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## Land use alters trophic redundancy and resource flow through stream food webs

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2 food webs

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18 **Running Title:** Urbanisation modulates food webs

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21 **Keywords:** Bottom-up control, diet estimates, energy flow, stable isotope analysis, trophic  
22 redundancy, urban streams.

**23 Abstract**

24 1. The changes to physical and chemical ecosystem characteristics as a response to  
25 pervasive and intensifying land use have the potential to alter the consumer-resource  
26 interactions and to rewire the flow of energy through entire food webs.

27 2. We investigated these structural and functional properties of food webs in stream  
28 ecosystems distributed across woodland, agricultural and urban areas in the Zagreb region of  
29 Croatia. We compared resource availability and consumer diet composition using stable  
30 isotope mixing models and tested how the isotopic variance of basal resources, primary  
31 consumers, macroinvertebrate predators, and other food-web characteristics change with  
32 different land use types.

33 3. Combination of increased loading and altered composition of nutrients, lower water  
34 discharge and higher light availability at urban sites likely promoted the contribution of  
35 aquatic macrophytes to diets of primary consumers. Macroinvertebrate predators shifted their  
36 diet, relying more on active filterers at urban sites relative to woodland and agricultural sites.  
37 Urban food webs also had lower trophic redundancy (i.e. fewer species at each trophic level)  
38 and a more homogenised energy flow from lower to higher trophic levels. There was no  
39 effect of land use on isotopic variation of basal resources, primary consumers or  
40 macroinvertebrate predators, but all these trophic groups at urban and agricultural sites were  
41  $^{15}\text{N}$ -enriched relative to their counterparts in woodland stream food webs.

42 4. The physical and chemical ecosystem characteristics associated with intensive land  
43 use altered the resource availability, trophic redundancy and the flow of energy to other  
44 trophic levels, with potentially negative consequences for community dynamics and  
45 ecosystem functioning. These empirical findings indicate that reducing nutrient pollution,

- 46 agricultural runoffs and maintaining riparian vegetation can mitigate the impacts of land use  
47 on structure and function of stream ecosystems.

## 48 **Introduction**

49 Intensive land use represents the leading threat to Earth's ecosystems and biodiversity (Sala  
50 et al., 2000; Vitousek, Mooney, Lubchenco, & Melillo, 1997). In particular, urbanization is  
51 profoundly altering abiotic and biotic ecosystem characteristics and it has become a leading  
52 cause of population extirpation across a wide range of species (Clergeau, Croci, Jokimäki,  
53 Kaisanlahti-Jokimäki, & Dinetti, 2006; McKinney, 2006). Similarly, industrial-scale  
54 agriculture and associated changes to nutrient cycling increase rates of species extinctions  
55 through dominance of few superior competitors that often reduce species richness and  
56 biodiversity (Carpenter, Cole, Kitchell, & Pace, 1998; Chapin et al., 2000; Guignard et al.,  
57 2017). However, the processes that underpin the structure and function of ecological  
58 communities may differ substantially among ecosystems influenced by different land use.  
59 Although the impacts of severe degradation, reduction and loss of habitats caused by  
60 intensive land use activities are widespread among taxonomic groups and ecosystem types,  
61 these impacts are particularly pervasive in freshwater ecosystems (Ormerod, Dobson,  
62 Hildrew, & Townsend, 2010; Strayer & Dudgeon, 2010).

63 The initial responses to land use changes may occur at a level of trophic interactions,  
64 resource use, and feeding behaviour of primary and secondary consumers (Alley, 1982;  
65 Beaugrand, Mackas, & Goberville, 2013). Consumers can buffer changes in the resources  
66 availability via feeding plasticity (Friberg & Jacobsen, 1994; Zah, Burgherr & Bernasconi  
67 2001), shifting their feeding preferences to new resources in response to habitat disturbance  
68 (Zah, Burgherr & Bernasconi 2001). High functional redundancy (i.e. large proportion of  
69 species with similar trophic ecologies) allows an ecosystem to maintain its function despite  
70 some taxa going locally extinct. Conversely, low functional redundancy usually weakens  
71 ecosystem resilience to stressors such as climate and land use changes (Cardinale, Palmer &  
72 Collins 2002). In aquatic systems, the ecosystem resilience to environmental change can also

73 be indicated by the relative contribution of allochthonous to autochthonous resources to food  
74 webs (Recalde, Postali, & Romero 2016). For instance, a stream food web with a high  
75 dependence on allochthonous material may undergo a disruptive shift in nutrient budgets if  
76 the surrounding land became urbanized and the vegetation in the catchment is reduced  
77 (Finlay, Khandwala, & Power 2002). On the other hand, autochthonous primary producers  
78 can provide a better nutritional resource than terrestrial litter (Brett, Kainz, Taipale, &  
79 Seshan, 2009; Junker & Cross, 2014; Thorp & DeLong, 2002), leading to higher biomass  
80 production of top consumers (Karlsson et al., 2015). Such shifts toward resources with high  
81 nutritional quality in streams with open canopy, in combination with higher transfer  
82 efficiency of these resources to primary consumers, can elongate food chains in comparison  
83 to woodland streams with closed canopy cover (Lau, Leung, & Dudgeon, 2009).  
84 Consequently, the impact of different land use on the taxonomic and nutritional composition  
85 of basal resources can cascade to higher trophic levels, altering the structure and flow of  
86 energy through the entire food web (De Castro et al., 2016; Kratina & Winder, 2015;  
87 Layman, John, Peyer, & Allgeier, 2007).

88       Recent advances in stable isotope analyses allow us to estimate community-wide  
89 characteristics such as variety of resources, trophic diversity, trophic redundancy and other  
90 metrics closely related to resource use, diet specialization and degree of omnivory (Layman,  
91 Arrington, Montaña, & Post, 2007; Nielsen, Clare, Hayden, Brett, & Kratina, 2018). These  
92 analyses often rely on quantifying existing differences in the nitrogen and carbon stable  
93 isotope composition of food resources (Newsome, Rio, Bearhop, & Phillips, 2007; Rader et  
94 al., 2017). Stable isotope analyses can determine the maximum trophic position through  
95 comparing nitrogen stable isotope ratios of all food web components and disentangle the  
96 pathways of energy flow from primary producers through to primary consumers and  
97 predators through a comparison of carbon stable isotope ratios. However, the application of

98 isotopic metrics to understand how ecological communities respond to different types of land  
99 use are scarce and the impacts of human activities in urban zones are rarely compared to the  
100 impacts in agricultural and woodland areas.

101 To understand the community-level impacts of different types of land use, we  
102 compared the resource availability and composition, variance in isotopic composition of  
103 macroinvertebrate consumers and the resilience-related food-web properties in urban,  
104 agricultural and woodland stream habitats. We hypothesised that stream sites with stronger  
105 urban and agricultural influences show: (i) shifts in basal resource availability, characterized  
106 by  $\delta^{13}\text{C}$  values that change minimally with trophic transfer, but can vary substantially across  
107 different resource types (McCutchan Jr, Lewis Jr, Kendall, & McGrath, 2003; Newsome, Rio,  
108 Bearhop, & Phillips, 2007); (ii) an increased contribution of aquatic (autochthonous)  
109 resources relative to terrestrial (allochthonous) resources, which is reflected in the stable  
110 isotope values of primary consumers; (iii) higher  $\delta^{15}\text{N}$  values of macroinvertebrate consumers  
111 (as a consequence of greater in-stream additions of urban wastes that usually increase basal  
112 resource-stable isotope values), or a longer food chain revealed by predators with high  $\delta^{15}\text{N}$   
113 values relative to basal resources; and (iv) fewer basal resources being exploited and lower  
114 functional (i.e. trophic) redundancy of macroinvertebrate assemblages shown through fewer  
115 species occupying a similar position in isotopic-niche space. Such empirical evidence could  
116 improve our understanding of the land use effects on the flow of energy through food webs  
117 and provide deeper mechanistic insights into the functioning of ecosystems in human-  
118 modified landscapes.

119

## 120 **Materials and methods**

### 121 *Study sites*

122 We collected samples of macroinvertebrates and their potential food resources from five  
123 streams in the region of Zagreb, Croatia (Fig. 1): Vrapčak (V), Kustošak (K), Veliki potok  
124 (VP), Bliznec (B) and Trnava (T). Zagreb is the largest city of Croatia with a population of  
125 approximately 800,000, representing the Croatian centre of economic and municipal  
126 activities. The stream network of Zagreb consists of 31 low-order streams flowing from the  
127 less human-impacted regions concentrated at the north of the city, through both agricultural  
128 and urban downstream areas where they are increasingly affected by anthropogenic (i.e.  
129 residential, municipal, industrial, agricultural) activities and physical modifications. Whereas  
130 agricultural land use prevails in the eastern part of the region, a high-density residential,  
131 municipal and industrial land use dominates the central and western part of the Zagreb area  
132 (Fig. 1). The streams flow into the River Sava, a tributary to the second largest river in  
133 Europe, the Danube River. The upper reaches of the five focal streams are situated within the  
134 forested area of Medvednica Nature Park to the north/northwest of Zagreb. The sampling  
135 sites were classified as woodland (n = 5), agricultural (n = 4) or urban (n = 6) based on the  
136 surrounding land use and proximity to the city centre. The woodland sites were characterised  
137 by a dense canopy cover, low light availability and sparse in-stream vegetation. However,  
138 there were dense stands of in-stream vegetation in the open canopy at urban and agricultural  
139 sites characterized by scarce riparian vegetation (mostly C4-grasses). The elevation of  
140 woodland sites ranged from 206-395 m a.s.l., agricultural sites from 132-217 m a.s.l., and  
141 urban sites from 155-161 m a.s.l. (Fig. 1). The physical, chemical and biological  
142 characteristics were measured at each location between late April and early May 2017.

143



144 *Physical and chemical parameters*

145 Physical and chemical stream parameters were measured to identify environmental  
146 characteristics that have the potential to alter macroinvertebrate diets, isotopic composition,  
147 and food web structure across the study sites (Table S1). The average stream width, depth  
148 and flow velocity (flow velocity meter P600, Dostman electronic GmbH) at the three cross-  
149 sectional stream areas were measured, to give an estimate of the stream discharge. We also  
150 measured in situ water temperature ( $^{\circ}\text{C}$ ), dissolved oxygen concentration ( $\text{mg L}^{-1}$ ) and  
151 saturation (%) using oximeter OXI 96 (WTW, Germany), conductivity ( $\mu\text{S cm}^{-1}$ ) using  
152 conductivity meter Hach Sension 5 (Hach Company, USA), and pH using pH-meter 330i  
153 (WTW, Germany). At each site, an additional 1-L water sample was taken for laboratory  
154 analysis of the chemical parameters that could not be measured *in situ*. Alkalinity and total  
155 water hardness (TWH) were measured to describe the amount of calcium or magnesium  
156 carbonate dissolved in water. Alkalinity measures the amount of negative carbonate ( $\text{CO}_3^{2-}$ )  
157 and bicarbonate ( $\text{HCO}_3^-$ ) ions, while water hardness describes the amount of positive calcium  
158 ( $\text{Ca}^{2+}$ ) and magnesium ( $\text{Mg}^{2+}$ ) ions. Alkalinity, total water hardness, and concentrations of  
159 nitrite, nitrate and orthophosphates were determined using the respective standardized  
160 methods described by APHA (1985). Total chemical oxygen demand (COD), used to assess  
161 the content of dissolved organic matter in water, was determined following the procedure in  
162 Deutsches Institut für Normung (1986).

163

164 *Consumer and resource sampling and processing*

165 We collected macroinvertebrates using a kick and sweep sampling method by disturbing the  
166 stream bed with a kicking action and using a benthic hand net (250- $\mu\text{m}$  mesh size), ensuring  
167 that individuals from all microhabitats were represented in each sample. From the samples  
168 collected at each site, we immediately separated predatory species (to prevent predation) and

169 all individuals were manually placed in containers filled with clean stream water and  
170 refrigerated at 4°C for 24 hours in order to empty their guts. We identified all  
171 macroinvertebrate individuals to the lowest possible taxonomic resolution, mainly genus  
172 (Table S2). We have sampled 2-20 individuals from each of the dominant taxa (depending on  
173 body size) and there were  $9.4 \pm 1.03$  dominant taxa (mean  $\pm$  SE) per site (Table S1). A total  
174 of 28 macroinvertebrate taxa from the 15 study sites were classified as non-predatory primary  
175 consumers, and 19 taxa were classified as predators. Based on their dietary preferences and  
176 following Moog (2002), we further classified the non-predatory primary consumers into five  
177 functional feedings groups. These functional feedings groups (FFGs) included detritivores,  
178 shredders, grazers, passive filterers, and active filterers. Because this method characterises  
179 each FFG as proportional contributions to a macroinvertebrate feeding function, each taxon  
180 was assigned to the FFG with the greatest contribution to its diet. For the subsequent  
181 analyses, we estimated dietary contributions of each predatory taxa at each site to yield  
182 multiple estimates at each site. The same method was applied to individual functional groups  
183 in the primary consumer diet estimates.

184 Potential dietary items from both allochthonous and autochthonous resources, i.e.  
185 periphyton separated from associated filamentous algae; particulate organic matter including  
186 leaf litter and other coarse particulate organic matter (CPOM – particles > 1 mm in diameter),  
187 as well as fine particulate organic matter (FPOM – particles 0.45  $\mu$ m – 1 mm in diameter),  
188 moss, aquatic and terrestrial macrophytes were collected at each site and stored in separate  
189 falcon tubes or polythene plastic bags. Terrestrial vegetation was sampled within a two-metre  
190 riparian zone from the stream edge. The finest organic matter fraction (FPOM) was collected  
191 directly into the falcon tube from slow-flowing areas at the edge of each stream and  
192 concentrated by repetitive sieving (250- $\mu$ m mesh size). In the laboratory, we manually  
193 removed animals and coarse minerals from the FPOM samples, to avoid the potential

194 interference among stable isotope ratio values. Periphyton was brushed off randomly selected  
195 rocks (with at least 50% coverage of biofilm) and subjected to manual exclusion of small  
196 invertebrates and detritus that might contaminate the samples and affect the  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$   
197 values of the biofilm. Two replicates of periphyton were processed for the respective content  
198 of chlorophyll-*a* (Chl *a*,  $\mu\text{g cm}^{-2}$ ) following the ethanol extraction procedure of Nusch (1980).  
199 All collected resource and macroinvertebrate samples were stored at  $-80^\circ\text{C}$  and then dried at  
200  $60^\circ\text{C}$  until processed for isotope analysis.

201

### 202 *Stable isotope analysis*

203 For the isotope analysis of the larger predatory taxa (e.g., Heteroptera, Odonata, Plecoptera),  
204 2-5 individuals were used, whereas for the analysis of the smaller taxa (e.g., Chironomidae,  
205 Simuliidae, Baetidae), at least ten individuals were pooled. In total, we analysed 359  
206 invertebrate samples for carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) stable isotope ratios.

207 Dried samples were grounded to a fine powder and stored in plastic tubes. Aliquots of  
208  $0.8 \pm 0.05$  mg (for invertebrates) and  $2.5 \pm 0.05$  mg (for resources) were placed in 8 x 5 mm  
209 tin capsules and analyzed by CF-IRMS (Sercon Integra 2 Stable Isotope Analyser, Crewe,  
210 UK). Carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) stable isotope ratios were calculated as  
211  $[(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000\text{‰}$ , where R is the ratio of heavy to light isotope,  $R_{\text{sample}}$  is from  
212 the sample, and  $R_{\text{standard}}$  is the international standard value. The isotopic standards were  
213 atmospheric air for nitrogen and PeeDee belemnite for carbon. Sercon software automatically  
214 corrected the delta values for the effects of drift between reference material combustions.  
215 Because lipids are depleted in  $^{13}\text{C}$ , they can bias the  $\delta^{13}\text{C}$  values of a bulk sample relative to  
216 the variation in lipid content between organisms (Perkins et al., 2013; Post et al., 2007). To  
217 account for variable lipid contents in animal and plant tissues, we measured the total C and N

218 content of each sample using CF-IRMS, and then applied lipid-correction models to stable  
219 isotope data as described in McConnaughey & McRoy (1979).

220

### 221 *Statistical analyses*

222 In order to estimate the effect of land use on the resource flow through the stream food web,  
223 we employed a SI (stable isotope) mixing model in the R package *MixSIAR* (Stock &  
224 Semmens, 2013) and estimated the proportional contribution of different food sources to the  
225 diets of macroinvertebrate consumers. For each site, separate SI mixing models were used to  
226 estimate dietary contributions of basal resources to primary consumers, and of prey to  
227 predators. These estimates were derived from contrasts in stable isotope values between  
228 dietary resources, and the consequent fractionation of the heavier isotope upon consumption  
229 (Jackson, Inger & Parnell 2011; Parnell et al., 2013). Because the trophic enrichment factors  
230 (TEF) vary across a range of environmental characteristics (McCutchan Jr, Lewis Jr &  
231 Kendall 2003; Vanderklift & Ponsard, 2003), we calculated our own FFG-specific TEF  
232 values based on our data as described in Caut et al., (2009). These were  $0.98 \pm 0.29\%$  (for  
233  $^{13}\text{C}$ ) and  $1.82 \pm 1.27\%$  (for  $^{15}\text{N}$ ) for the predator SI mixing models, and we averaged the  
234 calculated TEF values of individual primary consumer FFGs to yield a single value of  $0.94 \pm$   
235  $0.33\%$  ( $^{13}\text{C}$ ) and  $1.95 \pm 1.27\%$  ( $^{15}\text{N}$ ) for the primary consumer SI mixing models.

236 To increase the SI mixing model's performance, we pooled the basal resources for the  
237 primary consumer SI mixing models into three ecologically similar groups: LAR - lower  
238 aquatic resources (periphyton, FPOM, filamentous algae), HAR - higher aquatic resources  
239 (aquatic moss, submerged and emergent aquatic macrophytes) and terrestrial resources  
240 (CPOM including leaf litter, terrestrial macrophytes) (Brett, 2014; Nielsen et al., 2018;  
241 Phillips et al., 2014). Submerged aquatic macrophytes live entirely beneath the water surface,

242 whereas emergent plants are rooted in the stream bottom, but have parts projecting above the  
243 water surface. The potential prey taxa for the predator SI mixing model were classified into  
244 five functional feeding groups as shredders, grazers, detritivores, passive filterers and active  
245 filterers. Prior to the analysis, we used MANOVA to show that the individual prey groups  
246 (Wilks' lambda = 0.391,  $P < 0.001$ ) and resource groups (Wilks' lambda = 0.808,  $P < 0.001$ )  
247 differ in their nitrogen ( $\delta^{15}\text{N}$ ) and carbon ( $\delta^{13}\text{C}$ ) stable isotope ratios. The results of the SI  
248 mixing models were used to compare the contribution of each resource to its consumers  
249 across the three land use types by carrying out a MANOVA and then employing one-way  
250 bootstrapped analyses of variance (ANOVAs), with 1000 iterations. The significance was  
251 conservatively assessed with Bonferroni adjustments of alpha values. For this analysis, we  
252 used the functions *boot* and *ran.gen* from the *boot* package in R.

253 We used the R package SIBER to estimate an isotopic variance of predators, their  
254 potential prey (primary consumers), basal resources and two functional feeding groups  
255 (detritivores and grazers) that were common at the majority of sites (Table S3). We estimated  
256 isotopic variance based on multivariate, ellipse-based metric (SEAc, % $^2$ ), which is robust to  
257 small and unequal sample sizes (Jackson, Inger & Parnell 2011). Moreover, we calculated the  
258 mean nitrogen ( $\delta^{15}\text{N}$ ) and carbon ( $\delta^{13}\text{C}$ ) stable isotope ratios for each of these groups. All  
259 these metrics were calculated at the site level, to yield single site-based estimates. We also  
260 calculated four community-wide characteristics using the carbon and nitrogen stable isotope  
261 ratios for all macroinvertebrate taxa present at individual sites (Table S4): (i) mean nearest  
262 neighbour distance in isotopic niche space (MNND), indicating the resilience of the food web  
263 to environmental change through trophic redundancy (i.e. several functional groups at each  
264 trophic level); (ii) standard deviation of the nearest neighbour distance in the isotopic niche  
265 space (SDNND), indicating the uniformity of isotopic signature within groups, providing a  
266 further estimate of food web stability; (iii)  $\delta^{15}\text{N}$  and (iv)  $\delta^{13}\text{C}$  ranges, reflecting the variety of

267 trophic levels and basal resources that are exploited as a food source by the macroinvertebrate  
268 assemblages (Jackson, Inger & Parnell 2011; Layman, Arrington & Montaña 2007; Parnell et  
269 al., 2013). Finally, we estimated the length of the food chain as a difference in nitrogen stable  
270 isotope ratios between a consumer with the highest  $\delta^{15}\text{N}$  signature and a basal resource with  
271 the lowest  $\delta^{15}\text{N}$  signature. We then applied the linear mixed effects model (LME) to test  
272 whether these characteristics differ among the three land use types. We treated individual site  
273 as a random factor to account for non-measured (random) variation among the sites (Pinheiro  
274 & Bates, 2000).

275 Finally, we analysed the impact of key physico-chemical characteristics (Fig. S1a and  
276 b) associated with the different land use types on the isotopic food-web metrics. To reduce  
277 the potential for multicollinearity among the physico-chemical characteristics, we applied a  
278 Principal Component Analysis (PCA). The axis that explained the most variation in the data  
279 (PC1; Table S5) was used as a predictor of the food-web metrics using the linear mixed  
280 effects model (LMEs); PC1 was a fixed factor and the individual site was a random factor.  
281 All statistical analyses were performed using the language environment R version 3.2.2 (R  
282 Development Core Team, 2015).

283

## 284 **Results**

### 285 *Resource flow through food webs*

286 We surveyed 47 macroinvertebrate taxa (Table S2). Woodland sites were dominated by  
287 Ephemeroptera (37% of the taxa), agricultural sites were dominated by the family  
288 Chironomidae (40% taxa), whereas urban sites were dominated by family Simuliidae (40%  
289 taxa).

290 The contributions of basal resources to the diets of primary consumers, inferred from  
291 the SI mixing model, were influenced by the surrounding land use (MANOVA; Wilks'  
292  $\lambda = 0.52$ ,  $P < 0.001$ , Fig. 2a). Submerged and emergent aquatic macrophytes (HAR)  
293 contributed more to the diets of primary consumers at urban areas than to the diet of primary  
294 consumers at either agricultural or woodland sites (bootstrapped ANOVA,  $t = 20.7$ ,  $P = 0.03$ ,  
295 Fig. 2a). In contrast, terrestrial resources and lower LARs did not differ in their relative  
296 contributions to the diets of primary consumer among the three land use types (terrestrial:  $t =$   
297  $3.06$ ,  $P = 0.192$ ; LARs:  $t = 2.62$ ,  $P = 0.245$ ; Fig. 2a).

298 Catchment land use modified the contribution of the different prey functional groups  
299 to the diets of macroinvertebrate predators (MANOVA; Wilks'  $\lambda = 0.38$ ,  $P = 0.009$ ,  
300 Fig. 2b). This effect was mostly driven by active filterers that were not found at either  
301 agricultural or woodland sites and therefore contributed less to predator diets at those sites  
302 (bootstrapped ANOVA,  $t = 3.5$ ,  $P = 0.02$ , Fig. 2b).

303

#### 304 *Isotopic variance and food-web metrics*

305 The land use type had no effect on the isotopic variation (SEAc) of basal resources (LME,  $F_{2, 12}$   
306  $= 2.80$ ,  $P = 0.100$ ; Fig. 3a), potential prey (LME,  $F_{2, 12} = 0.53$ ,  $P = 0.601$ ; Fig. 3b), or  
307 macroinvertebrate predators (LME,  $F_{2, 9} = 0.05$ ,  $P = 0.948$ ; Fig. 3c). However, there was a  
308 strong effect of land use on the mean  $\delta^{15}\text{N}$  of basal resources (LME,  $F_{2, 12} = 6.83$ ,  $P = 0.011$ ;  
309 Fig. 4a), potential prey (LME,  $F_{2, 12} = 10.46$ ,  $P = 0.002$ ; Fig. 4b), and macroinvertebrate  
310 predators (LME,  $F_{2, 9} = 21.64$ ,  $P < 0.001$ ; Fig. 4c). All trophic groups at agricultural and urban  
311 sites were enriched in  $\delta^{15}\text{N}$  relative to those at woodland sites (Fig. 4). There was no effect of  
312 land use on the mean  $\delta^{13}\text{C}$  of resources, potential prey or predators (Table S6). The effect of  
313 land use type on the isotopic variation (Fig. S2),  $\delta^{15}\text{N}$ , and  $\delta^{13}\text{C}$  of detritivores and grazers

314 closely matched the effects found for predators and prey, except for grazers being more  
315 enriched in  $\delta^{13}\text{C}$  at agricultural and urban sites (Table S6).

316 The mean neighbour distance in isotopic space (MNND) was higher (indicating  
317 lower resilience) at urban sites than at agricultural and woodland sites (LME;  $F_{2,12} = 4.51$ ,  $P$   
318  $= 0.035$ ). The standard deviation of nearest neighbour distance (SDNND) was marginally  
319 more uniform at urban sites compared to agricultural and woodland sites (LME;  $F_{2,12} = 3.73$ ,  
320  $P = 0.055$ ). However, there was no effect of land use on the  $\delta^{15}\text{N}$  range (LME;  $F_{2,12} = 2.35$ ,  $P$   
321  $= 0.137$ ) and  $\delta^{13}\text{C}$  range (LME;  $F_{2,12} = 0.59$ ,  $P = 0.570$ ) of macroinvertebrates or on the  
322 length of the food chain (LME;  $F_{2,12} = 1.22$ ,  $P = 0.330$ ).

323 The PC1 axis explained 51.1% of the variation in the data of the physico-chemical  
324 characteristics (Table S5). Water conductivity, total water hardness, nitrite, nitrate and  
325 orthophosphate were all positively correlated with the PC1 axis, whereas discharge was  
326 negatively correlated with PC1 (Fig. S1a, Table S5). Temperature, pH, and chlorophyll-*a* and  
327  $\text{O}_2$  concentrations were positively correlated with the PC2 axis (explaining 15.5% of the  
328 variation; Fig. S1a; Table S5). PCA illustrated the environmental differences among sites  
329 according to the water physico-chemical characteristics (Fig. S1a and b). PCA aligned most  
330 woodland and agricultural sites along a gradient of increasing discharge. Urban sites were  
331 mostly aligned along gradients of increasing conductivity, total water hardness, nutrient,  
332 chlorophyll-*a*, oxygen concentrations, pH and water temperature (Fig. S1a).

333 The suite of physico-chemical site characteristics was related to the food-web metrics.  
334 There was a significant positive relationship between PC1 and the measure of trophic  
335 redundancy (MNND) (LME;  $F_{1,13} = 16.10$ ,  $P = 0.002$ , Fig. 5a), PC1 and the standard  
336 deviation of niche measures (SDNND) (LME;  $F_{1,13} = 8.95$ ,  $P = 0.010$ , Fig 5b), and between  
337 PC1 and the mean  $\delta^{15}\text{N}$  (LME;  $F_{1,13} = 9.30$ ,  $P = 0.009$ , Fig. 5c). However, there was no



338 relationship between PC1 and the  $\delta^{15}\text{N}$  range (LME;  $F_{1,13} = 2.58$ ,  $P = 0.132$ , Fig 5d) or  
339 between PC2 and any of the food-web metrics (Table S7).

340

## 341 **Discussion**

342 Whereas previous work has focused on the effect of morphological habitat features on the  
343 functioning of urban streams (Walsh et al., 2005), we demonstrate that changes to the  
344 physical and chemical characteristics in urban and agricultural zones shift the composition  
345 and availability of resources for aquatic consumers, and alter the flow of energy through the  
346 entire stream food web. The changes in physical, chemical and biological characteristics  
347 associated with intensive land use resulted in higher  $\delta^{15}\text{N}$  values of stream communities,  
348 reduced trophic redundancy (MNND), and increased omnivorous feeding (as suggested by  
349 similar  $\delta^{15}\text{N}$  values between macroinvertebrate predators and primary consumers) and niche  
350 uniformity (SDNND). These findings improve the mechanistic understanding of community  
351 structure and function under the influence of intensive land use.

352 The changes in diets of primary consumers and predators in response to composition of  
353 resources across different land use indicate strong bottom-up control of macroinvertebrate  
354 communities. Such bottom-up control has been reported in various freshwater (Kiffney,  
355 Buhle, Naman, Pess, & Klett, 2014; Shurin, Clasen, Greig, Kratina, & Thompson, 2012),  
356 marine (Capuzzo et al., 2017) and terrestrial (Halvorson, Fuller, Entrekin, Scott, & Evans-  
357 White, 2018; Lister & Garcia, 2018) ecosystems. Our results show that the bottom-up effects  
358 of land use may extend beyond individual consumer-resource interactions, and cascade to the  
359 structure of the entire food web. The positive relationship between the standard deviation of  
360 niche measures and the PC1 axis characterised by nutrient inputs suggests that there are less  
361 diverse dietary resources available to consumers, and more homogeneous pathways of energy

362 flow to the upper trophic positions at the sites with high nutrient load and lower discharge.  
363 Trophic redundancy among all macroinvertebrate taxa was highest, suggesting more complex  
364 food webs (Cucherousset & Villéger, 2015), at woodland and agricultural sites with low  
365 levels of nutrients and high discharge. In contrast, the urban sites with high nutrient loading  
366 and lower discharges were characterised by having lower trophic redundancy and a more  
367 homogenised energy flow as indicated by higher MNND and SDNND values, respectively.  
368 Local extinctions in ecosystems with low trophic redundancy can lead to a collapse of a  
369 functional group (Mason, Mouillot & Graham 2013) and negatively affect the functioning of  
370 the entire ecosystem (Heilpern, Weeks, & Naeem, 2018; Vinebrooke et al., 2004; Wallace &  
371 Webster, 1996).

372       The nitrogen stable isotope ratios were strongly influenced by catchment land use. In  
373 particular, all trophic groups had higher  $\delta^{15}\text{N}$  values along an increased urban and agricultural  
374 influence, in agreement with other studies (Baumgartner & Robinson, 2017; Pastor et al.,  
375 2014). Similar  $\delta^{15}\text{N}$  enrichment of macroinvertebrate consumers can indicate longer food  
376 chains in habitats with higher influence of autochthonous resources of higher nutritional  
377 quality (Lau et al., 2009; Junker & Cross, 2014). However, there was no support for longer  
378 food chains at urban or agricultural sites, potentially due to the weaker influence of  
379 productivity in smaller ecosystems (Ward & Mccann, 2017). Enrichment of basal resources  
380 (Chen, McGowan, Zeng, Xu, & Yang, 2017; Cole et al., 2004) and stream organisms  
381 (Harrington, Kennedy, Chamberlain, Blum, & Folt, 1998) in  $^{15}\text{N}$  has been also linked to  
382 higher nitrate input (Bergfur, Johnson, Sandin, & Goedkoop, 2009) and can be caused by  
383 sewage-sourced nitrogen pollution and greater inputs of polycyclic aromatic hydrocarbons  
384 (Saito et al., 2008). Whereas the natural and fertilizer sources of nitrogen are generally  
385 depleted in  $^{15}\text{N}$  (Risk, Lapointe, Sherwood, & Bedford, 2009), the sewage derived nitrogen  
386 inputs are generally enriched in  $^{15}\text{N}$  because of the preferential use of the lighter isotope by

387 bacteria during denitrification (Heaton, 1986). The sewage pollution in combination with low  
388 water discharge might have also contributed to the lower trophic redundancy of  
389 macroinvertebrates in some urban sites (Coors & De Meester, 2008; Vinebrooke et al., 2004).

390 The similar  $\delta^{15}\text{N}$  values between macroinvertebrate predators and primary consumers  
391 may be driven by predators feeding predominantly on prey with lower  $\delta^{15}\text{N}$  signature. Some  
392 predators and primary consumers can be omnivorous, which may increase  $\delta^{15}\text{N}$  for primary  
393 consumers or reduce  $\delta^{15}\text{N}$  for predators. Moreover, the basal resources at our sites are  
394 composed of diverse groups that widely vary in  $\delta^{15}\text{N}$ . Furthermore, the urban and agricultural  
395 sites have rapidly changing environmental conditions and rapid shifts in the composition of  
396 basal resources over time (E. L. Price and M. Sertić Perić, personal observation, February  
397 2016 – May 2017). Consequently, the lower  $\delta^{15}\text{N}$  in predators may reflect the discrepancy  
398 between the isotope composition of the rapidly changing resources and the primary and  
399 secondary consumers, especially at these urban and agricultural sites. Commonly assumed  
400 constant trophic enrichment factor between predators and their potential prey is not always  
401 found under the changing field conditions (Post, 2002; Vanderklift & Ponsard, 2003).

402 The changes in land use can alter the composition and availability of dietary resources  
403 for consumers, since higher nutrient loads facilitate the growth of a different community  
404 assemblage (Allan, 2004; Dülger, Heidbüchel, Schumann, Mettler-Altman, & Hussner,  
405 2017). Whereas high nutrient concentrations likely contributed to the increased population  
406 densities of passive filterers and reduced densities of shredders at our urban sites, large  
407 predaceous Plecoptera (that are sensitive to nutrient pollution) were found at our woodland  
408 sites only (Table S2). Closed canopy cover in woodland sites also led to a reduction in  
409 periphyton primary production and a scarcity of in-stream higher aquatic resources. The  
410 greater contribution of macrophytes to the diets of primary consumers at urban sites reflected  
411 their prevalence at those sites relative to agricultural and woodland sites. Macrophytes can

412 reduce the water flow velocity and the total discharge, which agrees with the negative  
413 relationship between discharge and nutrient levels found in our study and elsewhere (Baldy,  
414 Trémolières, Andrieu, & Belliard, 2007; Dodds & Biggs, 2002; Fig. S1a and b). Subsequent  
415 decomposition of macrophytes and their ability to trap fine particles and aquatic organisms  
416 within their roots and stems (Jones, Collins, Naden, & Sear, 2012; Sertić Perić, Miliša,  
417 Kepčija, Primc-Habdija, & Habdija, 2011) further enhances their contribution to the diet of  
418 macroinvertebrates. By removing the epiphytic cover from macrophytes, macroinvertebrate  
419 grazers might further promote their growth (Bronmark, 1985; Sand-Jensen & Borum, 1984).  
420 In agreement with recent findings (Rovira, Alcaraz, & Trobajo, 2016), our work suggests that  
421 intensive land use may increase the role of macrophytes in stream food webs.

422         The grouping of dietary items, into the higher and lower aquatic resources and  
423 terrestrial resources, can be applied to examine larger-scale ecological patterns in resource  
424 use (Neres-Lima et al., 2017; Phillips, Newsome, & Gregg 2005). We expected terrestrial  
425 resources to be more important at woodland sites as leaf litter dominates the nutrient input of  
426 many forested streams, and the canopy reduces light availability for growth of autochthonous  
427 primary producers (Neres-Lima et al., 2017; Rounick, Winterbourn, & Lyon 1982). However,  
428 besides leaf litter, the terrestrial resources also included terrestrial plants (mainly grasses and  
429 riparian herbaceous plants), which largely contributed to the consumers' diet at urban and  
430 agricultural sites. The lack of leaf litter and the dominance of riparian grass (i.e. C4 plants) at  
431 the urban sites was further reflected in the absence of macroinvertebrate shredders, which  
432 mainly rely on processing the leaf litter-CPOM (Moog, 2002). Furthermore, considering their  
433 range in  $\delta^{13}\text{C}$  values (-39.4 to -11.4 ‰), primary consumers can switch their diet from  
434 riparian vegetation sources (ranging from -27 ‰ to -13 ‰ within the terrestrial C3 and C4  
435 plants, respectively) to aquatic macrophytes ( $\delta^{13}\text{C}$  range: -27 ‰ to -20 ‰) and periphyton  
436 ( $\delta^{13}\text{C}$  range: -35 ‰ to -18 ‰) (Finlay & Kendall, 2007). This suggests that the herbivorous

437 and omnivorous macroinvertebrates can select autochthonous resources, even when terrestrial  
438 food resources are common, which agrees with invertebrate feeding patterns in Danish forest  
439 streams (Friberg & Jacobsen, 1994).

440 Despite the difference in the dietary sources, macroinvertebrate consumers had similar  
441 overall isotopic variance across the three land use categories. This may indicate that a similar  
442 range of habitats is being exploited by consumers (Rader et al., 2017). However, the measure  
443 of isotopic variance may include some individuals that may have obtained their isotopic  
444 signature from a region with a contrasting land use to the sites where they were sampled. We  
445 must also consider that isotopic estimates of diet contributions can be influenced by non-  
446 trophic determinants (Gorokhova, 2017), that dietary estimation can lack reliability when  
447 applied to complex diet mixtures (Nielsen et al., 2018) and is highly sensitive to missing  
448 resources (Phillips et al., 2014). Still, the isotope approach offers a robust space- and time-  
449 integrated overview of diet composition, which gives an insight beyond the limitations of  
450 morphological and molecular faecal and gut analyses.

451 We provide evidence for the strong influence of land use on  $\delta^{15}\text{N}$  enrichment of  
452 predators, primary consumers and basal resources. Functional and isotopic composition of  
453 basal resources and prey across land use types were reflected at the level of primary  
454 consumers and predators, respectively. This indicates a bottom-up control of food webs  
455 surrounded by intensive agriculture and urban development. More fragile food webs  
456 evidenced by low trophic redundancy in urban zones with high nutrient loads may be less  
457 resistant to ongoing and accelerating global and local environmental change. These findings  
458 demonstrate how alterations to land use reshuffle the flow of biomass and energy through  
459 ecosystems. Human population growth and increasing impacts of urbanization and  
460 agricultural land use across all trophic levels need to be considered in our efforts to  
461 understand, conserve and restore the human-modified ecosystems.

462

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474

**475 Author Contributions**

476 PK and MSP conceived the idea and designed the study; MSP and ELP collected the data;  
477 GQR, PK and ELP performed the statistical analyses. ELP and PK drafted the manuscript  
478 with inputs from all authors. All authors contributed substantially to revisions and the final  
479 format of the manuscript.

480

**481 Data Accessibility**

482 Data will be archived in the public archive Dryad (<http://datadryad.org>).

483

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739

740 **Figure Legends**

741 **Figure 1.** Locations of the fifteen study sites (red crosses) across the region of Zagreb,  
742 Croatia. The dark grey lines indicate the stream network in Zagreb, flowing from the northern  
743 area of Medvednica Nature Park through the human-modified areas and into the River Sava  
744 (thick black line). Text boxes linked to the sites contain information on the land-use category  
745 (W – woodland, A – agricultural, U – urban), altitude (m a.s.l.) and the mean  $\delta^{15}\text{N}$  values of  
746 macroinvertebrates at each site. The coloration of each box corresponds to its mean  $\delta^{15}\text{N}$   
747 value as indicated by the colour-key.

748

749 **Figure 2.** (a) Proportional contributions (mean  $\pm$  SE) of lower aquatic resources (LAR),  
750 higher aquatic resources (HAR) and terrestrial resources to the diets of primary consumers at  
751 urban, woodland and agricultural sites, as calculated by the SI mixing model. (b) Proportional  
752 contributions (mean  $\pm$  SE) of the detritivores, grazers, shredders, passive filterers, and active  
753 filterers to the diets of macroinvertebrate predators in urban, woodland and agricultural sites.

754

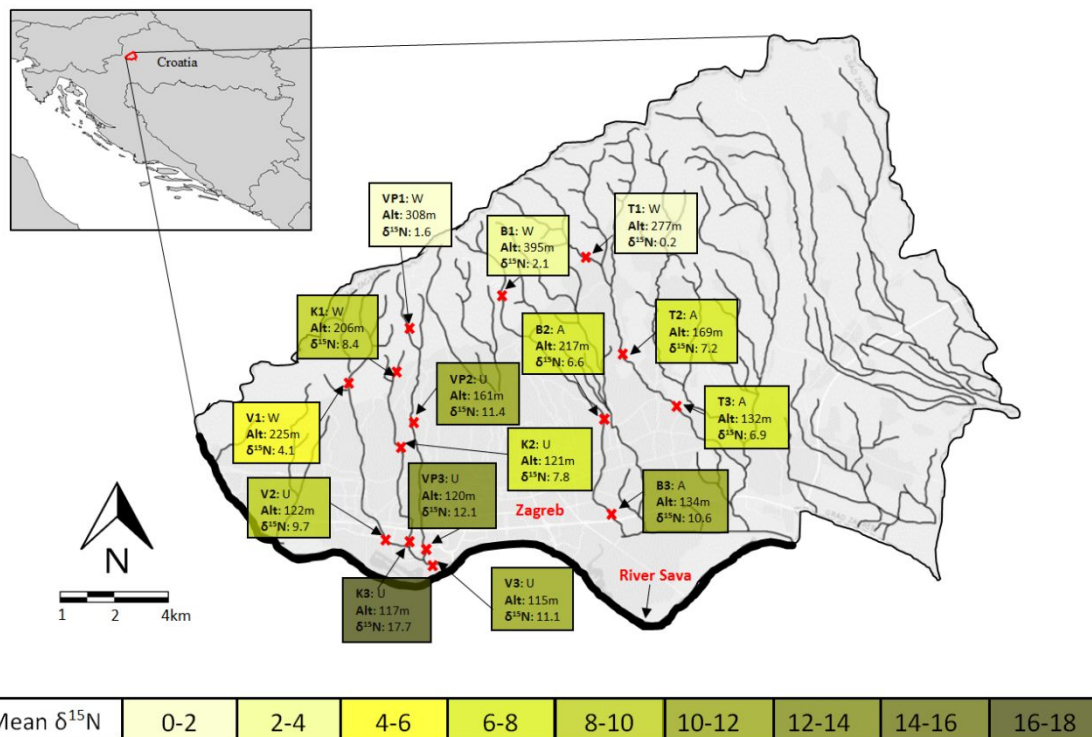
755 **Figure 3.** The isotopic variance illustrated as a size of ellipses ( $\text{SEAc}$ ,  $\%o^2$ ) for (a) basal  
756 resources, (b) potential prey, and (c) predators at each site. Red ellipses and symbols  
757 represent urban sites, black ellipses and symbols represent agricultural sites, and green  
758 ellipses represent woodland sites. The ellipses were calculated only for the sites that included  
759 at least five samples from the focal trophic group. Each data point represents one individual  
760 or an accumulation of individuals in one sample where a single specimen did not contain  
761 enough dry weight.

762

763 **Figure 4.** Nitrogen stable isotope ratios ( $\delta^{15}\text{N}$ , ‰) of (a) basal resources, (b) potential prey  
764 (primary consumers), and (c) predators across the three land use categories. The box plots  
765 illustrate the median (inner line), the interquartile range of the data (box), and the tails of the  
766 distribution (bars = 1.5 x interquartile range). Capital letters above the box plots denote  
767 treatments (land use categories) not significantly different from each other.

768

769 **Figure 5.** Relationship between the physico-chemical characteristics, represented by the  
770 Principal Component 1 axis (PC1; Fig. S1a & b) and (a) trophic redundancy (MNND), (b)  
771 standard deviation of niche measures (SDNND), (c) mean  $\delta^{15}\text{N}$ , (d)  $\delta^{15}\text{N}$  range at each site.  
772 The black circles show food-web metrics calculated at each site, the blue line represents a  
773 significant fit of the linear mixed effects model to the data, and the shaded area is the 95%  
774 confidence interval. There was no significant relationship between the PC1 and the  $\delta^{15}\text{N}$   
775 range (see Results). PC1 explained 51.1% of the variation in the physico-chemical  
776 characteristics at each site, and the concentrations of nitrites, nitrates, orthophosphates,  
777 conductivity and total water hardness were the strongest positive contributors to the PC1 axis.

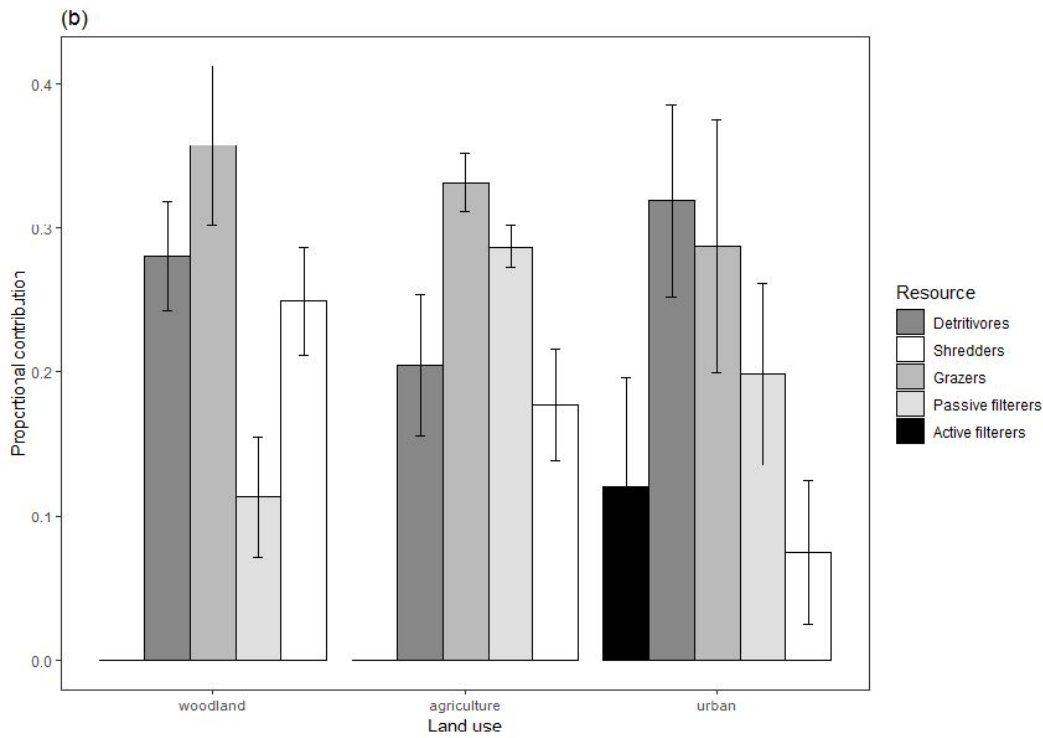
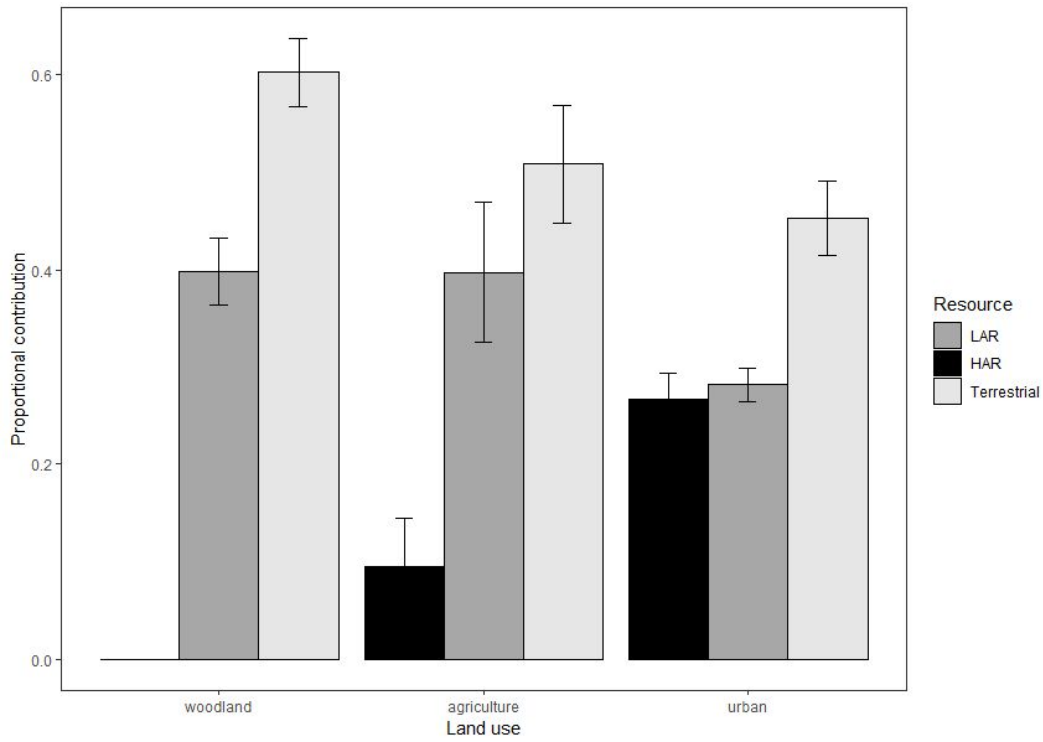


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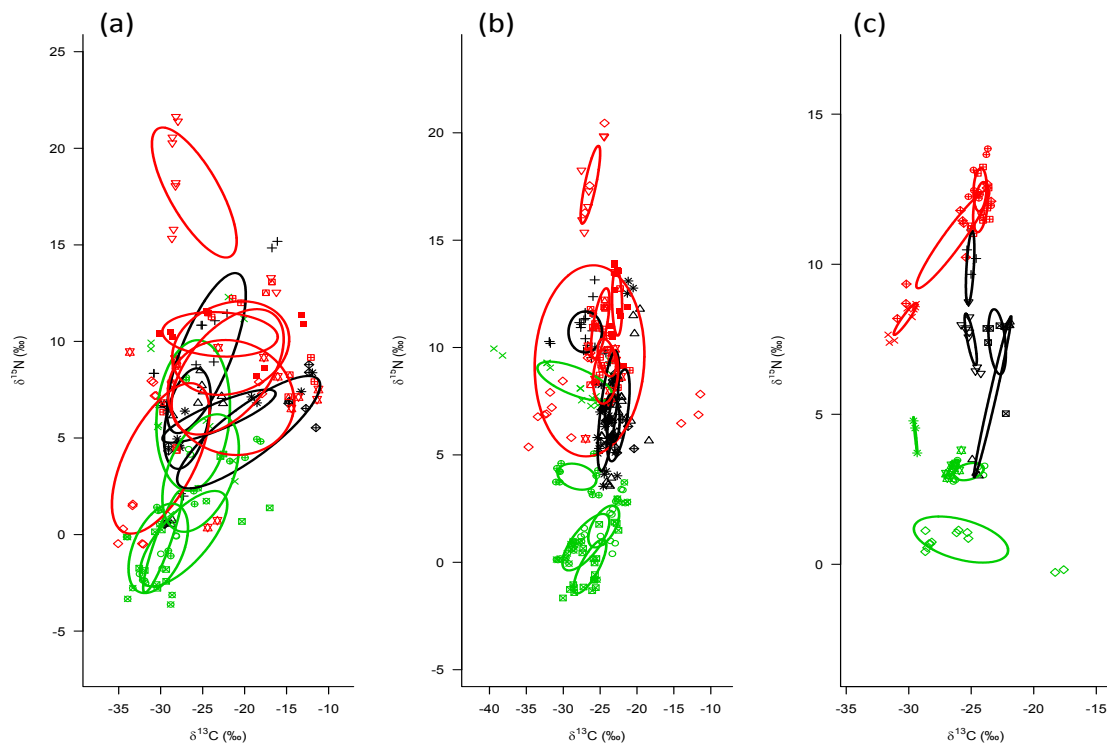
781 **Figure 1**



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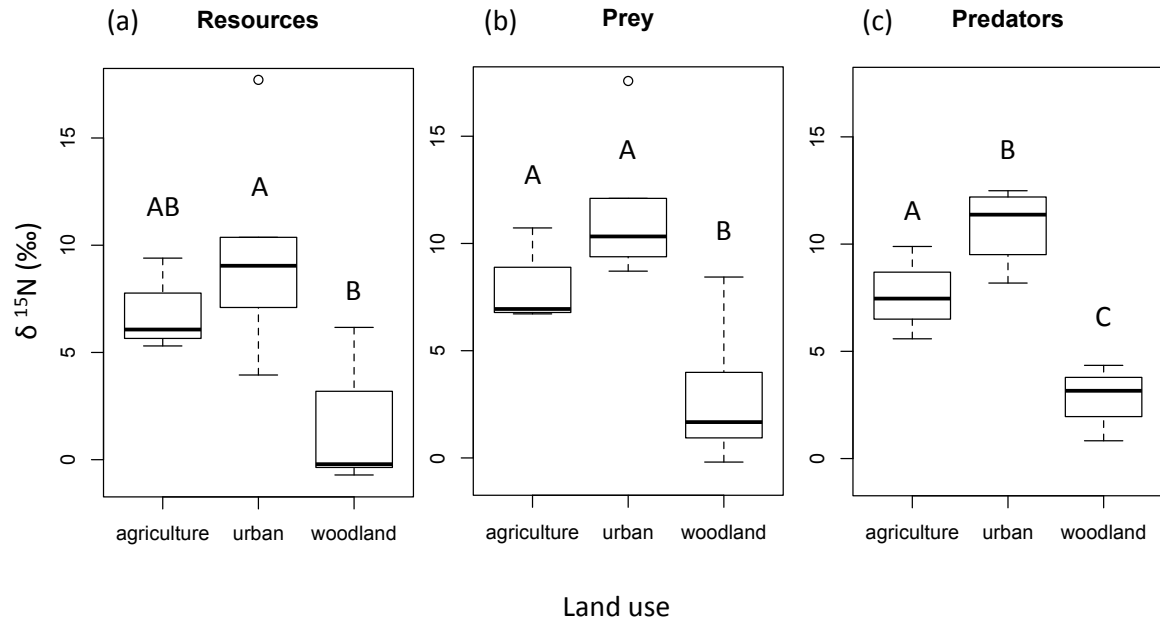
784 **Figure 2**



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786

787 **Figure 3**

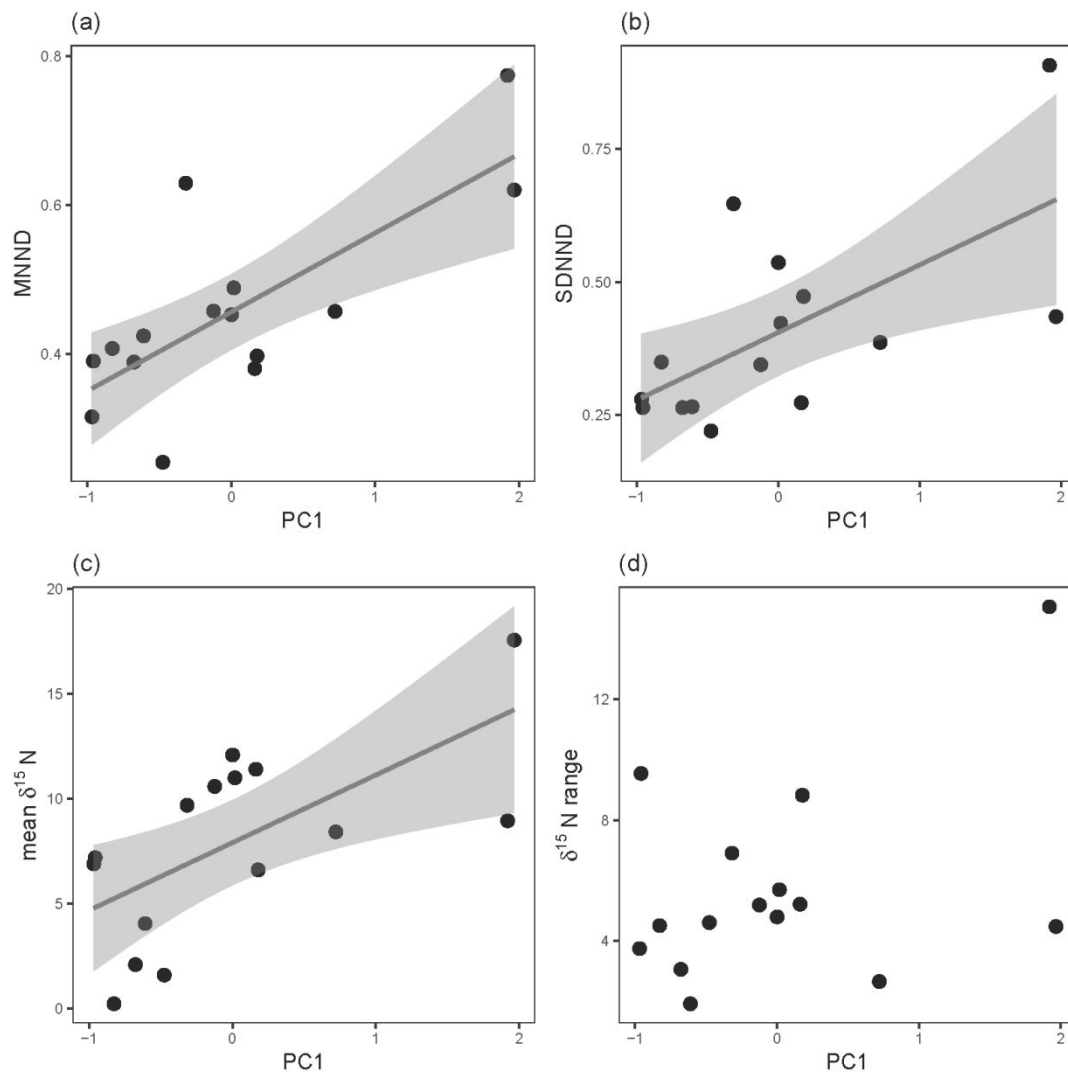


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790 **Figure 4**





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793 **Figure 5**

## Land use alters trophic redundancy and resource flow through stream food webs

### Supplementary Information

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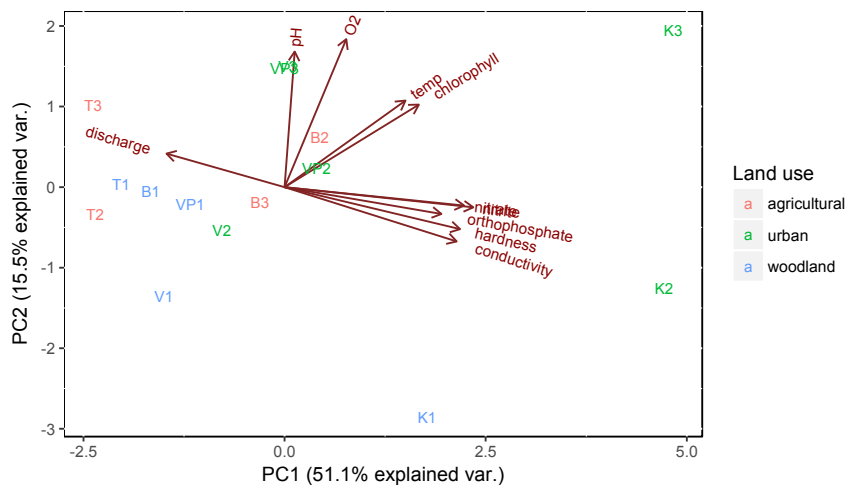
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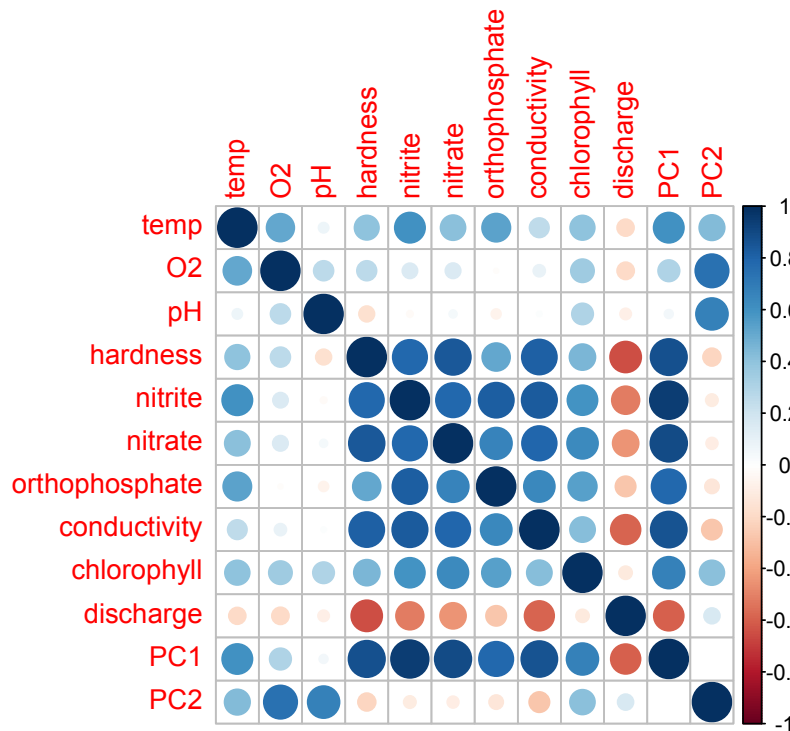
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## SUPPLEMENTARY FIGURES

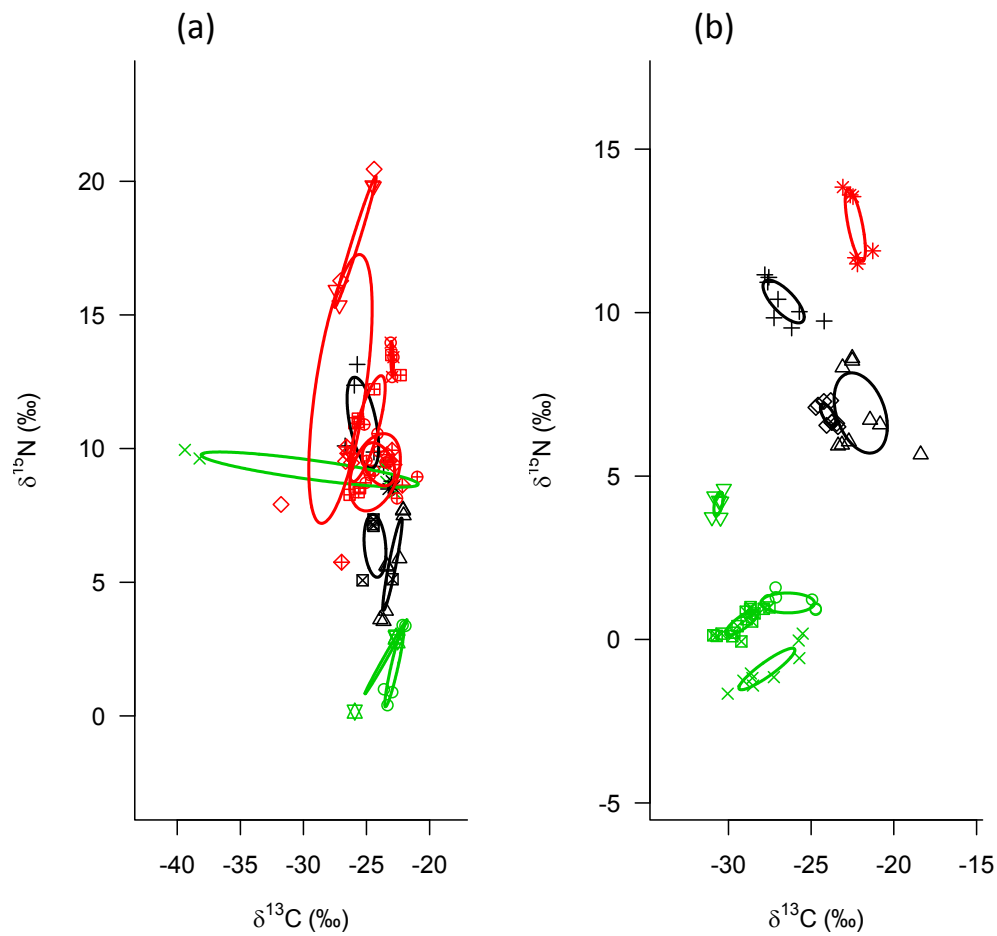
a)



b)



**Figure S1. (a)** The relationship between explanatory variables and the PC1 and PC2 axis for physico-chemical parameters. Explained variation (%) refers to how much of the total variation in physico-chemical characteristics can be described by each axis. The greater the length of the arrow, the greater the contribution of that variable to PC1 and PC2. Coloured points represent the relationship of each site with PC1 and PC2. O<sub>2</sub> – oxygen concentration (mg L<sup>-1</sup>); temp – water temperature (°C); chlorophyll - chlorophyll-*a* (Chl *a*, µg cm<sup>-2</sup>) concentration in periphyton samples. **(b)** Correlations matrix among explanatory variables and the PC1 and PC2 axis for physico-chemical parameters with circle size and colour intensity indicating the strength of the correlations.



**Figure S2.** The isotopic variance illustrated as a size of ellipses (SEAc, ‰<sup>2</sup>) for **(a)** detritivores and **(b)** grazers at each site. Red ellipses and symbols represent urban sites, black ellipses and symbols represent agricultural sites, and green ellipses represent woodland sites. The ellipses were calculated only for the sites that included at least five samples from the focal feeding group.

## SUPPLEMENTARY TABLES

**Table S1.** Physical and chemical characterization of the sampling sites under the three different land uses; Woodland (W), Agricultural (A) and Urban (U).

Stream	Site	Land use	Temperature	O <sub>2</sub>	pH	COD	TWH	Nitrite	Nitrate	Orthophosphate	Conductivity	Chlorophyll <i>a</i>	Discharge
			(° C)	(mg L <sup>-1</sup> )		(mg O <sub>2</sub> L <sup>-1</sup> )	(mg CaCO <sub>3</sub> L <sup>-1</sup> )	(mg L <sup>-1</sup> )	(mg L <sup>-1</sup> )	(mg L <sup>-1</sup> )	(µS cm <sup>-1</sup> )	(µg cm <sup>-2</sup> )	(m <sup>3</sup> s <sup>-1</sup> )
Vrapčak	V1	W	11.7	10.2	7.21	4.64	215.4	0.107	2.629	0.057	365	0.929	3.1
	V2	U	20.8	10.6	7.43	4.01	225.2	0.114	3.611	0.064	331	0.499	3.0
	V3	U	22.9	13.6	8.32	4.52	235.9	0.121	4.070	0.082	287	1.026	1.7
Kustošak	K1	W	12.9	9.7	7.31	2.00	283.9	0.249	5.305	0.169	674	0.000	0.5
	K2	U	24.6	8.2	8.05	6.99	298.2	0.458	6.629	0.267	660	3.167	0.6
	K3	U	26.1	15.9	8.35	5.42	287.5	0.392	6.152	0.229	636	4.114	0.8
Veliki potok	VP1	W	12.6	9.5	8.68	2.79	188.7	0.141	3.552	0.038	409	0.453	1.3
	VP2	U	16.7	9.7	8.85	3.85	197.6	0.147	4.394	0.192	476	1.391	2.4
	VP3	U	19.0	13.3	8.84	3.22	215.4	0.154	2.917	0.030	507	1.098	0.7
Bliznec	B1	W	10.4	10.2	8.51	7.23	211.8	0.097	1.820	0.050	367	1.010	2.0
	B2	A	12.2	10.7	8.45	3.65	222.5	0.130	5.405	0.102	445	3.897	4.2
	B3	A	13.4	10.3	8.33	4.32	233.2	0.143	4.941	0.060	476	1.267	4.8
Trnava	T1	W	14.1	9.7	8.10	2.04	145.1	0.102	2.082	0.112	261	1.281	3.1
	T2	A	16.3	9.7	7.87	1.93	147.7	0.093	1.776	0.108	332	0.000	5.0
	T3	A	18.9	10.6	8.17	2.12	151.3	0.105	2.023	0.097	278	1.184	8.7

**Table S2.** Taxonomic information and functional feeding groups (FFG) of stream macroinvertebrates found at each site and the respective land use. SHR – shredders, GRA – grazers, DET – detritivores, AFIL – active filterers, PFIL – passive filterers, PRE – predators. Land use: W – woodland, A – agricultural, U – urban. For the site codes and locations refer to Fig. 1 and Materials and Methods.

CLASS/ORDER/Family	Subfamily/Genus/Species	FFG	Presence	
			Site	Land use
<b>PLATYHELMINTHES</b>				
Tricladida	<i>Polycelis felina</i>	PRE	B2, T3, V1, VP1	W, A
<b>GASTROPODA</b>				
Lymnaeidae	<i>Pseudosuccinea columella</i>	GRA	B3, T2	A
	<i>Stagnicola</i> sp.	GRA	VP3, K3, V2	U
Physidae	<i>Physa</i> sp.	GRA	K2	U
<b>BIVALVIA</b>				
Sphaeriidae	<i>Pisidium</i> sp.	AFIL	K2	U
<b>OLIGOCHAETA</b>				
Lumbricidae	<i>Eiseniella tetraedra</i>	DET	B2, K2, T2, VP2	A, U
<b>HIRUDINOMORPHA</b>				
Hirudinomorpha gen. sp.		PRE	B2	A
<b>AMPHIPODA</b>				
Gammaridae	<i>Gammarus fossarum</i>	SHR	B1, B2, K1, T1, T2, T3, V1, VP1	W, A
<b>ISOPODA</b>				
Asellidae	<i>Asellus aquaticus</i>	DET	B3, K3, V2, V3	A, U
<b>COLEOPTERA</b>				
Elmidae	Elmidae gen. sp.	GRA	T1	W
<b>DIPTERA</b>				
Athericidae	<i>Atherix</i> sp.	PRE	T1	W
	<i>Ibisia marginata</i>	PRE	T1, VP1	W
Ceratopogonidae	Ceratopogonidae gen. sp.	PRE	B3	A
Chironomidae	Chironomini gen. sp.	DET	K3, V3	U
	Chironomus sp.	DET	B2, B3, V3, VP2, VP3, K2, T2, T3, V2	A, U
	Orthoclaadiinae gen. sp.	GRA/DET	B2, B3, K3, V3	A, U
	Tanypodinae gen. sp.	PRE	K2, T2, T3, V2, VP2	A, U
	Tanytarsini gen. sp.	DET	VP3	U
Limoniidae	Limoniidae gen. sp.	PRE	K1, K2	W, U
	<i>Limnophila</i> sp.	PRE	B1	W
Pediciidae	<i>Dicranota</i> sp.	PRE	T1	W
Simuliidae	<i>Prosimulium</i> sp.	PFIL	T2, T3	A
	<i>Simulium</i> sp.	PFIL	B2, B3, K2, T1, T2, V1, V2	W, A, U
Tipulidae	Tipulidae gen. sp.	SHR	T2, T3, VP3	A, U
<b>EPHEMEROPTERA</b>				
Baetidae	<i>Baetis</i> sp.	GRA/DET	B1, B3, VP1, VP2, T1, V1	W, A, U
	<i>Centroptilum luteolum</i>	GRA/DET	K1, T3	W, A
	<i>Procladius</i> sp.	DET	B2, VP1	W, A
Caenidae	<i>Caenis</i> sp.	DET	B3, T2, V3	A
Ephemerellidae	<i>Ephemerella</i> sp.	GRA/DET	B1	W
Ephemeridae	<i>Ephemera</i> sp.	AFIL	VP2	U
Heptageniidae	<i>Ecdyonurus</i> sp.	GRA/DET	B1, K1, T1, VP1	W
	<i>Heptagenia</i> sp.	GRA/DET	VP1	W
	<i>Rhitrogena</i> sp.	GRA	T3, VP1	W, A
<b>HETEROPTERA</b>				
Nepidae	<i>Ranatra</i> sp.	PRE	V2	U
<b>ODONATA</b>				
Aeshnidae	Aeshnidae gen. sp.	PRE	V2	U
Calopterygidae	<i>Calopteryx</i> sp.	PRE	V3	U
Coenagrionidae	<i>Coenagrion</i> sp.	PRE	V2, V3	U
Cordulegastridae	Cordulegastridae gen. sp.	PRE	T1, T3	W, A
Gomphidae	<i>Onychogomphus forcipatus</i>	PRE	B1, T3, V3, VP2, VP3	W, A, U
Platycnemididae	<i>Platycnemis pennipes</i>	PRE	V3	U
<b>PLECOPTERA</b>				
Chloroperlidae	<i>Chloroperla</i> sp.	PRE	VP1	W
Perlidae	<i>Perla</i> sp.	PRE	B1, VP1, T1	W
<b>TRICHOPTERA</b>				
Hydropsychidae	<i>Hydropsyche</i> sp.	PFIL	B2, B3, T1, T2, T3, VP3, K1	W, A, U
Limnephilidae	<i>Drusus</i> sp.	GRA	T1	W
	Limnephilidae gen. sp.	SHR	VP1	W
Rhyacophilidae	<i>Rhyacophila</i> sp.	PRE	V1, B2, T2	W, A
Sericostomatidae	<i>Sericostoma</i> sp.	SHR	B2	A

**Table S3.** The isotopic variance illustrated as a size of ellipses ( $SEAc$ ,  $\%o^2$ ) for all potential prey (primary consumers), predators, basal resources, detritivores and grazers per each site. We only calculated the ellipses for trophic and feeding groups that included at least five samples from the same site.

<i>Site</i>	<i>Land Use</i>	<i>SEAc</i> <i>PREY</i> ( $\%o^2$ )	<i>SEAc</i> <i>PREDATORS</i> ( $\%o^2$ )	<i>SEAc</i> <i>RESOURCES</i> ( $\%o^2$ )	<i>SEAc</i> <i>DETRITIVORES</i> ( $\%o^2$ )	<i>SEAc</i> <i>GRAZERS</i> ( $\%o^2$ )
<b>B1</b>	<i>Woodland</i>	5.57	1.25	9.02	1.70	1.94
<b>B2</b>	<i>Agricultural</i>	8.52	2.77	22.45	1.74	7.46
<b>B3</b>	<i>Agricultural</i>	7.00	1.46	45.14	7.46	2.42
<b>VP1</b>	<i>Woodland</i>	9.27	0.23	25.29	0.98	1.54
<b>VP2</b>	<i>Urban</i>	5.18	1.62	66.30	6.29	NA
<b>VP3</b>	<i>Urban</i>	3.50	NA	27.19	0.39	1.66
<b>T1</b>	<i>Woodland</i>	5.69	8.61	30.43	NA	2.09
<b>T2</b>	<i>Agricultural</i>	9.73	0.88	17.05	4.10	NA
<b>T3</b>	<i>Agricultural</i>	3.52	2.63	46.85	0.18	0.61
<b>K1</b>	<i>Woodland</i>	11.22	NA	57.40	12.80	NA
<b>K2</b>	<i>Urban</i>	108.21	0.61	60.63	38.91	NA
<b>K3</b>	<i>Urban</i>	5.14	NA	39.09	3.25	NA
<b>V1</b>	<i>Woodland</i>	5.19	0.14	42.22	NA	0.39
<b>V2</b>	<i>Urban</i>	7.45	5.32	74.31	9.77	NA
<b>V3</b>	<i>Urban</i>	3.40	1.26	59.43	3.30	NA

**Table S4.** Trophic metrics of each food web at all 15 sites at the three land use types in the surrounding catchments. The metrics for each network are  $\delta^{15}\text{N}$  range (NR),  $\delta^{13}\text{C}$  range (CR), total convex hull area (TA), mean distance to centroid (CD), mean distance to nearest neighbour (NND) and standard deviation of nearest neighbour distance (SDNND).

<i>Site</i>	<i>Land Use</i>	<i>NR</i>	<i>CR</i>	<i>NND</i>	<i>SDNND</i>
<b>B1</b>	<i>Woodland</i>	3.07	6.76	0.3895269	0.2644774
<b>B2</b>	<i>Agricultural</i>	8.84	6.53	0.3976789	0.4733168
<b>B3</b>	<i>Agricultural</i>	5.2	8.26	0.4580102	0.3451934
<b>VP1</b>	<i>Woodland</i>	4.62	9.6	0.2549206	0.2205836
<b>VP2</b>	<i>Urban</i>	5.23	4.05	0.3807053	0.2737085
<b>VP3</b>	<i>Urban</i>	4.81	2.28	0.453063	0.537001
<b>T1</b>	<i>Woodland</i>	4.52	12.44	0.4078513	0.3500275
<b>T2</b>	<i>Agricultural</i>	9.56	5.27	0.3908846	0.2643519
<b>T3</b>	<i>Agricultural</i>	3.76	4.51	0.3160091	0.2800542
<b>K1</b>	<i>Woodland</i>	2.67	16.62	0.4575171	0.3869496
<b>K2</b>	<i>Urban</i>	15.08	23.28	0.7743367	0.9074948
<b>K3</b>	<i>Urban</i>	4.49	3.1	0.6205092	0.4354267
<b>V1</b>	<i>Woodland</i>	1.93	5.83	0.4245844	0.2662198
<b>V2</b>	<i>Urban</i>	6.92	8.75	0.6296454	0.6474061
<b>V3</b>	<i>Urban</i>	5.71	4.24	0.4890857	0.4229855



**Table S5.** Results of Principal Component Analysis showing how much of the total variation can be explained by each PC axis (1-6), and the loadings of each physico-chemical parameter within each PC. Positive values and their corresponding parameters are inversely related to those with negative values.

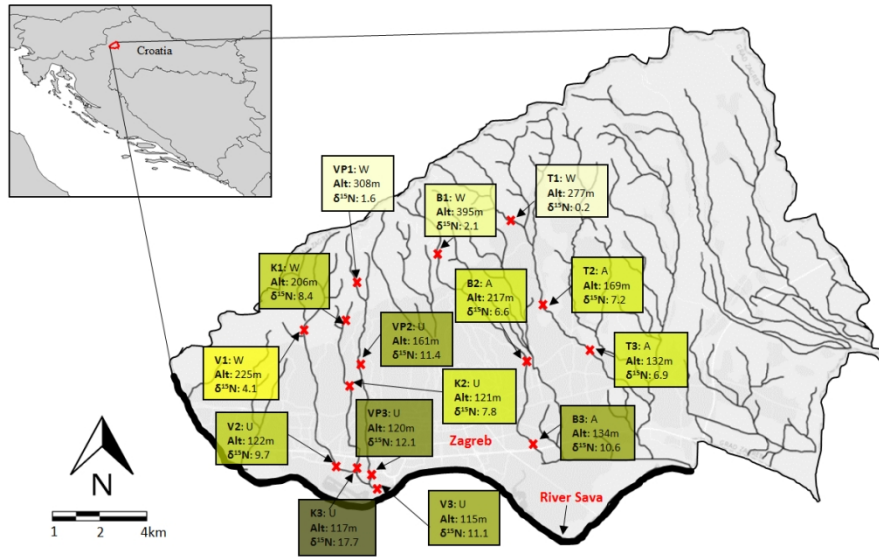
	<i>PC1</i> (51.1 %)	<i>PC2</i> (15.5 %)	<i>PC3</i> (10.6 %)	<i>PC4</i> (9.5 %)	<i>PC5</i> (5.8 %)	<i>PC6</i> (2.8 %)
<b>Temperature (° C)</b>	0.27	0.35	-0.29	-0.46	0.43	-0.22
<b>O<sub>2</sub> (mg L<sup>-1</sup>)</b>	0.14	0.59	0.25	-0.45	-0.28	0.02
<b>pH</b>	0.02	0.55	0.27	0.63	0.33	-0.26
<b>Total water hardness (mg CaCO<sub>3</sub> L<sup>-1</sup>)</b>	0.39	-0.17	0.22	-0.16	-0.29	-0.17
<b>Nitrite (mg L<sup>-1</sup>)</b>	0.42	-0.08	-0.13	0.00	0.18	0.04
<b>Nitrate (mg L<sup>-1</sup>)</b>	0.40	-0.07	-0.02	0.15	-0.28	-0.33
<b>Orthophosphate (mg L<sup>-1</sup>)</b>	0.35	-0.11	-0.43	0.10	0.35	0.22
<b>Conductivity (µS cm<sup>-1</sup>)</b>	0.38	-0.22	0.18	0.17	-0.04	-0.35
<b>Chlorophyll a (µg cm<sup>-2</sup>)</b>	0.30	0.33	-0.26	0.32	-0.44	0.54
<b>Discharge (m<sup>3</sup>s<sup>-1</sup>)</b>	-0.26	0.13	-0.66	0.08	-0.35	-0.53

**Table S6.** Linear mixed effects model summary statistics for the effect of land use type on the mean carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) stable isotope ratios for individual trophic groups. Individual sites were treated as a random effect.

	<i>Treatment</i>	<i>Statistics</i>	<i>P-value</i>
Resources	$\delta^{13}\text{C}$	$F_{2,12} = 3.01$	<i>0.090</i>
Prey	$\delta^{13}\text{C}$	$F_{2,12} = 3.56$	<i>0.061</i>
Predators	$\delta^{13}\text{C}$	$F_{2,9} = 1.89$	<i>0.207</i>
Detritivores	$\delta^{13}\text{C}$	$F_{2,10} = 0.44$	<i>0.657</i>
Grazers	$\delta^{13}\text{C}$	$F_{2,12} = 5.04$	<i>0.026</i>
Detritivores	$\delta^{15}\text{N}$	$F_{2,10} = 6.08$	<i>0.019</i>
Grazers	$\delta^{15}\text{N}$	$F_{2,12} = 9.71$	<i>0.003</i>

**Table S7.** Linear mixed effects model summary statistics for the effect of physico-chemical site characteristics, represented by the PC2, on the low level of trophic redundancy indicated by high MNND, the uniformity of niche measures SDNND, the mean  $\delta^{15}\text{N}$  and the  $\delta^{15}\text{N}$  range. Individual sites were treated as a random effect.

<i>Treatment</i>	<i>Statistics</i>	<i>P-value</i>
MNND	$F_{1,13} = 0.12$	<i>0.734</i>
SDNND	$F_{1,13} = 0.08$	<i>0.778</i>
mean $\delta^{15}\text{N}$	$F_{1,13} = 2.31$	<i>0.152</i>
$\delta^{15}\text{N}$ range	$F_{1,13} = 0.04$	<i>0.837</i>



Mean δ <sup>15</sup> N	0-2	2-4	4-6	6-8	8-10	10-12	12-14	14-16	16-18
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