1    **Title:** Regulation of trophic architecture across spatial scales in a major river network

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13   3B2.

14   **Author contributions**

15   EH and FA designed the research; FA provided the data; EH processed and analysed the

16   data; EH wrote the first draft of the manuscript; EH and FA contributed for further

17   manuscript revisions.

18   **Abstract**

19   Moving beyond species count data is an essential step to better understand the effects of

20   environmental perturbations on biodiversity and ecosystem functions, and to eventually

21   better predict the strength and direction of those effects. Here, coupling an integrative

22   path analysis approach with data from an extensive countrywide monitoring program, we

23   tested the main spatial, environmental and anthropogenic drivers of change in stream

24   macroinvertebrate trophic structure along the entire Swiss Rhine river catchment. Trophic

25   structure was largely driven by inherent altitudinal variation influencing and cascading to

26   regional scaled factors such as land use change and position in the riverine network,

27   which, in turn, transformed local habitat structure variables. Those cascading effects

28   across scales propagated through the biotic community, first affecting preys and, in turn,

29   predators. Our results illustrate how seemingly less important factors can act as essential

30   transmission belts, propagating through direct and indirect pathways across scales to

31   generate the specific context in which each trophic group will strive or not, leading to

32   characteristic landscape wide variations in trophic community structure.

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34   **Keywords**: Dendritic network, biodiversity, land-use change, metacommunity, trophic

35   networks, food webs

## INTRODUCTION

36

37    River ecosystems constitute iconic examples of spatial complexity with complex regional

38    scale vertical structures (from upstream to downstream; the river network) constraining

39    organism and energy movement[1–5], but also strong localized horizontal interactions with

40    the terrestrial matrix influencing local habitat characteristics through changes in cross-

41    ecosystem subsidy[6–8]. The shape of river networks, which all follows the same geometric

42    scaling properties[2], has been shown to influence biological community dynamics and

43    local species richness patterns[3,5,9–12]. However, recent studies have found that the relative

44    importance of the regional river network and local habitat characteristics is somewhat

45    context-dependant as a function of species traits (e.g., dispersal mode) and location-

46    specific conditions such as terrestrial land-use and biotic interactions[13–15]. Although those

47    studies tend to emphasize the importance of considering both local and regional factors to

48    understand variations in aquatic community, total explanatory power remains generally

49    low[16]. In that context, the use of well-defined functional or trophic groups each including

50    taxonomically different but functionally similar taxa could improve explanatory power by

51    generating groups of taxa with more uniform response to specific environmental or

52    spatial characteristics[17].

53    In addition, current approaches tend to focus on the relative importance of regional versus

54    local factors to identify the dominant drivers while totally ignoring the inherent structure

55    of interdependences among regional and local factors leading to a general loss of

56    explanatory power[16,18–23]. The often-assumed dichotomy between regional and local

57    factors generally erodes when considering the mechanisms behind those effects[22,24]. For

58    instance, many regional factors, such as altitude, do not have any direct mechanistic

59     effects on community structure, but rather influence local factors that, in turn, will

60     causally impact communities. Other regional factors, however, such as land-use cover are

61     likely to have both direct (e.g., changes in habitat structure) and indirect (e.g., changes in

62     water chemical quality) impacts on aquatic communities. Thus, local factors that may

63     seem less important at first might effectively act as transmission belts, propagating a part

64     or the total effects of some regional factors on community structure. Those effects are

65     then likely to propagate within biological communities as a function of biotic interactions

66     (e.g., effects on preys, which in turn, affect predators). Overall, we cannot rely on whole-

67     community endpoint biodiversity measurements only, such as local species richness, to

68     understand the direct and indirect pathways by which regional and local factors interact

69     and propagate through biological communities to influence their structure and function[25–

70     27].

71     Here, we disentangled the main spatial, environmental and anthropogenic drivers shaping

72     stream macroinvertebrate trophic structure across an entire river catchment. Starting from

73     abundance data from a Swiss-wide biodiversity-monitoring program we collected

74     functional traits on each taxon to reconstruct the trophic structure of each local

75     community for 364 sites covering the entire Swiss Rhine river catchment. Integrating

76     data related to land-use change, local water chemical and physical properties, regional

77     factors related to altitude and position along the dendritic network, we used an integrative

78     path analysis framework to identify specific pathways by which factors interact across

79     spatial scales to affect stream invertebrate trophic structure.

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4

82    **RESULTS**

83    Testing the main spatial, environmental and anthropogenic drivers of aquatic

84    macroinvertebrate trophic structure along the Swiss Rhine river catchment we found that

85    variations in relative (Figure 1,2) and absolute (Figure 3) abundances of each trophic

86    group across the whole river basin was largely driven by altitudinal variations (Table 1

87    and Figure 2). In turn, altitude influenced several other regional and local scale factors

88    leading to a complex array of direct and indirect pathways across spatial scales,

89    eventually leading to landscape wide variations in trophic community structure (Figure 1

90    & 3).
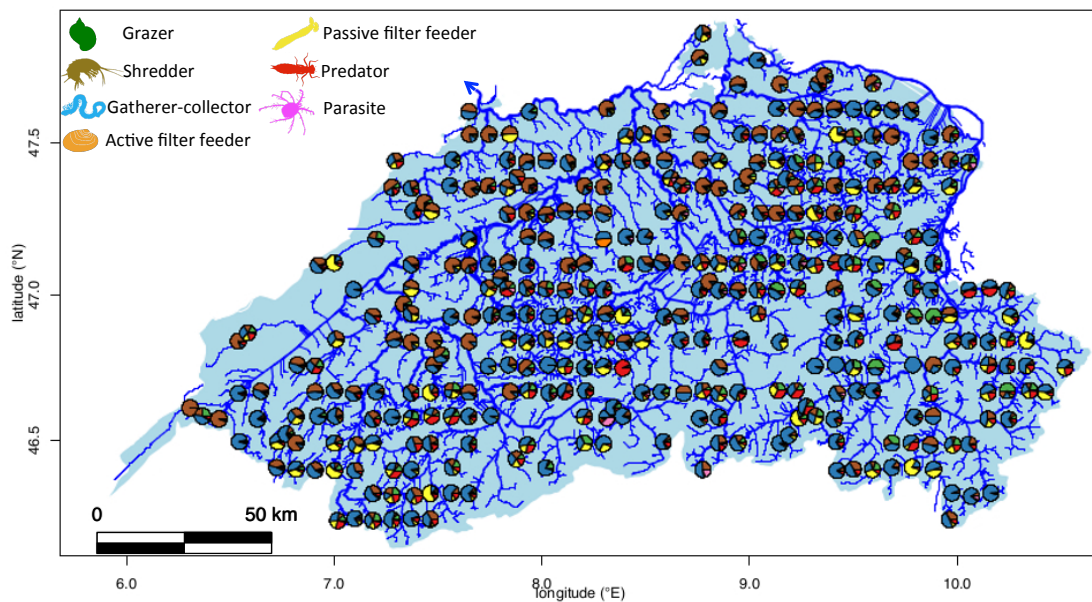


91
92    **Figure 1.** Spatial variation in trophic structure of riverine macroinvertebrates. The figure shows the Rhine
93    river basin. All 3$^{rd}$ order stream or larger are shown (arrow indicates direction of flows). Each pie chart
94    represents the trophic structure (relative abundance of each trophic group in the community) for one of the
95    364 sampling sites across the river basin. Each functional group is represented by a silhouette of one of its
96    iconic taxon: Gatherer-collector (Oligochaeta), Grazer-scraper (Limnaeidae), Predator (*Cordulegaster*),
97    Passive filter feeder (Simuliidae), Active filter feeder (Sphaeridae), Parasite (Hydracaria), Shredder
98    (Gammaridae).

99

100    More specifically, altitude led to a decline in deciduous forest cover, was associated with

101    an increase in distance to river outlet and drove land-use change from high settlement and

102    agricultural lands to high altitudinal natural meadows (Figure 3). In turn, those regional

103    factors influenced local habitats with transition to natural meadows leading to lower

104    water foam levels (a proxy of eutrophication), and increased distance to outlet leading to

105    higher turbidity level (Fig. 3). Lowland upstream sites were associated with higher

106    probability of finding modified streams (see negative effects of altitude and positive

107    effects of distance to outlet on river modification index on Figure 3). Local habitat factors

108    then affected various trophic groups with mud level negatively impacting shredder,

109    passive filter feeder and grazer-scraper abundances (Figure 3), foam (proxy of

110    eutrophication) positively impacting gatherer-collector and passive filter feeder, river

111    habitat modification positively influencing grazer-scraper, gatherer-collector and parasite,

112    and higher riverbed variations in depth positively affecting passive filter feeder (Figure

113    3). Finally, all those regional and local factors affected predator abundance through

114    affecting their preys (Figure 3).
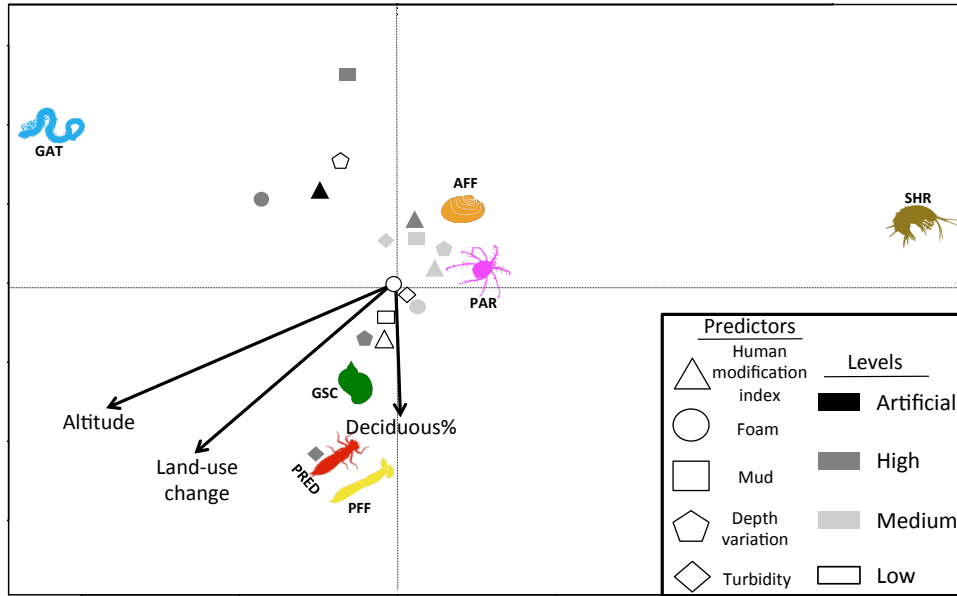
**Figure 2.** Main environmental and spatial drivers of riverine macroinvertebrate trophic structure. The ordination figure is the final db-RDA model selected by an automatic stepwise model building approach based on adjusted $R^2$. The first and second axes respectively explain 67% and 18% of the total variation in trophic structure (relative abundance of each trophic group *per* community, see Methods). A specific geometric shape represents each categorical predictor, with the gray gradient representing the level of each predictor. Each functional group is represented by a silhouette of one of its iconic taxon: GAT: Gatherer-collector (Oligochaeta), GSC: Grazer-scraper (Limnaeidae), PRED: Predator (*Cordulegaster*), PFF: Passive filter feeder (Simuliidae), AFF: Active filter feeder (Sphaeridae), PAR: Parasite (Hydracaria), SHR: Shredder (Gammaridae).

We also found evidence for direct effects of regional factors on some trophic groups.

Altitude had a direct negative impact on passive filter feeder and shredder abundances

(Figure 3), potentially mediated by unmeasured (i.e., missing) local variables. Land-use

transition to natural meadows had a direct positive effect on predator abundance

suggesting that predators tend to fare better in high altitudinal streams surrounded by

natural meadows than in low altitude zones characterized by a matrix of agricultural

lands and human settlements, and a negative effect on grazer-scraper (Figure 3). Distance

to outlet directly influenced gatherer-collector and parasite abundances negatively

(Figure 3), illustrating that location along the river network has both indirect (mediated

135    by local habitat factors, see above) and direct effects on aquatic invertebrate trophic

136    structure.

137    There were also causal pathways among variables at each spatial scale as described above

138    for altitude and regional factors. Among local factors, river modifications negatively

139    impacted stream depth variation, which in turn, negatively influenced turbidity (Figure

140    3). Thus river modifications had an indirect positive effects on turbidity mediated by a

141    change in riverbed depth variation.

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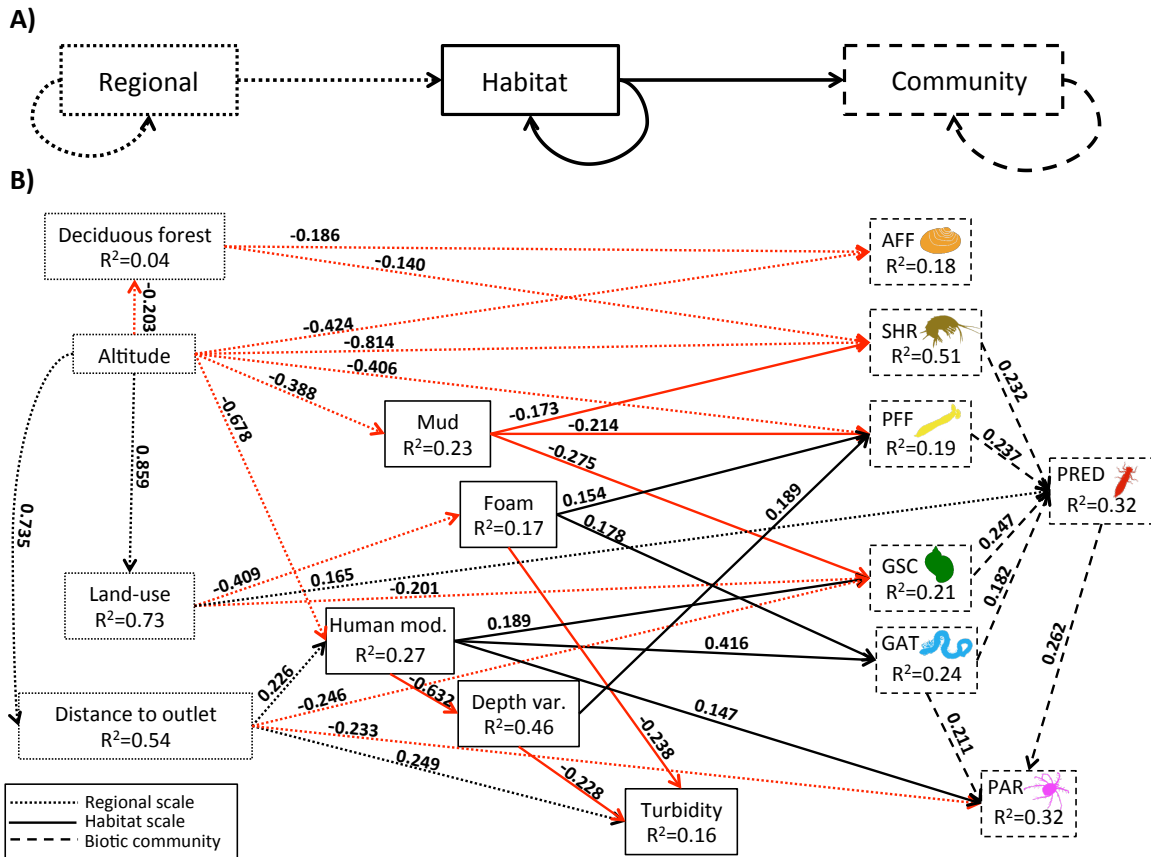


**Figure 3.** Direct and indirect pathways by which regional and local drivers influence riverine
macroinvertebrate trophic structure. A) We hypothesized that most regional (dotted lines) factors would
influence the biotic community (dashed lines) indirectly via an effect on local habitat factors (solid lines).
We also expected within spatial scale interaction structure at both regional and local scales (looped arrows).
Changes to biotic communities are usually analysed assuming that each predictor influence each taxa or
functional group in the community, however we hypothesized that the specific structure of interactions

150  within a biotic community would rather drive the propagation of effects from specific entry points (preys)
151  to the entire community (looped arrow on the community box). B) Final structural equation model
152  illustrating the different direct and indirect pathways by which regional (dotted lines) and local (solid line)
153  factors interact and then propagate through the trophic community (dashed lines). Each value is the
154  standardized coefficient (standardized estimate from each partial regression), representing the strength of
155  the effect of one variable on another. Red arrows represent negative effects and black arrows positive ones.
156  Each functional group is represented by a silhouette of one of its iconic taxon: GAT: Gatherer-collector
157  (Oligochaeta), GSC: Grazer-scraper (Limnaeidae), PRED: Predator (*Cordulegaster*), PFF: Passive filter
158  feeder (Simuliidae), AFF: Active filter feeder (Sphaeridae), PAR: Parasite (Hydracaria), SHR: Shredder
159  (Gammaridae).

160

161  Overall, our results illustrate the complex interactions among local and regional scale

162  predictors in shaping trophic structure along an entire catchment (Figure 3) and how the

163  outcome of those interactions across-scale generate the specific context in which each

164  trophic group will strive or not, leading to large spatial scale variations in trophic

165  community structure (Figure 1 and 2).

166

167  **DISCUSSION**

168  Testing for the main environmental and spatial drivers of trophic structure in stream

169  macroinvertebrates we found a complex array of direct and indirect pathways by which

170  regional and local drivers interact to influence relative and absolute abundances of

171  aquatic macroinvertebrate trophic groups, eventually leading to landscape wide variations

172  in trophic community structure. More specifically, cascading effects across spatial scales

173  starting with altitude as a key driver influencing other regional factors, which in turn

174  affected various local habitat characteristics directly to influence trophic group

175  abundances. Most effects propagated through the community by first affecting preys,

176  which in turn, affected predator abundances.

177    The importance of the river network has been shown to be context-dependant as a

178    function of location-specific conditions such as terrestrial land-use and biotic

179    interactions[14]. Our results suggest that those location-specific conditions can, in part,

180    interact with some river network properties because they are not distributed randomly

181    along the network but rather located at specific substructures in the network. Those

182    effects constitute in themselves indirect effects of the river network rather than the

183    absence of effect. More specifically, we showed that distance to outlet affected trophic

184    groups directly but also indirectly via its positive effect on the human modification index.

185    A main component of this result is the observation that lowland headwater locations are

186    systematically more affected by human-induced riverbed and riverbank modifications

187    than headwaters at higher elevations. Consequently, our results illustrate how the

188    significance of spatial and regional factors can be masked by location-specific conditions

189    when indirect pathways are not being taken into account[28].

190    Our results also emphasize the complex response of each individual trophic group (see

191    Figure 3) to each individual environmental and spatial factor. Interpreting any of these

192    patterns independently can thus be misleading and only an integrative approach allows a

193    coherent understanding of community structure, and eventually predicting shifts in

194    response to multiple environmental changes[24,28,29]. Although our predictors are

195    hierarchically organized (e.g., regional factors influencing local factors influencing preys,

196    which in turn impact predators) rather than multiplicative, our study echoes recent calls to

197    take a more integrative approach to the study of multiple-stressors and environmental

198    changes, especially in aquatic ecosystems[25,30–32].

199    Shifts in trophic structure are a well-known driver of ecosystem processes[33–36]. Predicting

200    those shifts, however, is a challenging endeavour because of multiple stressors interacting

201    at different spatial scales and potentially affecting different trophic levels simultaneously.

202    Our results suggest that effects mainly spread from preys to predators across the whole

203    river network, and we observed important shifts in trophic group's relative abundances.

204    For instance, our ordination analysis identified an important gradient from gatherer-

205    collector-dominated to shredder-dominated communities (see Figures 1 & 2). This

206    observation is also visible with the structural equation modeling where higher gatherer-

207    collector abundance is mainly associated with high levels of riverbed and bank

208    modifications, while shredders seem to strive in less disturbed environments (Figures 2 &

209    3). At the functional level, we postulate that this shift from coarse (shredder) to fine

210    particle (gatherer-collector) feeders along those environmental gradients is linked to

211    variations in the type of resource available[37]. Such shifts in trophic structures have also

212    implications for energy transfer and stoichiometric constraints in the community because

213    shredders mainly feed on allochthonous leaf particles, which tend to be rich in carbon but

214    nitrogen poor, while fine particles associated to agricultural lands tend to be nutrient rich

215    but a poorer source of carbon.

216    Looking at the functional or trophic structure of communities is an essential step to better

217    understand the effects of environmental perturbations on biodiversity and ecosystem

218    functions, but also to eventually better predict the strength and direction of those

219    effects[26,27,38]. Our results illustrate the complex interactions among local and regional

220    scale predictors in driving trophic structure and how the outcome of those interactions

221    across-scale generate the observed large scale variations in aquatic trophic community

222    structure.

223

224    **METHODS**

225    **Data**

226    Our study used the aquatic macroinvertebrate abundance data from 364 sites across the

227    whole Rhine river catchment in Switzerland, covering about 30,000 km$^2$ and eventually

228    flowing into the North Sea. The data is collected and curated by a Swiss governmental

229    monitoring program ("Biodiversity Monitoring in Switzerland BDM"; BDM

230    Coordination Office, 2014). Sampling is done following a systematic sampling grid, and

231    was conducted in wadeable streams, 2$^{nd}$ order or larger in size, thus excluding standing

232    waterbodies, 1$^{st}$ order streams and large rivers inaccessible by wading[39]. Each site was

233    sampled once between 2009–2014 with seasonal timing of sampling adjusted with

234    respect to elevation: the sampling period for a site was based on local phenology so as to

235    collect as many macroinvertebrate taxa as possible for a given elevation[39].

236    The survey was done using a standard kick-net (25 x 25 cm, 500 μm mesh) sampling

237    procedure defined in the Swiss "Macrozoobenthos Level I" module for stream benthic

238    macroinvertebrates (BDM Coordination Office, see [39,40]). Briefly, a total of eight kick-net

239    samples were taken at each site to cover all major microhabitats within a predefined

240    section of the river (area covered per site was width x 10 times the average width in

241    length). Therefore, all locally represented habitat types (including various sediment types

242    such as rocks, pebbles, sand, mud, submerged roots, macrophytes, leaf litter and artificial

243    river-beds) and water velocities were sampled. Samples were preserved in 80% ethanol

244    and returned to the laboratory for processing. In the laboratory, all macroinvertebrates

245    used in this study were sorted and identified to the family level by trained taxonomists

246    (total of 63 families see Table S1 for a list). For further details on the sampling method

247    and the database, see also [40–42].

248

249    **Predictors**

250    We used 38 predictors representative of regional, local and hydrological conditions, as

251    well as land-use coverage and position in the dendritic network (see Table S2 for a

252    complete list of each variable with description). Regional predictors included altitude at

253    the sampling site and catchment size. Local predictors represent instream habitat

254    conditions that were measured directly at sampling site. Local predictors included

255    features of channel cross-section (e.g., width, depth, and their variability), riverbed

256    conditions (e.g., mud deposition and attached algae), aquatic conditions (e.g., turbidity

257    and dissolved iron sulfide concentration), and a discrete ranking of human alterations to

258    riverbank and riverbed (see [39] for details). Hydrological predictors are factors

259    representing geometry conditions of the river network in the upstream catchment of a

260    sampling site. Those predictors included geomorphological (e.g., riverbed slope),

261    hydrological (e.g., mean discharge) and chemical (e.g., inflowing wastewater volume)

262    conditions. Land use predictors represent terrestrial conditions surrounding a sampling

263    site. Those predictors included 6 land use classes considering adjacent influences to the

264    local site with a lateral buffer distance of either 500 meters, 1, 5, 10, 100 or 1000

265    kilometers[42]. We know from previous work on this data that the 5 km scale is most

266    significant in affecting stream invertebrate diversity[24], thus we used only the 6 land use

267     classes with lateral buffer distance of 5 kilometers in our analyses.  Network predictors

268     represent the position of each sampling site in the river dendritic network (e.g., centrality

269     and distance to the outlet).

270     Many land use predictors were strongly skewed toward zero leading to important loss of

271     information and degrees of freedom when analysing each variable individually. Instead,

272     to emphasize a more continuous transition between each land-use type, for further

273     analysis, we used scores from a canonical correspondence analysis representing a gradual

274     shift in land-use from high proportion of human settlement and agricultural lands to high

275     proportion of natural meadows (see Fig. S1). Such gradient is dominant in Switzerland

276     with low lands representing most of the urban and agricultural lands. Grouping our land-

277     use data this way reduced our total number of predictors to 34 for 364 sites.

278

279     **Trophic structure**

280     We built the trophic structure of each stream macroinvertebrate community for each site,

281     using the 'freshwaterecology' European database[43] and extracting the 'feeding type'

282     metric (*sensu* [44]) for each of our 63 stream macroinvertebrate families. The data from the

283     'freshwaterecology' database was at the species level. Thus, we used averaged values

284     across all species within family to determine the dominant feeding type of each 63

285     family. At the end, our data was comprised of abundance data for 63 families across

286     seven functional feeding groups (following definition by [44], see Table S1) defining

287     overall trophic structure. The seven groups were: grazer scrapers (13 families, mainly

288     feeding on particulate organic matter from endolithic and epilithic algal tissues and

289     biofilm), shredders (10 families, mainly feeding on coarse particulate organic matter from

290    fallen leaves and plant tissue), gatherer collectors (10 families, mainly feeding on

291    sedimented fine particulate organic matter), active filter feeders (1 family, mainly feeding

292    on suspended particulate organic matter actively filtered from the water column), passive

293    filter feeders (2 families, mainly feeding on suspended particulate organic matter

294    passively trapped from running water), predators (24 families, mainly feeding on preys),

295    and parasites (2 families, mainly feeding from hosts).

296

297    **Analyses**

298    *Ordination*

299    To identify the main environmental and spatial drivers of the trophic structure of stream

300    macroinvertebrate communities we used a distance-based redundancy analysis on

301    Euclidean distances (db-RDA, following [45]) followed by an automatic stepwise model

302    building approach for constrained ordination based on the adjusted $R^2$ of the full model

303    (499 permutations, following [46]). The significance level at P<0.05 of the final model, and

304    of each selected term were tested using a permutation ANOVA (200 permutations). The

305    uses of pairwise Euclidean distances ensure that our analyses really emphasize changes in

306    the relative proportion of each trophic group within each community rather than between

307    site changes in absolute abundance or composition[47]. Because we did not have any *a*

308    *priori* knowledge on which predictors might be most important, we used all 34 predictors

309    into our analytical pipeline. At the end 8 predictors were selected with first and second

310    axes respectively explaining 67% and 18% of the total variance for the constrained axes.

311    *Structural equation model*

312    Ordination approaches provide insightful information on main drivers, however they do

313    not provide information on the potential interactions and pathways by which each driver

314    affect different trophic levels. For instance, a regional factor such as altitude does not

315    have any direct ecological relevance. Rather, altitude will affect trophic groups via its

316    effects on local factors (e.g., temperature or deciduous forest cover). Thus, even variables

317    that may seem less important at first might act as transmission belts for the effects of

318    other factors on stream invertebrate trophic structure. Moreover, factors affecting

319    predators can do so by affecting the predator directly (e.g., high turbidity decreasing

320    hunting efficiency) or indirectly by affecting its preys. Based on the information from the

321    db-RDA analysis, we built a meta-model representing the potential links of importance in

322    the system and how they affect trophic structure. We hypothesized that effects would

323    mainly cascade from regional factors affecting local factors which in turn affect different

324    trophic group (Fig. 1a). We then used structural equation modeling to test the fit of this

325    initial meta-model against the data. Subsequently, we used the residual co-variance

326    matrix and modification indices[48] to identify potentially important missing links that were

327    not included in the original meta-model. After adding those links to the model we then

328    identified and pruned least important links (based on p-values and effect on model fit) to

329    avoid over-parameterization and over estimation of explanatory power. Because we used

330    categorical factors, we measured the fit of our model to the data with a robust diagonally

331    weighted least square estimator (DWLS, see [48]). Our final model converged after 105

332    iterations and showed a good fit to the data (n = 364, DWLS = 63.36, Degree of freedom

333    = 62, P = 0.428).

334    All analyses were conducted with R 3.1.2 (R Core Team 2016), using the 'vegan'

335     package[49] for the db-RDA ('capscale' function) and stepwise model building ('ordistep'

336     function), the 'igraph' package[50] to compute network metrics, and the 'lavaan' package[48]

337     for SEM analysis.

338

339     **Acknowledgement**

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472     **Table 1.** Permutation ANOVA (200 permutations) on the final db-RDA model.

| | Df | SS | F | $P$-value |
|---|---|---|---|---|
| Altitude | 1 | 3.63 | 22.75 | 0.001 |
| Human Mod. Ind. | 3 | 2.16 | 4.51 | 0.001 |
| Foam level | 2 | 0.97 | 3.04 | 0.006 |
| Mud level | 2 | 0.88 | 2.75 | 0.004 |
| Land-use gradient | 1 | 0.81 | 5.10 | 0.001 |
| Depth variation | 2 | 0.95 | 2.98 | 0.012 |
| Deciduous cover | 1 | 0.60 | 3.80 | 0.011 |
| Turbidity level | 2 | 0.72 | 2.27 | 0.031 |
| Residual | 193 | 30.86 | | |

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