

River restoration and the trophic structure of benthic invertebrate communities across 16 European restoration projects

Benjamin Kupilas · Nikolai Friberg · Brendan G. McKie ·
Maik A. Jochmann · Armin W. Lorenz · Daniel Hering

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Abstract River restoration enhances not only habitat diversity in the stream channel and riparian zone, but also retention of organic matter, which together are expected to enhance aquatic-terrestrial linkages, and the range of autochthonous and allochthonous resources. Consequently, alterations of food-web structure and trophic relationships can be expected. We applied stable isotope analysis ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) to characterize changes in the trophic structure of benthic invertebrate communities between paired restored and unrestored river reaches across 16 European catchments. We sampled dominant taxa of invertebrate

assemblages belonging to different functional feeding groups and calculated $\delta^{13}\text{C}$ range to estimate the diversity of basal resources assimilated, $\delta^{15}\text{N}$ range as an indicator of the trophic length and standard ellipse area corrected for small samples as a measure of isotopic niche width. We analysed (1) if restoration influences the trophic structure of invertebrates, (2) if effects of restoration depend on the extent of restoration effort, and (3) if effects of restoration depend on restoration measures applied. Our European-scale comparison indicates that river habitat restoration effects trophic structure, primarily by increasing the breadth of resources assimilated by consumers; this effect increases with restoration effort and it depends on restoration measure type.

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B. Kupilas (✉) · A. W. Lorenz · D. Hering
Department of Aquatic Ecology, University of Duisburg-
Essen, Universitätsstr. 5, 45141 Essen, Germany
e-mail: benjamin.kupilas@uni-due.de

N. Friberg
Section of Fresh Ecology, Norwegian Institute for Water
Research, Gaustadalléen 21, 0349 Oslo, Norway

B. G. McKie
Department of Aquatic Sciences & Assessment, Swedish
University of Agricultural Sciences, P.O. Box 7050,
75007 Uppsala, Sweden

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M. A. Jochmann
Instrumental Analytical Chemistry, University of
Duisburg-Essen, Universitätsstr. 5, 45141 Essen, Germany

Introduction

Restoration of river hydromorphology has the potential to affect not only structural ecosystem features, including species composition and diversity, but also ecosystem functioning (Palmer et al., 2014). Despite this, the most-widely used parameters for assessing the success or failure of restoration projects are almost exclusively based on changes in community composition of different biological groups. In the context of the EU Water Framework Directive the composition of organism groups like fish, phytoplankton and benthic fauna and flora are most commonly investigated, and the response of these assemblages to hydromorphological restoration has been relatively well characterized (Lepori et al., 2005a; Jähnig et al., 2010; Sundermann et al., 2011; Lorenz et al., 2012; Haase et al., 2013; Friberg et al., 2014; Schmutz et al., 2014; Stoll et al., 2014). Functional metrics, even though widely applied in basic studies of aquatic systems (e.g. Vander Zanden & Rasmussen, 1999; Hieber & Gessner, 2002; Fischer et al., 2005; Friberg et al., 2009; Gücker et al., 2009; McKie & Malmqvist, 2009), are rarely in assessments of river restoration (but see Lepori et al. 2005b, 2006; Flores et al., 2011). Consequently, the outcomes of restoration for key ecosystem processes and trophic transfers of energy and nutrients remain poorly understood (Lepori et al., 2006).

Hydromorphological river restoration typically enhances not only habitat diversity in both the stream channel and riparian zone (Jähnig et al., 2010; Januschke et al., 2014), but also retention of organic matter (Lepori et al. 2005b, 2006; Flores et al., 2011), which together are expected to enhance aquatic-terrestrial linkages, and the availability of both autochthonous and allochthonous food sources. Therefore, significant alterations of food-web structure and trophic relationships can be expected: A higher diversity of both feeding- and physical habitat-related niches can contribute to changes in food-web structure, particularly if a higher variety of resources is available to increase the number of trophic pathways (Layman et al., 2007a; Woodward, 2009). Apart from increases in retention of allochthonous matter (Lepori et al., 2005b; Flores et al., 2011), restoration also might increase the availability of autochthonous sources, e.g. caused by enlarged shallow habitats providing more space for autotrophs (Lorenz et al.,

2012). Furthermore, stronger connections between river and floodplain, e.g. caused by a more shallow profile or the removal of hardened, channelized banks, have potential to increase inundation frequency and hence resource transfers from land to water. Furthermore, improving niche space for larger bodied predators through, e.g., the creation of pools or removal of dispersal obstacles is likely to increase food-chain length (Woodward et al., 2005). These changes all have implications for complexity of the food web and the relative trophic position of different organisms within the web (Woodward & Hildrew, 2002; Woodward, 2009).

Stable isotope composition of carbon and nitrogen ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) is commonly used to study food-web structure as they provide information on the material assimilated by organisms (Abrantes et al., 2014). $\delta^{15}\text{N}$ trophic fractionation changes about +3‰ between trophic levels (Minagawa & Wada, 1984; McCutchan et al., 2003) and is generally used to calculate the trophic position of an organism (Post, 2002). Because $\delta^{13}\text{C}$ trophic fractionation is less, changing only 0–1‰ from source to consumer (DeNiro & Epstein, 1978; McCutchan et al., 2003) and can vary among different producers, it is often used to identify the resource base (Vander Zanden & Rasmussen, 1999). A set of community-wide metrics has been introduced by Layman et al. (2007b) to gain more quantitative information from stable isotope data at the species or community level. These metrics have been used to investigate effects of ecosystem fragmentation on niche width (Layman et al., 2007a), to study effects of flooding on community structure (Calizza et al., 2012), to compare the trophic structure of communities within different lakes (Cooper & Wissel, 2012), in invasion ecology (Jackson et al., 2012), and to identify patterns in food-web structure related to different environmental conditions (Abrantes et al., 2014). Recently, these metrics have further been reformulated in a Bayesian framework by Jackson et al. (2011) which enables statistical comparison between sites without standardized sampling design or between different sampling periods (Jackson et al., 2012; Abrantes et al., 2014).

In this study, we applied stable isotope analysis of carbon and nitrogen to quantitatively characterize changes in trophic structure following both larger- and smaller scale river restoration projects. We sampled dominant benthic invertebrate taxa belonging to

different functional feeding groups (FFG) on paired restored and degraded river sections in 16 catchments throughout Europe, allowing comparison of restored sections with degraded “control sites” located upstream (Hering et al., 2015). Two types of restoration projects were investigated; comprehensive flagship projects representing best-practice examples and typically involving extensively restored river sections at a larger scale, and smaller projects including single restoration measures only. We focus on benthic invertebrate communities, which are commonly applied indicators of ecosystem health, and which are trophically diverse, encompassing herbivorous, detritivorous, and predacious species. However, benthic invertebrates in streams also typically show a high degree of dietary flexibility, and thus have the potential to respond to new resources as they become available (Mihuc, 1997; Layer et al., 2013), leading to potentially rapid uptake into the food web (Göthe et al., 2009). For example, species typically classified as detritivores are capable of incorporating algae into their diets when available (Friberg & Jacobsen, 1994), and many species feed at different levels in the food web (both primary consumer and predator) at different points in their lifecycle (Wissinger et al., 2004; Layer et al., 2013). Furthermore, two of the largest feeding groups (collector-gatherers and filterers) feed on particulate organic matter, derived from both allochthonous and autochthonous sources, providing another pathway for novel sources of energy and nutrients to enter stream food webs following restoration (Webster & Meyer, 1997).

We used a set of quantitative community metrics: $\delta^{13}\text{C}$ range (CR) and $\delta^{15}\text{N}$ range (NR) following Layman et al. (2007b), and standard ellipse area (SEA) according to Jackson et al. (2011) of the dominant feeding types of benthic invertebrate communities to quantify changes in trophic structure between restored and degraded sections. The restoration effect was quantified by comparing each restored river section to an upstream non-restored section. We expected that our isotopic metrics would show evidence for changes in trophic organization following river restoration, reflecting increases in habitat diversity, resource diversity, and aquatic-terrestrial linkages. Specifically, we hypothesized that (i) the CR metric would increase (i.e. an increase in $\delta^{13}\text{C}$ range), reflecting the availability of a more varied food source following restoration and that (ii) the NR metric would also

increase (increasing $\delta^{15}\text{N}$ range), if changes in habitat diversity and increased availability of basal resources allow an increase on food-chain length. Based on this, we further hypothesized that (iii) the SEA metric would increase, reflecting a larger isotopic niche of benthic invertebrate communities following restoration. We further expected these effects would (iv) increase with restoration extent, reflecting stronger changes in habitat complexity and aquatic-terrestrial connectivity, and that these effects are (v) related to the type of restoration measure employed, with projects which mainly aim at river widening (usually affecting both instream habitats and connectivity of water and land and thereby enhancing availability of autochthonous and allochthonous carbon resources) affecting food webs more strongly than projects which applied measures mainly affecting the river channel itself (e.g. instream measures or flow restoration).

Materials and methods

Study sites

The study on benthic invertebrate communities and stable isotopes was undertaken in river sections in 16 catchments across Europe (Table 1; and compare Muhar et al., 2015, Hering et al., 2015), either medium-sized lowland rivers or medium-sized mountain rivers. In each of these catchments, a restored and a nearby non-restored river section were sampled. Two types of restoration projects were investigated: large restored river sections with an extensive restoration effort representing best-practice examples (R1), and smaller projects relying on mainly single, local restoration measures (R2). For each large and small project, a representative sampling reach was selected in the downstream part of the restored river section to account for effects of the restored river length. The restored sections were compared to non-restored, degraded “control sections” (D1/D2) located directly upstream of the corresponding restored sections. As the distance between restored and degraded reaches was small relative to overall stream size (mean distance: 3.0 km, $n = 16$), natural shifts in basal resources are not anticipated over this length of the streams, thus it is highly unlikely that anything other than the human impacts could cause shifts in isotopic signals. We therefore did not expect effects on isotopic

Table 1 Overview of large-scale (R1) and small-scale (R2) restored sites

Site name	FI_R1	SE_R1	DK_R1	PL_R1_1	DL_R1	DM_R1	CZ_R1	AT_R1
Country	Finland	Sweden	Denmark	Poland	Germany	Germany	Czech Republic	Austria
River name	Vääräjoki	Emån	Skjern	Narew	Lippe	Ruhr	Becva	Drau
River type	Gravel-bed	Gravel-bed	Sand-bed	Sand-bed	Sand-bed	Gravel-bed	Gravel-bed	Gravel-bed
Latitude (N)	64.054433	57.149095	55.9380926	53.1500527	51.663675	51.44093	49.4968975	46.75454
Longitude (E)	24.2206639	16.441897	8.6279814	22.8716193	8.23248	7.96223	17.5211533	13.309393
Altitude (m a.s.l.)	60	10	10	139	72	153	232	570
Catchment geology	Organic	Siliceous	Siliceous	Organic	Siliceous	Siliceous	Siliceous	Siliceous
Mean discharge (m ³ /s)	9.9	29.3	36.6	16.9	17.7	15.2	16.6	62.6
Stream order	4	6	5	2	3	3	7	7
Ecoregion	Fenno-scandian shield	Fenno-scandian shield	Central plains	Eastern plains	Central plains	Central Highlands	Hungarian lowlands	Alps
Restoration length (km)	1.4	0.9	26	9	2	0.75	0.45	1.9
Restoration date	1997–2006	2006–2011	2003	1995-cont.	1997	2008	1997	2002–2003
Measure type	Other	Widening	Other	Other	Widening	Widening	Widening	Widening
Main restoration action	Instream measures	Hydro RivCon (dam removal, naturalize flow regime, fishway construction, salmonid spawning gravel and boulder additions)	Remeandering and reconnection of wetlands	Reconnection side channels (rise water level by thresholds)	Remeandering	Riverbed widening	Riverbed widening	Riverbed widening; (partial removal of bank fixation; initiation of secondary channel; reconnection of one sidearm)
Time of sampling (together with degraded section)	August 2012	August 2013	August 2013	July 2012	August 2013	June 2013	September 2012	July 2013

Table 1 continued

Site name	FI_R2	SE_R2	DK_R2	PL_R2	DL_R2	DM_R2	CZ_R2	AT_R2
Country	Finland	Sweden	Denmark	Poland	Germany	Germany	Czech Republic	Austria
River name	Kuivajoki	Mörrumsån	Stora	Warta	Spree	Lahn	Morava	Enns
River type	Gravel-bed	Gravel-bed	Sand-bed	Sand-bed	Sand-bed	Gravel-bed	Gravel-bed	Gravel-bed
Latitude (N)	65.6860429	56.336005	56.3614934	52.1930314	52.377747	50.86588	49.6570728	47.42112
Longitude (E)	25.6349874	14.700237	8.4982852	17.8974616	13.878897	8.79088	17.2179975	13.816094
Altitude (m a.s.l.)	74	87	10	75	35	191	218	692
Catchment geology	Organic	Siliceous	Siliceous	Calcareous	Siliceous	Siliceous	Siliceous	Calcareous/siliceous
Mean discharge (m ³ /s)	12.8	12	16.1	45.3	14	12	17.7	21.5
Stream order	4	6	5	2	6	3	7	5
Ecoregion	Fenno-scandian shield	Fenno-scandian shield	Central plains	Central plains	Central plains	Central Highlands	Hungarian lowlands	Alps
Restoration length (km)	0.4	3.3	0.3	3	0.95	0.24	0.22	0.6
Restoration date	2002–2006	2003–2012	2012	2008	2005	2000	1997	2003–2004
Measure type	Other	Other	Other	Widening	Other	Widening	Widening	Widening
Main restoration action	Instream measures	Hydro RivCon (increased flow, fishway construction and salmonid spawning gravel additions)	Instream measures (habitat restoration: salmonid spawning gravel)	Reconnection floodplain	Remeandering	Riverbed widening	Riverbed widening	Riverbed widening (partial removal of bank fixation; initiation of one secondary channel)
Time of sampling (together with degraded section)	August 2012	August 2013	August 2013	July 2013	July 2013	July 2013	September 2012	July 2013

signals due to the position of the sampling reaches in the river network. The degraded sections were selected to be similar to the restored reaches and to differ only in the absence of restoration activities (Hering et al., 2015). Therefore, comparing each restored river section with the nearby still degraded river section enabled quantifying the restoration effect. One flagship project (R1/D1) and one smaller project (R2/D2) were investigated in the following regions: Finland (FI), Sweden (SE), Denmark (DK), Poland (PL), Germany lowlands (DL) and mountains (DM), the Czech Republic (CZ) and Austria (AT). Further information about the general study design, restoration measures and environmental characteristics of the rivers is given in Muhar et al. (2015).

Sampling and laboratory analysis

Sampling was performed in summer 2012 or 2013, at the time of maximum biomass in each region (Table 1). We used a standardized sampling design across all 32 river sections, which allowed direct comparison of each restored river section with the nearby still degraded “control section”: At each sample section, we collected dominant benthic invertebrate taxa representing different functional feeding groups (FFG) to obtain an overview of the isotopic signatures of consumers at different trophic levels. Restored and degraded sections were sampled in the same field campaign. The invertebrates were taken from different habitats in the section using a shovel sampler (mesh size 500 μm) and a hand net. We sampled late-instar larvae (and larger individuals in case of hololimnic species), representative taxa for the following functional feeding groups:

- Grazers (e.g. *Baetis* sp., *Rhithrogena* sp.)
- Shredders (e.g. *Gammarus* sp., *Asellus* sp., *Nemoura* sp.)
- Collector-gatherers (e.g. Oligochaeta)
- Collector-filterers (e.g. *Hydropsyche* sp., Simuliidae gen. sp.)
- Predators (e.g. *Rhyacophila* sp., *Sialis* sp.)

Each sample consisted of several individuals of the same taxon to obtain sufficient material for stable isotope analysis, and we aimed to collect at least one representative sample per FFG (see Online Resource 1 for a list of taxa sampled at each section). In the field, individuals were presorted, counted and kept

separated by functional feeding groups to avoid contact between predators and prey. The samples were then placed in a cool box and subsequently transported to the laboratory.

In the laboratory, the benthic invertebrates were kept individually in filtered stream water for 12–24 h to allow for gut evacuation. Afterwards, the specimens were identified to the lowest level possible (most often genus). To prepare samples for stable isotope analysis, the animals were freeze-dried until all water was removed, and then ground with mortar and pestle. Four replicates of each taxon from each river section were loaded into tin capsules ($\sim 800 \mu\text{g}$). Content of carbon and nitrogen and stable isotopes of carbon and nitrogen were analysed with an elemental analyser (CE Instruments EA 1110 CHNS, Carlo Erba, Milan, Italy) connected via a ConflowIV interface to a Thermo Finnigan MAT 253 isotope ratio mass spectrometer (both Thermo Fischer, Bremen, Germany) at University of Duisburg-Essen’s Stable Isotope Facility (Instrumental Analytical Chemistry). Data from the stable isotope analysis are expressed as relative difference between ratios of samples and standards (VPDB for $\delta^{13}\text{C}$ and atmospheric nitrogen for $\delta^{15}\text{N}$) as described by the equation:

$$\delta^{13}\text{C}, \delta^{15}\text{N} = \left[\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right] \times 1000,$$

where $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$.

The analytical precision over all measurements (standard deviation from 791 in-house standards) was 0.08‰ for $\delta^{13}\text{C}$ and 0.19‰ for $\delta^{15}\text{N}$.

Data analysis

We displayed the isotopic composition of benthic invertebrate assemblages in $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ -isotope space (compare Online Resource 2). Quantitative community metrics, as introduced by Layman et al. (2007b), were calculated independently for each section. These metrics describe the trophic structure of communities and their trophic diversity by the position of species or groups in the $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ -isotope space. Here, we particularly focused on two of these metrics: (i) $\delta^{15}\text{N}$ range (NR), calculated as maximum $\delta^{15}\text{N}$ minus minimum $\delta^{15}\text{N}$; and (ii) $\delta^{13}\text{C}$ range (CR), calculated as maximum $\delta^{13}\text{C}$ minus minimum $\delta^{13}\text{C}$. Both NR and CR describe the distance between the two species or groups with the most enriched and most depleted $\delta^{15}\text{N}$

or $\delta^{13}\text{C}$ values, respectively (Layman et al., 2007b). We used NR as an indicator for the trophic length of the communities and CR as an indicator of the range of assimilated carbon sources. We calculated two sets of metrics. The first were calculated across all invertebrate species sampled at each river section, and are subsequently referred to as total range values (NR_{total} and CR_{total}). The second were calculated by classifying the invertebrate species into five feeding groups (predators, shredders, grazers, collector-filterers, collector-gatherers), and then using the mean values of each feeding type to calculate ranges across the FFGs. They are hereafter referred to as mean FFG range ($\text{NR}_{\text{meanFFG}}$ and $\text{CR}_{\text{meanFFG}}$). Feeding types were assigned with data from www.freshwaterecology.info (Schmidt-Kloiber & Hering, 2015).

Layman et al. (2007b) also calculated the area of a convex hull drawn around all species in $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ -isotope bi-plot to indicate the isotopic niche of the community. This approach was further extended by Jackson et al. (2011) by using standard ellipse area (SEA ; expressed in $\%_0^2$), which is to bivariate data as standard deviation is to univariate data (Batschelet 1981). The SEA contains *c.* 40% of the data and can therefore be used to measure the mean core community isotopic niche (Jackson et al., 2011). Here, the standard ellipse area corrected for small samples (SEA_C) was calculated as a measure of the isotopic niche, and was therefore used in the following analysis to quantify restoration effects. The small sample size correction leads to a slightly increased SEA_C in order to adjust bias towards underestimation (Jackson et al., 2011). SEA_C was further applied to test for isotopic niche overlap between restored and corresponding degraded sections, which gives a measure of dietary similarity/dissimilarity (Jackson et al., 2012). We finally pairwise tested the probability if SEA of the degraded section is smaller than SEA of the restored section based on the Bayesian standard ellipse area (SEA_B). We refer to Jackson et al. (2011) for a comprehensive description of SEA , SEA_C and SEA_B .

To quantify restoration effects across all 16 catchments, we first pairwise compared CR, NR, and SEA_C between restored and corresponding degraded sections (R vs. D) and between large and small restored sections (R1 vs. D1 and R2 vs. D2). This allowed first investigation of patterns in trophic structure related to river restoration. We further used an effect size by

calculating the response ratio according to Osenberg et al. (1997):

$$\Delta r = \ln \left(\frac{\bar{X}_R}{\bar{X}_D} \right)$$

with \bar{X}_R and \bar{X}_D being $\delta^{13}\text{C}$ range, $\delta^{15}\text{N}$ range or the standard ellipse area corrected for small samples of restored and degraded sections, respectively; values >0 are denoting a positive effect (e.g. an increase in $\delta^{13}\text{C}$ range), and values <0 are indicating a negative effect. One-sample *t* test was used to assess if effect sizes differed significantly from 0. The effect sizes based on CR, NR and SEA_C were compared. Both, an overall comparison of effect sizes (R1 and R2 pooled) and a comparison between large and small restoration projects (R1 vs. R2) were carried out to test if there was an overall positive effect of restoration, and if the effect of restoration depends on the restoration effort. Although the restored sections were selected to differ only in terms of restoration intensity (R1 vs. R2), there were differences in restoration measures employed independently from restoration extent: some projects aimed at river widening, while others applied measures mainly affecting the river channel itself (e.g. instream measures or flow restoration) (Table 1). Therefore, we re-grouped the sections based on the restoration measure employed (widening vs. others) and tested if effect sizes differ between restoration projects which mainly aimed at river widening (usually affecting both instream habitats and connectivity of water and land and thereby enhancing availability of autochthonous and allochthonous carbon resources) and projects which established other, less extensive measures affecting the river channel itself (instream measures, flow restoration, re-meandering, anastomosing). For selected restored and degraded sections, we worked out changes in trophic structure in more detail, based on niche overlaps and probabilities as inferred from SEA_C .

For the calculation of community-wide metrics (CR and NR), we used the package Stable Isotope Analysis (SIAR: Parnell et al., 2008, 2010) in R (R Development Core Team, 2007). The standard ellipse areas (SEA) were calculated using the SIBER package (Stable Isotope Bayesian Ellipses in R; Jackson et al., 2011) of SIAR (Parnell et al. 2008, 2010). Further statistical analyses, including Wilcoxon Matched Pair tests, *t* tests (one-sample *t* test against 0) and Mann–Whitney U tests, were run in Statistica 12 (StatSoft).

Results

General patterns of river restoration on CR and NR metrics of benthic invertebrates

The pairwise comparison of benthic invertebrate communities between restored (R) and degraded (D) sections (large and small projects pooled) across all 16 catchments showed minor differences in both $\delta^{15}\text{N}$ range and $\delta^{13}\text{C}$ range. The difference between restored and degraded sections was not significant, neither for the total range, nor mean FFG range used for the calculation of NR and CR (Wilcoxon Matched Pair test, $P > 0.06$, $n = 16$, Table 2). The median NR_{total} was equivalent to the distance between two trophic levels (3.68 ‰ in restored sections and 3.12 ‰ in degraded sections, $n = 16$, Table 2). The $\text{NR}_{\text{meanFFG}}$ was smaller (restored sections: 2.21‰; degraded sections: 2.28‰).

For the general comparison of effect sizes according to Osenberg et al. (1997), values above zero indicate enhanced $\delta^{15}\text{N}$ range or $\delta^{13}\text{C}$ range in restored sections. Restoration had an overall positive

effect on CR_{total} as the effect size ratio differed significantly from zero (t test, $P < 0.05$, Fig. 1), while $\text{CR}_{\text{meanFFG}}$ ratio was not significantly larger than zero (t test, $P > 0.15$). Effect sizes for neither $\text{NR}_{\text{meanFFG}}$ nor for NR_{total} were different from zero (t test, $P > 0.6$).

Effects of large and small restored sections on CR and NR metrics of benthic invertebrates

The pairwise comparison between the four groups of sections (large restored sections: R1; corresponding degraded sections: D1; small restored sections: R2; corresponding degraded sections: D2) showed minor differences for $\delta^{15}\text{N}$ ranges and $\text{CR}_{\text{meanFFG}}$ (Table 2). In contrast, CR_{total} differed significantly between R1 and D1 (Wilcoxon Matched Pair test, $P < 0.05$, $n = 8$), but not between R2 and D2 (Wilcoxon Matched Pair test, $P > 0.89$, $n = 8$).

Similarly, the pairwise calculated effect sizes, expressed as response ratios following Osenberg et al. (1997), revealed a positive effect of restoration on CR_{total} on large restored river sections (R1) (t test,

Table 2 Pairwise comparison of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ranges for R vs. D, R1 vs. D1 and R2 vs. D2 using Wilcoxon Matched Pair test. The analysis is based on total range values (i.e. all taxa are considered; not grouped into feeding types) and mean values (i.e. mean values of the feeding types were used). 25 and 75 % percentiles are given in parentheses. Significant differences ($P < 0.05$) are indicated by bold median values

	Total range values				FFG mean range values				<i>n</i>
	$\delta^{15}\text{N}$ range (‰)		$\delta^{13}\text{C}$ range (‰)		$\delta^{15}\text{N}$ range (‰)		$\delta^{13}\text{C}$ range (‰)		
	Median	<i>P</i>	Median	<i>P</i>	Median	<i>P</i>	Median	<i>P</i>	
R1 and R2 pooled									
R	3.68 (2.24–4.8)	0.80	6.29 (5.42–8.89)	0.06	2.21 (1.62–3.02)	0.96	4.70 (3.89–5.93)	0.18	16
D	3.12 (2.45–4.27)		5.64 (4.12–8.33)		2.28 (1.53–3.12)		3.80 (3.22–5.08)		16
Large projects									
R1	3.68 (2.32–4.17)	0.78	7.46 (5.19–10.29)	0.01	1.99 (1.64–2.65)	0.78	4.01 (3.65–4.76)	0.33	8
D1	2.94 (2.4–4.01)		6.39 (4.12–8.33)		1.80 (1.52–2.51)		3.43 (3.22–4.43)		8
Small projects									
R2	3.71 (2.14–5.32)	1.00	5.72 (5.42–6.87)	0.89	2.30 (1.62–3.36)	0.89	5.72 (4.52–6.20)	0.33	8
D2	3.14 (2.54–4.49)		5.20 (4.17–7.98)		2.89 (1.83–3.66)		4.35 (2.81–6.00)		8

$P < 0.05$, Fig. 2) but not for the small restored sections (R2) (t test, $P > 0.33$), suggesting that the range of assimilated sources is positively related to restoration extent. There were no significant effects of

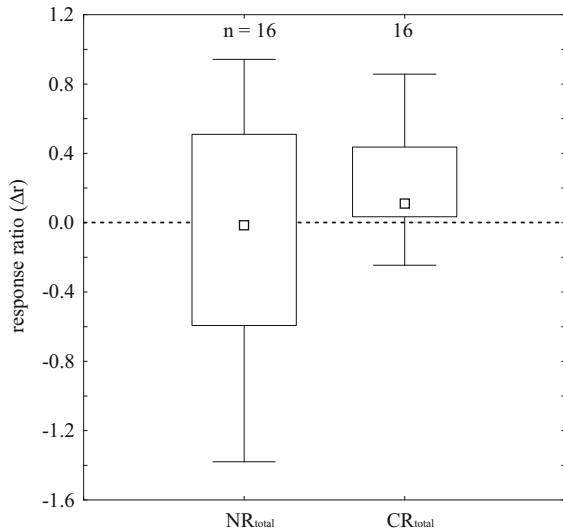


Fig. 1 General restoration effect (R1 and R2 pooled) calculated as response ratio after Osenberg et al. (1997) for total range values of NR and CR (Median; Box: 25–75%; Whisker: Min–Max). Effect sizes were pairwise calculated for each pair of restored and degraded sections

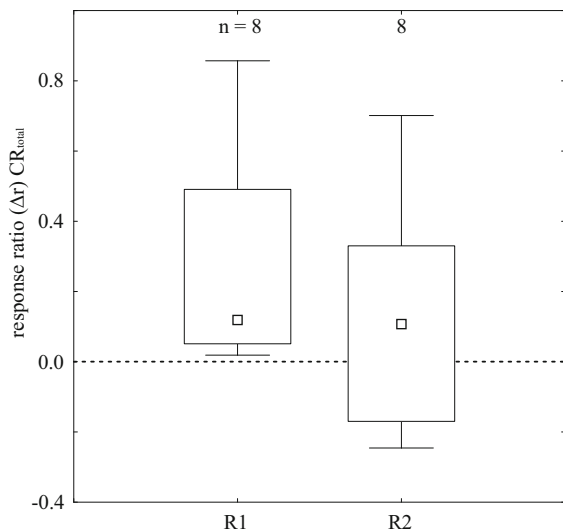


Fig. 2 Comparison of response ratios after Osenberg et al. (1997) based on CR_{total} in large (R1) and small (R2) restoration projects; effect sizes were pairwise calculated (Median; Box: 25–75%; Whisker: Min–Max)

restoration on $CR_{meanFFG}$, NR_{total} , and $NR_{meanFFG}$, neither for the large nor for the small restoration projects (t tests, $P > 0.17$). Moreover, the comparison of the effect sizes between more- and less extensive restored sections (i.e. response ratios of R1 compared to the response ratios of corresponding R2 sections) did not reveal a significant difference for any of the metric values (Wilcoxon Matched Pair test, $P > 0.2$).

Relationship of the metric values and the type of restoration measures

The alternative grouping of sections was based on the restoration measure employed (widening vs. others) and was therefore independent from restoration extent. The comparison of the effect sizes according to Osenberg et al. (1997) between restoration projects which mainly aimed at river widening ($n = 9$) and projects which applied other less extensive measures mainly affecting the river channel itself ($n = 7$) showed a positive effect for CR_{total} in sections where measures focused on river widening (Fig. 3). Here, the effect size for $\delta^{13}C$ range was significantly larger than zero (t test, $P < 0.05$). Effect sizes for $\delta^{15}N$ range were not significantly different from zero, neither using total range values nor mean values for the

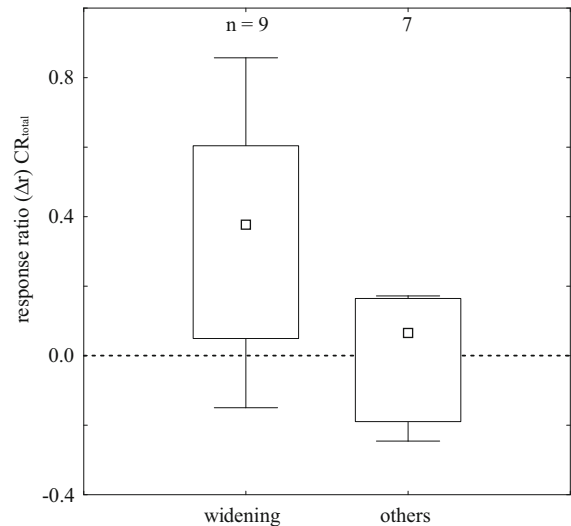


Fig. 3 Comparison of response ratios after Osenberg et al. (1997) based on CR_{total} in restored sections with widening and restored sections with other measures (e.g. improvement of instream habitats); effect sizes were pairwise calculated (Median; Box: 25–75%; Whisker: Min–Max)

calculation of NR. The response ratios were not different between measures which aimed at river widening and other measures (Mann–Whitney U test, $P > 0.2$).

Effects of river restoration on isotopic niche metric of benthic invertebrate communities

The entire statistical comparisons described above were simultaneously run based on standard ellipse area corrected for small samples (SEA_C). There was no support for a general restoration effect on SEA_C across all 16 catchments, i.e. neither pairwise comparison nor the effect sizes calculated according to Osenberg et al. (1997) revealed a significant difference; including the general comparison between R vs. D, the test if restoration extent has an effect (R1 vs. D1 and R2 vs. D2), and the re-grouping considering the type of restoration measure applied (widening vs. others). However, changes in SEA_C were apparent between some specific restored and degraded sections (Fig. 4; Table 3). In five of our eight study regions, SEA_C was bigger in R1 sections compared to the corresponding D1 sections, suggesting a larger isotopic niche following restoration. These sections are located in Finland, Sweden, Poland, Germany (mountains) and Austria (Fig. 4; Table 3). Similarly, the probabilities that D1 had smaller SEA_B than the corresponding R1 were 72% in Finland, 92% in Sweden, 95% in Poland, 86% in Germany (mountains) and 81% in Austria, respectively. The comparison between small restored sections with the degraded “control-sites” only showed bigger SEA_C in the R2 sections in Finland, Sweden, Germany (lowlands) and Austria. The associated probabilities that D2 had smaller SEA_B than the corresponding R2 sections were 71% in Finland, 72% in Sweden, 93% in Germany (lowlands) and 67% in Austria. In contrast, there were no larger SEA_C in R1 nor R2 sections compared to the corresponding D1/D2 in Denmark and in the Czech Republic. There were no distinct patterns in dietary similarity/dissimilarity by comparing the overlap between R2/D2 sections with those of the corresponding R1/D1 sections. In some cases, the overlap between R2/D2 was bigger compared to the corresponding R1/D1 sections (e.g. Czech Republic), suggesting that the diets of invertebrate communities were more similar in the less intensively restored sections (Fig. 4; Table 3). Anyhow, this effect did not

appear across all sections (e.g. in Denmark), and more often the difference between isotopic niches of restored and corresponding degraded section seemed to be independent from restoration extent (Fig. 4).

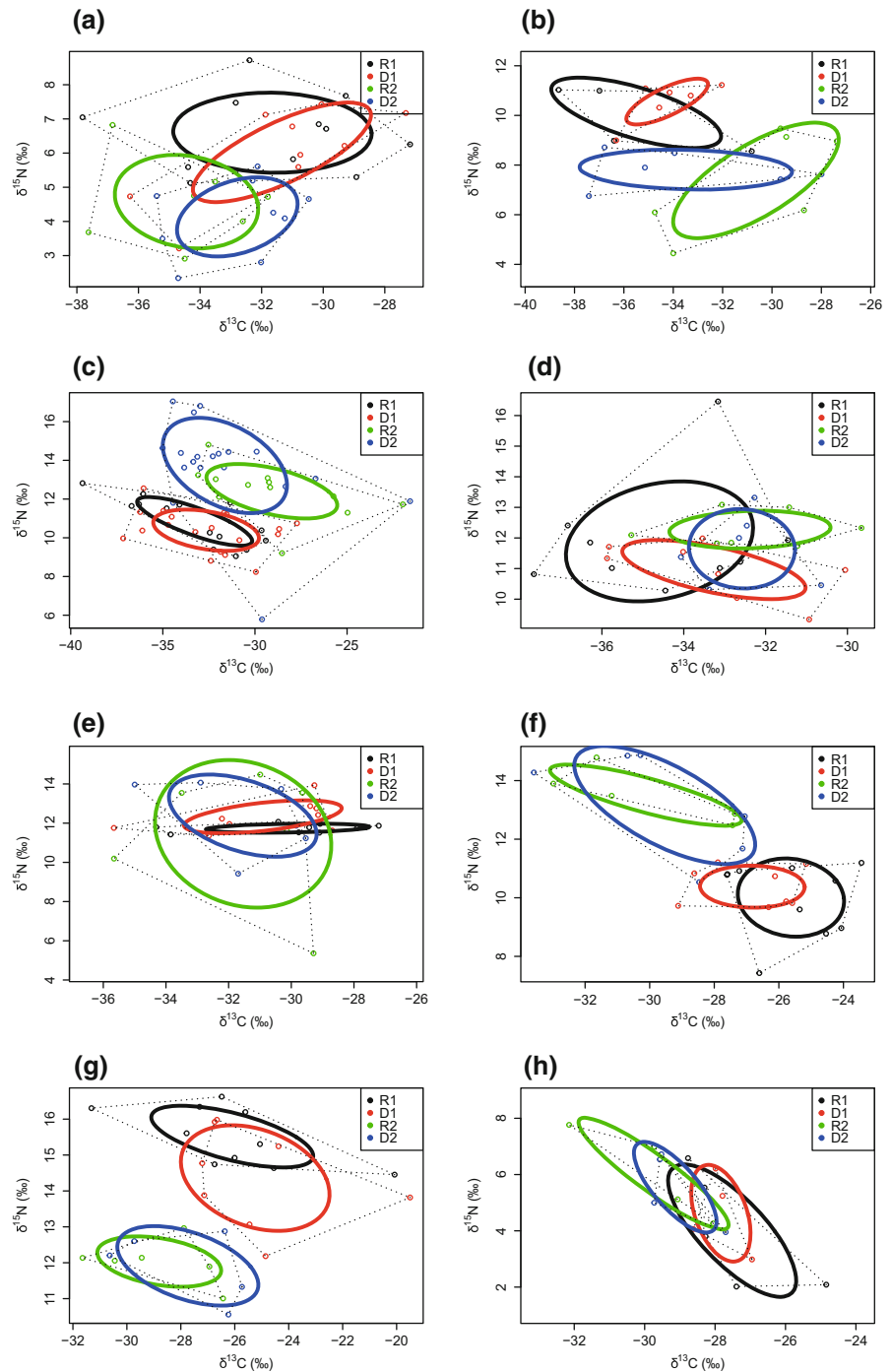
Discussion

Restoration of rivers is expected to increase the diversity of both habitat- and resource-based niches, which together have potential to affect the trophic structure of invertebrate communities. In line with this, we expected changes in the isotopic signatures of benthic invertebrate consumers indicative both of increased resource breadth (indicated by $\delta^{13}C$ range), and increases in trophic length (indicated by $\delta^{15}N$ range) following river restoration, which together favour larger isotopic niches of invertebrate assemblages (indicated by SEA_C). We further expected that the larger the restoration the bigger the impact. We found some support for an increase in resource breadth associated with restoration across all 16 restored sections, with these effects stronger for larger-scale restoration projects, and especially projects which aimed at river widening. In contrast, there was no support for a general increase in trophic length across all 16 catchments, though increases in NR ratios were apparent between some specific degraded and restored sections, suggesting such effects depend on local assemblage composition and/or environmental conditions. In line with this, changes in isotopic niche width of invertebrate assemblages were obvious between some specific restored and degraded sections. These findings suggest that river restoration results in modest changes in trophic structure. However, this is largely dependent on positive effects on the variety of resources assimilated by consumers (confirming hypothesis 1), rather than trophic length (rejecting hypothesis 2), with both effects further depending on restoration extent, the type of restoration measures employed and local environmental and community characteristics.

Restoration effects on trophic structure of benthic invertebrate communities

When using total community range values (CR_{total}), shifts in the $\delta^{13}C$ isotopic signatures of benthic consumers indicate an overall increase in the variety

Fig. 4 Mean stable isotope composition of the different benthic invertebrates from the eight study regions: **a** Finland, **b** Sweden, **c** Denmark, **d** Poland, **e** Germany lowland, **f** Germany mountain, **g** Czech Republic and **h** Austria. *Solid lines* enclose the standard ellipses area (SEAc), containing *c.* 40% of the data, showing the isotopic niche of representative benthic invertebrate communities at each site. *Dotted lines* are the convex hull areas of benthic invertebrate communities for each site, corresponding to the area encompassing all invertebrates in the $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ plot. R1 = large restoration, R2 = small restoration, and D1/ D2 = corresponding degraded control-sites. Axes are idealized for each region



of resources assimilated following restoration (widening of CR). We further found that the increase in CR_{total} was significantly greater in more extensively restored sections (i.e. comparing R1 and D1), relative to the less extensive restorations (between R2 and D2).

Similar results are apparent when comparing pairwise calculated effect sizes, expressed as response ratio after Osenberg et al. (1997), confirming the importance of restoration effort in dictating potential changes in the resource base and consumer responses.

Table 3 Standard ellipse area corrected for small samples (SEAc), probability that the SEA in the degraded section is smaller than the SEA in the restored section, overlap in SEAc between pairs of sites (restored and degraded), and overlap in % of respective area

	SEAc (% ²)	Probability that SEA _D < SEA _R	Overlap in SEAc between R and D (% ²)	Overlap in % of respective SEA
Large restored (R1)				
FI_R1	11.8	0.723	6.1	51.76
SE_R1	11.5	0.916	1.8	16.03
DK_R1	7.4	0.320	5.5	74.34
PL_R1	13.7	0.953	3.1	22.51
DL_R1	1.8	0.185	0.8	44.75
DM_R1	6.9	0.860	2.3	33.47
CZ_R1	6.3	0.173	3.6	56.12
AT_R1	8.9	0.810	3.9	43.44
Degraded (D1)				
FI_D1	8.8			69.22
SE_D1	3.2			57.55
DK_D1	8.9			61.47
PL_D1	5.4			57.59
DL_D1	5.7			14.39
DM_D1	3.7			62.66
CZ_D1	12.1			29.31
AT_D1	4.1			93.56
Small restored (R2)				
FI_R2	9.9	0.705	3.8	38.87
SE_R2	17.3	0.715	3.9	22.41
DK_R2	13.5	0.055	8.0	59.36
PL_R2	3.8	0.416	2.4	64.32
DL_R2	32.9	0.926	13.9	42.24
DM_R2	5.7	0.170	5.1	90.81
CZ_R2	4.7	0.309	4.0	84.36
AT_R2	5.3	0.666	3.1	57.45
Degraded (D2)				
FI_D2	6.7			57.05
SE_D2	10.8			35.93
DK_D2	23.7			33.80
PL_D2	5.3			46.01
DL_D2	13.9			99.99
DM_D2	13.2			38.78
CZ_D2	8.0			50.01
AT_D2	3.9			78.22

The increased CR_{total} ratio might reflect an increased availability of habitats suitable for autochthonous productivity, and/or a higher availability of allochthonous carbon resources either due to an intensified aquatic-terrestrial interaction or to the higher retentivity of restored sections. These possibilities are supported by results presented in Poppe et al. (2015)

who showed that measures were significantly impacting the hydromorphology of our sections, and by Göthe et al. (2015) who found positive effects of restoration on riparian vegetation adjacent to our reaches. Effects on hydromorphology in particular were greater in the more extensively restored sections (Poppe et al., 2015). We sampled representatives of

the same functional groups from all reaches, hence the change in the CR_{total} of invertebrates can partly be attributed to the dietary flexibility of many species, including those representing more specialized functional groups, allowing the food web as a whole to respond to the availability of novel resources (Mihuc, 1997; Göthe et al., 2009; Layer et al., 2013). Increases in the variety of available resources may also help support the more flexible taxa among the invertebrates, at times or year or during particular disturbances when their preferred resource may be scarce. Overall, a greater range of basal resources allows for heterogeneous energy flow pathways, which is an important factor for stabilizing food webs (Rooney et al., 2006; Layman et al., 2007b). We found that river widening is a particularly effective restoration measure for increasing the breadth of resources available to consumers. Whereas CR_{total} increased markedly following river widening, projects which applied other less extensive measures mainly affecting the river channel itself (instream measures, flow restoration, meandering, anastomosing) had no similar effects. River widening increases the surface area of instream habitats, and increases lateral connectivity between the river and its floodplain and can thereby enhance the availability of autochthonous and allochthonous carbon resources. Lepori et al. (2006) found no effect of increased detritus retentivity following restoration on the $\delta^{13}C$ signature of consumers, suggesting either that detritus was not limiting for consumers, or that the increase in retentivity was insufficient to alter carbon flows in the food web. The type of restoration studied by Lepori et al. (2006) aimed primarily at restoring instream habitats, and thus may be comparable to the predominantly “instream” measures assessed in our study. Overall, our results provide strong evidence that the magnitude of food web changes following restoration can indeed depend strongly not only on the scale, but also type of restoration.

In contrast with the relatively consistent changes in the range of resource assimilation following restoration at the European scale, there were no overall effects on trophic length. Thus, regardless of whether we compared NR_{total} directly between reaches, or analysed response ratios, we could not detect any shifts in the range of $\delta^{15}N$ signatures. Effects on NR also did not differ between restoration measures. Furthermore, when considered in light of trophic fractionation, we also have no evidence for the clear

addition of trophic levels following restoration. The value of trophic fractionation within food webs is often given with *c.* 3 ‰ (e.g. 3.4 ‰ in Minagawa and Wada, 1984; Post, 2002). We therefore assumed the $\delta^{15}N$ value of a consumer to be enriched by this value over that of its diet (Vander Zanden & Rasmussen, 2001). We observed the median $\delta^{15}N$ range of our invertebrate communities (NR_{total}) to span the space between two trophic levels (median restored sections: 3.68 ‰, median degraded sections: 3.12‰, $n = 16$). The results are in line with our expectations, as we sampled primary and secondary invertebrate consumers (e.g. grazers and predators) that should be separated by approximately one trophic level. Thus, based on the organisms we sampled, it appears that effects of the restoration on both the hydromorphology of the restored sections (increased habitat diversity and habitat size, e.g. depth, compare Poppe et al., 2015) and the variety of basal resources (indicated by CR) assimilated by consumers have not altered the trophic length of food chains. One possible reason for this is that, in choosing the most abundant invertebrate predators at each site, we were not sampling high enough in the food chain to detect real changes in food-chain length, associated with large predators such as fish that might enter the food web due to increased habitat size and diversity (Woodward and Hildrew, 2002, Woodward et al., 2005, 2010). Other factors which might have obscured a change in food-chain length include the possibilities that isotopic signatures of primary consumers might already be higher enriched (e.g. by scavenging on dead animal material), and reducing the relative difference between primary consumer and predator (i.e. minimum $\delta^{15}N$ and maximum $\delta^{15}N$) may not show the absolute higher position of predators in restored sections. Nevertheless, we did see increases in NR in some instances, suggesting that given the right community configurations and/or local environmental conditions, increases in trophic position lower in the food chain are possible following restoration.

We expected SEA to be larger in the restored sections compared to the degraded “control sections” following Layman et al. (2007a), who showed that the trophic niche width of the top predator *Lutjanus griseus* collapsed due to ecosystem fragmentation. He explains this effect with the reduction in diversity of prey taxa, which in turn is related to uniform energy flow pathways throughout the food web. Therefore, we

assumed the isotopic niche of benthic invertebrate assemblages to increase with restoration, due to the higher diversity of both habitat- and resource-based niches (Poppe et al., 2015). We found no support for a general increase of isotopic niche width following restoration across our 16 catchments, though increases in SEA_C ratios were apparent between some specific degraded and restored sections. For those sections, the increases in SEA_C were further supported by the probabilities that degraded sections had smaller SEA_B than the corresponding restored sections (calculated based on Bayesian statistics). It is well known that the isotopic niche of a community largely depends on CR and NR as it is based on the distribution of the mean core community in isotope space (Jackson et al., 2011) and thereby combines nitrogen and carbon ranges. This explains why an overall positive effect following restoration is absent: The missing general restoration effect on trophic length (indicated by NR) also negatively affects a potential increase in SEA_C . For example, SEA_C in R1 of the Czech Republic was smaller compared to the degraded “control section”, although the corresponding CR was bigger. Thus, it appears that the smaller SEA_C results from a corresponding smaller NR. Overall, our results indicate that the primary effect of restoration on food-web structure lower down in the benthic food web is an increase in the variety of resources assimilated, rather than an extension of food-chain length.

Type of data used

The results of our analysis were partly determined by the type of data used: Significant differences in $\delta^{13}C$ range, e.g. between long restored sections compared to the corresponding degraded sections (R1 and D1), were only obtained with values for the total range of community signatures. Mean values of the organisms representing individual feeding types possibly reduced the corresponding $\delta^{15}N$ and $\delta^{13}C$ range, minimizing the influence of species occurring at either end of the isotopic gradients. This indicates that the increased variety of resources assimilated was primarily driven by a few taxa extending their range of resource intake. In fact, the outliers might reflect a higher diversity of the resource base, as stated in our second hypothesis. Consequently, outliers might be a result of restoration as the corresponding invertebrates assimilated sources that were only present at the restored sections.

Recommendations for river management

In this comparative analysis across multiple, heterogeneous restoration projects, we used a representative set of samples to test for restoration effects on trophic structure of benthic invertebrates communities, using a selected set of isotope-based community-wide metrics. To cover a large number of restored sites, we aimed to be pragmatic, straightforward, cost- and time-effective, i.e. we used a representative set of samples, considered time in the lab, and applicability of metrics. This approach could easily be adapted for more expanded sampling, particularly in more regional assessments focused more strongly on particular restoration projects. For instance, future sampling for stable isotope analysis could be coupled to the multihabitat sampling design (Haase et al., 2004). In this case, data about abundance of different taxa would be considered in later assessment of restoration effects, to account for different relevance of basal resources. If a standardized sampling design cannot be implemented or data from different sampling campaigns should be compared, we recommend the Bayesian approach to these metrics introduced by Jackson et al. (2011), and see McCarthy (2007) for an introduction to Bayesian statistics. Overall, this study demonstrates that these isotope-based metrics are useful to identify patterns in trophic structure related to river restoration and that the integration of functional metrics in river management practice can be useful to determine the outcomes of restoration for key ecosystem processes such as trophic transfers of energy and nutrients.

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