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4 **The effects of top-down and bottom-up controls on macroinvertebrate**
5 **assemblages in headwater streams**

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20 **Abstract:** Headwater stream macroinvertebrates play an important role in processing

21 allochthonous leaf litter, which suggests that bottom-up forces control

22 macroinvertebrates. However, because larvae of stream-breeding salamanders are

23 predators of macroinvertebrates and are abundant consumers in these ecosystems,

24 macroinvertebrates in fishless headwater streams might also be controlled by top-

25 down forces through predation by salamander larvae. The aim of this study was to test

26 if and to what degree taxa richness, abundance and biomass of macroinvertebrates are
27 affected by bottom-up and top-down forces. We selected headwater streams with high
28 abundances of fire salamander larvae (1.2-2.6 individuals per 1 m of shorelength) and
29 manipulated bottom-up and top-down forces on macroinvertebrates by leaf litter
30 addition and by the exclusion of salamander larvae. The amphipod *Gammarus*
31 *fossarum* Koch, 1836 was the dominant taxon and responded positively to litter
32 addition. Linear models showed that neither predator exclusion or leaf litter addition
33 affected richness. However, variation in biomass and density were both explained by
34 the individual and joint effects of bottom-up and top-down forces. These findings
35 suggest that macroinvertebrates in these streams are strongly dependent on the
36 organic matter input and salamander larvae, and headwater streams interact strongly
37 with their adjacent terrestrial areas.

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40 **Keywords:** headwater streams, leaf litter, fire salamander, macroinvertebrates,
41 predation

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45 **Introduction**

46

47 Forested headwater streams have strong interactions with their adjacent terrestrial
48 areas. Small channel size and closed canopy cover create a physical habitat template
49 of reduced light input, high input of organic matter (leaf litter), and low primary
50 production (Clarke et al., 2008). Thus, the structure and composition of riparian

51 forests are crucial to the functioning of headwater streams (Cummins, 2002; Wallace
52 et al., 1997) in as much as these aquatic ecosystems highly depend on the input of
53 organic matter as the principal carbon source.

54

55 A wide variety of macroinvertebrate taxa colonize leaf litter in these forested streams
56 (Dobson et al., 1992), and use this organic matter both as food and substrate
57 (Richardson, 1992). Additionally, because a large portion of the allochthonous leaf
58 litter is colonized, decomposed, and consumed mainly by shredders (Cummins, 1973),
59 macroinvertebrates are thought to play an important role in leaf litter processing
60 (Cummins, 2002; Gessner et al., 1999). According to Wallace et al. (1997) the
61 exclusion of terrestrial leaf litter input to headwaters can result in a strong bottom-up
62 effect suggesting macroinvertebrates are controlled by bottom-up forces (via
63 limitation of leaf litter) in these aquatic ecosystems.

64

65 Top-down forces should also be considered in the study of trophic interactions, since
66 most ecosystems in nature are tritrophic, meaning they are formed by detritus (or a
67 plant), a detritivore (or a consumer) and a predator (Power et al., 1992). Although
68 field experiments indicate that fishes have a negative and taxon specific effect on
69 macroinvertebrate abundance (Dahl, 1998; Williams et al., 2003; Meissner & Muotka,
70 2006), information on how top-down forces structure macroinvertebrates in fishless
71 headwater streams is limited (but see Ruff & Maier, 2000; Keitzer & Goforth, 2013).

72

73 Larvae of stream-breeding salamanders are predators of stream invertebrates and are
74 abundant consumers in many stream ecosystems, particularly in small, fishless
75 headwater streams (Keitzer & Goforth, 2013; Reinhardt et al., 2013). Although the

76 biomass and trophic position of these larvae suggest that they may influence
77 macroinvertebrates through top-down effects, salamander larvae are often overlooked
78 as top-predators in headwater stream ecosystems and there is only a limited
79 understanding of their role (Davic & Welsh, 2004; Keitzer & Goforth, 2013).

80

81 Only a small number of studies have examined how bottom-up and top-down forces
82 combine to structure macroinvertebrate communities. While coastal stream predatory
83 insects were only impacted by top-down forces (Sircom & Walde, 2009), lake
84 macroinvertebrates and stream detritivores have been found to be impacted both by
85 bottom-up and top-down forces (Liboriussen et al., 2005; Jabiol et al., 2014). We
86 predicted that if salamanders are present in fishless forested headwater streams then
87 macroinvertebrate assemblages may also be structured both by bottom-up (via
88 limitation of leaf litter) and top-down (via predation by salamander larvae and other
89 predatory invertebrates) forces. To test this hypothesis, we examined a leaf litter
90 macroinvertebrates fire salamander tritrophic food chain. In our system, the fire
91 salamander (*Salamandra salamandra* (Linnaeus, 1758)), a widely distributed species
92 in central Europe, served as predator. Adult fire salamanders inhabit old broadleaf
93 forests and typically deposit their larvae into first order streams. In these fishless
94 habitats, larvae of salamanders are the top vertebrate predators (Thiesmeier, 2004;
95 Reinhardt et al., 2013).

96

97 To study bottom-up and top-down forces under natural conditions, we selected
98 forested headwater streams with high abundance of fire salamander larvae and
99 manipulated bottom-up and top-down forces on macroinvertebrates by leaf litter
100 addition and exclusion of salamander larvae through six, one-week experimental
101 periods from June through September 2013. The general aim of this study was to test

102 if and to what degree taxa richness, abundance and biomass of macroinvertebrates are
103 affected by the individual and joint effects of leaf litter addition (bottom-up force) and
104 salamander exclusion (top-down force) through summer and early fall, when
105 salamander larvae are present in high density in these systems.

106

107

108 **Material and methods**

109

110 *Site selection*

111

112 Three fishless headwater streams with fire salamanders were selected for this study;
113 Buechholdenbächli (7° 46'17.79" E, 47° 27'35.02" N), Talbächli (7° 47'07.59" E,
114 47° 27'19.88" N) and Teufelgrabenbach (7° 37'38.32" E, 47° 31'13.32" N). These
115 streams, in the Rhine River basin, are near Basel, northwestern Switzerland and range
116 in elevation from 300 - 600 m above sea level. They are representative of natural
117 forested streams in Central Europe, are fishless and have a high density of salamander
118 larvae (1.2-2.6 individuals per one m of shorelength). The forest around the streams
119 is mainly composed of beech (*Fagus sylvatica* Linnaeus 1753) and oak (*Quercus*
120 *robur* Linnaeus 1753). The mean annual temperature of the region is 9.6 °C and the
121 mean annual precipitation is 778 mm (MeteoSwiss, 2013).

122

123

124 *Experimental design*

125

126 Historical records of the three selected headwater streams suggested that salamander
127 larvae would be present in these streams. To confirm this prediction, the streams were
128 surveyed for 5 min along a 10 m stream section at three different sites to ensure that
129 salamander densities were sufficient for further experimentation.

130

131 Within each stream, four pools containing salamander larva were then selected to test
132 the effects of bottom-up and top-down forces on macroinvertebrate communities.

133 Four plastic trays (10 cm x 10 cm x 2 cm deep) were filled with 3-4 equal sized pieces
134 of stone from the stream. The first tray contained only pieces of stone in order to
135 mimic the natural stream bottom (Control). A second tray was prepared as for the
136 control then covered also with 5 mm polyester mesh, which not only excluded some
137 large-sized, predatory macroinvertebrate taxa, but also, early-stage salamander larvae.

138 This was the predator-free treatment (Salamander exclusion, abbreviated as SaEx).

139 The third tray was prepared as for the control then 1 g of leaf litter was added to it
140 (Litter addition, abbreviated as LiAd). Leaf litter was prepared by collecting leaves
141 from a single beech tree in November 2012 immediately after senescence. The leaves
142 were dried in the lab, kept at air temperature until use, and measured on a Sartorius
143 balance (0.1 mg precision). In the fourth tray both the SaEx and the LiAd were
144 applied (Both). In sum, the experimental design allowed us to test the effects of top-
145 down (SaEx), bottom-up (LiAd) and the joint effects of bottom-up and top-down
146 controls (Both) influences on macroinvertebrate communities.

147

148 We installed 48 experimental trays (4 treatments x 4 sites [replicates] x 3 streams),
149 which were then sampled at 1 week intervals over a six week period (dates). Although
150 macroinvertebrates can colonize hard substrate in a day (Koetsier, 2002), leaf decay

151 experiments suggest leaf litter needs conditioning to be labile for stream
152 macroinvertebrates, so we sampled trays after one week (Gessner & Chauvet, 2002).
153 Sampling of more than one week was considered undesirable because of the risk of
154 spates and also a longer conditioning exposure would increase the chance of the trays
155 being removed by passers by.

156

157

158 *Field work and identification*

159

160 Female of the fire salamanders in Central Europe deposit larvae from March until
161 June mostly into headwater streams (Thiesmeier, 2004). To use a period with a high
162 density of larvae (1.2-2.6 individuals per 1 m of shore length), our experiment started
163 on 18 June 2013. Although the winter of 2012/2013 was relatively long in
164 Switzerland, fire salamander larvae density was high in the study streams when the
165 experiment began. Because salamander larvae were never counted in the SaEx
166 treatment, we conclude that the mesh efficiently excluded these predators.

167

168 One week after installation, invertebrates were collected from each of the four trays
169 and preserved in 80% ethanol. Material was replaced in each tray after each sampling
170 event. Any trays filled by sediment or displaced from their initial position were
171 eliminated from the experiment. In the laboratory, macroinvertebrates were counted
172 and identified to the lowest practical taxonomic level under a dissecting microscope
173 (Leica MZ-8) using the dichotomous keys of Wolfgang (1989), Lechthaler (2009) and
174 Tachet et al. (2010). The wet weight of each taxon per sample was measured to the
175 nearest 0.1 mg using a Sartorius balance. To reduce the influence of the conservation

176 fluid on the wet weight, each sample was put into water for 1 min prior to weighing
177 and then dried on paper towel for 1 min. External materials like caddisfly cases were
178 removed before weighing (shells of molluscs were included) following Wirth et al.
179 (2010). Biomass was determined as weight per m².

180

181 To examine the seasonal changes in the macroinvertebrate communities, the
182 experiment was carried out on six dates (from June to September 2013). Because
183 metamorphosed salamander larvae leave streams from July to October (Thiesmeier,
184 2004), the experiment was terminated in the Buechholdenbächli and
185 Teufelgrabenbach streams on 19 September 2013. As the Talbächli stream dried out
186 in late August the experiment was prematurely terminated in this stream. Although
187 the planned experiment was predicted to result in 288 experimental units (4 treatment
188 x 3 streams x 4 sites [replicates] x 6 dates), the drying of Talbächli (loss of 64
189 experimental units) and the loss or damage of 16 additional trays resulted in 208
190 experimental units for analysis.

191

192

193 *Statistical analyses*

194

195 We examined how taxa richness, macroinvertebrate abundance and biomass were
196 affected by the individual and joint effects of SaEx and LiAd as well as by sampling
197 date and stream identity using linear models. (Crawley, 2007). As taxa richness
198 showed only integer values, we applied a generalized linear model with Poisson
199 distribution, while macroinvertebrate abundance and biomass were modeled with
200 linear models using normal distribution and double square-root transformationed

201 values for invertebrate biomass and abundance. A minimal adequate model was
202 selected using corrected Akaike Information Criterion corrected for small sample size
203 (AICc). Statistical models were compared using the difference in AICc values
204 between the best model and competing models ($\Delta AICc$), using the probability that a
205 particular model is the best fit to the data relative to the other models (AICc weight)
206 and using evidence ratio which indicates the level of support for two or more
207 competing models based on AICc weight (see Zeug et al. 2011).

208

209 In order to determine the taxa benefited from SaEx and LiAd, we used the indicator
210 species approach proposed by Dufrene & Legendre (1997) rather than usual statistical
211 tests such as ANOVA following Mouillot et al. (2008). All statistical analyses were
212 performed in the R environment (R Core team, 2013).

213

214

215 **Results**

216

217 A total of 4,943 individual macroinvertebrates from seven orders and 14 families
218 were collected during the study (Table 1). The macroinvertebrate community was
219 dominated by Amphipoda: *Gammarus fossarum* (2316 individuals/m², 97.47% of all
220 individuals, mean population biomass 23.46 g/m²) followed by Ephemeroptera:
221 Baetidae (29 individuals/m², 1.23% of total individuals, 0.09 g/m² biomass) and
222 Diptera *Simulium* (9 individuals/m², 0.004% of total individuals, 0.04 g/ m² biomass).
223 Other taxa were represented by less than 10 individuals/m² (Table 1). Indicator
224 species analysis identified *Gammarus fossarum* as a single indicator taxon of LiAd

225 (indicator value = 0.626, $P = 0.001$). Indicator species analysis did not find any other
226 indicator taxa.

227

228 The comparison of alternative statistical models explaining taxa richness showed that
229 the model without any predictor (null model) explains best the observed pattern of
230 taxa richness (Table 2). This model showed that taxonomic richness did not vary
231 enough for differences to be detectable across treatments and there was no statistical
232 evidence that SaEx, LiAd or the sampling date changed the taxa richness of
233 macroinvertebrate communities in the experimental trays. However, the low $\Delta AICc$
234 values, small changes in AICc weight values and moderately increasing evidence ratio
235 suggest that there is no strong evidence for one model over the others (Table 2). The
236 second best model, where the value of $\Delta AICc < 2$, predicts that only LiAd had an
237 effect on macroinvertebrate taxa richness (Table 2).

238

239 We also compared the performance of different statistical models predicting
240 macroinvertebrate abundance (Fig. 1) and found that the best-fit model includes the
241 effects of SaEx, LiAd, date, as well as the interaction of SaEx and LiAd (Table 3).
242 This model showed that SaEx and LiEx had a positive effect on macroinvertebrate
243 abundance while sample date and the interaction of SaEx and LiAd had a negative
244 effect (Table 4). The decrease in the mean density of macroinvertebrates over the six
245 sampling dates was as follows: 269.2, 186.4, 123.8, 95.0, 95.0 and 100
246 individuals/m². The second best model indicates that LiAd and sample date had an
247 effect on macroinvertebrate abundance, while the other alternative models showed
248 $\Delta AICc$ values higher than 2 (Table 3).

249

250 The linear model using salamander exclusion, litter addition, sample date and the
251 interaction of salamander exclusion and litter addition explains best the biomass of
252 macroinvertebrates (Table 5). This model showed that salamander exclusion and litter
253 addition had a positive effect on macroinvertebrate biomass, while the interaction of
254 these terms had a marginally significant negative effect (Table 6, Fig. 2). This model
255 also indicated that the biomass of the macroinvertebrates decreased with time (Table
256 6). Other alternative statistical models also explained well the observed patterns in
257 biomass (Table 5). Three of these had an evidence ratio smaller than 2, all of them
258 indicated an effect of litter addition and sample date, two of them the effect of
259 salamander exclusion, and only one the effect of stream identity and the interaction of
260 salamander exclusion and litter addition (Table 5).

261

262

263 **Discussion**

264

265 Our results show for the first time that macroinvertebrate assemblages in fishless
266 headwater streams are structured both by bottom-up and top-down forces, if larvae of
267 fire salamander are present. These findings suggest that macroinvertebrates in these
268 streams are strongly dependent on the bottom-up organic input and the larvae of
269 salamanders that have a top-down effect on macroinvertebrates in these systems.

270

271 The communities we examined were dominated by a single species and only three
272 taxa were represented by more than 10 individuals. Although the use of the one-week
273 experimental period was necessary to avoid the risk of spates, our experimental
274 design indicate only early colonization events of macroinvertebrates, where leaves

275 might provide both substrate and food for macroinvertebrates (Richardson, 1992;
276 Gessner & Chauvet, 2002). The observed significant differences among treatments
277 indicate that stream macroinvertebrates colonize the substrate very quickly
278 (Townsend & Hildrew, 1976). Compared to other studies (Heino et al., 2003;
279 Schmera & Erős, 2004), the recorded number of macroinvertebrate taxa was low. A
280 possible explanation for this is that small headwater streams have low taxa richness
281 (Heino et al., 2005; Clarke et al., 2008; Schmera et al., 2012). Another explanation is
282 that the colonization of the trays used in our experimental design was only through the
283 water column, and not the substratum. Therefore, only a highly mobile fauna living
284 close to the surface was sampled (Weigelhofer & Waringer, 2003).

285

286 The macroinvertebrate communities examined were dominated by the amphipod
287 *Gammarus fossarum* and this species responded positively to litter addition. This
288 species is a shredder (see Cummins, 1973) and is widespread in Central Europe
289 (Meijering, 1972). *Gammarus fossarum* is the main food source for the larvae of fire
290 salamander in headwater habitats (Thiesmeier, 1982; Ruff & Maier, 2000).

291

292 Litter input from riparian vegetation has been identified as a major energy component
293 of stream food webs (Cummins, 1973; Wallace et al., 1997). Although the best-fit
294 statistical model suggested that taxa richness did not respond to any treatment and
295 indicator analyses showed that only *G. fossarum* responded to litter addition, the
296 second best statistical model indicated that litter addition had an impact on taxa
297 richness. Our results, which show that macroinvertebrate abundance and biomass
298 increases in response to litter addition, are in agreement with other studies reporting
299 that stream macroinvertebrates are under pressure from a strong bottom-up effect

300 (Flory & Milner, 1999; Johnson & Wallace, 2005). These findings are in agreement
301 with the observation that shredding macroinvertebrates show aggregated spatial
302 distribution (Murphy et al. 1998) and mostly follow the patchy distribution of leaf
303 packs on the stream bottom (Dobson & Hildrew, 1992; Schmera, 2004). The
304 increasing abundance and biomass in response to the exclusion of salamanders
305 suggests that macroinvertebrates are also under predatory pressure from salamanders.
306 Although experimental studies have reported similar results (Huang & Sih, 1991;
307 Keitzer & Goforth, 2013; Reinhardt et al., 2013), our study is the first to
308 simultaneously examine the effects of leaf litter and salamander larvae on stream
309 macroinvertebrates. The minimal adequate models examining macroinvertebrate
310 abundance and biomass had an estimate value for litter addition that was always
311 larger than the estimate value for salamander exclusion. Moreover, the alternative
312 models more frequently included litter addition than salamander exclusion. Together
313 this suggests that bottom-up forces have a stronger impact on macroinvertebrate
314 abundance and biomass than top-down forces. On the other hand, the negative
315 interaction between leaf litter addition and salamander exclusion suggests that the
316 combination of salamander exclusion and litter addition does not increase
317 macroinvertebrate abundance and biomass in the way that would be assumed based on
318 the additive effect of individual treatments. A possible explanation is that the mesh
319 size used to exclude salamander larvae could easily have also excluded larger
320 *Gammarus fossarum* individuals (length >8 mm), which was by far the most abundant
321 macroinvertebrate species. The control trays are likely to have provided little
322 protection from predation by the salamander larvae, and as expected,
323 abundance/biomass was reduced in comparison to mesh-covered trays. In trays with
324 leaves, abundance/biomass was always higher than in trays without leaves, as again

325 expected. In these trays it was thought that leaves provided cover and protection from
326 predation, preventing the salamander larvae from reducing the *Gammarus* abundance
327 so easily. All of these findings suggest that our systems can easily be modeled by a
328 litter amphipod salamander larvae food chain with a stronger bottom-up and a weaker
329 top-down control.

330

331 In conclusion, we demonstrated that macroinvertebrate abundance and biomass in
332 fishless headwater streams were structured both by bottom-up and top-down forces.
333 We found that headwater streams interact strongly with adjacent terrestrial areas and
334 the riparian buffer zone is extremely important for these streams. This buffer zone
335 provided food source for macroinvertebrates in the form of allochthonous leaf litter
336 and the top predators of these streams, the salamander larvae, come from this zone. In
337 sum, our study emphasizes the importance of the riparian buffer zone in the structure
338 of macroinvertebrate communities and also the function of headwater streams
339 (Richardson & Danehly, 2007; Clipp & Anderson, 2014; Olson et al., 2014).

340

341

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343

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485 Table 1: Mean density of taxa (individuals/m²/sampling occasion) in the different
 486 treatments.

Order	Family	Taxon	Treatment			
			Control	Salamander exclusion	Litter addition	Both
Tricladida	Dugesiiidae	<i>Dugesia gonocephala</i> (Duges, 1830)	9.62	0	5.77	15.38
Amphipoda	Gammaridae	<i>Gammarus fossarum</i> Koch, 1836	1546.15	1921.15	3023.08	2775.00
Diptera	Dixidae	<i>Dixa sp.</i>	1.92	0	0	0
	Simuliidae	<i>Simulium sp.</i>	5.77	13.46	11.54	5.77
	Stratiomyidae		0	0	1.92	0
	Tipouidae	<i>Dicranota sp.</i>	0	1.92	3.85	5.77
	Tipulidae	<i>Tipula sp.</i>	1.92	0	0	0
Ephemeroptera	Baetidae	<i>Baetis sp.</i>	23.08	21.15	42.31	30.77
	Ephemeridae		1.92	0	0	0
	Heptageniidae	<i>Heptagenia sp.</i>	1.92	0	5.77	1.92
	Leptophlebiidae		1.92	5.77	3.85	3.85
Plecoptera	Perlodidae		1.92	0	0	3.85
Trichoptera	Polycentropodidae	Plectrocnemia	0	1.92	1.92	0

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488

489 Table 2: The best five statistical models explaining taxa richness of
 490 macroinvertebrates. Models are arranged from the best to worst based on evidence
 491 ratios. AICc: Akaike's Information Criterion corrected for small sample size, Δ AICc:
 492 the difference in AICc values between the best model and competing models, AICc
 493 weight: the relative likelihoods of a model given the data, evidence ratio: relative
 494 likelihood of each model vs. the best model
 495

Model	AICc	Δ AICc	AICc weight	Evidence ratio
	503.80	0.00	0.23	1.00
Litter addition	504.27	0.47	0.19	1.26
Salamander exclusion	505.83	2.04	0.08	2.77
Date	505.84	2.04	0.08	2.77
Salamander exclusion + Litter addition	506.32	2.52	0.07	3.53

496
 497

498 Table 3: The best five statistical models explaining abundance of macroinvertebrates.
 499 Models are arranged from the best to worst based on evidence ratios. AICc: Akaike's
 500 Information Criterion corrected for small sample size, $\Delta AICc$: the difference in AICc
 501 values between the best model and competing models, AICc weight: the relative
 502 likelihoods of a model given the data, evidence ratio: relative likelihood of each
 503 model vs. the best model

504

Model	AICc	$\Delta AICc$	AICc weight	Evidence ratio
SaEx + LiAd + Date + SaEx:LiAd	268.46	0.00	0.41	1.00
LiAd + Date	269.82	1.36	0.21	1.98
SaEx + LiAd + Date + Stream + SaEx:LiAd	270.50	2.04	0.15	2.77
SaEx + LiAd + Date	271.03	2.57	0.11	3.62
LiAd + Stream + Date	271.82	3.36	0.08	5.36

505 SaEx: Salamander exclusion, LiAd: Litter addition, SaEx:LiAd: interaction of salamander
 506 exclusion and litter addition

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508

509 Table 4: The summary table of the minimal adequate model explaining
510 macroinvertebrate abundance using different predictors.

Predictors	Estimate	SE	t-value	P
Salamander exclusion (SaEx)	0.195	0.089	2.188	<0.001
Litter addition (LiAd)	0.418	0.089	2.188	0.029
Season	-0.026	0.006	-4.253	<0.001
SaEx:LiAd	-0.271	0.126	-2.152	0.033

511 SaEx:LiAd: interaction of salamander exclusion and litter addition

512

513

514 Table 5: The best five statistical models explaining biomass of macroinvertebrates.
 515 Models are arranged from the best to worst based on evidence ratios. AICc: Akaike's
 516 Information Criterion corrected for small sample size, Δ AICc: the difference in AICc
 517 values between the best model and competing models, AICc weight: the relative
 518 likelihoods of a model given the data, evidence ratio: relative likelihood of each
 519 model vs. the best model

520

Model	AICc	Δ AICc	AICc weight	Evidence ratio
SaEx + LiAd + Date + SaEx:LiAd	-159.8	0.00	0.27	1.00
LiAd + Date	-159.4	0.37	0.22	1.20
SaEx + LiAd + Date + Stream + SaEx:LiAd	-158.6	1.16	0.15	1.79
SaEx + LiAd + Date	-158.6	1.19	0.15	1.82
LiAd + Stream + Date	-158.2	1.51	0.13	2.13

521 SaEx: Salamander exclusion, LiAd: Litter addition, SaEx:LiAd: interaction of
 522 salamander exclusion and litter addition

523

524

525

526 Table 6: The summary table of the minimal adequate model explaining
527 macroinvertebrate biomass.

Predictors	Value	SE	t-value	P
Salamander exclusion (SaEx)	0.066	0.032	2.072	0.039
Litter addition (LiAd)	0.148	0.032	4.654	<0.001
Date	-0.011	0.002	-5.038	<0.001
Leaf:Mesh	-0.081	0.044	-1.808	0.072

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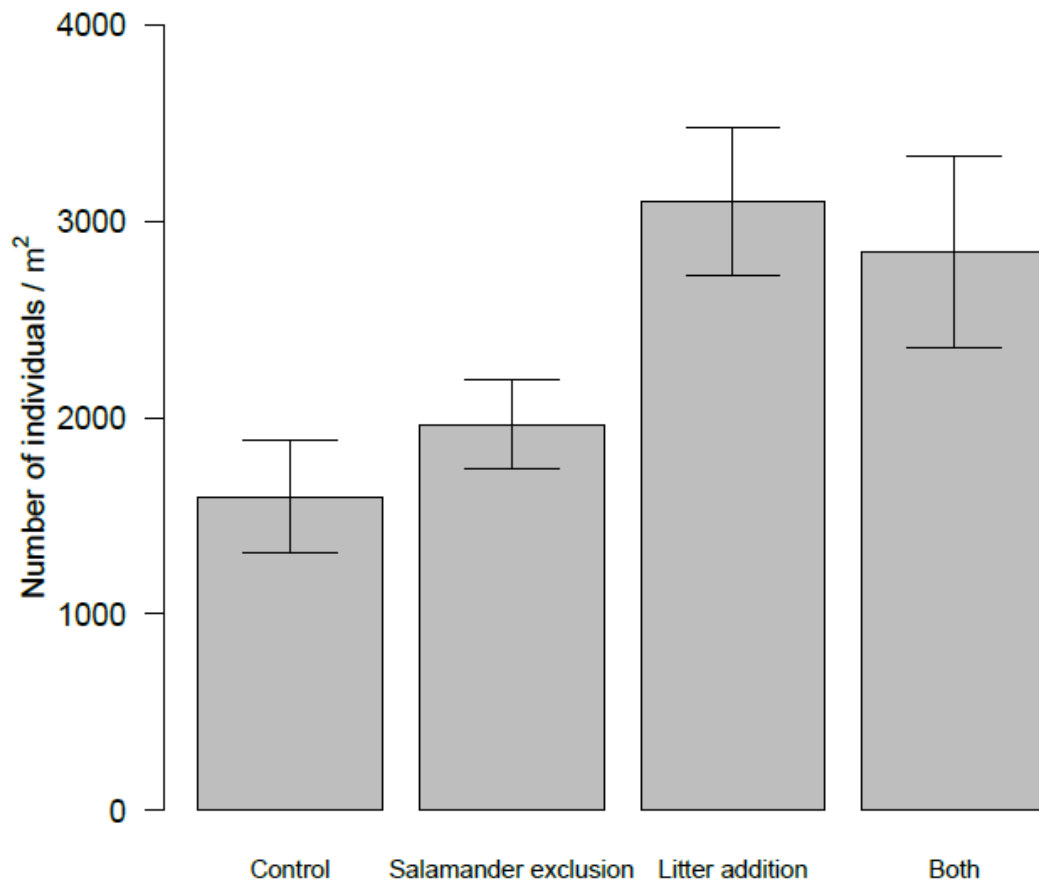
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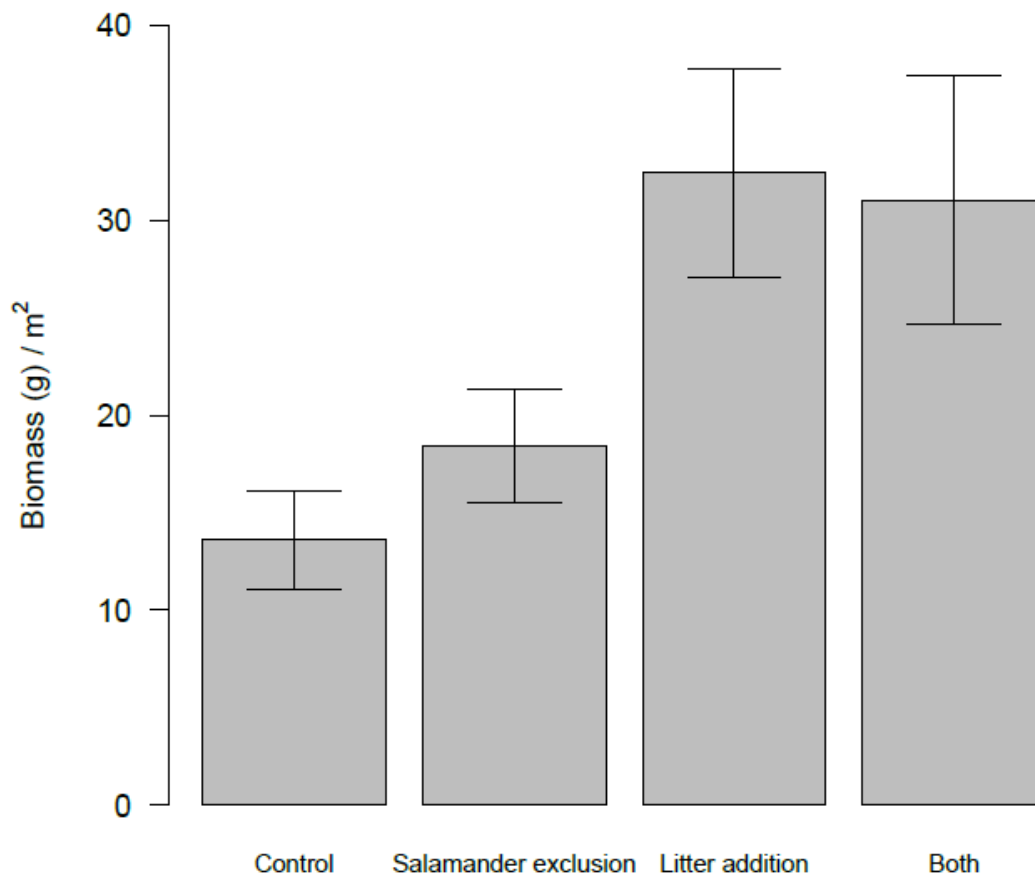
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535 Fig. 1: Distribution of macroinvertebrate abundance (individuals / m²) among
536 different treatments. Bars show mean values while vertical lines standard errors.

537



538

539 Fig. 2: Distribution of macroinvertebrate biomass (g / m²) among different treatments.

540 Bars show mean values while vertical lines standard errors.

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