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4 NICHE SEGREGATION BETWEEN TWO CLOSELY RELATED  
5 GAMMARIDS (CRUSTACEA, AMPHIPODA) – NATIVE VS. NATURALISED  
6 NON-NATIVE SPECIES

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8 BY

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17

18 ABSTRACT

19 Closely related species may occupy similar niches, but are often found to diverge  
20 by one or more traits when they inhabit the same habitat. In this study, we examined  
21 how two co-occurring gammarids - the native Gammarus fossarum and the  
22 naturalised G. roeselii – are distributed among microhabitats, depending on their  
23 sympatric or allopatric distribution. We hypothesized that the larger body sized  
24 species (G. roeselii), exploiting their advantages in competition, restrict smaller  
25 species to microhabitats with smaller particle sizes. Four headwaters were sampled in

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26 Mecsek Mountains (SW Hungary) in May, July and October 2009, and 37 local scale  
27 environmental variables at each site were measured. Although G. fossarum is smaller  
28 in size, significantly more individuals were collected from the more favourable lithal  
29 and biotic microhabitats, whereas a strong negative association was observed between  
30 the two species. Gammarus roeselii occurred at sites characterised by degraded  
31 riparian vegetation, which indicates stronger anthropogenic impacts, but still has a  
32 disadvantage in competition in mountainous streams under anthropogenic influence.

33       Keywords: Gammarus fossarum, Gammarus roeselii, habitat segregation, co-  
34 existence, environmental variables;

35

37 In the last one hundred years, through the accelerated industrialization, the state  
38 and conditions of watercourses have worsened a lot, that opened the gate for the  
39 spread of invasive species (Van der Velde et al 2000), which may have been  
40 contributed the extinction of native species from the middle section of river Danube  
41 (Bódis et al. 2012). This process could be responsible for the increase of the numbers  
42 of invasive species in large European rivers like, Oder, Rhine or Vistula (Jazdzewski  
43 1980, Jazdzewski & Konopacka 2000, Bij de Vaate et al. 2002, Konopacka and  
44 Jazdzewski 2002, Borza 2009). Native gammarid communities are exposed to the  
45 impacts of invasive species (MacNeil & Platvoet 2005). That process is remarkable,  
46 because gammarids are common and play important functional role in fresh and  
47 brackish running water systems across Europe (Jazdzewski 1980). They could be  
48 considered as key species in aquatic assemblages, especially in food web interactions  
49 (Piscart et al. 2011). These species owe their success to their relatively short  
50 generation time, fast sexual maturation and high reproductive ability (Bij de Vaate et  
51 al. 2002, Grabowski et al. 2007). Invasive gammarids have restricted native species  
52 from numerous large rivers, to smaller mountainous streams, where the absence of  
53 invasive species presumably related to the special physico-chemical condition of  
54 habitats (e.g. high water velocity, low level of salinity) (Wijnhoven et al. 2003, Piscart  
55 et al. 2009). Changes in amphipod assemblages after the colonization by invasive  
56 species have been well known (e.g. Dick 1996, Jazdzewski et al. 2005, Josens et al.  
57 2005, Grabowski et al. 2006, Piscart et al 2011, Mayer et al. 2012), but interactions  
58 among native species assemblages are poorly known.

59 Among gammarids, several closely related species share highly similar ecological  
60 niches (van Riel et al. 2009). Thus, strong interactions could occur between them (van

61 Riel et al. 2007). On the other hand, it is well known that changes in resource  
62 allocation could help to avoid interference or competitive exclusion (Schoener 1983).  
63 Among gammarids, shifts in life-cycles and microhabitat preference could limit the  
64 niche overlap and competition between species (Korpinen & Westerbom 2009). Such  
65 shifts could create horizontal (Czarnecka et al. 2010) and, if the depth permits,  
66 vertical separations (Kley & Maier 2005). An interesting phenomenon of horizontal  
67 separations is that the native gammarid species are usually restricted to biotic habitats  
68 (roots and leaf litter) after the colonization of an invasive species (Dick 1996; Piscart  
69 et al. 2007; van Riel et al. 2007). Nevertheless, precisely describing the structure of  
70 native communities is important for estimating the effects of further invasions. To  
71 survey changes in habitat segregation among gammarids, we chose two sympatric  
72 species, which are showing similarity in several ecological traits; the native G.  
73 fossarum Koch, in Panzer 1836 and the non-indigenous, but naturalised G. roeselii  
74 Gervais, 1835. Gammarus fossarum is generally considered as a widely distributed  
75 freshwater species in Europe (e.g. Karaman & Pinkster 1977) and also the most  
76 abundant native amphipod in freshwater streams of mountainous areas in Central  
77 Europe (Pöckl et al. 2003). Gammarus roeselii was introduced from the Balkans  
78 (Karaman & Pinkster 1977, Jazdzewski & Roux, 1988) as an early invader, and today  
79 is considered as a naturalised species (Piscart et al. 2009) in the Eastern- and Central-  
80 European rivers, where it usually occupies the lower parts of watercourses  
81 (Jazdzewski & Roux 1988; Janetzky 1994). The appearance of this species in  
82 mountain streams is relatively unusual (Nesemann et al. 1995).

83 For this reason the aims of this study were to examine (1) how two closely related  
84 gammarid species - G. fossarum and G. roeselii – are distributed among  
85 microhabitats, depending on their sympatric or allopatric distribution, and (2) the

86 variability in their biotic interactions if they are sympatric. Our aim was to assess the  
87 primary influencing factors (at temporal and different spatial scales) structuring the  
88 distribution patterns of G. fossarum and G. roeselii. We hypothesized that, as the  
89 result of interspecific competition, the two species show spatial segregation at the  
90 level of microhabitat, if they co-occur. We also sought the abiotic environmental  
91 variables that could determine the occurrence of G. fossarum and G. roeselii at the  
92 reach scale. We examined the biotic interactions between the two species within  
93 different microhabitats and seasons.

94

## 95 MATERIAL AND METHODS

96

### 96 Sampling sites and data collection

97 The study area is located in Mecsek Mountains in south-western Hungary. The  
98 350 km<sup>2</sup> area is considerably isolated from other mountainous regions and bordered  
99 by low plain and hilly territories. Macroinvertebrate samples were taken at four sites  
100 (fig. 1) from second-order headwaters running in deep, cool and shadowed valleys. In  
101 two of the four streams, the only occurring species is *G. fossarum*. Investigating the  
102 biotic interactions and the changes in habitat preference of the two gammarid species  
103 were possible in the two other streams (fig. 1). Samples were taken from a 100 m long  
104 section of each site between 6-20 of May, 21-25 of July and 19-23 of October in  
105 2009. The macroinvertebrates were quantitatively collected according to Integrated  
106 Assessment System for the Ecological Quality of Streams and Rivers throughout  
107 Europe using Benthic Macroinvertebrates (AQEM) protocol (AQEM Consortium,  
108 2002), which focuses on a multihabitat scheme designed for sampling major habitats  
109 in proportion to their presence within 100 m long sampling reaches. A sample  
110 consisted of 20 'sampling units' taken from all microhabitat types at each sampling

111 site with a share of at least 5% coverage. The 20 'sampling units' were distributed  
112 according to the proportion of microhabitats. A 'sampling unit' was taken from a total  
113 of 0,25 \* 0,25 m<sup>2</sup> area by 'kick and sweep' sampling method using a handnet (1 mm  
114 mesh size). In case of macrolithal type samples were collected from the given surface  
115 of the rocks and among the fine sediment between them. Thus, a total of 1.25 m<sup>2</sup> area  
116 was sampled for benthic macroinvertebrates at each site. In this study, seven different  
117 types of habitat were determined according to the original AQEM microhabitats (table  
118 1). The 'sampling units', which contained the complete assortment of  
119 macroinvertebrates, were fully and separately sorted in the field. The collected  
120 gammarids were identified in laboratory from the sorted samples, based on the keys  
121 and descriptions of Cărauşu et al. (1955) and Kontschán et al. (2002).

122

#### 123 Environmental variables

124 At each site, 37 local scale environmental variables were measured in all seasons  
125 related to streambed morphology (9), physicochemical attributes (15), riparian  
126 vegetation (9) and hydrology (4) (table 2). Water samples for physicochemical  
127 analyses were taken prior to the biological sampling. The water temperature was  
128 measured during the sampling periods, 3 data points at each location, one data from  
129 the upper (0m), one from the lower edge of the stream section (100m), and one at the  
130 middle (50m). Habitats and their degradation state were determined according to the  
131 standards of the Hungarian Habitat Mapping Project (Bölöni et al. 2007). In details,  
132 vegetation of the sampling sites consisted mainly of natural beech and hornbeam-oak  
133 forests, which on some places had been turned into degraded habitat types as a result  
134 of land use. The human activity in the valley floors have cleared mostly for meadows  
135 and pastures, but these have been abandoned recently and turned into high herb

136 vegetation (*Equisetum telmateia*, *Petasites hybridus*, *Urtica dioica*), secondary bushes  
137 (e.g. of *Cornus sanguinea*, *Corylus avellana*), and secondary riparian forests (*Salix*  
138 *alba*, *Salix fragilis*).

139

140 Statistical analyses

141 Prior to all analysis, the abundance data of the two species were  $\log_{10}(x+1)$   
142 transformed to reduce heteroskedasticity.

143 To identify the seasonal shifts in microhabitat preferences, we calculated  
144 additional Kruskal-Wallis tests within each season. To compare the abundances of G.  
145 fossarum directly from sites with and without the other species were carried out with  
146 Mann-Whitney U tests. For these analyses, we reduced the seven available  
147 microhabitat types into three wider habitat groups (table 1). Thus, we cumulated the  
148 abundance of each species and referred them to 1m<sup>2</sup> because different numbers of  
149 sampling units of single microhabitat types were available at sampling sites.  
150 Furthermore, to explore the differences between the abiotic factors of the two types of  
151 site, independent samples t-tests were used. These analyses were implemented with  
152 software R ver. 2.14.0 (R Development Core team 2011).

153 Coexistence analyses were made in Microsoft Excel Macro, based on the work of  
154 Schmera et al. (2007). Co-existence indices ( $CI_{ij}$ ) between the species were calculated  
155 using the formula  $CI_{ij} = \sum_{a=1}^N x_{ai} * x_{aj}$ , where  $CI_{ij}$  is the co-existence index (i.e. degree  
156 of association) between i and j species,  $x_{ai}$  is the relative abundance of species 'i' in  
157 sample 'a',  $x_{aj}$  is the relative abundance of species 'j' in sample 'a', N is the total  
158 number of samples. Altogether 1000 random pseudo-assemblages were generated,  
159 species' abundances were kept constant in a sample. If the observed value falls in the  
160 upper marginal tail of the random distribution, it presumes a positive association (e.g.

161 aggregation). If the observed value falls in the lower marginal tail of the distribution,  
162 then the species pair shows negative association (e.g. competition) (Schmera et al.  
163 2007).

164

## 165 RESULTS

### 166 Temporal and spatial distribution patterns

167 During the survey, a total of 27,445 specimens were identified. There was no  
168 significant difference in abundances of the species among sites (Kruskal-Wallis test:  
169  $\chi^2 = 6.385$ ,  $df = 2$   $p = 0.094$ ).

170 The temporal shift in the microhabitat preference, based on the Kruskal-Wallis  
171 tests did not show significant differences in quantitative distribution between  
172 microhabitat types at sites where only G. fossarum was present (spring:  $\chi^2 = 0.432$ ,  $df$   
173  $= 2$ ,  $p = 0.806$ ; summer:  $\chi^2 = 3.545$ ,  $df = 2$ ,  $p = 0.170$ ; autumn:  $\chi^2 = 1.054$ ,  $df = 2$ ,  $p =$   
174  $0.590$ ) (fig. 2). However, when both species were present (fig. 3) a significant  
175 difference occurred in the microhabitat preference of G. fossarum in spring and  
176 summer (spring:  $\chi^2 = 10.744$   $df = 2$ ,  $p = 0.005$ ; summer:  $\chi^2 = 14.617$ ,  $df = 2$ ,  $p =$   
177  $0.001$ ). In autumn, no significant difference was found in habitat preference ( $\chi^2 =$   
178  $1.618$ ,  $df = 2$ ,  $p = 0.445$ ) (fig. 3).

179 The abundance of G. roeselii was low in spring, and no difference was found in  
180 the abundance between microhabitats ( $\chi^2 = 0.614$ ,  $df = 2$ ,  $p = 0.736$ ) (fig. 4), whereas  
181 significant differences were found in the abundance between the microhabitat types in  
182 summer and autumn (summer:  $\chi^2 = 11.349$ ,  $df = 2$ ,  $p = 0.003$ ; autumn:  $\chi^2 = 14.080$ ,  $df$   
183  $= 2$ ,  $p = 0.001$ ) (fig. 4).

184 Based on the Mann-Whitney U tests, the comparison of the abundances of G.  
185 fossarum with and without G. roeselii showed no differences in most cases. We found



186 exceptions in spring in the lithal and gravel microhabitats and in the biotic one in  
187 summer (table 3.)

188

189 Coexistence

190 Throughout the year, negative associations were found between the species in  
191 almost every habitat type, which indicates interference. The only exception was the  
192 gravel microhabitat, where positive associations were observed in autumn (table 4).

193

194 Comparing abiotic conditions of the two groups of sites with different species  
195 composition

196 Comparing the two different groups of sites we found difference in some factors  
197 of bed morphology and degradation state together with an ion concentration and the  
198 proportion of the xylal microhabitat type ( $t = -2.684$ ,  $p = 0.028$ ). The biggest  
199 difference among factor of bed morphology was found in water depth ( $t = -3.556$ ,  $p =$   
200  $0.007$ ). Furthermore, significant difference was found in the degradation state of  
201 riparian vegetation. The secondary (degraded) site number was higher at sites where  
202 G. roeselii was present at the scale of valley floor ( $t = -3.437$ ,  $p = 0.009$ ) and slope ( $t$   
203  $= -5.817$ ,  $p = 0.001$ ). Additionally concentration (mg/l) of  $\text{Ca}^{2+}$  ion was higher ( $t = -$   
204  $4.530$ ,  $p = 0.002$ ) at sites where both species were present. Also, significant difference  
205 was found in coverage of riparian shrub ( $t = -2.623$ ,  $p = 0.031$ ) and forest ( $t = 3.217$ ,  $p$   
206  $= 0.012$ ) between the two sites.

207

208 DISCUSSION

209 Our study provides information about the spatial niche segregation of two  
210 gammarid species (G. fossarum, G. roeselii) in small headwaters. We also made an  
211 attempt to identify factors affecting the distribution patterns.

212 We revealed different microhabitat preference of the gammarid species at sites  
213 where they co-occurred (fig. 3, 4). We also showed that differences in microhabitat  
214 preference did not exist during the whole year and its rate changed among seasons  
215 (fig. 3, 4). Gammarus fossarum showed microhabitat preference only, if it co-  
216 occurred with G. roeselii. In those cases, G. fossarum was mostly abundant in the  
217 optimal lithal and biotic microhabitats, whereas it was less dominant in gravel ones.  
218 On the contrary, G. roeselii was almost completely absent from the lithal  
219 microhabitats, but it was usually frequent in the biotic ones. Our results partly  
220 confirmed some previous studies in which competition could be observed between G.  
221 fossarum and G. roeselii at stream reaches if they co-occurred (e.g. Pöckl &  
222 Humpesch 1990). Besides, the reproduction is not restricted to a short period and may  
223 occur throughout the year (Beracko et al. 2012), thus we consider that the seasonal  
224 investigation might not be sufficient to show the shift of their life-cycles.  
225 Nevertheless, former studies (e.g. van Overdijk et al. 2003, McGrath et al. 2007,  
226 Korpinen & Westerbom 2009) also focused mostly on the spatial resource partition,  
227 especially on habitat separation. In a laboratory experiment, G. pulex and G. roeselii  
228 did not show any change in habitat preference when co-occurring (van Riel et al.  
229 2007). On the contrary, a high degree of divergence in substrate choice was found  
230 between the aggressive invader Dikerogammarus villosus and the non-indigenous G.  
231 roeselii (Kley et al. 2009). The weak interactions between G. roeselii and G. pulex  
232 were supported by a field survey, which provided for G. roeselii to colonize the more  
233 favourable habitats that are less acceptable to G. pulex (Kaldonski et al. 2008).

234 Thereby, G. roeselii could permanently co-exist with other native species. On the  
235 other hand, Túri et al. (2003) observed a competitive exclusion and checkerboard  
236 pattern between two native species (G. fossarum, G. balcanicus) in mountainous  
237 small streams in NE Hungary. Regarding the habitat segregation, several previous  
238 studies revealed that larger species, exploiting their advantages in competition,  
239 restrict smaller species to microhabitats with smaller particle sizes (e.g. Hacker &  
240 Steneck 1990, Olyslager & Williams 1993). Despite that, G. fossarum is smaller in  
241 body size (Pöckl 1992), even though we collected significantly more individuals from  
242 larger grained lithal microhabitats; moreover G. fossarum was relatively frequent in  
243 the biotic microhabitats. According to several investigations, G. roeselii prefers  
244 slower and warmer stream sections (e. g. Meijering 1972; Dahl & Greenberg 1996;  
245 Toman & Dall 1998), and it is not able to colonize springs and spring outlets (e. g.  
246 Wijnhoven et al. 2003, Piscart et al. 2009). Furthermore, our results show that G.  
247 roeselii occurred at sites characterised by abiotic habitat features resembling  
248 downstream sections of streams with degraded riparian vegetation, which indicates  
249 stronger anthropogenic impacts (table 2, fig. 5). It is well known that environmental  
250 factors have non-negligible effects on the distribution pattern (Früh et al. 2012),  
251 besides that G. roeselii shows some kind of expansion as it appears in sufficiently  
252 degraded second order streams. Nevertheless, we supposed that small, mountainous  
253 headwaters were less optimal habitats for G. roeselii; thereby the typical mountain  
254 species G. fossarum could be a stronger competitor. This presumption was also  
255 confirmed, according to the permanence microhabitat preference of G. fossarum  
256 (table 3). Several authors (Dick 1996; Piscart et al. 2007; van Riel et al. 2007) found  
257 similar distribution patterns of native and presumably weaker competitor species  
258 being restricted to biotic microhabitats and excluded from the, lithal ones following

259 invasions. Based on the previous statement, we can assume that, being the stronger  
260 competitor, G. fossarum restricts G. roeselii from optimal lithal microhabitats, while  
261 still dominant in the biotic ones, characterised by higher amounts of detritus  
262 deposition.

263 Coexistence analyses confirmed the influence of biotic interactions on the  
264 distribution patterns. Presumably, G. fossarum could be the stronger competitor,  
265 whereas a strong negative association was found between the two species, which  
266 confirms the habitat segregation between the two species. Positive association could  
267 be found only between the species in autumn in the gravel microhabitats. Throughout  
268 the year, the fine particulate substrate was characterised by small numbers of  
269 individuals. Therefore, when large quantities of allochthonous organic matter (e.g.  
270 leaf litter) appeared in autumn, habitat structure changes for gammarids, providing  
271 shelter and nutritive as well.

272 To sum up, our aim was to describe the effect of an expanding species (G.  
273 roeselii) on a closely related species (G. fossarum) belonging to the same functional  
274 guild and utilizing similar niches (Nesemann et al. 2002). Thus strong competition  
275 could be assumed between them. The most notable is that a simple practical model  
276 based on a field study supported the previous theoretical models that described the  
277 main opportunity to avoid competitive exclusion based on niche segregation (Tilman  
278 1987). In this particular case, this segregation appeared as spatial resource allocation.  
279 Our study revealed whether the native or the ‘expanding’ species has the advantage  
280 in the competition in a certain environmental condition (small mountainous streams).  
281 Since we worked in mostly natural habitats, G. roeselii which arrived from the lower  
282 sections of streams still had a disadvantage in competition. In fact, we did not expect  
283 the appearance of G. roeselii in these natural stream sections; however, it spread

284 already at the moderately disturbed reaches. Lastly, we conclude, that the  
285 degradation of near-pristine headwater sites could thus enable the naturalized non-  
286 native species to get into action for further expansion of its area.

287

288

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294

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- 460

461 TABLES

462 **Table 1.**

<b>Groups</b>	<b>Type</b>	<b>Definition</b>
Gravel	Psammal	Sand; diameter 6 $\mu$ m–2 mm
	Akal	Fine to medium-sized gravel; diameter 2mm-2 cm
Lithal	Microlithal	Coarse gravel with medium to fine gravel; diameter 2-6 cm
	Mesolithal	Cobbles with a variable percentage of gravel and sand; diameter 6-20 cm
	Macrolithal	Coarse cobbles, gravel and sand; diameter 20-40 cm
Biotic	Xylal	Tree trunks, dead wood, branches, roots
	CPOM	Deposits of coarse particulate organic matter

463

Variables	Sites with <u>G. fossarum</u> only	Sites with <u>G. fossarum</u> and <u>G. roeselii</u>	Transform.
<b><i>Streambed morphology</i></b>			
<b>Substrate composition</b>			
% Macrolithal	0.00...4.22...13.22 (6.28)	0.00...0.95...3.17 (1.45)	$\arcsin(x/100)^{0.5}$
% Mesolithal	31.78...46.69...60.05 (9.49)	4.76...28.41...63.33 (24.88)	$\arcsin(x/100)^{0.5}$
% Microlithal	0.79...10.39...18.73 (7.42)	4.76...15.18...28.44 (8.45)	$\arcsin(x/100)^{0.5}$
% Akal	0.79...8.81...17.62 (6.49)	0.00...10.78...24.60 (10.11)	$\arcsin(x/100)^{0.5}$
% Psammal	0.52...12.14...26.70 (9.71)	6.87...15.49...39.68 (12.18)	$\arcsin(x/100)^{0.5}$
% Xylal	1.05...3.71...9.09 (2.88)	3.81...6.81...16.13 (4.72)	$\arcsin(x/100)^{0.5}$
% CPOM	0.00...6.53...20.08 (8.83)	0.00...9.88...26.56 (9.65)	$\arcsin(x/100)^{0.5}$
Number of riffles in 100 m	3.00...5.50...7.00 (1.51)	5.00...7.33...9.00 (1.63)	$\ln(x+1)$
Number of pools in 100 m	3.00...4.33...8.00 (1.86)	4.00...5.50...7.00 (1.04)	$\ln(x+1)$
Channel width (m)	0.94...1.34...1.72 (0.26)	1.8...2.09...2.29 (0.19)	$\ln(x+1)$
Water depth (m)	0.04...0.05...0.07 (0.01)	0.08...0.15...0.34 (0.09)	$\ln(x+1)$
Number of bends in 100 m	2.00...3.83...6.00 (1.72)	3.00...4.83...8.00 (2.13)	$\ln(x+1)$
Number of woods in 100 m	3.00...5.16...9.00 (2.99)	6.00...10.33...13.00 (2.80)	$\ln(x+1)$
% Detritus	6.70...24.47...54.00 (18.39)	19.05...35.12...52.38 (13.99)	$\arcsin(x/100)^{0.5}$
% Washaway	4.55...20.04...42.86 (17.34)	4.76...19.21...35.71 (15.54)	$\arcsin(x/100)^{0.5}$
<b><i>Physicochemical attribute</i></b>			
pH	7.97...8.39...9.00 (0.38)	7.12...7.91...8.50 (0.50)	$\exp(x/100)$
Water temperature (°C)	6.40...13.01...19.40 (5.15)	10.10...12.65...17.83 (2.67)	$\ln(x+1)$
Conductivity (µS/cm)	572.00...722.23...886.00 (158.43)	649.70...795.93...899.30 (89.60)	$\exp(x/100)$
Concentration of dissolved oxygen (mg L <sup>-1</sup> )	5.10...6.91...8.10 (1.17)	5.20...6.50...8.20 (1.34)	$\ln(x+1)$
NH <sub>4</sub> <sup>+</sup> (mg L <sup>-1</sup> )	0.02...0.49...1.00 (0.43)	0.04...0.41...1.20 (0.53)	$\ln(x+1)$
NO <sub>2</sub> <sup>-</sup> (mg L <sup>-1</sup> )	0.01...0.02...0.03 (0.01)	0.01...0.05...0.32 (0.05)	$\ln(x+1)$
NO <sub>3</sub> <sup>2-</sup> (mg L <sup>-1</sup> )	0.20...0.93...2.10 (0.78)	0.40...1.55...2.70 (0.93)	$\ln(x+1)$
PO <sub>4</sub> <sup>3-</sup> (mg L <sup>-1</sup> )	0.18...0.46...0.84 (0.28)	0.14...0.40...0.76 (0.20)	$\ln(x+1)$
SO <sub>4</sub> <sup>2-</sup> (mg L <sup>-1</sup> )	0.30...41.84...120.00 (47.09)	1.05...57.37...140.00 (52.15)	$\ln(x+1)$
Ca <sup>2+</sup> (mg L <sup>-1</sup> )	50.04...83.57...110.43 (20.96)	115.46...134.59...165.18 (21.01)	$\ln(x+1)$

Mg <sup>2+</sup> (mg L <sup>-1</sup> )	19.56...33.96...45.24 (10.47)	14.97...43.91...102.05 (31.54)	ln(x+1)
Cl <sup>-</sup>	1.01...4.97...10.19 (3.99)	7.76...9.97...12.12 (1.69)	ln(x+1)
HCO <sub>3</sub> <sup>-</sup>	238.90...365.93...415.80 (66.30)	360.90...442.92...525.60 (69.63)	ln(x+1)
Chemical oxygen demand	3.04...3.70...4.75 (0.59)	0.77...1.96...3.12 (1.03)	ln(x+1)
m alkalinity	5.50...6.25...6.80 (0.52)	5.89...7.33...8.60 (1.08)	ln(x+1)
<b>Riparian vegetation</b>			
% Tree (0-1m)	8.75...19.60...29.76 (7.97)	14.67...20.01...26.12 (3.71)	arcsin(x/100) <sup>0.5</sup>
% shrubs (0-1m)	1.19...3.86...6.81 (2.03)	6.33...17.04...24.93 (7.29)	arcsin(x/100) <sup>0.5</sup>
% herbaceous (0-1m)	46.43...54.99...65.09 (8.62)	48.47...60.89...69.43 (7.70)	arcsin(x/100) <sup>0.5</sup>
% Forest coverage at the valley floor	90.00...95.00...100.00 (5.44)	100.00	arcsin(x/100) <sup>0.5</sup>
% of natural habitat of vegetation at valley floor	100.00	50.00	arcsin(x/100) <sup>0.5</sup>
% of degraded habitat of vegetation at valley floor	0.00	50.00	arcsin(x/100) <sup>0.5</sup>
% Forest coverage of at the nearest slopes	90.00...95.00...100.00 (5.44)	60.00...75.00...90.00 (16.43)	arcsin(x/100) <sup>0.5</sup>
% of natural habitat of vegetation at slope	50.00...75.00...100.00 (27.38)	33.00...54.16...0.75 (22.82)	arcsin(x/100) <sup>0.5</sup>
% of degraded habitat of vegetation at slope	0.00...25.00...50.00 (27.38)	25.00...45.83...66.00 (22.82)	arcsin(x/100) <sup>0.5</sup>
<b>Hydrology</b>			
Distance from source (km)	1.47...2.32...3.17 (1.20)	0.20...2.08...3.96 (2.65)	ln(x+1)
Altitude (m)	218.00...268.50...319.00 (71.41)	187.00...203.00...219.00 (22.62)	ln(x+1)
Aspect	96.12...138.75...181.37 (60.27)	108.60...124.77...140.94 (22.86)	ln(x+1)
Slope	4.00...6.50...9.00 (3.53)	7.00...8.00...9.00 (1.41)	ln(x+1)

466 **Table 3.**

Season / m.habitat	lithal	gravel	biotic
Spring	$Z = -2.559, p = 0.009$	$Z = -3.249, p = 0.001$	$Z = -0.387, p = 0.755$
Summer	$Z = -1.846, p = 0.065$	$Z = -1.736, p = 0.088$	$Z = -2.492, p = 0.011$
Autumn	$Z = -0.66, p = 0.948$	$Z = -1.827, p = 0.067$	$Z = -0.31, p = 0.976$

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**Table 4.**

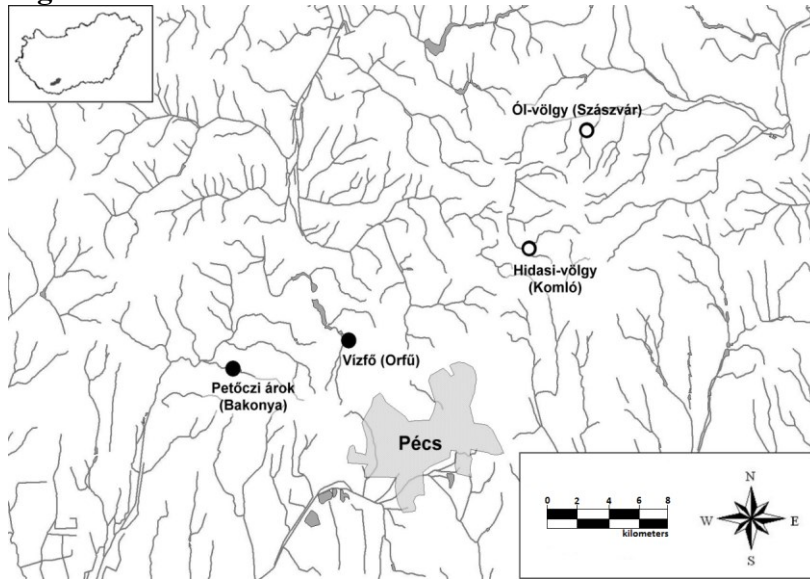
<b>Microhabitat type</b>	<b>CI<sub>ij</sub></b>	<b>Upper 2.5%</b>	<b>Lower 2.5%</b>	<b><i>p</i></b>	<b>type of association</b>
<b>Spring</b>					
Lithal	0.042	0.067	0.074	0.001	Negative
Gravel	0.074	0.156	0.173	0.001	Negative
Biotic	0.120	0.167	0.176	0.001	Negative
<b>Summer</b>					
Lithal	0.028	0.046	0.049	0.001	Negative
Gravel	0.109	0.211	0.223	0.001	Negative
Biotic	0.138	0.147	0.150	0.001	Negative
<b>Autumn</b>					
Lithal	0.035	0.056	0.060	0.001	Negative
Gravel	0.396	0.141	0.173	0.001	Positive
Biotic	0.228	0.288	0.308	0.001	Negative

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472 FIGURES

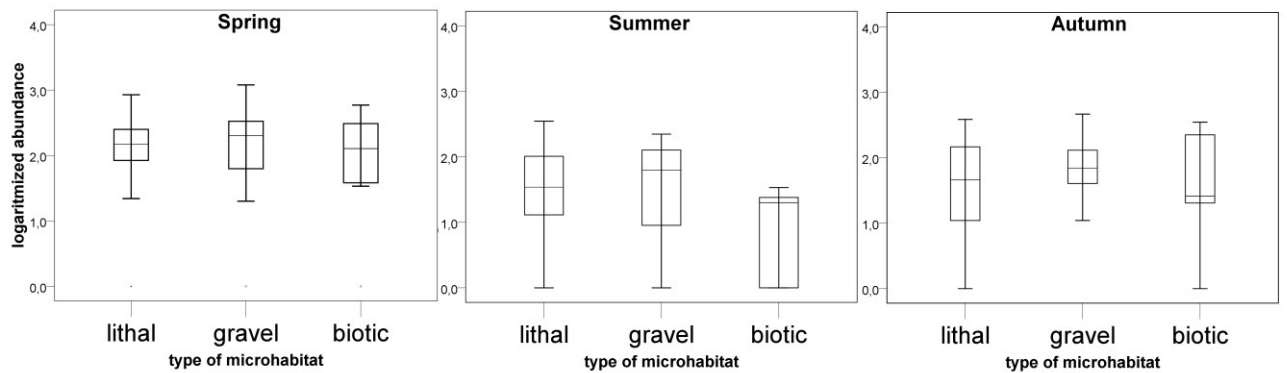
473 **Fig. 1:**



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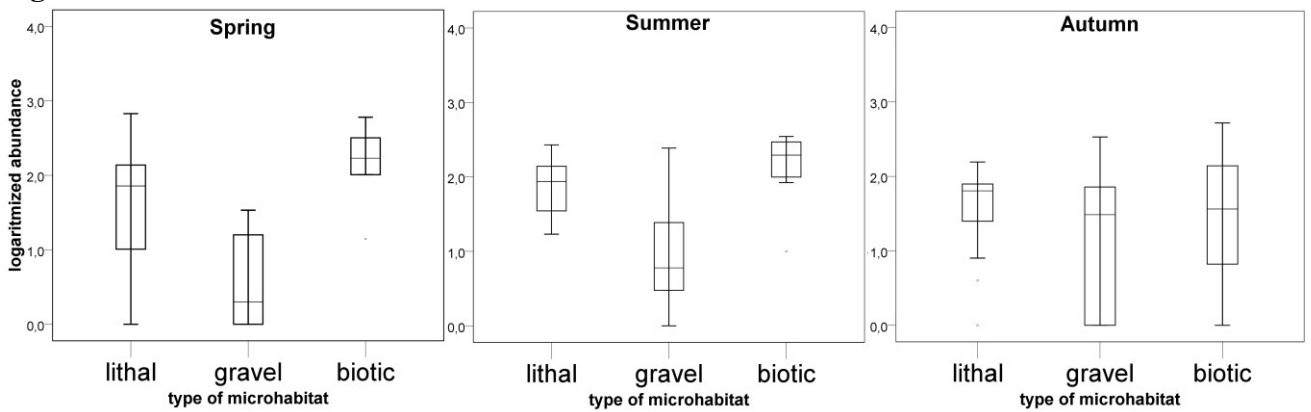
475

476 **Fig.2:**



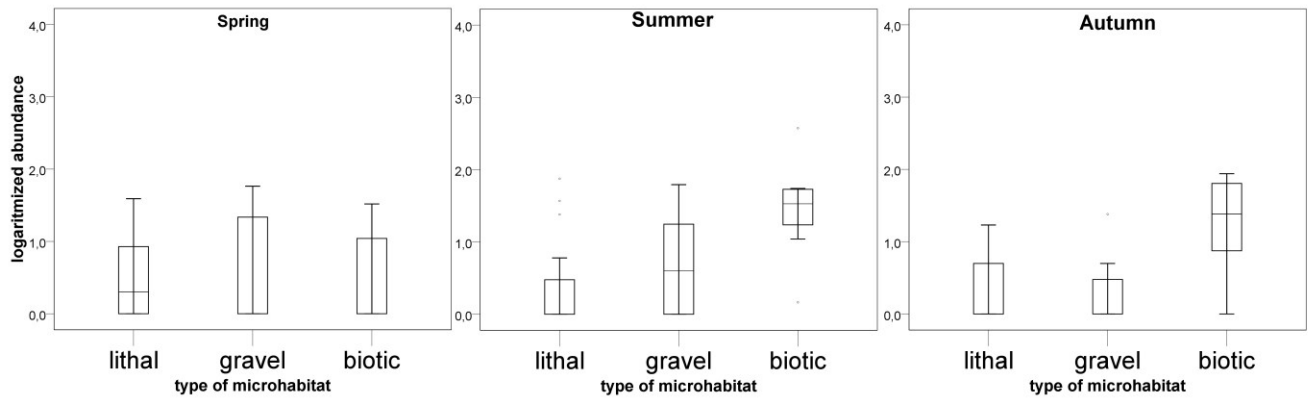
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478 **Fig.3:**



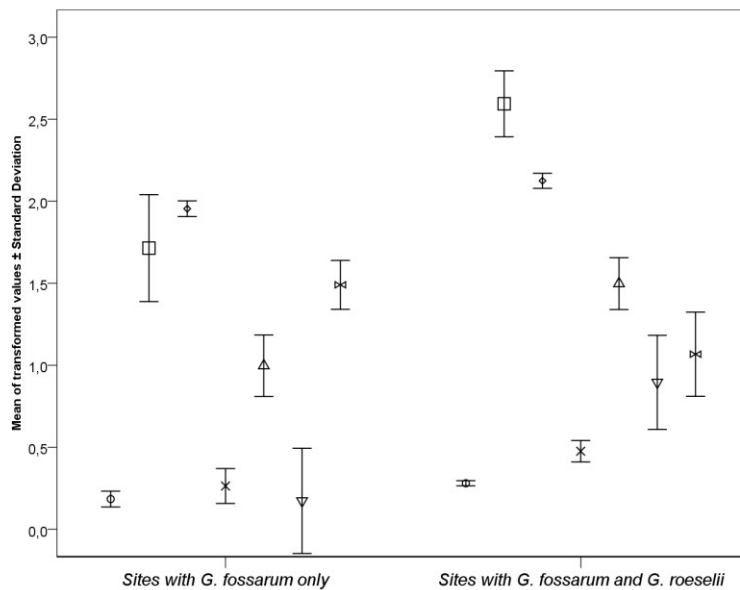
479

480 **Fig.4:**



481  
482

**Fig.5:**



483

484 Table and figure captions

485 **Table 1.** List of microhabitats from AQEM protocol (following Hering et al. 2004.)  
486 and the cumulative microhabitat groups used in this study.

487 **Table 2.** Minimum, mean and maximum (standard deviation) values of local  
488 environmental variables used in analyses and grouped into four variable groups, and  
489 their type of transformation.

490 **Table 3.** Comparison of the abundance data of G. fossarum with and without G.  
491 roeselii in each season separated by microhabitats, the bold values are representing the  
492 significant differences.

493 **Table 4.** Results of the co-existence analyses in seasonal partition, where  $CI_{ij}$  is the  
494 co-existence index, upper 2.5% means the value of random distribution top 2.5%,  
495 lower 2.5% is the value of random distribution bottom 2.5%.

496 **Fig. 1:** Map of the study area. '●' marked sites where G. fossarum and G. roeselii co-  
497 existed and '○' marked sites where G. fossarum is the only occurring gammarid.  
498 Petőczi-árok: Petőczi stream (Bakonya; N 46°07'17" E 18°03'42"; 187m a.s.l.);  
499 Vízfő: Vízfő spring (Orfű; N 46°08'21" E 18°09'37"; 219m a.s.l.); Hidasi-völgy:  
500 Hidas stream (Komló; N 46°11'46" E 18°19'06"; 319m a.s.l.), Ól-völgy: Ól stream  
501 (Szászvár, N 46°15'49" E 18°22'01"; 218m a.s.l.).

502 **Fig. 2:** Based on the mean of abundances, Gammarus fossarum showed no significant  
503 microhabitat preference in the case of its single occurrence in each season (□:  
504 interquartile range  $\top$ : standard error of mean SE, ○ outlier).

505 **Fig. 3:** Based on the mean of abundances, it is clearly visible that G. fossarum showed  
506 a remarkable change in microhabitat preference in the case of co-existence with G.  
507 roeselii compared with the habitat choice of its single occurrences (□: interquartile  
508 range  $\top$ : standard error of mean SE, ○ outlier).

509 **Fig. 4:** Based on the mean of abundances, a definite preference of microhabitat of G.  
510 roeselii was found in the case of co-existence with G. fossarum in each season (□:  
511 interquartile range  $\top$ : standard error of mean SE, ○ outlier).

512 **Fig. 5:** Comparison of the abiotic conditions of the two sites with different species  
513 composition suggests the degraded state of the sites where both species co-occurred  
514 (○: proportion of xylal microhabitat at the 100m section; □: water-depth; ◇:  
515 concentration of  $\text{Ca}^{2+}$  ion, ×: % shrubs (0-1m); △: Number of degraded riparian  
516 habitats; ▽: Number of degraded habitats at the nearest hill-side; ▷◁: the proportion  
517 of the forest coverage at the nearest slopes).

518