

CHAPTER 5

**THE CONTRIBUTION OF LATERAL AQUATIC HABITATS
TO MACROINVERTEBRATE DIVERSITY ALONG RIVER
CORRIDORS**

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The lateral dimension of biodiversity along river corridors has been given scant attention in river ecology. Therefore, the objective of the present study was to quantify the distribution and diversity of lateral aquatic habitats and their associated macroinvertebrate communities along three river corridors (Tagliamento, Thur, and Rhône) in the Alps. A nested sampling design was applied. Along each corridor, 1-km long segments were surveyed at 10-km distances (14 to 17 sections per corridor). Within each segment, the main channel, parafluvial ponds, backwaters, and tributaries were sampled for Ephemeroptera, Plecoptera and Trichoptera (EPT-taxa). Overall, 159 EPT-taxa were identified in 119 composite samples, which was between 73% and 77% of the total expected richness along each corridor. Lateral habitats contributed >50% to total corridor species richness. Diversity was hierarchically partitioned to quantify the relative proportion contribution of individual samples, habitats, and corridors to overall diversity (three river corridors). Among-sample and among-corridor diversity components contributed most to total EPT-taxa richness, while <15% was due to within-sample and among-habitat diversity components. The present study clearly emphasises the importance of lateral aquatic habitats for maintaining high aquatic biodiversity along river corridors. Consequently, these habitats need to be fully integrated in future conservation and restoration projects; particularly since these

are the first habitats that disappear as a consequence of river regulation and flow control.

INTRODUCTION

Biodiversity in river corridors is structured along longitudinal, lateral and vertical dimensions (Ward 1989). Various concepts predicting species diversity along river corridors have been developed (Vannote *et al.* 1980; Statzner & Higler 1986; Ward & Stanford 1995; Stanford *et al.* 1996). The river continuum concept (RCC, Vannote *et al.* 1980) proposed maximum biodiversity in middle reaches where environmental heterogeneity is expected to be maximized. Statzner and Higler (1986) suggested that maximized biodiversity is linked to hydraulic changes associated with geomorphological transition zones. In extension of the serial discontinuity concept (SDC), Ward & Stanford (1995) included the interactions between the river channel and its flood plain (i.e., lateral dimension). They proposed greatest diversity in transition zones between constrained and braided sections and in the meandering reach. Stanford *et al.* (1996) suggested a more complex and extended model, which predicts maximum diversity in floodplain reaches and lowest diversity in geomorphological transition zones.

Most concepts have been developed for single-thread rivers. Studies on the lateral organization of aquatic macroinvertebrates were restricted to individual floodplain segments (e.g., Amoros & Roux 1988; Castella *et al.* 1991; Foeckler *et al.* 1991; Obrdlik & Fuchs 1991; Van den Brink *et al.* 1996; Tockner *et al.* 1999; Arscott *et al.* 2003). Although backwaters, parafluvial ponds and tributaries are recognised as key elements of the river “discontinuum” (e.g., Vannote *et al.* 1980; Minshall *et al.* 1985; Perry & Schaeffer 1987; O'Leary *et al.* 1992; Homes *et al.* 1999; Rice *et al.* 2001; Solari *et al.* 2002; Benda *et al.* 2004), their contribution to biodiversity at the corridor scale (regional-scale diversity) has not been tested yet.

In addition, most diversity studies - not only in rivers - focused on alpha-diversity (i.e., local-scale diversity), neglecting hierarchical organization of biodiversity (e.g., Noss 1990; Ward & Tockner 2001). Relationship between scale of investigation and processes that influence species diversity is the basis of the

distinction between inventory diversity (α -, γ - & ϵ -diversity) and differentiation diversity (β -diversity) (Magurran 2004). Studies on beta-diversity (i.e., species turnover along environmental gradients), for example, can be crucial to the understanding of environmental factors that are responsible for observed diversity patterns in both aquatic and terrestrial ecosystems (Bornette *et al.* 2001; Ward & Tockner 2001; Pineda & Halffer 2004). Moreover, processes that operate over a range of scales likely influence the structure of communities along riparian corridors. However, mechanisms at one spatial scale might have larger relative effects on community structure than mechanisms that operate at another scale (Shmida & Wilson 1985; Wagner *et al.* 2000). Identification of such critical scales is of great importance for the successful conservation of riverine biodiversity.

In this study we focus on diversity of aquatic macroinvertebrates along river corridors by including the lateral dimension. Principal objectives are (1) to quantify the relative contribution of main channel, backwater, parafluvial pond and tributary habitats to river corridor diversity and (2) to study the hierarchical structure of biodiversity along river corridors. Based on this study, we discuss potential implications for conservation and management of river ecosystems. Emphasis was given on the insect orders Ephemeroptera, Plecoptera and Trichoptera (EPT). EPT-taxa form an important component of the benthic community of lateral aquatic habitats (Arscott *et al.* in press). Furthermore, they are frequently considered in basic research as well as for biomonitoring of aquatic ecosystems (e.g., Marchant *et al.* 1995; Hewlett 2000; Cereghino *et al.* 2003).

STUDY AREAS

Three Alpine river corridors were investigated for aquatic habitats and benthic macroinvertebrates (Figure 1). The Tagliamento drains into the Adriatic Sea, the Thur via the Rhine River into the North Sea, and the Rhône into the Western Mediterranean Sea. The three river corridors are comparable in their geomorphology and catchment size, although they differ in their anthropogenic alteration (e.g., water abstraction, channelization). The Tagliamento is the least modified, the Rhône the most impacted river.

Tagliamento

The Tagliamento is a large gravel-bed river located in north-eastern Italy (Friuli-Venezia Giulia; 46°N, 12°30'E; Figure 1). It rises at 1195 m a.s.l. in the Carnian Alps and flows 170 km to the Adriatic Sea. The catchment covers 2580 km² with more than 70% located in the Alps. The Tagliamento has an average discharge of 90 m³/s, whereas 2-, 5- and 10-year floods are estimated to be 1100, 1600 and 2150 m³/s (Petts *et al.* 2000). High flow is caused by snowmelt (spring) and heavy rainfall (autumn) with discharge maxima of ~4000 m³/s (Ward *et al.* 1999); minimum discharge is 20 m³/s. The near-pristine character of the Tagliamento is reflected in its complex channel morphology, a dynamic flood regime, and an idealized longitudinal sequence of constrained, braided and meandering sections. For detailed information on the catchment and the main study area see Ward *et al.* (1999), Gurnell *et al.* (2000), Arscott *et al.* (2000), and Tockner *et al.* (2003).

Thur

The Thur is a gravel-bed river located in north-eastern Switzerland (Figure 1). It rises in the alpine region at 2502 m a.s.l. and flows 135 km to the Upper Rhine (345 m a.s.l.). The catchment area covers 1750 km². Major parts of the upper catchment are in the pre-alpine zone. Average discharge is 47 m³/s, with minimum and maximum values of 2.2 m³/s and 1130 m³/s, respectively. The Thur is

channelized between the lower end of the pre-alpine zone (river-km 59) and its confluence with the River Rhine (river-km 135) (Uehlinger 2000).

Rhône

The Swiss part of the Upper Rhône River originates from the Rhône glacier at 1763 m a.s.l. and flows 166 km to the Lake Geneva (374 m a.s.l., Figure 1). The catchment area covers 5220 km² (Loizeau & Dominik 2000). Average annual discharge is 182 m³/s with a minimum and maximum discharge of 34 m³/s and 1370 m³/s, respectively (Bundesamt für Wasser und Geologie 2003). The Upper Rhône River is channelized from river-km 45 to Lake Geneva. Numerous hydroelectric dams have been constructed on the main stem and on tributaries, which strongly modify the flow characteristics of the river (hydropeaking). Dam operations cause rapid variations in discharge and water level fluctuations (>100 cm per day) (Loizeau & Dominik 2000).

METHODS

Sampling design

A nested design was used in this study (*sensu* Ward & Tockner 2001). In spring 2002 (March until May), at approximately mean annual discharge, and before most EPT-larvae emerge, lateral habitat-heterogeneity and the diversity of EPT-taxa were investigated along the three river corridors. Along each corridor, one-km long segments were surveyed at 10-km distances starting at river-km 5. Within each segment the main channel and lateral aquatic habitats (i.e., backwaters, parafluvial ponds, and tributaries) were mapped (Table 1).

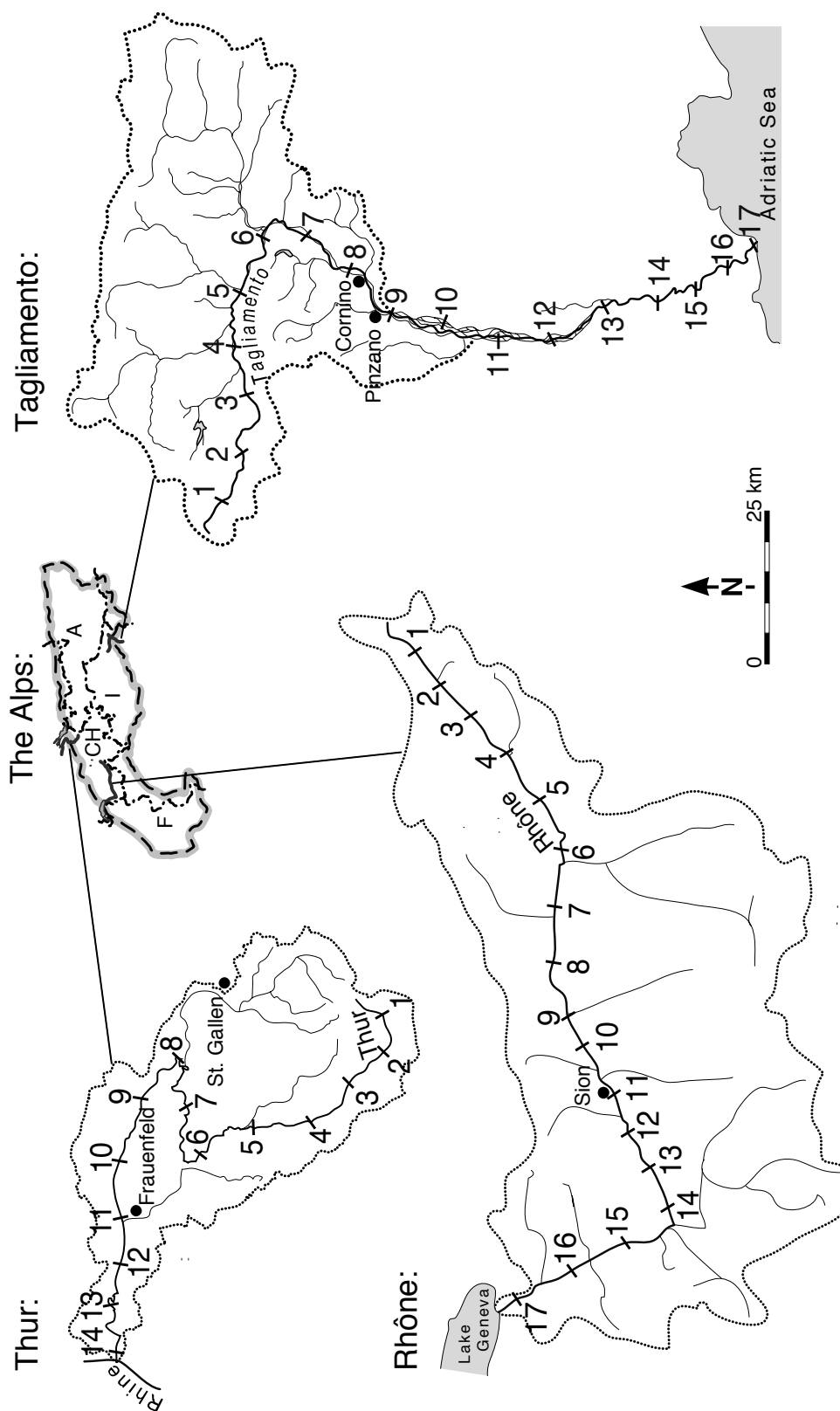


Figure 1. Catchment of the Tagliamento, the Thur, and the Rhône Rivers and location of individual sampling segments along each corridor (numbers; 1-km long segments each 10 km).

Table 1. Total number of composite samples (mc = main channel, p = pond, bw = backwater, t = tributary).

	mc	p	bw	t	Total
Tagliamento	15	9	10	5	39
Thur	14	5	5	13	37
Rhône	17	3	6	17	43
Total	46	17	21	35	119

Backwaters were defined as habitats with a permanent downstream connection to a lotic channel but with local conditions being lentic-like and often with fine sediment deposits. Parafluvial (*sensu* Fisher *et al.* 1998) ponds were disconnected lentic waterbodies within the active zone of the corridor (*sensu* Frissell *et al.* 1986). A tributary was defined as the smaller and the main channel as the larger of two intersecting channels (*sensu* Benda *et al.* 2004). We sampled tributaries upstream from their confluence with the main stem.

Macroinvertebrate sampling and treatment

Along the three river corridors, the main channel, ponds, backwaters, and tributaries were systematically surveyed. Lentic aquatic habitats (ponds and backwaters) were sampled subsequent to the mapping. In segments with >5 lentic habitats, five habitats per type were randomly selected. If <5 habitats were present, all were sampled. Semi-quantitative samples in all aquatic habitats were collected using a D-shaped kick-net (mesh size: 250 μm). To ensure that ecological data gathered from different aquatic habitat types could be directly compared, samples were collected from 50 m² area of the aquatic habitat type (Williams *et al.* 2004). Per segment, a total area of 50 m² in main channel, ponds, backwaters, and tributaries was sampled for 15 min. Duration of sampling was calculated according to the total area of the chosen aquatic habitat type (example: two ponds with an

area of 100 m² (pond 1) and 300 m² (pond 2) occur in a hypothetical segment. In pond 1 an area of 37.5 m² is sampled in 11 min and in pond 2 an area of 12.5 m² is sampled for 4 min). Microhabitats within individual aquatic habitat types (e.g., large wood, shallow shore areas, pool-riffle sequences) were sampled proportional to their area. Sub-samples from each aquatic habitat type of each segment were combined into a composite sample and preserved in 4% formaldehyde. In the laboratory, all EPT individuals were identified to the lowest practical taxonomic level, mostly to species level.

Data Analyses

Jackknife estimation of species richness

To standardize samples, jackknifed estimates (Jackknife-1, Heltshe & Forrester 1983) of taxa richness were generated for each individual habitat type (Programme EstimateS Version 6.0b1, Colwell 2001). Data were standardized both by number of samples and number of individuals. For each aquatic habitat type, jackknifed estimates were permuted at random 1,000 times. Furthermore, Jackknife analyses were used to estimate the total expected number of species for each individual river corridor (Krebs 1998).

Nestedness

Communities are considered to be nested when species-poor sites comprise a subset of species assemblages in richer sites (Patterson 1987). Nestedness was determined using the Temperature Calculator of Atmar and Patterson (1993; 1995). The calculated “temperature” (T) reflects the degree of order in presence-absence matrices. It ranges from T=0° (perfectly nested) to T=100° (random). The data were packed in rows (samples) and columns (taxa) to maximize nestedness. Monte Carlo randomization (1000 permutations) was used to test whether the

calculated T value of the matrix was significantly lower than the T value of a randomly calculated matrix.

Diversity measures

Based on the nested sampling design, different components of diversity (*sensu* Magurran 2004) were determined (Table 2). Alpha (α) and gamma (γ) diversity are direct measures of species richness that differ in their hierarchical nature (spatial scale). Two types of beta (β) diversity were used. (1) Harrison's beta-1 (β_1) (1992) has been calculated to determine the distinctness of species composition (spatial species turnover) at three different scales (Alps, corridor, habitat types; see Table 2) and among aquatic habitat types within each segment (within segment β_1). The scale "Alps" combines the three river corridors Tagliamento, Thur and Rhône; "corridor" means Tagliamento, Thur, or Rhône; the scale "habitat type" comprises main channel, pond, backwater, and tributary; the scale "sample" includes all individual samples taken during this study (see Table 1). Beta-1 is based on Whittaker's β -diversity (Whittaker 1977) and has been modified in order to compare transects of unequal size:

$$\beta_1 = \frac{\left(\frac{S}{\alpha - 1} \right)}{(N - 1)} \times 100$$

where N is the number of sites, S the regional species diversity and α the mean alpha-diversity. Beta-1 ranges from 0 (complete similarity) to 100 (complete dissimilarity). (2) Lande's beta-diversity (1996) was calculated in order to partition total diversity ("Alps") (Veech *et al.* 2002). Lande's β -diversity determines the diversity among sites (i.e., the mean number of species not found in each of the samples or habitats). Diversity can be partitioned into its components (alpha, beta and gamma) to evaluate the influence of each diversity component to total

diversity. Lande (1996) found that inventory and differentiation diversity can be partitioned by the equation:

$$\gamma = \alpha + \beta$$

where γ is the number of species in the corridor and α is the mean species richness of individual samples or habitats. Beta can be estimated as follows:

$$\beta = \gamma - \alpha.$$

This provides a measurement based on the number of species that is comparable with α -diversity. Therefore, diversity components at each hierarchical level can be calculated as $\beta_m = \gamma - \alpha_m$ at the highest level with $m =$ highest level and $\beta_{i+1} = \alpha_i - \alpha_{i+1}$ for each lower level with $i =$ any level beneath the highest level m . Then, the additive partitioning of diversity is:

$$\gamma = \alpha_1 + \sum_{i=1}^m \beta_i .$$

Based on this equation, total diversity along the corridors can be expressed as the proportional contribution of diversity at each hierarchical level (Table 2). In the present study, β_i of three different hierarchical levels was calculated (β_C , β_H , β_S ; Table 2).

Similarity

The mean similarity of EPT-taxa between all pairs of habitat types within each segment was calculated using Jaccard's similarity coefficient (Krebs 1998). An analysis of variance (ANOVA) was applied to test for differences among pairs of habitat types.

Table 2. Hierarchical framework of the sampling strategy of the present study in order to determine the different levels of biodiversity. Alps: Tagliamento, Thur & Rhône. See methods for further explanation.

Level	Scale	Inventory diversity	Differentiation diversity
1	Alps	ϵ_A	β_{1A}, β_A
2	Corridor	γ_C	β_{1C}, β_C
3	Habitat type	α_H	β_{1H}, β_H
4	Sample	α_S	β_S

RESULTS

Habitat distribution

Along the three corridors, a total of 46 1-km long segments were investigated (Table 1). The number of backwaters and ponds was highest along the Tagliamento and lowest along the Rhône (Figure 2).

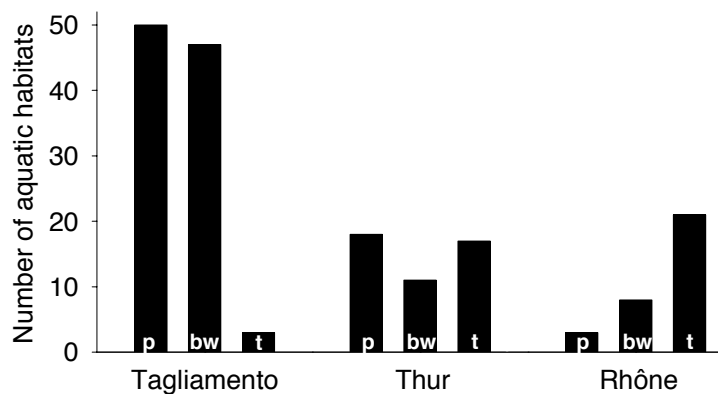


Figure 2. Total number of aquatic habitat types along Tagliamento, Thur and Rhône Rivers. P=pond, bw=backwater, t=tributary (see also Table 1).

The total number of tributaries peaked in the Rhône, with the highest number in headwater segments (Figure 3). Along the Tagliamento, ponds and backwaters occurred mainly in middle, and tributaries in headwater segments (Figure 3). Along the Thur, ponds were most abundant in lower segments (Figure 3).

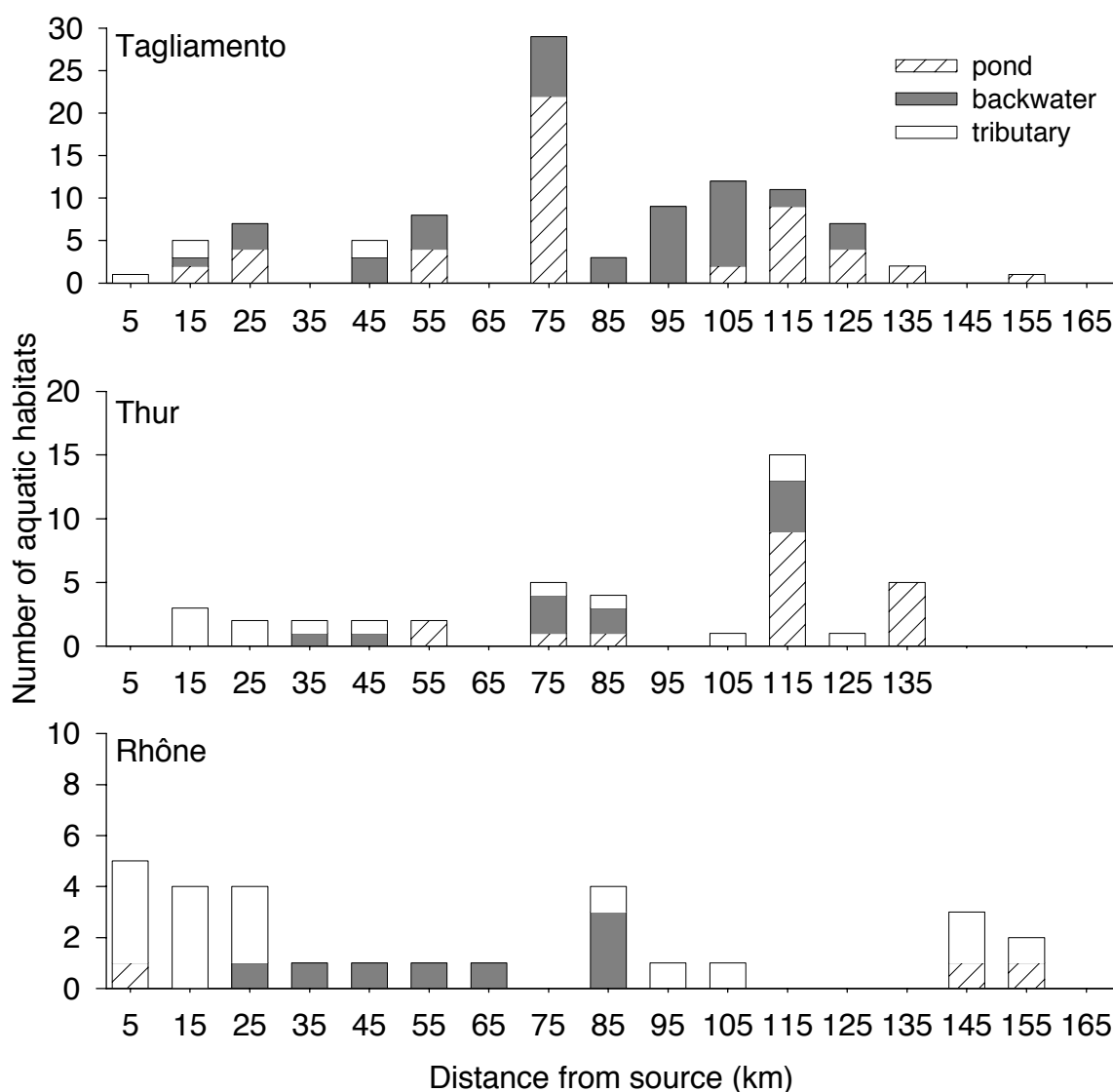


Figure 3. Lateral aquatic habitat distribution along the Tagliamento, Thur, and Rhône.

Species richness patterns

A total of 41918 individuals from 159 EPT-taxa was collected in 119 samples along the three corridors (Appendix, Table 1). Corridor diversity was highest along the Thur (112 taxa), followed by the Tagliamento (78) and the Rhône (65). Based on Jackknife analyses, between 73% (Tagliamento) and 77% (Rhône) of the total expected species richness was sampled. Rare taxa (<1% of total abundance)

accounted for 85%, 53%, and 88% of all taxa along the Tagliamento, the Thur, and the Rhône, respectively (Appendix, Table 1).

Estimates of species richness produced using Jackknife procedures, standardized for number of samples and individuals, exhibited a different increase of richness for individual aquatic habitat types (Figure 4). Based on samples, tributaries showed most species (Figure 4A); based on individuals, ponds exhibited a steeper increase in species richness (Figure 4B).

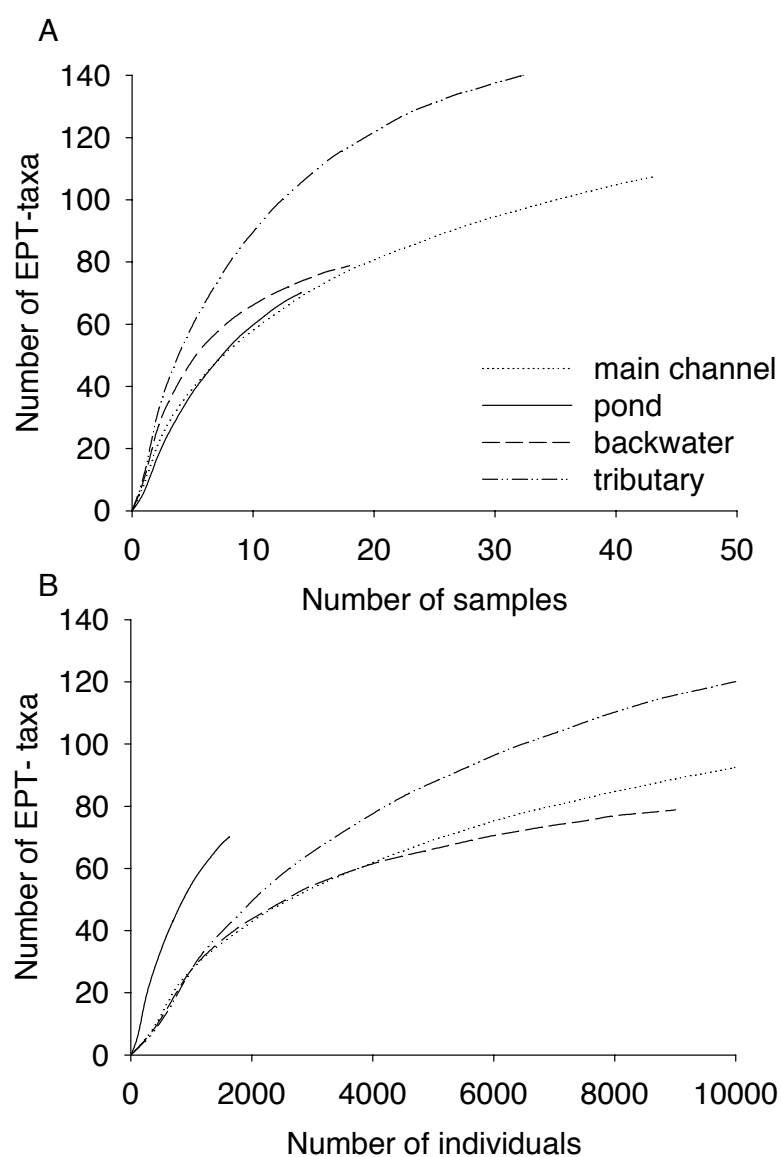


Figure 4. Predicted number of EPT-taxa in individual habitat types based on Jackknife analyses standardized for samples (A; surrogate for area) and individuals (B).

Lateral aquatic habitats (i.e., ponds, backwaters and tributaries) contributed >50% to total EPT-taxa richness, although the relative contribution of habitat types was different along the three corridors (Figure 5). Along the Tagliamento, 14% of total number of taxa was restricted in their occurrence to main channel habitats, 4% to ponds, 23% to backwaters, and 13% to tributaries; along the Thur, 17% was restricted to main channel habitats, 7% to ponds, 3% to backwaters, and 27% to tributaries; and along the Rhône, 12% of taxa was restricted to main channel habitats and 54% to tributaries. Ponds and backwaters were almost completely absent in the Rhône.

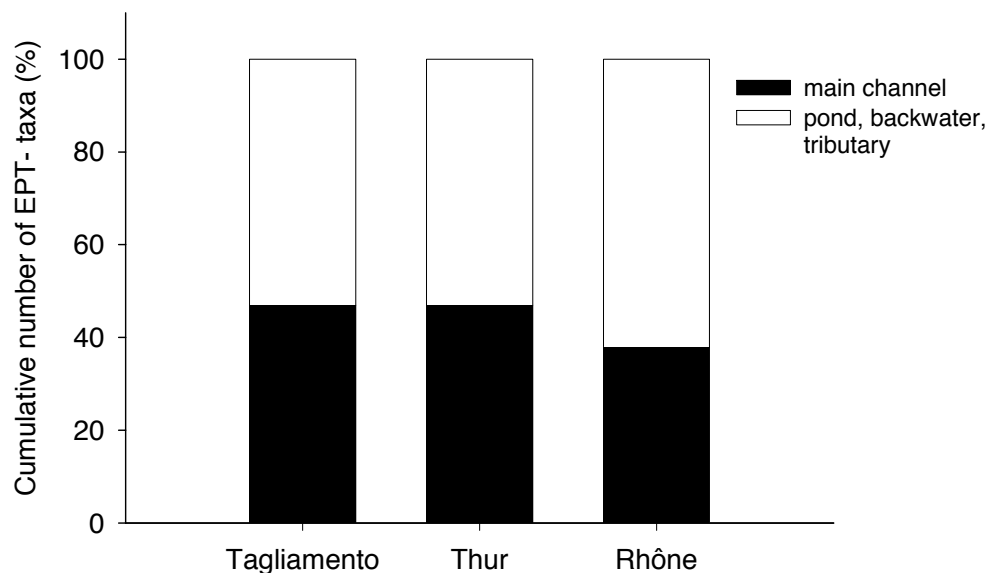


Figure 5. The cumulative relative (%) species richness along the Tagliamento, Thur and Rhône Rivers. Taxa not found in the main channel were cumulatively added.

Longitudinal diversity patterns differed among corridors (Figure 6). Along the Rhône River, diversity peaked in the headwater section. Habitats downstream of river-km 25 added only five new taxa to total corridor diversity. No clear longitudinal patterns occurred along the Thur and Tagliamento. In both rivers, cumulated richness increased continuously along the corridor, with a steeper increase along the Thur (Figure 6).

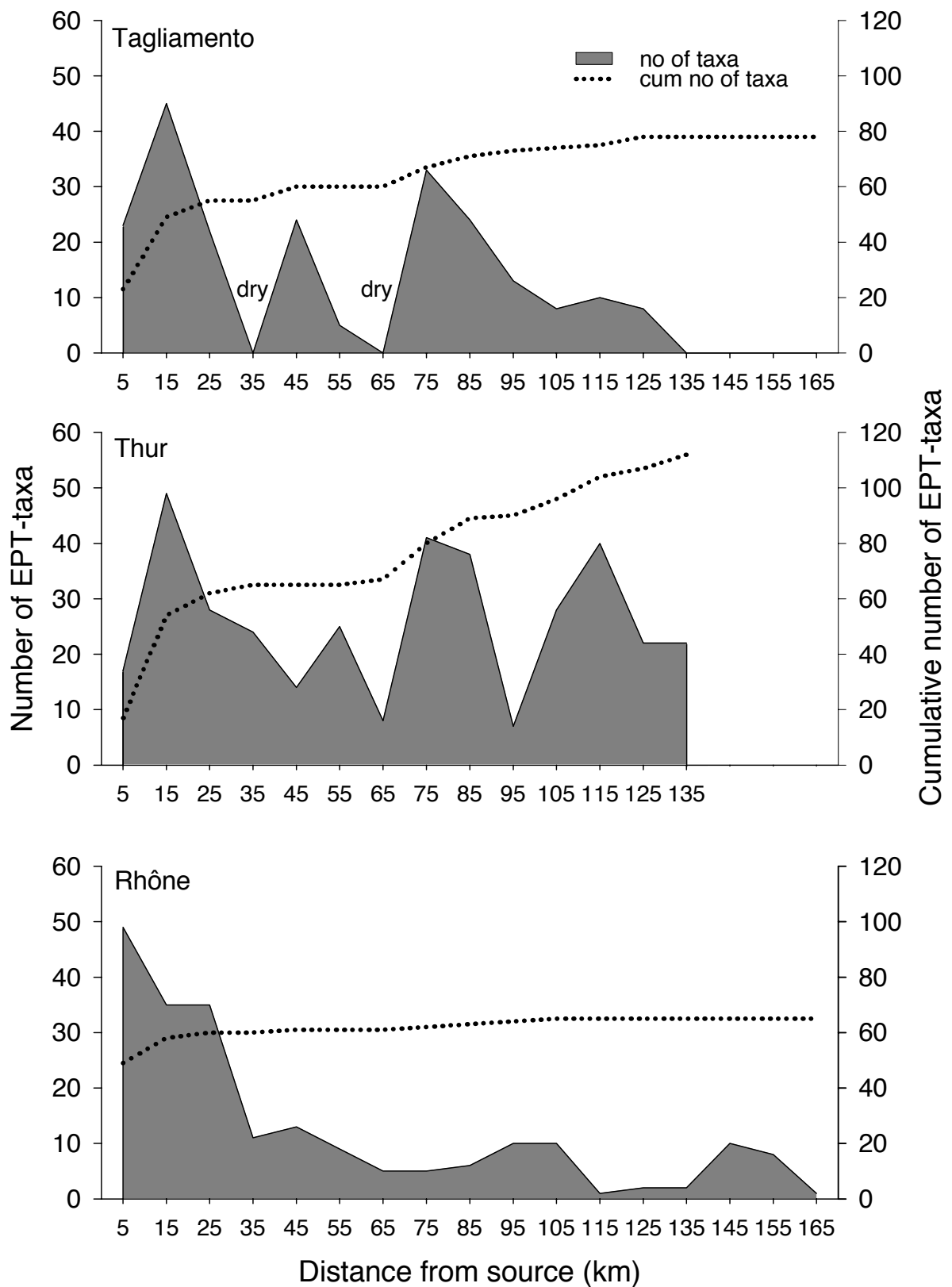


Figure 6. Taxa richness (total no of taxa per segment) and cumulative number (cum no of taxa; dotted line) along the three river corridors.

Nestedness and hierarchical organization

EPT-assemblages were highly nested within each corridor. The calculated temperatures (Tagliamento: 10.1°; Thur: 16.5°; Rhône: 6.6°) were significantly ($p < 0.001$) lower than values randomly produced by Monte Carlo simulations.

Point diversity (α -diversity) was highest along the Thur and lowest along the Rhône (Levels 2-4; Figure 7). Along each corridor, average species richness was lowest in pond habitats (Levels 3 & 4; Figure 7).

Species turnover (β_1 -diversity) varied across scales (Figure 7). Turnover rate was highest at the scale “Alps” (Level 1) and lowest at the corridor scale (Level 2).

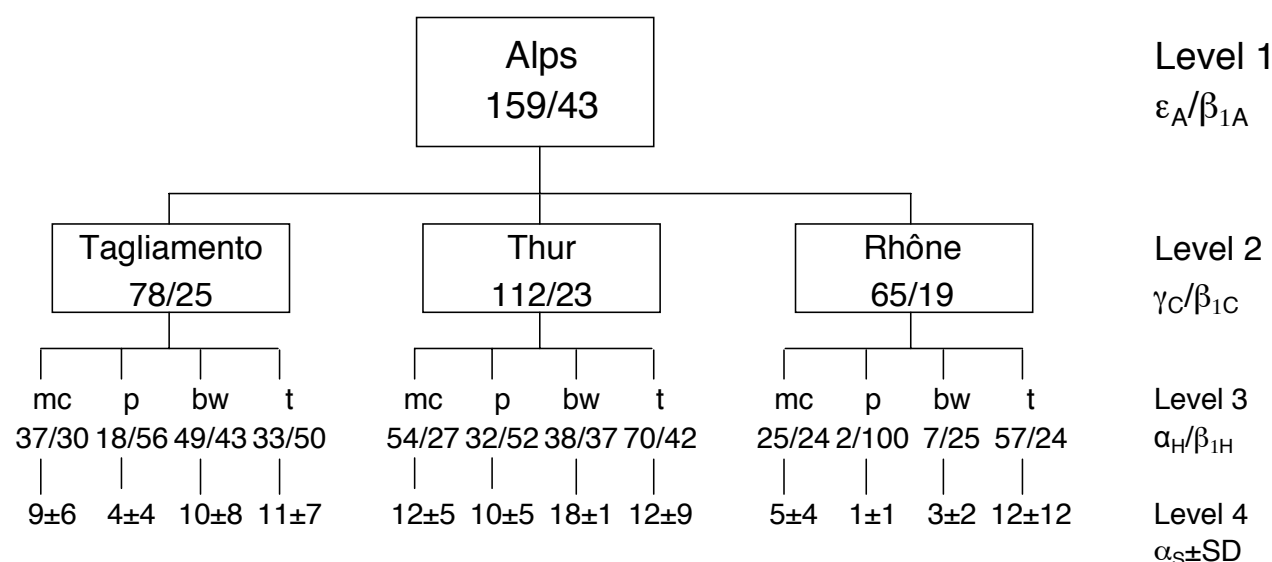


Figure 7. Hierarchical organization of species diversity. Level 1: Alps (ϵ_A =Alps epsilon; β_{1A} =Alps beta-1); Level 2: corridor (γ_C = corridor gamma ; β_{1C} = corridor beta-1); Level 3: habitat type (α_H = habitat type alpha; β_{1H} = habitat type beta-1); Level 4: individual sample (α_s = sample alpha). Mc=main channel, p=pond, bw= backwater; t= tributary.

Two additional trends could be observed: (1) Turnover rate, or β_{1H} -diversity, decreased (except for ponds) from the near-natural Tagliamento to the highly impacted Rhône (Figure 7). (2) β_{1H} -diversity decreased laterally (main channel<backwaters<ponds and tributaries) along the Thur and Tagliamento. Along the regulated Rhône, the number of backwaters and ponds was too low to detect any lateral trend in beta-diversity. Species-turnover rates among aquatic habitat types within each segment (within segment β_1) were high. Mean values \pm SD were 64 ± 16 , 63 ± 20 , and 59 ± 16 for Tagliamento, Thur and Rhône, respectively.

Total species diversity was partitioned into its hierarchical components. Along the three rivers, among-sample and corridor diversity components (β_S and β_C) contributed most to total EPT-taxa richness, while <15% was due to within-sample and habitat type diversity components (α_S and β_H ; Figure 8).

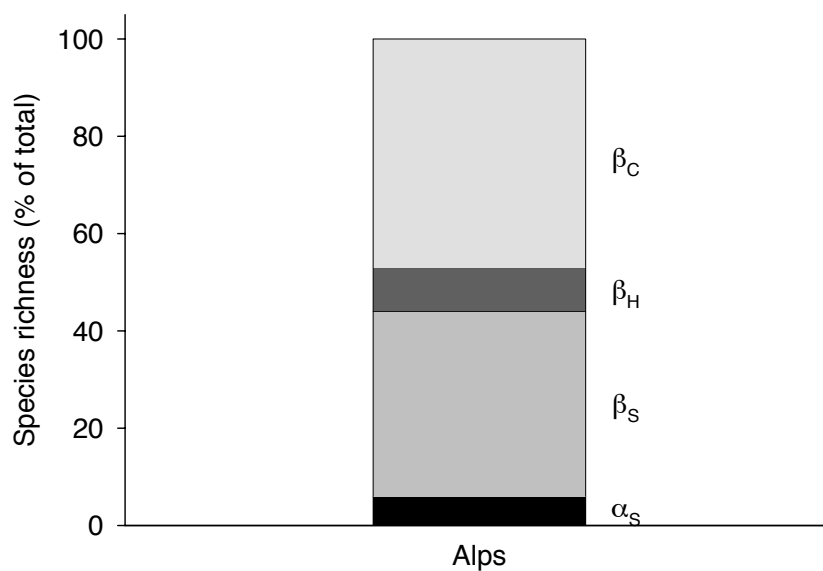


Figure 8. Additive partitioning of observed species richness across three spatial scales. Values are expressed as the percent of the total diversity of EPT-taxa diversity explained by each hierarchical level (see Table 2).

This means that the heterogeneity among individual habitats (i.e., individual samples) explained more of the total species richness than the heterogeneity within individual habitats and among habitat types (i.e., pond, tributary, backwater, main channel).

The average faunal similarity between pairs of aquatic habitat types was low, and differences between pairs were not significant (ANOVA; Table 3).

Table 3. Mean taxa similarity (\pm SD) between all pairs of aquatic habitat types along the three river corridors (mc=main channel, p=pond, bw=backwater, t=tributary).

	mc-bw	mc-p	mc-t	bw-p	bw-t	p-t
Tagliamento	0.18 \pm 0.09	0.16 \pm 0.19	0.15 \pm 0.11	0.1 \pm 0.11	0.18 \pm 0.13	0
Thur	0.22 \pm 0.12	0.22 \pm 0.14	0.14 \pm 0.07	0.17 \pm 0.07	0.09 \pm 0.09	0.04 \pm 0.05
Rhône	0.26 \pm 0.1	0.17 \pm 0.29	0.18 \pm 0.12	-	0.05 \pm 0.08	0

DISCUSSION

Habitat and species richness patterns

Species diversity patterns along rivers has been well studied. In particular, it is well known that species are replaced along the river channel due to changes in temperature, sediment structure, and stream metabolism (see Vinson & Hawkins 1998). However, most studies focused on single-thread rivers and excluded lateral habitats. In the present study, we included lateral aquatic habitats along entire river corridors. As a consequence, none of the existing concepts that have been developed to predict biodiversity along river corridors (e.g., Vannote *et al.* 1980; Ward & Stanford 1983; Statzner & Higgler 1986) can be supported by our data. Each river exhibited a distinct longitudinal pattern sequence in species diversity (Figure 6), which emphasizes the uniqueness of rivers. Hynes (1975), already proposed that ‘every stream is likely to be individual’. Moreover, each habitat type

contained a very distinct community, and faunal similarity among individual habitat types was very low (Table 3). The “individuality” of rivers as well as of habitat types, however, has been challenged by anthropogenic impacts. River regulation not only eliminates lateral habitats (see Figures 2 and 3) it also most likely leads to a homogenization of aquatic communities. Along the regulated Rhône, for example, main stem habitats were species-poor; remaining diversity was primarily allocated to tributaries (parafluvial ponds and backwaters were almost completely absent). In tributaries, which are less affected by hydropeaking and canalization, 87% of the present corridor species pool occurred (Appendix, Table 1).

Lateral aquatic habitats such as tributaries, backwaters, and parafluvial ponds are among the least-investigated habitat types along river corridors. Although these habitats cover only a small proportion of the total aquatic area (<8% in braided flood plains along the Tagliamento, Van der Nat *et al.* 2003), they contributed >50% to total species richness (Figure 5). In particular backwaters and tributaries contained rich communities that were different from main channel habitats. A modest contribution by parafluvial ponds can partly be explained by our focus on EPT-taxa. By considering other groups such as Mollusca, Crustacea, Odonata or, Coleoptera, we may expect a much higher contribution of lentic habitats (parafluvial ponds, backwaters) to total species diversity (U. Karaus, unpubl. data). Jackknife analyses, standardized by number of individuals, exhibited a steeper curve in ponds compared to other habitat types (Figure 4B). Between-pond heterogeneity is expected to be large, which was confirmed by higher turnover rates among ponds compared to other habitat types (Figure 7). From an ecological perspective, ponds can be regarded as “concave islands” with environmental properties strongly related to local conditions (Karaus *et al.* 2005). Generally, pond invertebrate diversity has been related to a range successional stages, and therefore, to disturbance frequency (Castella 1987; Schneider & Frost 1996; Homes *et al.* 1999) and to hydrological connectivity (Tockner *et al.* 1999).

Tributaries, on the other hand, are not only different from the main channel regarding environmental properties, but also are assumed to enhance the local heterogeneity at the confluence with the main channel (the network dynamics hypothesis, Benda *et al.* 2004). Brown & Coon (1994) reported higher fish density and different community composition in tributaries compared to the channel (Lower Missouri, US). They found a gradient in the faunal assemblage from small tributaries to large river sections, which corresponded to an environmental gradient from shallow streams with coarse substrate to deep rivers with finer sediments. The potential importance of tributaries for main stem communities is virtually unexplored. Tributaries may serve as important refugia for recolonising the main channel after disturbances (e.g., floods, droughts, pollution), and they are important habitats for early life stages of fish and invertebrates (Bruns *et al.* 1984; Rice *et al.* 2001).

In the present study, backwaters also contributed significantly to overall species richness along the three river corridors (Figure 7). They were colonized by a unique and species rich community. Similar differences in taxa richness between backwaters and main-channel habitats were found also in upland streams in Victoria (O'Leary *et al.* 1992). Solari (2002) found high plankton densities in backwaters of the Slado River (Argentina), a consequence of lentic conditions. Lentic conditions, a permanent hydrological connection to the main channel, and increased primary production can enhance species richness within backwaters (Cellot & Bournaud 1986; Schiemer *et al.* 2001). At mean and low discharge, backwaters exhibit lentic conditions, and they primarily accumulate organic matter (Amoros & Roux 1988) In their "Inshore Retention Concept", Schiemer *et al.* (2001) emphasized the importance of still-water habitats in the active channel for the development of phyto- and zooplankton and fish larvae. Backwaters were identified as important retentive habitats, which contributed to overall river biodiversity and production. However, further studies on local constraints on backwater communities (as well as on tributary communities) - in particular on the

potential role of backwaters as refugia during flood events - are required. This is especially intriguing for permanently connected habitats (backwaters and tributaries) where dispersal barriers are presumably absent.

Nestedness and hierarchical organization

River corridors are hierarchically organized and nested ecosystems. In the present study, the nested sampling design allowed to detect differences in species diversity at various spatial scales. As expected, communities were highly nested in all three river corridors. Nestedness is a common attribute of most communities (Wright *et al.* 1998). Aquatic invertebrates, however, have been regarded as an exception, because of their high diversity (Boecklen 1997). Malmqvist & Hoffsten (2000) detected a nested distribution for Ephemeroptera, Plecoptera, Trichoptera, and Simuliidae in Swedish streams and rivers. Nestedness was particularly pronounced in the Rhône River, where communities in the canalized middle and downstream sections formed distinct subsets of the less-impacted and more species-rich headwater reaches. The lower sections along the Rhône - heavily impacted by hydropeaking and river regulation - are very likely sinks for invertebrate species. Most species of the regional pool are expected to be able to disperse over large areas, therefore local conditions primarily determine the presence or absence of species within individual habitats (habitat filters, *sensu* Poff 1997). A lower degree of nestedness (higher system temperature T) in the less impacted Thur and Tagliamento Rivers could result from higher habitat heterogeneity.

In the present study, we applied a quantitative model that allows to partitioning at different spatial scales (see Wagner *et al.* 2000). This approach implies that what we measure as within-community diversity at a higher scale (e.g., corridor scale) is the combined effect of heterogeneity at various lower scales (habitat, river segment). In the present study, high differentiation diversity (beta-diversity) at the broadest spatial scale (Level 1 in Figure 7) reflected distinct biogeographic

differences among corridors (i.e., regional control of local diversity). All three rivers flow in different directions. In addition, human impacts were likely to increase differences among catchments.

The low within-corridor turnover (β_{1C}), in contrast to the high within- (β_{1H}) and between-habitat (within-segment β_1) type turnover, assumed that both regional and local factors control benthic communities. The influence of local factors (habitat heterogeneity and biotic interactions) and of regional factors (altitude, river style, land-use patterns) on the structure of stream invertebrates has been well documented (see review by Vinson & Hawkins 1998). However, the relationship between regional and local species richness has been rarely investigated for stream invertebrates. Studies on fish diversity showed a strong regional control on local diversity (Hugueny 1995), or an influence by both regional and local factors (Angermeier & Winston 1998). Vaughn (1997) reported a linear relationship between regional and local species richness for river-dwelling mussels, while Heino *et al.* (2003) detected regional species richness as the most influential variable contributing to local species richness. However, it is far from clear whether regional species richness consistently sets the limits to local species richness, or vice versa (Vinson & Hawkins 1998). We may consider the relationship between regional and local species richness as a feedback system where they influence each other. On the one hand, regional species richness sets the upper limit for local species richness; on the other hand, regional species richness is adapted to decrease or increase of local species richness. This implies that the regional species pool is sequentially reduced by environmental filters, which include disturbance regime, dispersal barrier, habitat condition, and biotic interaction (Tonn *et al.* 1990). Each filter operates at a distinctive spatiotemporal scale and leads to a characteristic species community.

Implications for conservation and management

River corridors are among the most threatened ecosystems world wide (Malmqvist & Rundle 2002; Tockner & Stanford 2002). In Europe, for example, ~90% of all former floodplains disappeared or are functionally extinct (Hughes 2003). Nowadays, restoration is a major issue in river management. However, a high proportion of restoration projects fail, mainly because of a fundamental lack of understanding of principal mechanisms that create and maintain biodiversity and biocomplexity along river corridors. Lateral habitats are among the first habitats that disappear as a consequence of river regulation and flow control. Since overall river biodiversity is strongly enhanced by the lateral habitat diversity (see: Figure 5), the formation and rejuvenation of ponds and backwaters needs to be promoted by restoration projects. Furthermore, we also need to more thoroughly understand the importance of tributary confluences as important ecological nodes along river corridors (see Benda *et al.* 2004). Tributaries and their intersections with the main channel may be critical for the resilience of entire river corridors.

At a regional scale, flood disturbance is a key factor promoting biodiversity (Pollock 1998). At a local scale, parafluvial ponds are often associated with dead wood and vegetated islands (Gurnell & Petts 2002; Karaus *et al.* 2005). Hence, dead wood and islands are expected to enhance aquatic habitat diversity (Arscott *et al.* 2000). Furthermore, biodiversity along the three river corridors was strongly nested and hierarchical. This is important since restoration has primarily focused on the reach scale or on individual species and habitats. Clarke (2003) proposed an eco-hydromorphic approach for restoration, which is based on the principle that both morphological and ecological components are closely interlinked and that channel form, system functioning, and species composition result from these interacting processes. A better understanding of the ecology and functioning of lateral aquatic habitats will therefore, support successful river restoration.

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APPENDIX

Table 1. Distribution (total abundance) of EPT-taxa along the three river corridors (mc=main channel, p=pond, bw=backwater, t=tributary). For further explanation see text.

	Tagliamento				Thur				Rhône				Sum	
	mc	p	bw	t	mc	p	bw	t	mc	p	bw	t		
Ephemeroptera														
<i>Baetis alpinus</i> Pictet			3	16				1531					4322	5872
<i>B. lutheri</i> Mueller-Liebenau								48					35	83
<i>B. muticus</i> Linné			1	2				45						48
<i>B. rhodani</i> Pictet			84	114			18	337				138	585	1276
<i>B. vernus</i> Curtis			4					99						103
<i>Baetis</i> sp. 6	896	3	98	3	2544	19	568	1877	3	362			6373	16
<i>Caenis lactuosa</i> Burmeister			1				15							15
<i>C. rivulorum</i> Eaton			4				11							38
<i>Caenis</i> sp. 3			1	7	3	27								135
<i>Centropilum lateolum</i> Mueller	8	34	87		1	5								10
<i>Centropilum</i> sp. 2					2	8								101
<i>Cloeon dipterum</i> Linné					49	52								4
<i>Cloeon</i> sp. 2					4									9
<i>Echyonurus beheticus</i> Eaton													9	5
<i>E. picteti</i> Meyer-Dür			3										5	7
<i>E. torrentis</i> Kimmins							1	6						17
<i>E. venosus</i> Eaton			4	2		7	4							6
<i>E. zelleri</i> Eaton			6											63
<i>Echyonurus</i> sp. 6	679		62	56	76	6	73	14	36				63	1065

	Tagliamento				Thur				Rhône				Sum
	mc	p	bw	t	mc	p	bw	t	mc	p	bw	t	
<i>Electrogena</i> sp.	4	4		3									11
<i>Epeorus assimilis</i> Eaton			1				1						2
<i>Epeorus</i> sp. 2				65									65
<i>Ephemera danica</i> Müller			4			9	1						14
<i>Ephemera ignita</i> Poda			1				6						18
<i>Ephemera</i> sp. 2			11				6						6
<i>Habroleptoides confusa</i> Sartori & Thomas	3	2	9	2			5	21					42
<i>Habroleptoides</i> sp. 2				4	1								5
<i>Habrophlebia lauta</i> Eaton			2			16	6						24
<i>Habrophlebia</i> sp. 2				11	11								22
Heptageniidae				4							1	39	44
<i>Heptagenia</i> sp.	25	367		13				1				32	438
Leptophlebiidae			2	1									3
<i>Paraleptophlebia</i> sp.				2	1								3
<i>Rhibrogena gratianopolitana</i> Sowa, Degrange & Sartori												11	11
<i>R. hybrida</i> Eaton			7			1	1						9
<i>R. landai</i> Sowa & Soldán			4										4
<i>R. semicolorata</i> Curtis			5			32	52						89
<i>Rhibrogena</i> sp. 5	5	1	13	677	14	11	93	96				36	946
<i>Serratella</i> sp.				28									28
<i>Siphonurus lacustris</i> Eaton			6874	1		18	64						6957
<i>Siphonurus</i> sp. 2	4	56	148	1	459	78	3						749

	Tagliamento				Thur				Rhône				Sum	
	mc	p	bw	t	mc	p	bw	t	mc	p	bw	t		
Plecoptera														
<i>Amphinemura</i> sp.	11	4	4	82	56	6	37	26						226
<i>Brachyptera risi</i> Morton								5						5
<i>B. trifasciata</i> Pictet											2			2
<i>Brachyptera</i> sp. 3	9				2									11
<i>Chloroperlidae</i>					2					1				3
<i>Chloroperla</i> sp.	385	23	64	1	69	33	16	5	1			2		599
<i>C. tripunctata</i> Scopoli			34				73	1						108
<i>Dictyogenus alpinum</i> Pictet												4		4
<i>D. fontium</i>												2		2
<i>Dictyogenus</i> sp. 3									11					11
<i>Dinocras megacephala</i> Klapálek								2						2
<i>Dinocras</i> sp. 2					19	5	5	1						30
<i>Isoperla grammatica</i> Poda			1				34	11						46
<i>I. lugens</i> Klapálek												124		124
<i>I. rivulorum</i> Eaton							4	31			2	74		111
<i>Isoperla</i> sp. 3	6	1	2	2	19	9	2	6	41		1	2		91
<i>Leuctra alpina</i> Kühtreiber												1		1
<i>L. braueri</i> Kempny													27	28
<i>L. inermis</i> Kempny			1				8	3			93	77		182
<i>L. leptogaster/major</i>			29											29
<i>Leuctra</i> sp. 5	242	57	85	15	712	293	344	767	1489		3	2661		6668

	Tagliamento				Thur				Rhône				
	mc	p	bw	t	mc	p	bw	t	mc	p	bw	t	Sum
<i>Nemouridae</i>				71								621	692
<i>Nemoura marginata</i> Pictet			1										1
<i>N. mortoni</i> Ris				1								17	18
<i>Nemoura</i> sp. 3	13		14	45	33		5	11	21			82	224
<i>Nemurella pictetii</i> Klapalek							1	1				1	3
<i>Perla grandis</i> Rambur								3					21
<i>Perla</i> sp. 2	2		11	5									1
Perlidae			1										1
<i>Perlodes intricatus</i> Pictet												1	1
<i>Perlodes</i> sp. 2					1	1		1	3				6
Perlodidae					1								1
<i>Protonemura lateralis</i> Pictet												11	11
<i>P. nimborum</i> Ris												3	3
<i>Protonemura</i> sp. 2	52		4	15	53	1		32	111			1734	2002
<i>Rhabdiopteryx alpinus</i> Kühtreiber								1					1
<i>R. neglecta</i> Aubert				2									2
<i>Rhabdiopteryx</i> sp. 3					17				11			99	136
<i>Siphonoperla torrentium</i> Pictet							2						2
<i>Siphonoperla</i> sp. 2								14				4	18
<i>Xanthoperla</i> sp.													1
Trichoptera													
<i>Agapetus ochripes</i> Curtis								7					7

	Tagliamento				Thur				Rhône				Sum
	mc	p	bw	t	mc	p	bw	t	mc	p	bw	t	
<i>H. subripes</i> Curtis	1												1
<i>H. guttata</i> Pictet	4												4
<i>H. incognita</i> Pitsch	2							2					4
<i>H. instabilis</i> Curtis	8		5	1	8				1			4	27
<i>H. pellucidula</i> Curtis	3		1		2								6
<i>H. siltalai</i> Döhler					54			7					61
<i>H. tenuis</i> Navas				4									4
<i>Hydropyche</i> sp. 10	11		1	6	32			49				2	101
<i>Hydroptila martini</i> Marshall			36										36
<i>H. sparsa</i> Curtis								312					312
<i>Hydroptila</i> sp. 3	75	68	11		59			315	77				605
<i>Hydroptila vectis</i> Curtis								1					1
<i>Lepidostoma hirtum</i> Fabricius			3		9		2	1					15
Limnephilinae			1	2	3		3	1		2		13	25
<i>Limnephilus affinis</i> oder <i>incisus</i>								1					1
<i>L. auricula</i> Curtis							2						2
<i>L. decipiens</i> Kolenati							1						1
<i>L. lunatus</i> Curtis			1	1	3		3						5
<i>Limnephilus</i> sp. 5								1					1
<i>Lithax niger</i> Hagen												2	2
<i>Lype phaeopa</i> Stephens										1			1
<i>Lype</i> sp. 2								1					1

	Tagliamento				Thur				Rhône				Sum
	mc	p	bw	t	mc	p	bw	t	mc	p	bw	t	
<i>Melampophylax mucoreus</i> Hagen				1									1
<i>Metanoea rhaetica</i> Schmid				5								2	7
<i>Metanoea</i> sp. 2							5						5
<i>Micrasema morosum</i> McLachlan			1										1
<i>Mystacides azurea</i> Linne					1								1
<i>Mystacides</i> sp.	2												2
<i>Odontocerum albicorne</i> Scopoli				1									1
<i>Oeetis</i> sp.					11		1						12
<i>Parachiona picicornis</i> Pictet												1	1
<i>Philopotamus ladicatus</i> McLachlan							2					18	20
<i>Plectrocnemia</i> sp.			1	4			4						9
<i>Polycentropus excisus</i> Klapalek	5	11	24	13									53
<i>P. flavomaculatus</i> Pictet		1			2	11	7	2					23
<i>Potamophylax cingulatus/laiipennis/luctuosus</i>			2	2				3				15	22
<i>Potamophylax</i> sp. 2	4	1			1			1	2				9
<i>Psychomyia pusilla</i> Fabricius					10	1	25						36
<i>Ptilocolepus granulatus</i> Pictet												7	7
<i>Rhyacophila dorsalis</i> McLachlan								29					29
<i>R. glareosa</i> McLachlan												3	3
<i>R. hirticornis</i> McLachlan									2				2
<i>R. intermedia</i> McLachlan									1			1	2
<i>R. pubescens</i> Pictet							4						4

	Tagliamento				Thur				Rhône				Sum
	mc	p	bw	t	mc	p	bw	t	mc	p	bw	t	
<i>Rhyacophila s. str.</i> sp.	83		2	26	73	1	3	62	1			11	262
<i>R. torrentium</i> Pictet	2		1						23			67	93
<i>R. trisix</i> Pictet				2	6		5					3	16
<i>Sericostoma personatum</i> Kirby & Spence	1						7						8
<i>S. flavicorne</i> Schneider			1		5	1							7
<i>Sericostoma</i> sp. 3												8	8
<i>Silo piceus</i> Brauer						1							1
<i>Stenophylax vibex</i> Curtis					4								4
<i>Tinodes dives</i> Pictet							5						5
<i>Tinodes</i> sp. 2							1						1
<i>Wormaldia copiosa</i> McLachlan	44											6	50
Sum	2623	640	7742	452	4963	957	1200	4553	7040	3	198	11547	41918