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**Stable isotope analysis indicates positive effects of river restoration  
on aquatic-terrestrial linkages**

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## 1 **Abstract**

2 Hydromorphological river restoration can significantly alter habitat configuration and modify  
3 invertebrate assemblages of rivers and floodplains. However, the consequences of these changes for  
4 ecosystem functioning and aquatic-terrestrial interactions are not known. As a restored shoreline has a  
5 more heterogeneous structure compared to a straightened river, restoration is likely to impact aquatic-  
6 terrestrial linkages in multiple ways, which might be captured based on biomarker indicators to  
7 characterize changes in food web functioning. We conducted a large scale comparative study targeting  
8 eleven river restoration projects in central and northern Europe to assess effects of river restoration on  
9 trophic patterns across the aquatic-terrestrial interface. We investigated the isotopic composition ( $\delta^{13}\text{C}$ ,  
10  $\delta^{15}\text{N}$ ) of prey and of invertebrate consumers stratifying between the aquatic, riparian and terrestrial  
11 zones. The isotopic distance of riparian arthropods to instream macroinvertebrates and terrestrial  
12 arthropods was used as a measure of trophic linkage, and its variation with riparian habitat  
13 composition was quantified. Restoration enhanced aquatic-terrestrial linkages, indicated especially by  
14 differentiation in the  $\delta^{15}\text{N}$  isotopic signatures between aquatic, riparian and terrestrial consumers,  
15 rather than by  $\delta^{13}\text{C}$  signatures. The  $\delta^{15}\text{N}$  isotopic signatures of riparian arthropods revealed a higher  
16 relative trophic position in restored sections ( $\delta^{15}\text{N}_{\text{Restored}}$ : 8.64‰, n = 11) as compared to non-restored  
17 sections ( $\delta^{15}\text{N}_{\text{Degraded}}$ : 8.05‰, n = 11), lending support to the conjecture that restoration increased the  
18 proportion of more highly enriched aquatic prey ( $\delta^{15}\text{N}_{\text{Restored}}$ : 10.01‰;  $\delta^{15}\text{N}_{\text{Degraded}}$ : 10.38‰) while  
19 simultaneously reducing the share of lower enriched terrestrial prey ( $\delta^{15}\text{N}_{\text{Restored}}$ : 4.88‰;  $\delta^{15}\text{N}_{\text{Degraded}}$ :  
20 5.53‰). Riparian habitat diversity and the share of exposed sand and gravel bars were positively  
21 related to the strength of aquatic-terrestrial linkages ( $R^2 = 0.28$  and  $R^2 = 0.31$ , respectively), pointing to  
22 the importance of habitat diversification in the riparian zone in promoting trophic linkages between  
23 river and floodplain. These findings expand our understanding of the multifaceted outcomes of  
24 hydromorphological restoration, beyond biodiversity in the aquatic environment. It highlights the need  
25 to expand our current set of indicators in order to mechanistic understand restoration effects on  
26 ecological networks spanning across boundaries. This knowledge is highly relevant for the large  
27 restoration efforts driven by legislative frameworks such as the Water Framework Directive in Europe.

28 **Keywords:** *restoration assessment, functional indicators, habitat diversity, food webs, riparian buffer,*  
29 *macroinvertebrates*

## 30 **1. Introduction**

31 The hydromorphology of most European rivers has been degraded by straightening, damming and  
32 removal of riparian vegetation (EEA, 2018). Measures to improve river and floodplain habitat  
33 diversity (hereafter referred to as “hydromorphological restoration”) are increasingly undertaken to  
34 enhance aquatic and riparian biodiversity and ecosystem functioning (e.g., Jähnig et al. 2010,  
35 Januschke et al. 2014, Poppe et al. 2016). The assessment of restoration success or failure has mainly  
36 focused on hydromorphological features and on the composition of different riverine communities  
37 (e.g., Kail et al. 2015, Hasselquist et al. 2018), including fish (e.g., Schmutz et al. 2015, Thomas et al.  
38 2015, Göthe et al. 2019) and macroinvertebrates (e.g., Sundermann et al. 2011, Pilotto et al. 2018), as  
39 well as on riparian communities (Göthe et al 2016), while other aspects such as hydro-geochemical  
40 processes measured using stable isotopes (Schulte et al. 2011, Mader et al. 2018) and ecosystem  
41 functioning has been rarely considered (Kupilas et al. 2017, Frainer et al 2018). In Europe, the focus  
42 on instream structural measures is grounded in the Water Framework Directive (WFD), where the  
43 deviation of these communities from a reference condition is the center of ecological status  
44 assessments (Hering et al. 2010, Friberg 2014). Nevertheless, several studies have revealed that  
45 riparian biota is positively affected by restoration, e.g., through increasing species richness and  
46 abundance of riparian carabid beetles (Jähnig et al. 2009, Januschke et al. 2014, Januschke &  
47 Verdonschot 2016). A major driver of change is the provision of a greater diversity of riparian  
48 habitats, such as unvegetated sand and gravel bars, along the river channel.

49 The use of assemblage composition as an indicator of restoration success, however, has some  
50 important limitations, since it does not necessarily reveal pathways between restoration measures and  
51 biotic effects, and is only indirectly related to ecosystem functioning. Direct measurements of  
52 ecosystem functioning may provide additional and more direct insights into cause-effect-chains  
53 between restoration and its effects on an ecosystem level, thus allowing for more targeted restoration  
54 planning (Frainer et al. 2018). Furthermore, functional aspects may be more sensitive than classical,

55 community-based parameters. Kupilas et al. (2016) observed changes in the trophic structure of  
56 macroinvertebrate communities associated with river restoration, while species richness and diversity  
57 of the same communities remained unaffected (Verdonschot et al. 2016). Contrasting responses of  
58 functional measurements and community composition have also been observed in the context of  
59 environmental impact assessments (e.g., Friberg et al. 2009, McKie & Malmqvist 2009, Niyogi et al.  
60 2013). While functional aspects may complement the monitoring of river restoration measures, and  
61 lead to a better mechanistic understanding of restoration effects (Young et al. 2008, 2009, Palmer &  
62 Febria 2012, Woodward et al. 2012, Friberg 2014), they are still rarely implemented (Palmer et al.  
63 2014).

64 The assessment of the success of restoration measures leading to changes in both instream and riparian  
65 habitats is particularly challenging, requiring consideration of changes in food web configuration and  
66 ecosystem functioning in a broader ecological network crossing habitat boundaries (Truchy et al.  
67 2015, Bruder et al. 2019). Changes in food web architecture (e.g., connectance, trophic complexity,  
68 trophic position, trophic niche of consumer groups) can be used to track stressor impacts (Bruder et al.  
69 2019), e.g. the intensity of droughts (Ledger et al. 2013), and ecosystem fragmentation (Layman et al.  
70 2007a). However, the interplay between degradation, restoration and food web properties remains  
71 poorly understood.

72 An important component of food webs in riverine landscapes that is likely to be affected by both  
73 instream and riparian restoration is the flow of materials, carbon and nutrients from land to water and  
74 vice versa. Previous studies have documented increased retention of terrestrial leaf litter in rivers  
75 following habitat restoration (Lepori et al. 2005, Flores et al. 2011), and an increased usage and uptake  
76 of terrestrially derived C into aquatic food webs (Kupilas et al. 2016, Frainer et al. 2018). However,  
77 less research attention has been given to the effects of riverine restoration on terrestrial food webs and  
78 the flow of energy and nutrients from water to land. In particular, rivers can be an important source of  
79 energy and nutrients for riparian biota such as predaceous ground beetles and spiders, through  
80 consumption of the emerging adults of aquatic insects and drifting aquatic organisms accumulating  
81 along the shoreline (Hering & Plachter 1997, Collier et al. 2002, Paetzold et al. 2005). Since the flux

82 of biomass between the river and its riparian zone is determined by habitat structure (Baxter et al.  
83 2005, Paetzold et al. 2005, Burdon & Harding 2008, Carlson et al. 2016), hydromorphological  
84 restoration may promote food web connectivity. Specifically, a restored heterogeneous shoreline  
85 structure, with a shallow river profile and without bank fixations, may enable riparian arthropods to  
86 stay close to the river channel and to more effectively prey on both the adult stages of aquatic  
87 organisms, and surface drifting aquatic organisms washed ashore.

88 To assess effects of hydromorphological restoration on trophic connectivity between water and land,  
89 we conducted a large-scale comparative study targeting eleven river restoration projects in central and  
90 northern Europe. We analyzed stable isotopes ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) for invertebrate taxa collected in three  
91 spatially-explicit zones: in the stream channel (instream macroinvertebrates), within a one meter strip  
92 along the shoreline (hereafter referred to as “riparian arthropods”), and in less dynamic, higher  
93 elevated habitats adjacent to the riparian zone (hereafter referred to as “terrestrial arthropods”). Our  
94 overall aim was to use stable isotopes as indicators of connectance between rivers and their riparian  
95 zones and to elucidate how restoration interventions influenced this link.

96 We used stable isotope composition of carbon and nitrogen ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ) and trophic fractionation, i.e.  
97 the enrichment or depletion in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  between diet and consumer, to elucidate food web  
98 responses to restoration. The trophic fractionation of  $\delta^{13}\text{C}$  is low, changing only 0-1‰ from source to  
99 consumer and the fractionation of  $\delta^{15}\text{N}$  is usually about 3‰ (Post 2002, Brauns et al. 2018). Based on  
100 this isotopic shift between prey and predator,  $\delta^{15}\text{N}$  is generally used to characterize the trophic position  
101 of a consumer in a food web and  $\delta^{13}\text{C}$  can be used to identify the ultimate carbon sources for an  
102 organism (Post 2002). Rather than an exhaustive quantification of different potential basal resources in  
103 the aquatic and terrestrial habitats, our analyses focussed on detecting shifts in the position of the  
104 organisms in isotope space (i.e., a  $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$  biplot where species are plotted based on their stable  
105 isotope signatures; Layman et al. 2007b). A special focus was on the position of riparian arthropods in  
106 isotope space following restoration to explore their potential as an indicator of restoration effects. We  
107 calculated the relative position of riparian arthropods to instream macroinvertebrates and to terrestrial  
108 arthropods in isotope space as a measure of trophic linkage. Our hypotheses were: (i) Isotopic

109 signatures of riparian arthropods in restored reaches show evidence for an increased trophic linkage  
110 between river and land; i.e., increased distance to terrestrial arthropods reflecting a smaller share of  
111 terrestrial prey, and higher similarity to instream macroinvertebrates reflecting an increased use of  
112 aquatic resources. (ii) Riparian habitat diversity and the presence of unvegetated side bars are  
113 positively related to the strength of aquatic-terrestrial linkages as reflected by isotopic distance.

## 114 **2. Methods**

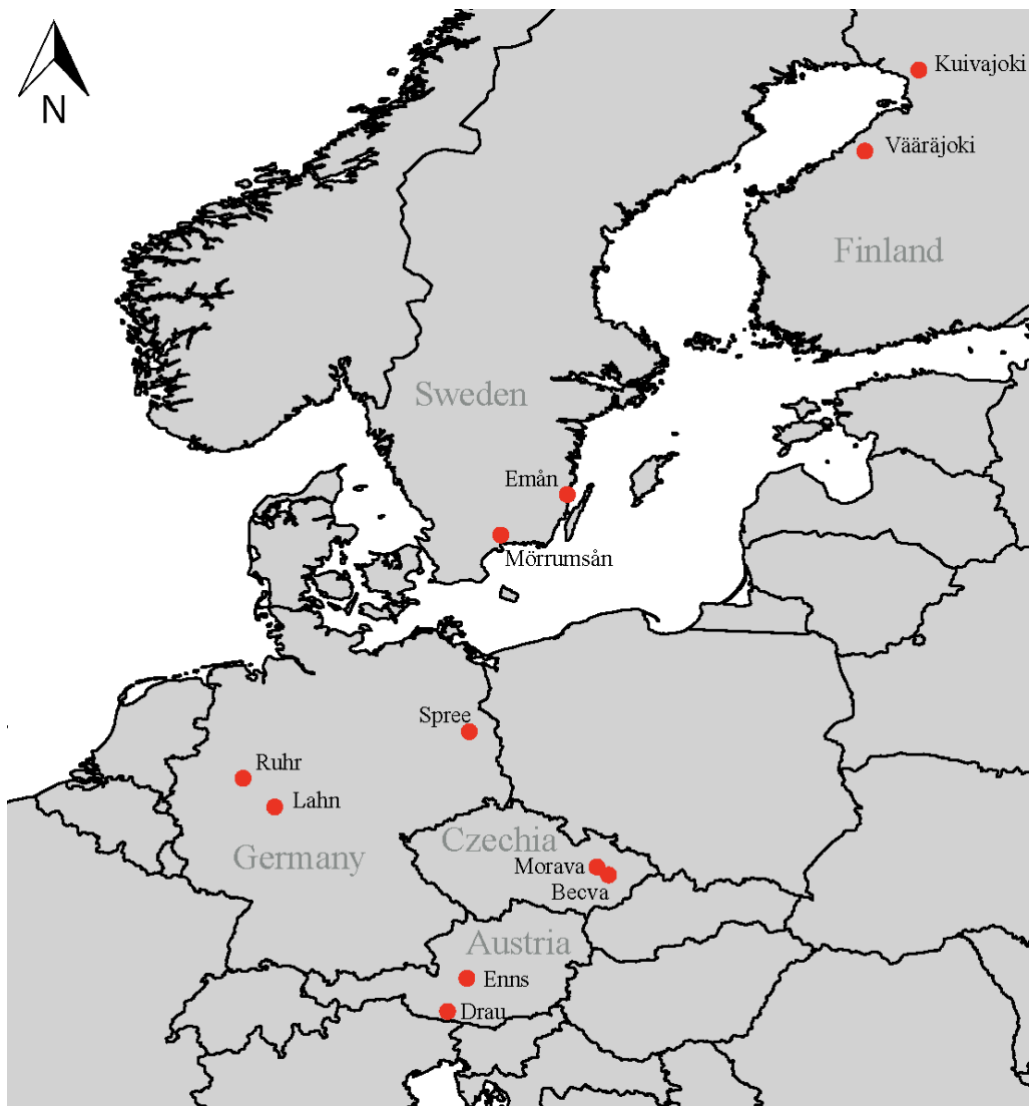
### 115 *2.1 Study sites*

116 We investigated the isotopic composition of consumers in aquatic, riparian and terrestrial habitats  
117 associated with eleven restoration projects conducted across central and northern Europe (Fig. 1, Table  
118 1, Muhar et al. 2016), encompassing both medium-sized lowland rivers and medium-sized mountain  
119 rivers (mean discharge: 10 to 60 m<sup>3</sup>/s). Along each river, we selected a representative sampling reach  
120 at the downstream end of a restored river section (R) and compared it to a non-restored,  
121 hydromorphological degraded “control section” (D) located upstream of the restored section. Both  
122 sections within each river had previously been similar to one another, prior to application of the  
123 restoration measures (Hering et al. 2015, Muhar et al. 2016). As the distance between restored and  
124 degraded river sections was small compared to overall river size (2.8 km, n = 11), background shifts in  
125 isotopic composition between the sections (e.g. arising from differences in geology or vegetation)  
126 unrelated to the restoration are unlikely. Detailed information about the restoration measures and  
127 environmental characteristics of the rivers is given by Muhar et al. (2016).

### 128 *2.2 Sample collection, preparation and laboratory analysis*

129 Study reaches were sampled in summer 2012 and 2013 (Table 1). At each sampling reach,  
130 invertebrates were collected in three spatially-explicit zones to obtain an overview of the isotopic  
131 signatures across the aquatic-terrestrial interface (Fig. 2): instream macroinvertebrates, riparian  
132 arthropods and terrestrial arthropods. Restored and degraded sections were always sampled in the  
133 same field campaign. From the instream habitats, we collected individuals of the dominant instream  
134 macroinvertebrate taxa representing different functional feeding groups (FFG; grazer, shredder,

135 collector, predator; Appendix 1), to infer isotopic signals of potential aquatic food sources of riparian  
136 arthropods. For insect taxa we targeted late-instar larvae, reflecting the isotopic composition of an  
137 aquatic insect at the time close to emergence, and thus most closely represent the composition of the  
138 adult stage prone to predation by riparian arthropods (Paetzold et al. 2005). For hololimnic species  
139 larger individuals were targeted. The sampling of instream macroinvertebrates is described in more  
140 detail by Kupilas et al. (2016). Multiple individuals of each species were pooled to get sufficient  
141 biomass for a sample, and where possible, enough for technical replication.



142

143 **Fig. 1:** Location of the restored sections.

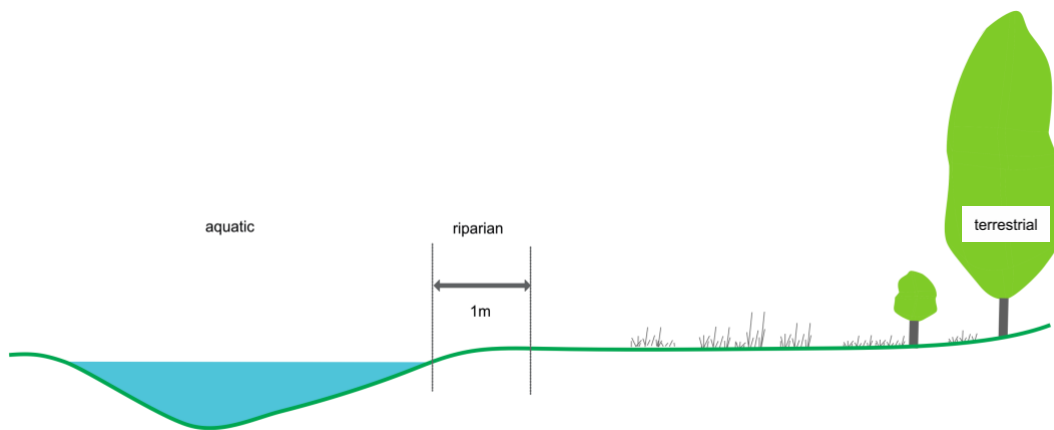


144 **Table 1:** Overview of restored study reaches based on data by Muhar et al. (2016).

145

Site name	FI_R1	SE_R1	DM_R1	CZ_R1	AT_R1	FI_R2	SE_R2	DL_R2	DM_R2	CZ_R2	AT_R2
Country	Finland	Sweden	Germany	Czech Republic	Austria	Finland	Sweden	Germany	Germany	Czech Republic	Austria
River name	Vääräjoki	Emån	Ruhr	Becva	Drau	Kuivajoki	Mörrumsån	Spree	Lahn	Morava	Enns
River type	Gravel-bed	Gravel-bed	Gravel-bed	Gravel-bed	Gravel-bed	Gravel-bed	Gravel-bed	Sand-bed	Gravel-bed	Gravel-bed	Gravel-bed
Latitude (N)	64.054433	57.149095	51.44093	49.4968975	46.75454	65.6860429	56.336005	52.377747	50.86588	49.6570728	47.42112
Longitude (E )	24.2206639	16.441897	7.96223	17.5211533	13.309393	25.6349874	14.700237	13.878897	8.79088	17.2179975	13.816094
Altitude (m a.s.l.)	60	10	153	232	570	74	87	35	191	218	692
Catchment geology	organic	siliceous	siliceous	siliceous	siliceous	organic	siliceous	siliceous	siliceous	siliceous	calcareous/ siliceous
Mean discharge (m <sup>3</sup> /s)	9.9	29.3	15.2	16.6	62.6	12.8	12	14	12	17.7	21.5
Stream order	4	6	3	7	7	4	6	6	3	7	5
Ecoregion	Fenno-scandian shield	Fenno-scandian shield	Central Highlands	Hungarian lowlands	Alps	Fenno-scandian shield	Fenno-scandian shield	Central plains	Central Highlands	Hungarian lowlands	Alps
Restoration Length (km)	1.4	0.9	0.75	0.45	1.9	0.4	3.3	0.95	0.24	0.22	0.6
Restoration date	1997-2006	2006-2011	2008	1997	2002-2003	2002-2006	2003-2012	2005	2000	1997	2003-2004
Main restoration action	instream measures	Hydro RivCon (dam removal, naturalise flow regime, fishway construction, salmonid spawning gravel and boulder additions)	riverbed widening	riverbed widening	riverbed widening; (partial removal of bank fixation; initiation of secondary channel; reconnection of one sidearm)	instream measures	Hydro RivCon (increased flow, fishway construction and salmonid spawning gravel additions)	remeandering	riverbed widening	riverbed widening	riverbed widening (partial removal of bank fixation; initiation of one secondary channel)
Time of sampling	August 2012	August 2013	June 2013	September 2012	July 2013	August 2012	August 2013	July 2013	July 2013	September 2012	July 2013

146 The non-aquatic consumers (*a priori* defined as “riparian” and “terrestrial”) either comprised  
147 predaceous ground beetles or spiders and were sampled in two separate zones along the study reaches.  
148 The first “riparian” zone comprised a one meter strip along the shoreline, representing a zone subject  
149 to highly variable hydrological dynamics, and consequently colonized by invertebrates well-adapted to  
150 those conditions (e.g., small and flat ground beetles), while the second “terrestrial” zone comprised  
151 embankments >1m from the shoreline characterized by less variable hydrological dynamics, and both  
152 higher elevated and more densely vegetated than the riparian zone, and often colonized by larger taxa  
153 with less specialized habitat preferences (compare Sadler et al. 2004, van Looy et al. 2005, Kedzior et  
154 al. 2016). Riparian and terrestrial arthropods were both collected at randomly chosen locations of the  
155 study reach using exhausters and forceps. Each sample of riparian and terrestrial arthropods consisted  
156 of several individuals to constitute a bulk sample (Appendix 2).



157

158 **Fig. 2:** Schematic overview of aquatic, riparian, and terrestrial habitats sampled at each study reach.

159

160 Instream macroinvertebrates, riparian arthropods, and terrestrial arthropods were presorted in the field,  
161 counted and kept separate from one another. The samples were transported to the laboratory in a cool  
162 box. In the laboratory, specimens were kept individually for 12 to 24 hours to allow for gut evacuation  
163 (instream macroinvertebrates were hold in filtered and aerated stream water). Afterwards, the  
164 specimens were identified to the lowest level possible (mostly species or genus; Appendix 1 and 2).  
165 To prepare samples for stable isotope analysis, we freeze-dried the samples to remove water, and then

166 ground them with mortar and pestle to obtain a homogenized composite sample- Multiple individuals  
167 were pooled to get sufficient biomass for a sample, and where possible, enough for technical  
168 replication. Depending on the amount of sample material, up to four replicates of each bulk sample  
169 from each river section were loaded into tin capsules (~800 µg).

170 Content of carbon and nitrogen and stable isotopes of carbon and nitrogen were analysed with an  
171 elemental analyser (CE Instruments EA 1110 CHNS, Carlo Erba, Milan, Italy) connected via a  
172 ConflowIV interface to a Thermo Finnigan MAT 253 isotope ratio mass spectrometer (both Thermo  
173 Fischer, Bremen, Germany) at University of Duisburg-Essen's Stable Isotope Facility (Instrumental  
174 Analytical Chemistry). Data from the stable isotope analysis are expressed as relative difference  
175 between ratios of samples and standards (VPDB for  $\delta^{13}\text{C}$  and atmospheric nitrogen for  $\delta^{15}\text{N}$ ) as  
176 described by the equation:

177  $\delta^{13}\text{C}, \delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$ , where  $R = {}^{13}\text{C}/{}^{12}\text{C}$  or  ${}^{15}\text{N}/{}^{14}\text{N}$ .

178 The analytical precision over all measurements (standard deviation from 791 in-house standards) was  
179 0.08‰ for  $\delta^{13}\text{C}$  and 0.19‰ for  $\delta^{15}\text{N}$ .

### 180 *2.3 Data analysis*

181 We displayed the isotopic composition of each study reach in  $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ -isotope space (Appendix 3).  
182 For instream macroinvertebrate communities, we computed the area of a convex hull drawn around all  
183 species in isotope space to indicate the isotopic niches occupied by the communities. For further  
184 analyses, we calculated mean isotopic values of each community (separately for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ; for  
185 number of taxa used *cf.* Appendix 1 and 3), reflecting the average isotopic signature of each river; the  
186 arithmetic mean of a community is similar to its centroid in isotope space. We used multiple Wilcoxon  
187 Matched pair tests (Fowler et al. 1998) between the three organism groups (instream  
188 macroinvertebrates, riparian and terrestrial arthropods) to explore the trophic organization across the  
189 aquatic-terrestrial interface for the total population of restored and degraded sections (n=22).

190 To characterize shifts in the position of riparian organisms in isotope space following restoration, we  
191 calculated two metrics based on the relative position of groups to each other in the  $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ -isotope

192 space: the distance of riparian arthropods to terrestrial arthropods, calculated as riparian arthropods  
193 minus terrestrial arthropods; and the distance of riparian arthropods to instream macroinvertebrates,  
194 calculated as riparian arthropods minus instream macroinvertebrates. This was done for each  
195 investigated section and separately for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ . Both metrics provide a measure of the trophic  
196 linkage between riparian arthropods and the terrestrial and aquatic system considering trophic  
197 fractionation. To quantify the restoration effect, we then compared the isotopic distances of riparian  
198 arthropods to terrestrial arthropods and to instream macroinvertebrates between restored and  
199 corresponding degraded reaches using Wilcoxon Matched pair tests.

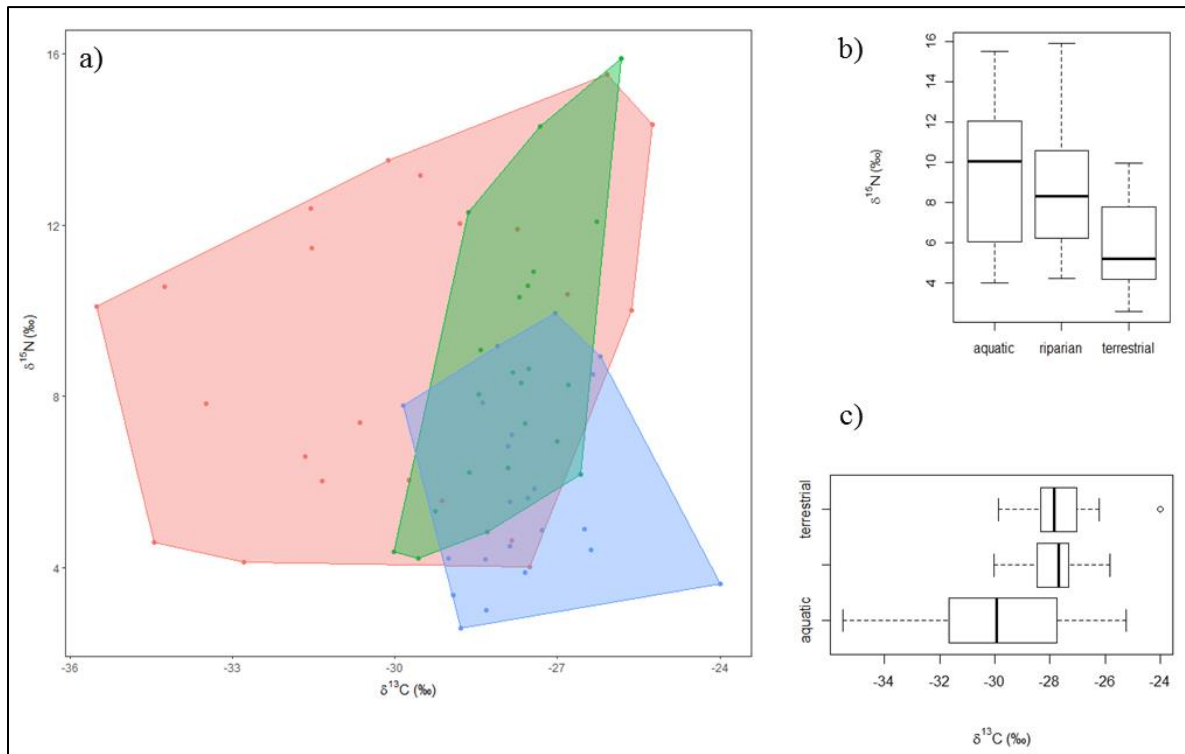
200 To explore the relationship between riparian habitat composition and the strength of trophic linkages,  
201 we extracted data on riparian habitats adjacent to our study reaches compiled by Poppe et al. (2016).  
202 Briefly, for each study reach riparian habitats were recorded along ten equidistant transects vertical to  
203 flow directions covering the entire floodplain area. The length of each riparian habitat feature was  
204 measured and their extent as a proportion of total habitat area was computed. We calculated riparian  
205 habitat diversity (Shannon-Wiener Index) based on the habitat composition at each study reach and  
206 correlated the resulting habitat diversity to the trophic linkage metrics (i.e. isotopic distances). In  
207 addition, the proportion of exposed side bars as key habitats for ground-dwelling riparian arthropods  
208 was correlated to the trophic linkage metrics. All statistical analyses were performed in R (Version  
209 3.2.2, <http://www.r-project.org/>).

### 210 **3. Results**

#### 211 *3.1 Isotopic signatures across the aquatic-terrestrial interface*

212 Isotopic composition of instream macroinvertebrates and terrestrial arthropods revealed a clear  
213 differentiation between the aquatic and fully terrestrial taxa (Wilcoxon Matched pair test,  $\delta^{15}\text{N}$ :  $P <$   
214  $0.001$ ,  $\delta^{13}\text{C}$ :  $P < 0.001$ ,  $n=22$ , Fig. 3, Appendix 3), with riparian arthropods taking an intermediate  
215 position (Fig. 3). Instream macroinvertebrates were significantly more enriched in  $\delta^{15}\text{N}$  compared to  
216 the terrestrial arthropods, as indicated by the median pairwise isotopic distance between the two  
217 groups ( $+3.7\text{‰}$ ;  $n = 22$ ; equivalent to one trophic level). Riparian arthropods were generally more

218 similar in their  $\delta^{15}\text{N}$  isotopic signatures to instream macroinvertebrates then to terrestrial arthropods  
 219 (Wilcoxon Matched pair test,  $\delta^{15}\text{N}$ :  $P < 0.001$ ,  $n=22$ , Fig. 3 b), indicating a larger proportion of more  
 220 highly  $\delta^{15}\text{N}$  enriched aquatic prey in their diet. Considering trophic fractionation, the  $\delta^{15}\text{N}$  isotopic  
 221 signatures of riparian arthropods reflected a mixed diet with a significant proportion of aquatic insects  
 222 and hence, an intermediate position in isotope space.



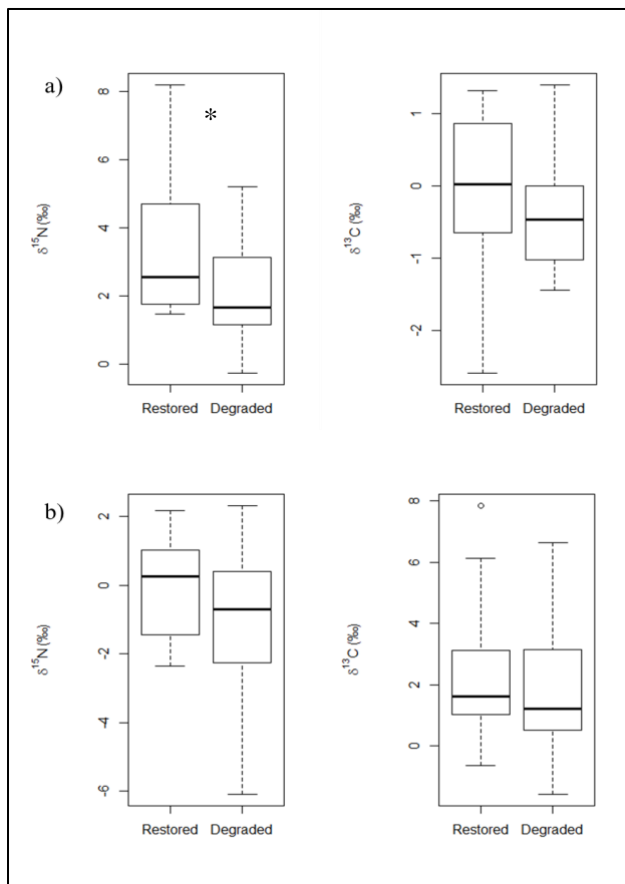
223  
 224 **Fig. 3:** Trophic organization across the aquatic-terrestrial interface as indicated by mean stable isotope composition ( $\delta^{15}\text{N}$ ,  
 225  $\delta^{13}\text{C}$ ) of invertebrates collected in aquatic, riparian and terrestrial habitats across all study reaches ( $n=22$ ): a) general  
 226 distribution of instream macroinvertebrates (red), riparian arthropods (green) and terrestrial arthropods (blue) in isotope  
 227 space, and pairwise comparison of b)  $\delta^{15}\text{N}$  and c)  $\delta^{13}\text{C}$  isotopic signatures between instream macroinvertebrates, riparian and  
 228 terrestrial arthropods (Median; Box: 25–75%; Whisker: Min–Max excluding outliers,  $\circ$  = Outliers).

229  
 230 Differences in the  $\delta^{13}\text{C}$  signatures were less clear than for  $\delta^{15}\text{N}$ , and indicating substantial overlap in  
 231 resources across the aquatic-terrestrial interface for the majority of study reaches (compare Fig. 3 c,  
 232 Appendix 3). Carbon isotope values for instream macroinvertebrates ranged widely, as expected if  
 233 aquatic invertebrates rely on both aquatic and terrestrial C sources. The  $\delta^{13}\text{C}$  isotopic signatures of  
 234 riparian arthropods were generally more similar to those of terrestrial arthropods than to those of  
 235 instream macroinvertebrates (Wilcoxon Matched pair test,  $\delta^{13}\text{C}$ :  $P < 0.001$ ,  $n=22$ , Fig. 3 c).  
 236 Considering trophic fractionation of  $\delta^{13}\text{C}$ , the median of pairwise calculated distances between riparian

237 arthropods and instream macroinvertebrates across all study reaches was still within the range of one  
238 trophic level (+1.5‰, n = 22). Overall, there were large differences between study reaches: riparian  
239 arthropods were more closely linked to the aquatic habitat in Austria, Germany (mountain) and partly  
240 in the Czech Republic and Finland. The majority of study reaches in Sweden, Finland and Germany  
241 (lowland) displayed more pronounced differences between riparian arthropods and instream  
242 macroinvertebrates (Appendix 3).

### 243 *3.2 Restoration effect*

244 The  $\delta^{15}\text{N}$ -distance of riparian arthropods to terrestrial arthropods revealed differences between restored  
245 and degraded sites (Wilcoxon Matched pair test,  $P < 0.05$ , n = 11, Fig. 4 a): The  $\delta^{15}\text{N}$  isotopic  
246 signatures of riparian arthropods differed more from those of terrestrial arthropods in restored reaches  
247 than in degraded reaches. Accordingly, riparian arthropods in restored reaches have a relatively higher  
248 trophic position than in degraded river reaches (as reflected by higher  $\delta^{15}\text{N}$ , Table 2), suggesting an  
249 increased proportion of higher  $\delta^{15}\text{N}$  enriched aquatic prey in the diet of riparian consumers and thus  
250 enhanced trophic linkages following restoration. This pattern is further supported by the pairwise  
251 comparison between restored and degraded reaches using the  $\delta^{15}\text{N}$ -distance of riparian arthropods to  
252 instream macroinvertebrates: although the comparison showed a minor effect (Wilcoxon Matched pair  
253 test,  $P = 0.08$ , n = 11), the findings suggest a closer relation between aquatic and riparian biota in  
254 restored reaches (Fig.4 b). No clear pattern regarding effects of restoration emerged using  $\delta^{13}\text{C}$ -  
255 distances of riparian arthropods to terrestrial arthropods and instream macroinvertebrates.



256

257 **Fig. 4:** Pairwise comparison of the isotopic distances of riparian arthropods to a) terrestrial arthropods and b) instream  
 258 macroinvertebrates between restored and corresponding degraded study reaches (Median; Box: 25–75%; Whisker: Min–Max  
 259 excluding outliers, ○ = Outliers): Significant differences ( $P < 0.05$ ) between pairs are indicated with \*.

260

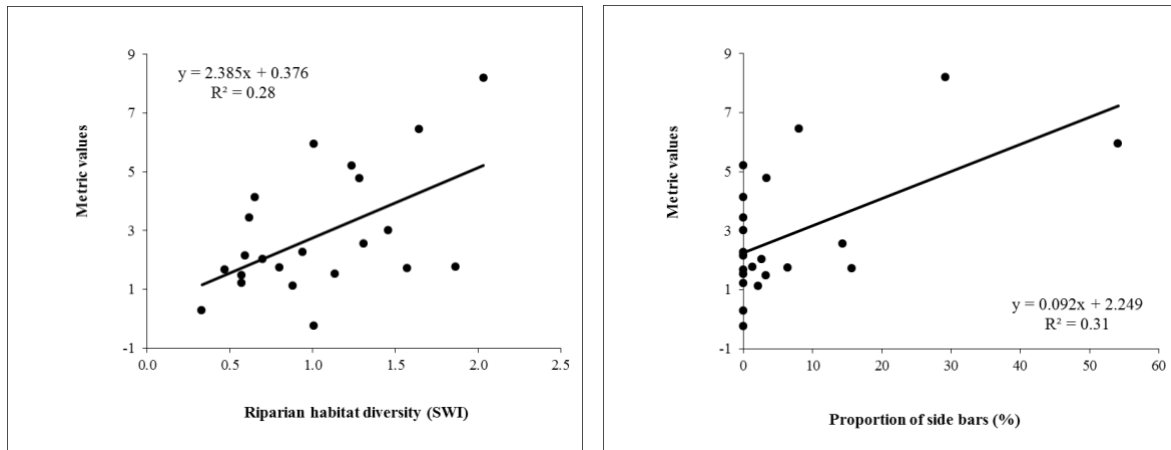
261 **Table 2:** Median  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of consumers in aquatic, riparian and terrestrial habitats separately for restored (R)  
 262 and degraded (D) study reaches.

	aquatic		riparian		terrestrial		n
	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	
R	-30.12	10.01	-27.52	8.64	-27.87	4.88	11
D	-29.53	10.38	-27.82	8.05	-27.84	5.53	11

263

### 264 3.3 Relationship between riparian habitat composition and trophic linkage

265 There was a positive, though weak, relationship between riparian habitat diversity and our trophic  
 266 linkage metrics as well as between the proportion of unvegetated side bars and trophic linkage metrics  
 267 (Fig. 5). We limited our analysis to  $\delta^{15}\text{N}$ -distance of riparian arthropods to terrestrial arthropods that  
 268 displayed the most pronounced differences between restored and degraded sites.



269

270 **Fig. 5:** Relationship between metric values ( $\delta^{15}\text{N}$ -distance of riparian arthropods to terrestrial arthropods in isotope space)  
 271 and a) diversity of riparian habitats (Shannon-Wiener Index) and b) proportion of unvegetated side bars.

272

#### 273 4. Discussion

274 Our findings reveal that restoration measures targeting riverine habitats affect not only instream food  
 275 webs (Kupilas et al. 2016), but also trophic linkages between stream food webs and riparian  
 276 consumers. Hypothesis (i) that hydromorphological restoration favours enhanced aquatic-terrestrial  
 277 linkages was confirmed across all eleven projects, supported especially by differentiation in the  $\delta^{15}\text{N}$   
 278 isotopic signatures between aquatic, riparian and terrestrial consumers, rather than by  $\delta^{13}\text{C}$  signatures.  
 279 Riparian  $\delta^{15}\text{N}$  signatures revealed a higher trophic position relative to other terrestrial consumers  
 280 following restoration, indicating decreased use of terrestrial and increased use of aquatic prey. We  
 281 further observed that the strength of aquatic-terrestrial linkages (as reflected by isotopic distance) is  
 282 positively related to riparian habitat diversity, pointing to the importance of habitat diversification in  
 283 the riparian zone in promoting trophic linkages between river and floodplain (confirming hypothesis  
 284 ii). In general, these findings suggest that hydromorphological restoration results in enhanced trophic  
 285 linkages between river and riparian zone, attributable especially to the provision of open sand and  
 286 gravel bars, and to the general diversification of riparian habitats.

##### 287 4.1 Isotopic signatures across the aquatic-terrestrial interface

288 We found a clear separation between instream macroinvertebrates and predaceous terrestrial  
 289 arthropods using stable isotopes ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ).  $\delta^{15}\text{N}$  signatures revealed that aquatic communities were



290 approximately one trophic level higher than fully terrestrial arthropods across all 22 study reaches.  
291 Riparian consumers also occupy a higher trophic position than terrestrial arthropods, indicating a  
292 significant proportion of  $\delta^{15}\text{N}$  enriched emerging aquatic insects and other stranded aquatic organisms  
293 in their diet. Aquatic biomass consumed by riparian arthropods is likely to be transferred further  
294 through terrestrial food webs given their importance for terrestrial consumers at higher trophic levels  
295 (Jackson & Fisher 1986), although a fraction might also be transferred back into aquatic food webs  
296 when riparian consumers fall to the water surface (Baxter et al. 2005). Our large-scale comparison,  
297 therefore, supports the role of riparian arthropods as a linkage between river and floodplain biota  
298 (Baxter et al. 2005, Paetzold et al. 2005).

#### 299 *4.2 Restoration effect and influence of riparian habitat composition on trophic linkage*

300 Our findings expand our understanding of the multifaceted outcomes of hydromorphological  
301 restoration, beyond the aquatic environment. In addition to previous findings that restoration promotes  
302 riparian habitat diversification (e.g., Jähnig et al. 2010, Januschke et al. 2011, Poppe et al. 2016),  
303 riparian plant diversity (Hasselquist et al. 2018) and riparian arthropod assemblages (e.g., Jähnig et al.  
304 2009, Januschke et al. 2014), our results provide evidence that hydromorphological restoration  
305 promotes trophic connectivity between river and floodplain. Aquatic-terrestrial linkages are essential  
306 for sustaining biodiversity and ecosystem functioning in riverine landscapes (Nakano & Murakami  
307 2001, Tockner & Stanford 2001, Tockner et al. 2008) and the reciprocal flow of matter between  
308 streams and their adjacent riparian zones underpins landscape integrity (Baxter et al. 2005). In  
309 particular, emerging adult aquatic insects represent an important prey subsidy for a wide range of  
310 riparian consumers such as arthropods, birds, lizards, and bats (Baxter et al. 2005, Burdon and Harding  
311 2008). Our findings indicated a significantly smaller share of terrestrial prey in the diet of riparian  
312 arthropods following restoration and suggested a modest increase of aquatic prey. This effect is largely  
313 inferred from the  $\delta^{15}\text{N}$  isotopic signatures of riparian arthropods, rather than changes in  $\delta^{13}\text{C}$   
314 signatures, as  $\delta^{15}\text{N}$  signatures revealed a higher relative trophic position of riparian biota following  
315 restoration. In terms of  $\delta^{13}\text{C}$  isotopic signals we observed almost no changes, though  $\delta^{13}\text{C}$  was  
316 originally expected to be a better indicator of changes in resource use (Collier et al. 2002, Post 2002).

317 Our findings suggest that there was no considerable shift in the use of ultimate carbon resources  
318 following restoration and that  $\delta^{15}\text{N}$  patterns were more consistent for describing trophic linkages of  
319 riparian arthropods.

320 Overall, patterns of  $\delta^{13}\text{C}$  across the aquatic-terrestrial interface were inconsistent between river reaches  
321 and were independent of their restored or degraded state: in some regions, the sections showed large  
322 differences between terrestrial and aquatic  $\delta^{13}\text{C}$ , while others reflected an overlap in  $\delta^{13}\text{C}$  signatures  
323 (Appendix 3). These findings suggest that differences in  $\delta^{13}\text{C}$  isotopic signatures between water and  
324 land were dictated by regional environmental characteristics and regional differences in community  
325 composition rather than restoration measures. One possible reason for a  $\delta^{13}\text{C}$ -overlap across the  
326 aquatic-terrestrial interface is the utilization of terrestrial carbon (leaves, wood) by instream  
327 invertebrates. Even aquatic biofilms are often “contaminated” with terrestrial carbon (trapped  
328 particles, bacteria growing in the biofilm, uptake of DOC of terrestrial origin). Hence, grazing or  
329 shredding instream macroinvertebrates may reflect isotopic signatures initially derived from terrestrial  
330 carbon instead of aquatic carbon so that riparian consumers can receive terrestrial C both primarily or  
331 secondarily, i.e. by consuming aquatic prey that has fed on terrestrial C in the aquatic environment.  
332 The use of another isotope (deuterium,  $\delta^2\text{H}$ ) has recently been highlighted as an application to  
333 explicitly determine between allochthonous and autochthonous nutrient sources (Vander Zanden et al.  
334 2016). ). In future studies, the use of deuterium isotopes should be considered in order to more clearly  
335 differentiate the usage of allochthonous vs. autochthonous resources in linked stream-riparian food  
336 webs.

337 Riparian arthropod predation is concentrated along the shoreline and habitat structure of the riparian  
338 zone determines not only composition of riparian arthropod assemblages but also aquatic insect  
339 emergence and the accumulation of surface drifting organisms (Hering & Plachter 1997, Hering 1998,  
340 Paetzold et al. 2005, Carlson et al. 2016). Open sand and gravel bars are major drivers of aquatic-  
341 terrestrial transfers as the boundary between river and shore is open for cross-habitat movements  
342 (Paetzold et al. 2005). Furthermore, aquatic insects leaving the water for emergence are particularly  
343 vulnerable to predation on open bars providing a minimum of shelter (Hering & Plachter 1997). In line

344 with this, we found a positive relationship between the provision of such habitats and the strength of  
345 aquatic-terrestrial linkages. However, we further highlighted that overall riparian habitat diversity is  
346 important for the strength of trophic linkages between river and floodplain. Different pathways for  
347 aquatic biomass to enter the riparian zone are made available by a diverse shoreline: spaces between  
348 stones for insect emergence, small lentic zones prone for stranding of aquatic organisms, and wet soils  
349 in which midge larvae (Chironomidae), a preferred prey of small ground beetles of the genus  
350 *Bembidion*, dwell (Hering 1998). Moreover, the high share of aquatic prey may simply be explained  
351 by the lack of terrestrial prey, which is much more abundant in vegetated zones and by the lack of  
352 shelter for emerging aquatic insects. Finally, hydromorphological restoration can affect the  
353 composition and dispersal of instream macroinvertebrates and shifts in the adult trait composition of  
354 the aquatic invertebrate assemblages can have substantial impact on the subsidy of stream  
355 invertebrates to terrestrial food webs (Carlson et al. 2016, McKie et al. 2018).

356 Our findings provide evidence for an enhanced stream-riparian linkage following restoration. As  
357 hydromorphological restoration typically enhances riparian arthropod abundances and species richness  
358 in the riparian zone (Günther & Assmann 2005, Lambeets et al. 2008, Jähnig et al. 2009, Januschke &  
359 Verdonshot 2016), we can assume that the quantitative energy flow into the terrestrial food web is  
360 also increased (i.e., more riparian predators are consuming more aquatic prey). This is in line with  
361 numbers of arthropods caught in our study reaches: the three reaches with highest  $\delta^{15}\text{N}$ -distance  
362 between riparian arthropods and terrestrial arthropods (indicating a smaller share of terrestrial prey in  
363 the diet of riparian consumers) also revealed higher abundances of riparian arthropods in restored  
364 compared to degraded reaches. This also applies for the expected increase in aquatic insect biomass as  
365 a result of restoration, which can serve as potential prey for riparian predators. Hering & Plachter  
366 (1997) and Burdon & Harding (2008) showed positive associations between aquatic insect biomass  
367 and riparian predator densities.

#### 368 *4.3 Conclusion*

369 Although hydromorphological restoration primarily addresses biodiversity of aquatic and floodplain  
370 habitats, our study highlights that restoration can also affect ecological networks spanning across

371 boundaries. Aquatic-terrestrial connectivity was enhanced following restoration, as revealed by the  
372 isotopic signatures of invertebrate in aquatic, riparian and terrestrial habitats. Our findings expand our  
373 understanding of the manifold outcomes of river restoration and reveal the necessity to expand our set  
374 of indicators used to assess restoration measures. Developing a predictive understanding of ecological  
375 responses to environmental change requires a set of structural and functional indicators. Future  
376 evaluation of hydromorphological restoration measures should incorporate indicators for food web  
377 configuration crossing habitat boundaries to facilitate a mechanistic understanding of ecological  
378 responses. Biomarkers including stable isotopes and poly-unsaturated fatty acids can be used to  
379 describe the trophic connectivity between stream and riparian food webs. We also saw that riparian  
380 habitat diversity is a key factor for promoting trophic linkages between water and land as it enhances  
381 the pathways for aquatic biomass entering the riparian zone. From a management perspective, the  
382 riparian zone should be more explicitly incorporated into future restoration planning because it acts as  
383 the interface for aquatic-terrestrial transfer, provides habitat for various organism groups and provides  
384 a wide range of ecosystem services (e.g., flood protection). Sustaining biodiversity becomes  
385 increasingly relevant during times of global species decline where freshwaters and floodplains are  
386 disproportionately contributing to global biodiversity.

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