RESEARCH PAPER

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Species diversity and functional assessment of macroinvertebrate communities in Austrian rivers

Received: June 25, 2004 / Accepted: April 13, 2006 / Published online: June 23, 2006

Abstract We applied an extensive data set from 211 locations along Austrian rivers to assess community structure and the ratios of functional feeding groups of benthic macroinvertebrates. A total of 569 taxa have been identified. At the catchment scale, the Enns, Salzach, and Traun Rivers exhibited the highest taxa richness whereas the Inn River showed the lowest richness. Beta-diversity was highest along the impounded and fragmented Enns and Drau Rivers. Consequently, high corridor diversity corresponded to a low degree of nestedness. Overall, scrapers and gathering-collectors dominated the benthic community. Further, the relationship between habitat conditions and metrics based on functional feeding groups were statistically analyzed to validate the potential of these metrics as indicators of ecosystem attributes. We examined four major ecosystem attributes: species diversity, material cycling, longitudinal material transport, and lateral material input. Multiple regression analyses for midorder rivers demonstrated that metrics were significantly related to habitat conditions. For example, the metric set indicating primary production was positively correlated with periphyton cover, dissolved oxygen, dominant sediment size, and average

annual discharge. Overall, most metrics exhibited unique responses to habitat conditions, implying that they are useful proxies of ecosystem attributes. Thus, a function-based approach based on macroinvertebrates has the potential to become an effective tool for the assessment of river ecosystems.

Key words Invertebrates · Biodiversity · Species diversity · Nestedness · Functional feeding groups · Ecosystem functions · Assessment

Introduction

Worldwide, streams and rivers are among the most threatened ecosystems (World Resources Institute 2001; Malmqvist and Rundle 2002). To assess the potential effects of multiple anthropogenic drivers on aquatic ecosystems, a function-based approach is required (Findlay et al. 2002). Such an approach uses structural and functional indicators as proxies of the ecological integrity and long-term sustainability of aquatic systems (Kerans and Karr 1994; Wright 2000). In general, ecological integrity is defined as the capacity of an ecosystem to support and maintain a balanced, integrated, and adaptive system having the full range of elements and processes expected in a region's natural habitat (Karr and Dudley 1981). Thus, functional assessment of the ecological integrity serves as a useful tool for assessing the state of ecosystems, although biological elements (e.g., rare and exotic species) have often been neglected.

Benthic macroinvertebrates are key components of aquatic food webs that link organic matter and nutrient resources (e.g., leaf litter, algae, and detritus) with higher trophic levels. By focusing on their multiple functional traits (e.g., feeding strategy, dispersal capacity), functional feeding groups (FFGs) have been applied to assess ecosystem-level processes in rivers and wetlands (Merritt et al. 1999; Rawer-Jost et al. 2000; Gayraud et al. 2003). However, individual FFGs react differently to increasing human impacts,

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Fig. 1. Location of the 211 sampling sites along Austrian rivers (Bundesministerium für Land- und Forstwirtschaft, Umwelt und Wasserwirtschaft 1997). Closed circles, 78 sites used for the functional assessment; numbers 1–7, location of the seven major catchments

Table 1. Total number of river segments with a catchment area $>10\text{km}^2$ in Austria (Wimmer et al. 2000) and the number of monitoring sites included in the present study

Stream order	1	2	3	4	5	6	7	8	9	Total
Rivers	72	416	964	531	146	33	5	3	1	2171
%	3.3	19.2	44.4	24.5	6.7	1.5	0.2	0.1	0.1	100
Monitoring sites	0	0	4	31	80	70	26	0	0	211
%	0	0	1.9	14.7	37.9	33.2	12.3	0	0	100

which may limit their application (Resh 1994; Barbour et al. 2001). Yet, only a few studies have tested the effects of habitat alteration on these functional indicators (Minshall et al. 1982). Therefore, it is crucial to identify the habitat factors that affect different functional indicators and the ways in which they do so.

In the present article, we took advantage of an extensive data set on benthic invertebrates and habitat conditions available for all major Austrian rivers. First, we evaluated taxa diversity at different spatial scales. Second, we calculated the degree of nestedness for seven major catchments. Nestedness is a community property typical of fragmented and isolated ecosystems (Wright and Reeves 1992; Boecklen 1997). Third, we applied multivariate analyses to examine the sensitivity of functional indicators against major habitat factors. Based on benthic invertebrate composition, we calculated 13 metrics that better indicate ecosystem functions than simple FFG abundance data.

Methods

Study sites

Austria covers $84,000\text{km}^2$ and has an average population density of 97 humans km^{-2} . The total length of the entire river network is $\sim 100,000\text{km}$ (Koller-Kreimel and Tomek 1999). The length of all rivers with a catchment area $>500\text{km}^2$ is $5,200\text{km}$ (in total, 52 rivers; Chovanec et al. 1996). The Danube River drains 96% of Austria.

From 1994 to 1997, aquatic invertebrates were sampled quantitatively at 211 monitoring sites (Fig. 1). Sites covered all 15 Austrian aquatic bioregions (Moog et al. 2001a) and included stream orders 4–7 (Wimmer and Moog 1994) (Table 1). Low-order streams and the Danube River (9th-order river) were not included in the present analysis for reasons of different sampling design and methodology. Based on degree of anthropogenic impacts, sites were

classified as 0 (pristine), 1 (seminatural), 2 (hydrologically impaired), or 3 (both morphologically and hydrologically impaired) (Bundesministerium für Land- und Forstwirtschaft, Umwelt und Wasserwirtschaft 1998). Among the 211 sites, 78 sites were selected for detailed statistical analyses. The selected sites are located in midorder streams (stream order, 4–7) in western and southern Austria (see Fig. 1).

Sampling design

All sites were sampled during low flow in January and February to minimize seasonal variations and short-term impacts by floods (Hawkins and Sedell 1981). In addition, winter is the preferable season of larval growth for many species (Moog 1995; Wallace and Anderson 1996). Thus, the relationship between macroinvertebrates and habitat conditions is expected to be most significant during the low-flow period. Macroinvertebrates were sampled with a Surber (sampling area, 0.1 m²) or a Hess sampler (area, 0.043 m²). Mesh size was 100 µm. Two to three replicates were taken at each site. All individuals were counted and identified to lowest possible taxonomic level, mostly to species level. Total invertebrate biomass of each sample was measured as grams dry weight (gDW).

At each site, dominant grain size fraction, periphyton cover, water velocity, and water temperature were measured. Surface water was sampled at bimonthly intervals (monthly intervals in transboundary rivers). Samples were analyzed using standard methods as described by Aubrecht et al. (1993). Twenty-two of 50 physicochemical parameters were included in the present analyses.

Assessment of species diversity

Detailed analyses were carried out for the seven primary catchments (see Fig. 1). Local species diversity (alpha-diversity) was calculated as the average number of taxa per site at the corridor and the catchment scale. A major component of biodiversity is beta-diversity, which provides an estimate of taxa turnover along a gradient (e.g., along a river corridor) (Ricklefs 1990). Beta-diversity is mostly neglected, although it can be an important indicator to assess the ecological integrity of rivers (Ward and Tockner 2001). We used the degree of dissimilarity as an index of beta-diversity (Soerenson index; Sorenson 1948). To estimate sampling efficiency and to develop a collector's curve for gamma-diversity (at the corridor and at the catchment scale) for the seven major rivers, macroinvertebrate data were "bootstrapped" following a jackknife procedure (after Heltshe and Forrester 1983). Before calculating diversity indices, we conducted taxonomic adjustment to avoid double counts of individual species. If individuals were identified to species level, individuals of that genus or at higher taxonomic levels were omitted.

The degree of nestedness was calculated using the "nestedness calculator" (Atmar and Patterson 1993). Its

metric, "system temperature" (T), reflects the extent of order in a presence-absence species matrix. Perfectly nested communities have a T = 0 and maximally disordered ones a T = 100. Presence-absence matrices have been packed into a state of minimum unexpectedness. The characteristic "T" of randomized matrices was calculated through Monte Carlo simulations (500 runs per test) and compared with observed "temperatures." Nestedness is an assemblage property typical of fragmented and isolated ecosystems (Wright and Reeves 1992; Boecklen 1997). Many communities exhibit a nested pattern when communities in areas with low diversity form subsets of richer sites (e.g., Kerr et al. 2000; Patterson and Atmar 1986).

Assignment of functional feeding groups

Most invertebrate species feed on various food sources, and they may change their feeding strategy depending on their life stage and on food availability (Wallace and Webster 1996). Thus, abundance and relative proportion (%) of each functional feeding group (FFG) was calculated using a ten-point system developed for Austrian and German rivers (Moog 1995; Bayerisches Landesamt für Wasserwirtschaft 1996). Ten points have been assigned for each taxon to indicate their feeding preferences (a list of taxa and FFG assignment is available at http://www.ccn.yamanashi.ac.jp/~chihiroy/FFG_assignment.xls). For example, *Baetis alpinus* has an equal feeding preference for attached algae and detritus. In this case, five points were assigned for scrapers and detritivores, respectively. For most taxa, except for Chironomidae (Diptera), feeding preferences were available at the genus level. The points for a shredder were equally divided to shredder-herbivores and shredder-detritivores if a separation was not provided in the relevant references.

Here, points were divided by ten and used to convert macroinvertebrate abundance from taxonomic classification to FFG as follows:

$$\mathbf{A} = \begin{pmatrix} \alpha_{1,1} & \cdot & \cdot & \cdot & \alpha_{1,10} \\ \cdot & \cdot & & & \cdot \\ \cdot & & \alpha_{i,j} & & \cdot \\ \cdot & & & \cdot & \cdot \\ \alpha_{s,1} & \cdot & \cdot & \cdot & \alpha_{s,10} \end{pmatrix} \quad (1)$$

$$\mathbf{N} = (n_1, n_2, n_3, \dots, n_s) \quad (2)$$

$$\mathbf{X} = \mathbf{N} \cdot \mathbf{A} \quad (3)$$

$$\mathbf{X} = (G_1, G_2, G_3, \dots, G_{10}) \quad (4)$$

where $\alpha_{i,j}$ is the point of taxon i assigned for a functional feeding group j ($0 \leq \alpha \leq 1, 0 \leq j \leq 10$), and S is total number of observed taxa. Abundance in taxonomic classification and FFGs is shown as $\mathbf{N}$ and $\mathbf{X}$, respectively. Equation 3 shows the conversion of abundance from a taxonomic to FFG classification.

Table 2. Functional feeding groups of macroinvertebrates related to ecosystem attributes

Metrics based on taxa and functional feeding groups		Ecosystem attributes
<i>Species diversity</i>		
F1	Number of taxa	Taxa richness
F2	Shannon–Weaver index	Diversity index (taxa composition)
<i>Material cycling</i>		
F3	Abundance of shredder-herbivores and scrapers, G1 + G3	Primary production
F4	Ratio of shredder-herbivores and scrapers to shredder-detritivores, filterers, and gathering-collectors, $(G1 + G3)/(G2 + G4 + G5)$	Autotrophy/heterotrophy
F5	Total biomass (dry weight)	Secondary production
F6	Abundance of shredder-detritivores and gathering-collectors, G2 + G5	Decomposition
<i>Longitudinal transport</i>		
F7	Abundance of filterers, G4	Longitudinal transport
F8	Ratio of filterers to shredder-detritivores and gathering-collectors, $G4/(G2 + G5)$	Relative longitudinal transport (ratio of suspended FPOM to benthic FPOM)
<i>Lateral input</i>		
F9	Abundance of shredder-detritivores, G2	Lateral input
F10	Ratio of shredder-detritivores to total abundance, $G2/\text{total abundance}$	Relative lateral input (ratio of CPOM input from riparian vegetation to total organic matter input)
<i>Others</i>		
F11	Ratio of shredder-detritivores to filterers and gathering-collectors, $G2/(G4 + G5)$	CPOM input/FPOM input
F12	Ratio of predators to total abundance, $G6/\text{total abundance}$	Top-down predator control
F13	Ratio of scrapers and filterers to total shredders and gathering-collectors, $(G3 + G4)/(G1 + G2 + G5)$	Habitat stability

G1, shredder-herbivore; G2, shredder-detritivore; G3, scraper; G4, filterer; G5, gathering-collector; G6, predator; FPOM, fine particulate organic matter; CPOM, coarse particulate organic matter

Functional assessment

We used abundance data and ratios of FFGs as proxy indicators to assess four major river ecosystem attributes: (a) maintaining high species diversity, (b) cycling of carbon and nutrients, (c) longitudinal organic matter transport, and (d) lateral organic matter input. A total of 13 metrics were calculated based on the abundance and the ratio of FFGs (Table 2).

a. Species (taxa) diversity (F1, F2)

In the present study, we calculated two metrics: taxa richness (F1) and Shannon–Wiener index (Krebs 1999) (F2). Taxa diversity was reported at a level that is sufficient to quantify the relative composition of FFG taxa. The level was mostly genus (Moog 1995; Bayerisches Landesamt für Wasserwirtschaft 1996).

b. Material cycling (F3–F6)

Material cycling (spiralling and retention of carbon and nutrients) is one of the most important ecosystem functions in which macroinvertebrates are involved (Newbold et al. 1982; Meyer et al. 1988). We indirectly assessed the following attributes: (i) primary production, (ii) the ratio of production to respiration, (iii) secondary production, and (iv) decomposition (F3 to F6 in Table 2). The abundance of scrapers and shredder-herbivores (F3) is an estimate of primary production because they feed on periphyton and aquatic macrophytes (Hawkins et al. 1982; Richardson 1993; Wallace and Webster 1996). Evans-White and Lamberti (2005) suggested that

scrapers may serve as “nutrient pumps” in stream ecosystems. The ratio of autotrophy to heterotrophy was analogized by the ratio of scrapers and shredder-herbivores to shredder-detritivores and total collectors (F4). It corresponds to the ratio of gross primary production to community respiration or, more generally, to the ratio of autotrophy to heterotrophy as used by Merritt et al. (1999). This ratio also reflects food and habitat conditions because turbidity, shading, or nutrient limitation may restrict autotrophy (Hawkins et al. 1982; Minshall et al. 1982). Secondary production was indicated by the total biomass of macroinvertebrates (F5). Finally, the total number of shredder-detritivores and gathering-collectors (F6) indicates the potential amount of coarse particulate organic matter (CPOM) and the capacity of the system to decompose CPOM (Hieber and Gessner 2002).

c. Longitudinal transport (F7, F8)

Abundance of filterers (F7) and their ratio to shredder-detritivores and gathering-collectors (F8) were used to indirectly assess longitudinal material transport. Filterers are often supported by high organic seston concentration and stable habitat condition (Parker and Voshell 1983; Wotton 1987). Thus, their abundance is closely related to POM concentration transported downstream, although suspended POM transport may be retarded by their POM acquisition (Wallace et al. 1977). The metric F8 is comparative to the ratio of suspended fine particulate organic matter (FPOM) to benthic FPOM (Merritt et al. 1999).

Table 3. Physicochemical variables used as independent variables in multiple regression analyses

Variables	Unit	Mean	Range		
Stream order	–	–	4	–	7
Mean annual discharge ^a	–	–	1	–	4
Main substrate ^b	–	–	1	–	6
Periphyton cover	%	38	0	–	90
Velocity	cm s ⁻¹	63	0	–	100
Anthropogenic impact on habitat ^c	–	–	0	–	3
Specific conductivity	µS cm ⁻¹	247	57	–	471
Dissolved oxygen (DO)	mg l ⁻¹	11.3	8.4	–	12.3
Dissolved organic carbon (DOC)	mg l ⁻¹	1.16	0.32	–	4.31
Total organic carbon (TOC)	mg l ⁻¹	1.44	0.32	–	6.92
Calcium	mg l ⁻¹	34.4	7.0	–	83.1
Sodium	mg l ⁻¹	3.3	0.8	–	14.9
Potassium	mg l ⁻¹	1.32	0.37	–	3.62
Nitrate-N	mg l ⁻¹	0.72	0.25	–	3.98
Total inorganic nitrogen	mg l ⁻¹	0.79	0.27	–	4.24
Phosphate-P	mg l ⁻¹	0.019	0.001	–	0.218
Sulfuric acid	mg l ⁻¹	26.3	5.7	–	120.8
Chlorine	mg l ⁻¹	3.1	0.5	–	15.4
Organic halogen compounds-Cl	µg l ⁻¹	4.3	1.0	–	12.2

^a A six-class system was adopted for mean annual discharge (see Fig. 1)

^b The value system for dominant substrate type ranged from 1 (gravel) to 6 (silt)

^c Anthropogenic impacts on habitat (four classes) were categorized according to the Austrian standard (for more details, see text)

d. Lateral input (F9, F10)

Allochthonous CPOM derived from terrestrial systems is an essential food source for shredders, playing a key role in the conversion of CPOM into FPOM (Cummins et al. 1989; Graça et al. 2001). Rivers receive a large proportion of their energy input as CPOM from terrestrial litter, which is the primary food source for shredder-detritivores (Cummins and Klug 1979; Dobson and Hildrew 1992). We calculated two metrics, namely, the number of shredder-detritivores (F9) and the ratio of shredder-detritivores to total abundance, as indicators of lateral organic matter input (F10).

e. Other ecosystem attributes (F11–F13)

Three additional ecosystem attributes were assessed: (i) the ratio of CPOM to FPOM, (ii) top-down predator control and (iii) habitat stability. They were indirectly calculated as (i) the ratio of shredder-detritivores to gathering-collectors and filterers (F11), (ii) the ratio of predators to total abundance (F12), and (iii) the ratio of scrapers and filterers to total shredders and gathering-collectors (F13) (Merritt et al. 1999).

Statistical analyses

Based on abundance and ratio of FFGs, 13 metrics (F1–F13) were calculated for all 211 sites to indicate ecosystem attributes. Among these sites, 78 sites for which detailed habitat information was available were selected for detailed analyses of the relationship between physicochemical variables and ecosystem functions (F1–F13). To exclude seasonality from statistical analyses, all 78 sites were sampled in winter (January–February). In addition, 19 physicochemical variables were selected as independent variables

to avoid redundancy by partial correlation analyses: those variables included carbon, nutrient, heavy metal, and chlorine concentrations (average annual values; Table 3).

The relationship between habitat conditions and individual metrics was calculated by multiple regression analyses (forward selection with $F > 1.0$; Statistica; Kernel release 6.0, StatSoft, Tulsa, USA). All metrics (F1–F13) were transformed (log or arcsine) to meet assumptions of normality and homogeneity. Before multiple regression analyses, relationships between these metrics and stream order were tested using analysis of variance (ANOVA). If stream order significantly affected individual metrics, it was expressed as a dummy variable and then included in multiple regression analyses. In addition, correlations between the metrics (F1–F13) were tested with sequential Bonferroni procedures (Rice 1989).

Results

Species diversity and nestedness

At 211 sampling sites, a total of 569 taxa of benthic invertebrates were identified, mostly to species level. The average density of benthic macroinvertebrates was 50,367 individuals m⁻² (range, 4,750–870,000). Chironomidae (221 taxa), Trichoptera (65), Oligochaeta (64), and Ephemeroptera (62) were the most diverse groups. The average number of taxa per site was 39 (±14), ranging from 4 to 73. Overall, 210 taxa were found in less than 1% of the sites (1–2 sites), 461 taxa in <10 % of all sites. Numerically dominant taxa (>1% of all individuals) included mainly oligochaetes and chironomids (Table 4). Together, the 10 most abundant

Table 4. Dominant taxa with a relative abundance >1.0% each (pooled data)

Taxon	Relative abundance (%)	Relative frequency (%) ^a
<i>Vejdovskyella</i> spp.	10.1	2.4
<i>Propappus volki</i>	9.8	54.5
<i>Nais elinguis</i>	8.4	49.3
<i>Microspectra atrofasciata</i>	6.3	24.2
<i>Limnodrilus hoffmeisteri</i>	3.7	27.5
<i>Stylodrilus heringianus</i>	3.1	67.8
<i>Synorthocladus semivirens</i>	2.6	50.7
<i>Nais alpina</i>	2.5	54.0
<i>Tvetenia calvescens</i>	1.8	66.8
<i>Orthocladus rivicola</i>	1.7	43.6
<i>Psychomyia pusilla</i>	1.7	53.6
<i>Gammarus fossarum</i>	1.7	40.3
<i>Nais bretscheri</i>	1.6	41.2
<i>Parametriocnemus stylatus</i>	1.5	70.1
<i>Paratrichocladus rufiventris</i>	1.4	73.0
<i>Orthocladus frigidus</i>	1.3	43.1
<i>Nais simplex</i>	1.3	5.2
<i>Cheumatopsyche lepida</i>	1.3	9.5
<i>Tubifex tubifex</i>	1.1	14.2
<i>Nais communis</i>	1.0	49.3
<i>Eukiefferiella devonica</i>	1.0	54.0
<i>Ancylus fluviatilis</i>	1.0	45.0
Total	65.8	—

^a Relative frequency, proportion (%) of sites occupied by each individual taxon

taxa accounted for 50% of all individuals. Generally, those abundant taxa were also the most frequent ones. However, *Vejdovskyella* spp. and *Nais simplex* were found in very high densities at a few locations (mainly along the impounded Drau River).

High corridor diversity (gamma-diversity) was observed along the Enns, Traun, Leitha, and Mur Rivers, where >140 taxa were estimated for a total of six sampling sites (jack-knifed diversity; Table 5). At the catchment scale, the Enns, Traun, Drau, and Salzach Rivers exhibited highest taxa richness (>200 taxa for 10 sampling sites), whereas the Inn River had only 114 taxa (10 sites). Diversity calculated by jackknife procedures was similar to observed values.

At the corridor scale, beta-diversity (dissimilarity between pairs of sites) ranged from 0.45 to 0.81. Corridors with higher local (alpha-)diversity exhibited lower beta-diversity. The highest beta-diversity (lowest similarity between pairs of sites) was found along the Enns River (0.81), followed by the Drau River (0.70). Beta-diversity between sites increased with spatial distance, indicating a gradual faunal change along corridors (Fig. 2). Dissimilarity between the most upstream and the most downstream site was always >0.5. Average dissimilarity was lowest along the main corridor of the Salzach River.

In general, high corridor diversity corresponded to a low degree of nestedness, except for the Enns River. In the Traun and Leitha Rivers system, temperature (T), an index of the degree of nestedness, was not significantly different from T calculated from a random community. This result means that each site within those catchments had a distinct macroinvertebrate community. In contrast, invertebrates in the Inn, Salzach, Enns, Drau, and Mur catchments were significantly nested.

Fig. 2. Average beta-diversity (dissimilarity) between all pairs of sites along selected Austrian rivers (average Soerenson index for each pair of sites). Distance between study sites ranged from 10 to 40km. Numbers in parentheses, gamma-diversity of the main corridor

Functional feeding groups

All macroinvertebrates (569 taxa from 211 sites; average density, 50,367 m⁻²) were classified according to their functional feeding preference (Fig. 3). However, for 32.8% of the individuals it was not possible to accurately assess their feeding preferences because information was not available or taxonomic resolution was too coarse. Gathering-collectors and scrapers dominated benthic communities (>50% of all individuals), which suggests that detritus and epilithic algae (periphyton) were the primary energy sources for macroinvertebrate communities. If unidentified individuals

Table 5. Summary statistics for major corridors and catchments

	Inn	Salzach	Traun	Enns	Leitha	Drau	Mur
<i>Main corridor</i>							
Sites along corridor	14	9	7	8	6	14	14
Local diversity ^a	32 ± 10	38 ± 12	48 ± 4	36 ± 19	45 ± 8	32 ± 15	38 ± 10
Corridor diversity ^a (calculated, 6 sites)	100 ± 6	116 ± 10	149 ± 9	192 ± 16	171 ± 7	130 ± 9	147 ± 11
Beta diversity	0.51	0.45	0.48	0.81	0.58	0.70	0.60
Nestedness (T)	38.2	35.3	64.2 (n.s.)	40.2	60.7 (n.s.)	33.0	40.6
<i>Catchment</i>							
Sites in the catchment	30	22	19	14	nd	33	25
Catchment diversity (observed)	117	206	190	198	nd	185	176
Catchment diversity ^a (calculated, 10 sites)	114 ± 5	213 ± 14	205 ± 11	244 ± 12	nd	239 ± 13	171 ± 12

Taxa diversity was predicted at the corridor and catchment scale following jackknife procedures (after Heltshe and Forrester 1983)

Local diversity, average (±SD) number of taxa per sampling site; beta-diversity, average degree of dissimilarity (Soerenson index); nestedness, system temperature (T) calculated after Atmar and Patterson (1993); n.s., calculated temperatures were not significantly different from randomly calculated temperatures (Monte-Carlo simulation, 500 runs); nd, not determined

Leitha catchment: all study sites were located along the main corridor

^aMean ± SD

Fig. 3. Relative proportion (%) of individuals belonging to individual functional feeding groups (pooled data from 211 sites). Average number of individuals per site was 50,367 m⁻²

were excluded, the proportions (based on abundance) of gathering-collectors and scrapers were 59.5% and 29.7%, respectively. Gathering-collectors were mainly composed of Chironomidae and Trichoptera taxa. Scrapers included many Trichoptera and Ephemeroptera taxa. In contrast, relative proportion of filterers and shredders was 3.5% and 1.6% (of individuals), respectively.

Ecosystem attributes

Among the 78 sites selected for detailed functional assessments, 8 sites were classified as pristine or seminatural. For all sites, the pH value ranged from 7.28 to 8.50 (mean, 7.94). Average concentration of dissolved organic carbon (DOC), nitrate-N, and soluble reactive phosphorus was 1.16, 0.72, and 0.019 mg l⁻¹, respectively (see Table 3). The saprobic value, an index of organic pollution (Zelinka and Marvan 1961), ranged from 1.44 to 3.31. Several monitoring sites were located in limestone areas. There, calcium and magnesium concentrations as well as specific conductance decreased from upstream to downstream sections.

Stream order significantly affected the biomass (F5) (ANOVA; $F = 4.3$, $P < 0.01$, $df = 3$) and the abundance of filterers (F7) ($F = 2.9$, $P = 0.041$, $df = 3$). For all other attributes, no significant differences among stream orders were found. All functional metrics (F1–F13) were well explained by physicochemical variables, with multiple correlation coefficients ranging from 0.44 to 0.73 ($P < 0.01$; Table 6). Among the metrics, abundance of filterers, as an indicator for longitudinal material transport (F7), exhibited the highest correlation coefficients. It had a significant positive correlation with stream order, periphyton cover, dissolved oxygen (DO), and chlorine concentration. The diversity index (F2) was significantly related to discharge, DO, total organic carbon (TOC), calcium, total inorganic nitrogen, and phosphate-P concentration. Especially discharge, TOC, and inorganic nutrients exhibited high partial correlation coefficients.

Among all independent variables, DO was the single most important variable that explained most macroinvertebrate-based metrics. Dissolved oxygen exhibited a significant correlation with six metrics (F2–F4, F7, F8, and F13). Correlation coefficients were positive except for F4 (ratio of herbivores to detritivores as an indicator of P:R ratio). Periphyton, DOC, TOC, sodium and potassium were

Table 6. Results from multiple regression analyses showing relationships between metrics based on functional feeding groups (F1–F13, see Table 2) and physicochemical parameters

Statistics/Parameter	Metrics based on taxa and functional feeding groups (see Table 2)												
	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10	F11	F12	F13
Mean	55	3.59	8812	0.95	16	10860	578	0.06	638	0.02	0.10	0.02	1.02
Maximum	100	4.96	78782	4.10	104	70310	8947	0.37	9848	0.12	0.77	0.15	3.88
Minimum	14	1.80	99	0.03	0	486	1	0.00	3	0.00	0.00	0.00	0.03
<i>R</i> (Multiple correlation coefficient)	0.51	0.57	0.56	0.49	0.70	0.51	0.73	0.66	0.44	0.64	0.61	0.46	0.57
<i>F</i>	3.58	4.19	4.68	3.80	9.72	3.54	10.1	5.95	4.44	8.39	6.86	2.75	3.54
<i>p</i>	0.002**	<0.001**	<0.001**	0.002**	<0.001**	0.002**	<0.001**	<0.001**	0.003**	<0.001**	<0.001**	0.014	0.001**
Standard error of estimate	1.55	3.91	0.92	0.17	0.68	16.2	1.21	0.09	1.27	0.09	0.14	0.08	0.21
Stream order α	NA	NA	NA	NA	0.53**	NA	0.28**	NA	NA	NA	NA	NA	NA
Stream order β	NA	NA	NA	NA	NA	NA	0.12	NA	NA	NA	NA	NA	NA
Mean annual discharge	–	–0.28**	0.16	–	–0.14	–	–	0.10	–0.13	–0.31**	–0.19	–0.19	–
Main substrate	–0.21	–	–0.14	0.13	–	–	–	–	–	0.13	–	0.23	–0.17
Periphyton cover	0.12	–	0.32**	–	0.24**	0.25*	0.22*	–	0.14	–0.17	–	–0.17	–
Velocity	–	–	–	–	–	–	–	–0.12	–	–	–	–	–
Anthropogenic impact on habitat	0.17	0.18	–	–0.12	–	–	–	0.10	–0.14	–	–	–	0.11
Specific conductivity	–	–	–	–	–	–0.81*	–	0.45**	–	–	–	–	0.28
Dissolved oxygen (DO)	0.15	0.24*	0.35**	–0.30*	–	–	0.36**	0.42**	–	–	–	0.16	0.43**
Dissolved organic carbon (DOC)	0.46**	–	–	–	–	–	–	–	–	–1.08*	–1.04*	–	–0.69
Total organic carbon (TOC)	–	–0.65**	–	–	0.28	–	–	–	–	0.93*	1.17**	–	0.49
Calcium	0.14	0.27*	–	–	–	0.55	–	–	–	–	0.20	–	–
Sodium	–	–0.18	–	–	–	–	–	0.27*	–0.40**	–0.37**	–0.24	0.17	–
Potassium	–	–	–	–0.30*	–0.20	–0.34*	–	0.32*	–	–	–	–	0.50**
Nitrate–N	–	–	–	–	–	–	0.31	–	–	–	–	–	–
Total inorganic nitrogen	–	1.11**	–	–	–	–	–	–	–	–	–	0.23	–
Phosphate–P	–0.13	–0.50**	0.14	0.21	–	0.35*	–0.14	–0.14	–	–	–	–	–0.20
Sulfuric acid	–	–	–	–0.23*	–	–	–	–0.18	–	–	–	–0.16	0.07
Chlorine	–	–	0.14	–	0.24	0.32	0.42*	–	–	–	–0.43	–	–
Organic halogen compounds–Cl	–	–	0.18	–	0.24*	0.25	0.15	–	–	–	–	–	–

Stream orders α and β were dummy variables expressing differences between 4th–6th and 7th, and 4th and 5th–7th order, respectively

$n = 78$

NA, not analyzed

Standardized partial correlation coefficients (**, $P < 0.01$; *, $0.01 < P < 0.05$) are shown for each parameter

Table 7. Correlation matrix of 12 metrics corrected with sequential Bonferroni procedures

	F1	F2	F3	F4	F5	F6	F7	F8	F9	F11	F12
F1											
F2	0.31										
F3	0.57**	−0.06									
F4	−0.31	−0.17	−0.54**								
F5	0.57**	0.09	0.51**	0.00							
F6	0.30	−0.28	0.65**	0.27	0.53**						
F7	0.45**	0.24	0.37**	0.01	0.65**	0.37*					
F8	0.28	0.42**	−0.02	−0.13	0.36*	−0.22	0.82**				
F9	0.24	−0.02	0.42**	−0.19	0.16	0.29	−0.01	−0.20			
F11	−0.01	0.17	−0.09	−0.30	−0.21	−0.39**	−0.25	−0.04	0.72**		
F12	−0.14	0.30	−0.49**	0.33	−0.03	−0.32	0.16	0.38*	−0.24	0.04	
F13	0.34	0.21	0.54**	−0.97**	0.05	−0.26	0.13	0.28	0.12	0.22	−0.26

$n = 78$

See Table 2 for the metrics (F1–F13); F10 (ratio of shredder-detritivores) was excluded from the analysis because it obviously was correlated to F9 (abundance of shredder-detritivores)

Significant correlation coefficients at $P = 0.01$ and $P = 0.05$ are marked with * and **, respectively

significantly related to several metrics (Table 6). Periphyton biomass, for example, was positively correlated with metrics indicating material cycling (F3, F5, and F6) and longitudinal material transport (F7). DOC exhibited a positive correlation with taxa richness (F1) and a negative correlation with the ratio of shredders to detritivores (F10). TOC was negatively correlated with diversity index (F2) and positively with ratio of shredders to detritivores (F10). Dominant substrate class, flow velocity, anthropogenic impact, and nitrate concentration, however, were not significantly related to any of the calculated metrics.

Correlation analyses among metrics revealed that F1 and F2 (species diversity) were positively correlated with F7 and F8, which are both based on abundance of filterers (Table 7). Taxa richness showed significant correlations (correlation coefficients >0.45) with F3 (abundance of herbivores) and F5 (total biomass). Metrics for material cycling (F3, F5, and F6) were correlated with metrics indicating longitudinal transport and lateral input (F7 and F9). Overall, F3 (abundance of herbivores) was correlated with most other metrics (F1, F4–F7, F9, F12, and F13). In addition, there was a negative correlation between F3 and F4 (the ratio of herbivores to detritivores).

Discussion

Species diversity

We identified 569 taxa, corresponding to 21% of the entire aquatic macroinvertebrate fauna listed for Austria, which includes all species living in running waters, lakes, wetlands, springs, and groundwaters (Moog 1995; Moog et al. 2001b). This proportion is considered as high because only medium-size rivers were considered and individual sites were only sampled once. Tributaries, especially along the Salzach and Drau Rivers, considerably increased total species richness at the catchment scale (see Table 5). In general, tributaries

exhibit fewer human alterations than the main corridor (Federal Environment Agency of Austria 2002). Multiple correlations indicated, as expected, that diversity (F1, F2) increased with natural habitat conditions (which occurred primarily in headwater sections). Our results suggest that some taxa are dominant in relatively large river sections as discharge was only significantly related to the diversity index (F2) but not to taxa richness (F1). Additional detailed hydrogeomorphic conditions might help to better explain the expected longitudinal trend (Lorenz et al. 2004).

In their natural state, river corridors are longitudinally connected systems, whereas ponds form more-isolated habitats. In lotic ecosystems, migration and dispersal are essential phenomena. Thus, habitat fragmentation as well as water abstraction can cause discontinuities along corridors, which may reduce the dispersal of aquatic organisms. Therefore, community structure at the catchment scale may reflect anthropogenic impacts and biogeographic differences. In the present study, the Enns River exhibited very high corridor and catchment diversity as well as a high turnover (high beta-diversity) between adjacent sites. This result indicates that each individual site harbours a rich and relatively unique macroinvertebrate community (see Table 5, Fig. 2). A high proportion of protected areas in the catchment might account for this high species diversity in the Enns River catchment, although only short sections along the main stem maintained good hydromorphological quality (Muhar et al. 2000). In contrast, the Inn and Drau Rivers, which are fragmented by impoundments, exhibited a low alpha-diversity but a high degree of nestedness. There, species-poor sites contained faunal subsets of the richest sites. In this case, the conservation of the most diverse sites, mainly headwaters, deserves highest priority.

Both biogeographic and anthropogenic factors are supposed to be responsible for differences in taxa diversity at the catchment scale (Bauernfeind and Moog 2000; Wimmer et al. 2000; Offenböck et al. 2002). Most study sites within the Inn catchment were located in the aquatic bioregions

“Glaciated Crystalline Alps” and “Limestone Alps.” Turbid glacial meltwater probably confines taxa diversity at the local level. In contrast, the Traun and Enns catchments, which include sites from different longitudinal regions (rhithral to hyporhithral), showed relatively high diversity. These catchments drain several biogeographic regions including the limestone area.

Functional metrics and ecosystem attributes

Multiple correlation analyses revealed significant relationships between habitat conditions and macroinvertebrate metrics, implying that these metrics can be used for the functional assessment of rivers. Functional feeding groups (FFGs) emphasise the multiple linkages that exist between food resources and the capability of invertebrates to successfully acquire these resources (Merritt et al. 1999; Wallace and Webster 1996; Barbour et al. 2001). Thus, a function-based assessment is more directly related to ecosystem processes than to solely taxonomic composition.

For example, species diversity (F1 and F2) was correlated with high DO, low TOC, and low phosphate concentration. Metrics used to indicate material cycling (F3–F6) were significantly related to DO and periphyton cover. Interestingly, higher phosphate concentration seemed to support microbial growth, which provides a better POM quality for detritivores (F6), as also reported by Lawson et al. (1984). Further, abundance of filterers (F7) increased downstream, which means that suspended organic matter also increased, as predicted by the River Continuum Concept (Vannote et al. 1980). We found some limitations to evaluate these metrics based on our database because parameters explaining hydrogeomorphic conditions were not equally documented from the sampling sites. Thus, further studies are required to investigate the meaning and validity of metrics, especially in respect to flow regime, local flow conditions, and habitat stability.

Inorganic nutrients stimulate periphyton and microbial growth. This biofilm is an important food source for scrapers and shredder-detritivores (Battin et al. 2003; Rezanka and Hershey 2003). Positive correlations between inorganic phosphorus and metrics indicating material cycling (primary and secondary production and decomposition by shredders) were found in the present study. However, inorganic phosphorus was negatively related to species diversity (F2), which suggests that an excess in phosphorus can lead to an unbalanced macroinvertebrate community dominated by scrapers. In contrast, total inorganic nitrogen was positively related to the diversity index (N range, $0.27\text{--}4.24\text{ mg l}^{-1}$).

High-order sites (7th order) differed significantly from 4th- to 6th-order sites relative to total biomass (F5) and abundance of filterers (F7) (see Table 6). Increased longitudinal transport of POM generally results from an increase of upstream organic matter input and/or increased in-stream production. Based on our statistical analyses, a longitudinal trend was found for secondary production, but not for primary production. However, abundance of herbivores

(F3) was positively correlated with periphyton cover, DO, and main substrate diameter and negatively with annual discharge (see Table 6). Thus, results indicated that these metrics, based on abundance of shredder-herbivores and scrapers, are sensitive enough to detect changes in primary production (Merritt et al. 1999; Rezanka and Hershey 2003).

Calcium concentration was positively related to diversity (F1, F2), decomposition (F6), and the ratio of CPOM to FPOM (F11). Limestone is the dominant underlying bedrock in several bioregions in Austria (Wimmer et al. 2000). Geology is a principal factor that explains the variation of ecosystem attributes across stream orders. It is, therefore, important to take regional characteristics into account when a functional assessment is applied to rivers.

Taxa richness (F1) was positively correlated with F3 and F5 (primary and secondary production; see Table 7). Thus, high in-stream productivity seems to be fundamental for maintaining species richness, at least in medium-size rivers. Metrics F3–F6 (material cycling) were in general positively correlated to F7 (longitudinal transport), implying a close relationship between in-stream production and energy transport. Surprisingly, F3 (primary production) was negatively correlated to the ratio of herbivores to detritivores (F4). Considering the positive response of F3 (primary production) to periphyton cover (Table 6), correlation analysis indicated that heterotrophic functional groups (detritivores) increase at a higher rate in abundance than autotrophic groups (herbivores) with increasing periphyton cover. Detritivores might prefer periphyton cover as a habitat, although it is not their primary food source.

Metrics for primary production (F3), secondary production (F5), decomposition (F6), and longitudinal transport (F7) were positively correlated with pollutants such as chlorine and organic halogen compounds, which represent direct anthropogenic (and partly toxic) impacts from agricultural and urban areas (Newman et al. 1987; Fukushima and Kanada 1999). This result implies that functional indicators are affected by toxic substances. For example, organic halogen compounds often result in a dominance of a few tolerant Chironomidae and Oligochaeta taxa (Barbour et al. 2001). As shown in our results, toxic substances may increase some metrics, for example, primary and secondary production, without enhancing ecosystem attributes. Thus, functional assessments should be carefully applied by setting clear targets of stressors because each macroinvertebrate species may exhibit a different response to toxic substances (Hurd et al. 1996; Soucek et al. 2001).

Overall, indicators of ecosystem attributes (metrics F1–F13) were closely related to environmental conditions in various ways. Therefore, a function-based approach using FFGs of benthic macroinvertebrates has the potential to be an effective tool for the assessment of the ecological integrity of streams and rivers (Lakly and McArthur 2000). However, future research is required (i) to understand relationships between food availability and macroinvertebrates, as well as their interactions with other biota (e.g., fish), (ii) to determine the sensitivity of individual indicators to vari-

ous impacts, and (iii) to define reference standards against which ecosystem attributes can be calibrated. In particular, macroinvertebrate abundances cannot simply be converted to biomass, which again is a better determinant of primary and secondary production (Grubaugh et al. 1996). Our results clearly suggest that a function-based approach could complement the more-traditional approaches used for the assessment of river ecosystems (Zelinka and Marvan 1961; Armitage et al. 1983).

Acknowledgments This study was supported by a grant from the Japan Society for the Promotion of Science (JSPS). We acknowledge the Austrian Ministry for Agriculture, Forestry, Environment and Water Management for providing data for the Austrian Monitoring Network. This manuscript was written while Klement Tockner was a sabbatical visitor at the Institute of Ecosystem Studies (IES), Millbrook, NY, USA. Comments by the editor and two anonymous reviewers helped very much to improve the manuscript.

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