 1 of the environmental habitat ordination (Figure 4a). Lotic taxa (that is, taxa that prefer high-flow velocities) were located at the right side of the ordination plot, whereas lentic taxa (that is, taxa that prefer low- or zero-flow conditions) were placed on the left side of the plot. The lentic species were pond species and an additional group of taxa that tolerate moderate-flow velocities (for example, the snail *Galba truncatula* and the water beetle *Haliphus* sp.) (Figure 4b).

The lotic species were separated along factor 2 into river and spring species. Typical species for the river habitats were the larvae of the stonefly *Perlodes* sp. and the caddis fly *Allogamus auricollis*. Spring habitat species were typified by the larvae of the caddis fly *Ptilocolepus granulatus* and the water beetle *Helodes* sp. Spring species contributed significantly to taxon richness of all habitats in the middle floodplain (22%: aggradated, meadow springbrooks; 18%: forest springbrook) but less to four

habitats in the lower floodplain (14%: forest; 8%: pasture; 3%: terrace springbrooks, hyporheic-fed channels). Factor 2 also showed a transition in habitat preferences for many lotic species. For instance, taxa such as the larvae of the mayfly *Baetis alpinus* were found in both habitats and lay between both groups on the plot. Factor 2 displayed a gradient developed by flooding frequency and the influence of adjacent land in terms of coverage, deposition of CWD, and presence of algae (Table 2). Dense terrestrial vegetation cover resulted in shade and low algal growth and high inputs of CWD.

Stenothermal aquatic beetles such as *Hydroporus ferrugineus* and *Hydraena nigrita* occurred specifically at exfiltration sites of cold alluvial and hillslope groundwater with soft substrates. Dragonflies are an example of a taxonomic group that was not found in river habitats but were indicative of particular environmental conditions in aquatic floodplain habitats. *Cordulegaster bidentata*, a mountain spring species, occurred in the middle floodplain at sites with exfiltration of hillslope groundwater with a constant temperature. *Cordulegaster boltoni*, a mountain stream dragonfly, inhabited cold-water

Figure 5. Coinertia analysis of scores obtained by principal component analyses of environmental habitat variables and aquatic fauna. Filled dots and arrows indicate ordination of sites according to physical habitat variables and fauna, respectively. Percentages in parentheses along the axes are the amount of variation explained by the principal component.

forest springbrooks with exfiltrated alluvial groundwater in the lower floodplain. The following dragonflies tolerate temperature fluctuations such as those that occurred in the lower floodplain: *Lestes viridis* was found in the slow-flowing terrace springbrook with marginal overhanging willows, which are necessary for reproduction. Lentic species such as *Coenagrion puella* and *Ischnura elegans* require stagnant conditions offered by the ponds. *Symptetrum striolatum/vulgatum* and *Platycnemis pennipes* were indicative of transitions between pondlike habitats and slowly flowing brooks. *Aeschna cyanea* occurred in all stagnant and slow-flowing habitats. Thus, the various water bodies of the lower floodplain offered habitats for several dragonfly species that did not occur in the middle floodplain.

Concordance between Environmental and Community Structures

The concordance between the faunal and environmental ordinations was high according to the coinertia analysis. The correlations of factors 1 and 2 between the two ordinations accounted for $r = 0.95$ for both, respectively. Permutation tests proved that the costructure was significant ($P < 0.001$). The coinertia analysis revealed four groups of habitats based on environmental and faunal data (Figure 5): (a) the riverine habitats, which refer to the Brenno, the Lesgiuna, and the closely located exfiltration

sides, which were fed by hyporheic water; (b) the springbrooks in the middle floodplain, (c) the springbrooks of the lower floodplain, and (d) the ponds of the lower floodplain. Comparisons with results obtained by measurements of chemical variables revealed the following origins of waters (Figures 2 and 3): Group a was fed by riverine surface water and by hyporheic water—that is, surface water that emerged after a short-term subsurface passage of a few hours. Basically, the hyporheic water altered its chemical characteristics by a slight increase in nutrients and a reduced pH, which did not affect the background characteristics markedly (Figure 3). Group b was fed by two types of groundwater that resembled waters of hillslope tributaries enriched in nitrate (group ii/iii in Figure 2) and the waters from a dolomite (that is, $\text{Ca}^{2+}/\text{Mg}^{2+}$ less than 5) subcatchment (group iv in Figure 2). Group c was mainly fed by waters from the alluvial aquifer of the Brenno that had infiltrated further upstream. Some sites also received subsurface water from the Lesgiuna or another source, as did the ponds of group d. The anoxic character and the discrete exfiltration at the margin of a terrace indicated that this water might originate from a top layer of groundwater that flowed through the root system of the floodplain vegetation and emerged as the slope of the terrain decreased toward the river channel. The ponds occasionally also received Brenno and Lesgiuna water during floods and precipitation. The quantitative contributions of surface water relative to subsurface inputs remained unresolved.

In the coinertia analysis, the length of the arrows indicated differences between the faunal and environmental scores (Figure 5). The invertebrate assemblages of the Lesgiuna and the hyporheic-fed channels were more similar than indicated by environmental conditions. The environmental conditions of the Brenno and Lesgiuna rivers were similar because of the dominating hydraulic/sediment gradient along factor 1, but faunal compositions differed slightly. The springbrooks of the middle floodplain were a distinct group, of which the aggradated springbrook displayed the closest relationship between environment and fauna. The springbrooks of the lower floodplain were a heterogeneous group, as they scattered along factor 2. The arrows of both the forest springbrook and the levee springbrook were long, but there was no overlap between any of the springbrooks. The costructure between the fauna and environmental variables of the terrace springbrook was very distinct. Each of the springbrooks in the lower floodplain was unique in terms of hydrogeomorphology and faunal assemblages.

Figure 6. Relationships between (a) alpha-diversity and intrahabitat structural diversity and (b) gamma diversity and interhabitat structural diversity. Alpha diversity is the taxon richness per habitat; gamma diversity is the regional diversity of combined habitats.

There was no overall concordance between surface connectivity assessed as recurrence interval of flooding and arrangements of habitats. Surface connectivity was similar within the groups fed by hill-slope groundwater (b) and, of course, by river water (a). The alluvial ground water group (c) and the ponds (d) of the lower floodplain were not arranged in a consistent gradient according to surface connectivity. A trend of connectivity occurs along factor 2 (Table 2).

Structural Habitat Diversity and Faunal Alpha and Gamma Diversities

Structural habitat diversity and recorded taxon richness per habitat (alpha diversity) were significantly correlated (Figure 6a). The pasture springbrook had a lower and the forest springbrook a higher taxon richness than would have been expected from their structural diversities. The low structural diversity of the levee springbrook, due to a dominance of sand, was reflected in its depauperate fauna. Yet taxon richness did not correlate significantly to intrahabitat dominance of substratum. Faunal beta diversity was highest in the lower floodplain and very variable in comparison of lateral floodplain habitats to riverine habitats as assessed by mean Jaccard index (range): middle floodplain, 0.47 (0.43–0.49); lower floodplain, 0.24 (0.09–0.35); middle versus lower floodplain, 0.26 (0.11–0.38); Brenno and Lesgiuna versus middle and lower floodplain; 0.25 (0.10–0.55).

The heterogeneity of the combined aquatic habitats of the middle floodplain was characterized by a low interhabitat and a high intrahabitat structural and faunal diversity (Figure 6a and b). The combination of the middle floodplain springbrooks with the Brenno River did not markedly increased either the structural or the gamma diversity. Many of the river species of

the Brenno also occurred in the springbrooks of the middle floodplain because these springbrooks share gravel beds and lotic conditions with the Brenno. The lower floodplain showed a higher degree of structural interhabitat diversity than of intrahabitat taxon richness (alpha diversity); gamma diversity was high because of high taxon turnover. The lower floodplain is characterized by an environmental distinctness of springbrooks and ponds, which did not allow high alpha diversities. The taxon richness of all floodplain habitats combined was about 2.5 times higher than in the Brenno and Lesgiuna rivers combined. Both floodplains combined had an interhabitat diversity and gamma diversity nearly equal if they were combined with those of the Brenno and Lesgiuna rivers. Thus, the major portion of the total diversity of the river–floodplain system was contributed by the floodplain habitats.

DISCUSSION

Surface Water–Groundwater Interaction: Groundwaters

The origins of groundwater exfiltration varied markedly within and between the two floodplains. The contribution of tributaries to groundwater recharge appeared to be small. In the middle floodplain, tributaries were totally disconnected from groundwater by an unsaturated zone of up to 4 m vertical distance between the saturated zones. The hydraulic conductivity of unsaturated sediment is one to three orders of magnitude lower than that of saturated sediment (Huggenberger and others 1998). Frequently, clogging by fine particles is restricted to the top sediment layer (Brunke 1999). This was most likely the case and prevented tributaries in the middle floodplain from seeping away before reaching the Brenno.

In the middle floodplain, some groundwaters had similar chemical compositions as water from the hillslope tributaries. Because of respiration processes, the middle floodplain subsurface water was enriched in carbon dioxide, which resulted in a higher alkalinity and lower pH. The enriched nitrate content reflected the effect of agricultural land use and recharge through the soil comparable to the hillslope groundwater of the Rhône system (Bornette and others 1998). Much of this groundwater probably enters the aquifer after snowmelt by percolating through the soil. This hillslope groundwater fed the meadow and pasture springbrooks. Snowmelt is also the main source of water for hillslope tributaries. Groundwater age estimations for the middle floodplain indicated a seasonal hydrological cycle based on local recharge of this groundwater in spring following snowmelt (Kipfer and others 2000). The exfiltration of groundwater in the aggradated bar of the middle floodplain contrasts with this sequence. Its different chemical composition indicated that the Brenno neither fed it further upstream nor was recharged locally by snowmelt or hillslope water. This strongly suggests that the groundwater must have originated from a lithologically different subcatchment with stronger geochemical dolomite characteristics because of the high Mg content. In spite of its longer subsurface passage, it was also rich in oxygen.

Brenno water infiltrates within the middle floodplain at several sites. However, the subsurface flowpaths were limited to the adjacent riparian sediments. The underflow and subsurface Brenno water did not reemerge to feed springbrooks. The hillslope aquifer extends to the floodplain as a fan. In the lower floodplain, Brenno water infiltrated locally at the beginning of the floodplain and re-emerged at hyporheic-fed channels mixed with different groundwater.

Surface Water–Groundwater Interaction: Springbrooks

According to the typology of floodplain channels reported by Tockner and others (1997), all springbrooks of both Brenno floodplains belong to groundwater channels, which have no upstream connection to the river. However, the various environmental characteristics of the springbrooks in this hydrosystem render them a nonuniform group and make further differentiation necessary. The various origins of exfiltrating groundwater with different properties (for example, in terms of dissolved oxygen, temperature, and pH) and substrate structures and the influence of the terrestrial vegetation, make each habitat of the lower floodplain a unique

case. For example, only the groundwater that feeds the terrace springbrook and ponds was depleted of oxygen. Both the temperature variations and the drainage out of the terrace indicated that this was surficial groundwater that flowed laterally through the root system of the floodplain vegetation, where metabolic oxygen depletion occurred.

The middle floodplain springbrooks were a distinct group in terms of hydrogeomorphology and fauna relative to the lower floodplain habitats. The chemical difference of the aggradated springbrook—that is, in terms of higher specific conductance and Mg content—did not seem to influence habitat characteristics significantly, since invertebrate assemblages were similar to forest and meadow springbrooks and ordinated in between both.

Tributaries did not appear to recharge the middle floodplain groundwater. The contributions of hillslope groundwater to alluvial groundwater and floodplain water bodies have frequently been underestimated or neglected (Burt and Haycock 1996); for the structure of this floodplain (in terms of springbrooks and vegetation) hillslope groundwater was essential. The down-valley slope of the middle floodplain promoted hillslope groundwater flow beneath the floodplain and induced interstitial drainage parallel to the river channel. The Mg-rich groundwater probably reached the middle floodplain via this pathway. Nevertheless, the Brenno water undergoes intense exchanges with its adjacent underflow. In the lower floodplain, the exfiltration of shallow and deep alluvial groundwater prevailed to feed springbrooks. However, locally, river and tributary water also infiltrated and re-emerged after hyporheic passage, which contributed to the spatial mosaic of river–groundwater interactions.

Hydrogeological Patchiness of the Two Floodplains

At the macroscale, hydrogeological patchiness is expressed as the difference between the floodplains with respect to the role of groundwater emergence to floodplain structure and the origin and physicochemical properties of waters. In both floodplains, the exfiltration of groundwater creates several types of surface water bodies, which are significant for the structure of the floodplains. However, the two floodplains differed in their hydrological regime. In the middle floodplain, hillslope groundwater from different subcatchments prevails. In the lower floodplain, alluvial groundwater is more prominent than in the middle floodplain, and hyporheic groundwaters contribute to emergence patterns. In the lower floodplain, tributary waters feed hypo-

rhic exfiltrations, and the major tributary—the Lesgiuna—has a strong influence on floodplain aquatic habitat structure. Because of the rarity of macroscale studies, we are just beginning to appreciate the role played by tributaries in diversity of floodplains, which can differ at the mesoscale but can contribute greatly to macroscale biodiversity (Godreau and others 1999).

At the mesoscale, hydrogeological patchiness is expressed as the heterogeneity among waters within the two floodplains. Waters of the middle floodplain originate from two subcatchments. River water interacts with the groundwater adjacent to the channel. So differences between waters were small, and the springbrooks, which are fed by hill-slope groundwater, are homogeneous in their physicochemical properties. In contrast, water circulation in the lower floodplain is more complex. Here, several types of surface and groundwaters infiltrate and exfiltrate, creating a high heterogeneity between aquatic habitats.

The contributions to landscape patchiness by one or both floodplains viewed together are different. The contributions of groundwaters in terms of quality and quantity, which are frequently overlooked, are probably more significant for the diversity of floodplains than has been recognized. These results indicate that measuring groundwater levels for floodplain studies and management may not be sufficient to understand the complete role played by groundwater and by its interactions with surface waters in functional processes, such as organic matter decomposition (Claret and others 2001), and in the diversity of floodplains.

Aquatic Habitat Diversity and Invertebrates

The close costructure in ordination analyses between environmental and faunal data suggests that an investigation at the mesoscale was adequate for a characterization of abiotic and biotic diversities. Despite the often-stated linkage between geomorphologically diverse habitats or landscapes and biotic diversity of plants and animals (Rosenzweig 1995), the tight relationship between structural intrahabitat diversity and taxon richness was unexpected. First, we did not classify all taxonomic groups to the finest level of resolution. Second, the diversity index did not distinguish between the nature of substratum (that is, mud and sand were treated as equivalent to gravel or dead woody debris as habitats). Several studies indicate that fine sediments offer fewer microhabitats and refugia for aquatic invertebrates (see for example, Richards and others 1994; Brunke and others 2002). Third, the structural index of spatial resources and their

diversity barely reflected the supply of nutritional resources and the influence of disturbances, both of which should be relevant for biological diversity (Huston 1994). Taxon richness does not account for community composition. However, a high faunal beta diversity was evident for the Brenno–floodplain system, so the species turnover was not considered in the relationship between intrahabitat structural diversity and taxon richness (alpha diversity).

The occurrence of specialized species in particular habitats—such as stenothermic beetles at cold groundwater exfiltration sites or obligate mountain spring species (crenobionts)—proved that factors other than structural habitat diversity determine assemblages. For example, the occurrence of the crenobiontic caddis fly *Ptilocolepus granulatus* depends on the emergence of groundwater at a constant temperature and the growth of moss, which serves as a microhabitat providing food and leaves that are used to build the case. Furthermore, such crenobiontic species are not adapted to riverine disturbances (Zollhöfer and others 2000). In the Brenno River–floodplain system, only the exfiltration of hillslope groundwater in conjunction with the more isolated location of the springbrooks in the middle floodplain offered such conditions. Similar species level occurrences were recorded for other trichopterans, odonates, coleopterans, and mollusks. Ferreira and Stohlgren (1999) emphasized the species-specific response of floodplain plants as opposed to a community-level response to flooding and the importance of habitat heterogeneity for creating and maintaining species and landscape diversity.

Many of the structural characteristics and the mean oxygen content found in our study were a consequence of hydraulic forces—results comparable to those from another southern alpine river (Arscott and others 2000). At the landscape scale, when all habitats were considered, the lentic–lotic gradient was the prominent factor governing transitions and discriminating among assemblage compositions. This coincides with findings for other river–floodplain systems in Australia and Europe (Boulton and Lloyd 1991; Greenwood and Richardot-Coulet 1996). The aquatic habitats were ordinated along the hydraulic gradient in sequence from river water, hillslope groundwater-fed habitats, and alluvial groundwater-fed habitats to ponds, which received waters of different origins. This array indicates a relationship between the source of the water, slope, and geomorphology. Ambient terrestrial surroundings further differentiated environmental habitat conditions, which was also reflected in the faunal costructure. A high de-

gree of coverage by surrounding vegetation resulted in depositions of CWD, which were not flushed due to the minor hydraulic influence in the more isolated habitats and thus hindered the growth of algae. Boulders guaranteed sufficient temporal stability for the development of extensive moss covers in a hydraulically intermediately demanding habitat. Thus, hydraulics determined lotic–lentic composition at the landscape scale because of the valley gradient. Physicochemical and terrestrial factors operated at the mesoscale to provide various microhabitats, resulting in a high species turnover.

Temperature and dissolved oxygen variations were inversely related to exfiltration of hillslope and alluvial groundwater. The importance of terrestrial inputs was highest for habitats that had the lowest lateral hydrological connectivity and, in concordance, where vertical hydrological connectivity determined the physicochemical milieu. So the most ecologically relevant direct influences of groundwater emergence partly overlap with inputs from terrestrial vegetation. Thermal heterogeneity of floodplain water bodies enriched the spectrum of structural habitats at the landscape scale owing to various volumes and origins of groundwater inputs, as was proposed by Brunke and Gonser (1997). The springbrooks probably provide thermal refugia for fish in addition to functioning as refugia during erosive floods in the main stem.

In the Brenno system, invertebrate alpha diversity was highest in the less disturbed aquatic habitats of the middle floodplain because of the co-occurrence of spring and riverine species. A low temporal variability in environmental conditions in conjunction with cold groundwater emergence is a prerequisite for the existence of most aquatic mountain flora and spring fauna (Bornette and others 1998; Zollhöfer and others 2000). Beta diversity was higher in the lower floodplain, where habitats were subjected to a differential surface connectivity by flooding and where the influence of the terrestrial surroundings were also different between habitats.

Somewhat different relationships have been found for other large European river systems. In the Regelsbrunner Aue of the Danube in Austria, beta diversity was higher in general for isolated and fragmented channels (Tockner and others 1999). A separate analysis of odonates, mollusks, macrophytes, and amphibians revealed that diversity patterns varied strongly, mainly depending on a mixture of group- and species-specific tolerances against autogenic and allogenic hydrogeomorphic successions of floodplain water bodies along a lateral connectivity gradient. Habitat size seemed not to be a relevant causal variable or was overridden

by the effect of lateral connectivity (Tockner and others 1999). A comparison between two adjacent sections in the Upper Rhone system in France revealed contrasting diversity patterns for aquatic invertebrates. Aquatic habitats of the dynamic Ain floodplain near the confluence were characterized by a high alpha diversity, whereas fragmented habitats in the floodplain of the regulated Rhône displayed a high beta diversity (Castella and others 1991). The different sizes of the limited number of investigated systems and the sparseness of data currently make a general synthesis on decisive factors for invertebrate diversity patterns in river–floodplain systems impossible. Surface and subsurface connectivity clearly exert a dominant influence on colonization pathways, which was also shown for dryland rivers (Sheldon and others 2002), but many other factors are important in structuring biological diversity at the meso- and macroscale. Taxon richness and composition is generally determined not only by local environmental factors, but also by the larger taxa pool at the basin scale (Vinson and Hawkins 1998). In the Brenno, this macroscale factor is reflected by the occurrence of river taxa in the springbrooks in the middle floodplain. Most of the abiotic and biological diversity is contained in the floodplains of the Brenno system.

The role of the origin of groundwater on faunal diversity is difficult to assess, because it overlaps with other variables in the river–floodplain system of the Brenno catchment. Nonetheless, coinertia analysis revealed different assemblages for different water sources. Structural diversities of habitats were not related to groundwater emergences. Structural diversity was fundamental for alpha diversity, but a high gamma diversity that integrates alpha and beta diversity depends on further qualitative factors. Hydraulics, terrestrial influence, and hydrogeomorphology acted across scales to form the habitat template of aquatic water bodies. Vertical and lateral connectivity regulates the distinctness of species compositions. Groundwater emergence was essential for maintaining most aquatic floodplain habitats and enabled the occurrence of several specialized and rare species because of their distinct physicochemical characteristics.

From a holistic perspective, these results underscore the interrelatedness between lateral and vertical connectivity as well as the importance of terrestrial influence for mesohabitat characteristics. Therefore, vertical hydrologic connectivity should always be included in analyses of floodplain biodiversity and management policies designed to preserve the mosaic of habitats.

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