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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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45   **Introduction**

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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 tropic 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 m^2.

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 (ΔAICc), 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 indivdiduals/m^2, 97.47% of all

220 individuals, mean population biomass 23.46 g/m^2) followed by Ephemeroptera:

221 Baetidae (29 individuals/m^2, 1.23% of total individuals, 0.09 g/m^2 biomass) and

222 Diptera *Simulium* (9 individuals/m^2, 0.004% of total individuals, 0.04 g/ m^2 biomass).

223 Other taxa were represented by less than 10 individuals/m^2 (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 ΔAICc

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 ΔAICc < 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/m^2. The second best model indicates that LiAd and sample date had an

247 effect on macroinvertebrate abundance, while the other alternative models showed

248 ΔAICc 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 macroinvertebrte communities and also the function of headwater streams

339 (Richardson & Danehly, 2007; Clipp & Anderson, 2014; Olson et al., 2014).

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485　Table 1: Mean density of taxa (individuals/m^2/sampling occasion) in the different

486　treatments.

Order	Family	Taxon	Treatment			
			Control	Salamander exclusion	Litter addition	Both
Tricladida	Dugesiidae	*Dugesia gonocephala* (Duges, 1830)	9.62	0	5.77	15.38
Amphipoda	Gammaridae	*Gammarus fossarum* Koch, 1836	1546.15	1921.15	3023.08	2775.00
Diptera	Dixidae	*Dixa sp.*	1.92	0	0	0
	Simuliidae	*Simulium sp.*	5.77	13.46	11.54	5.77
	Stratiomyidae		0	0	1.92	0
	Tipouidae	*Dicranota sp.*	0	1.92	3.85	5.77
	Tipulidae	*Tipula sp.*	1.92	0	0	0
Ephemeroptera	Baetidae	*Baetis sp.*	23.08	21.15	42.31	30.77
	Ephemeridae		1.92	0	0	0
	Heptageniidae	*Heptagenia sp.*	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, ΔAICc:

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	ΔAICc	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, ΔAICc: 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	ΔAICc	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

507

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, ΔAICc: 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	ΔAICc	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

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526   Table 6: The summary table of the minimal adequate model explaining

527   macroinvertebrate biomass.

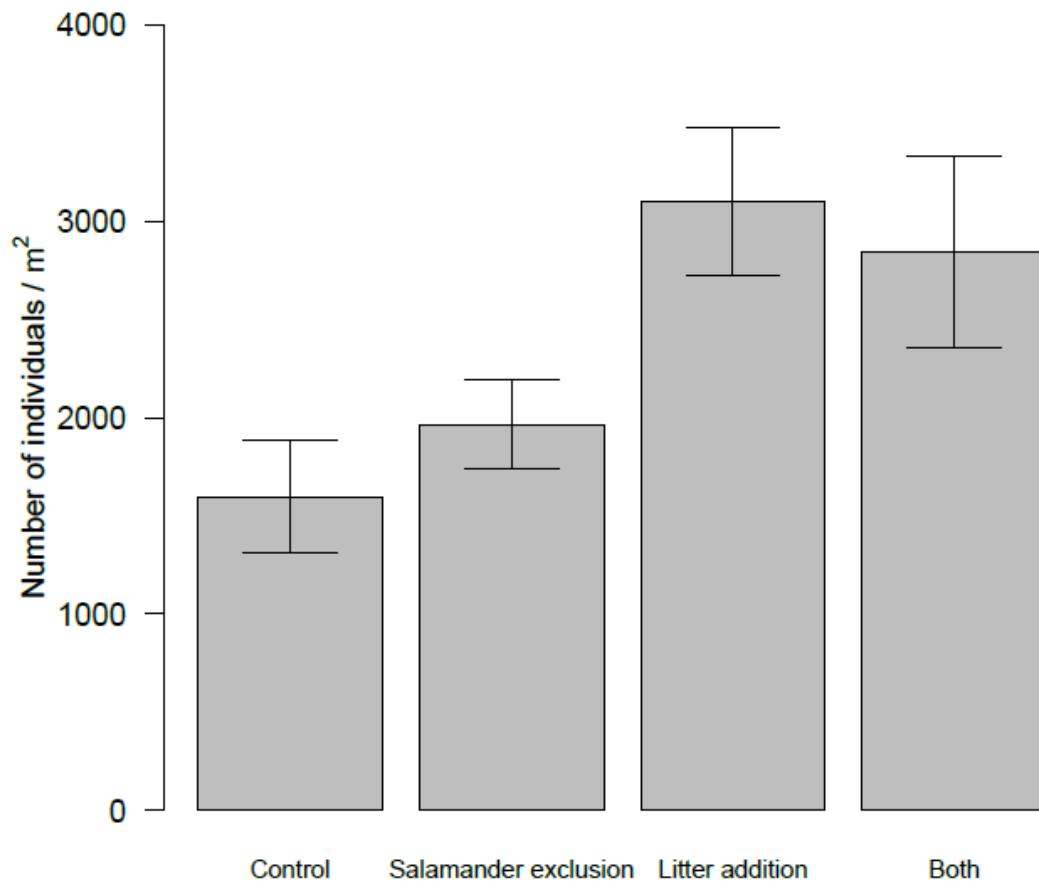| Predictors	Value	SE	t-value	P
Salamander exclusion (SaEx)	0.066	0.032	2.072	0.039
Litter addition (LiAd)	0.148	0.032	4.654	<0.001
Date	-0.011	0.002	-5.038	<0.001
Leaf:Mesh	-0.081	0.044	-1.808	0.072

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535   Fig. 1: Distribution of macroinvertebrate abundance (individuals / m^2) among

536   different treatments. Bars show mean values while vertical lines standard errors.

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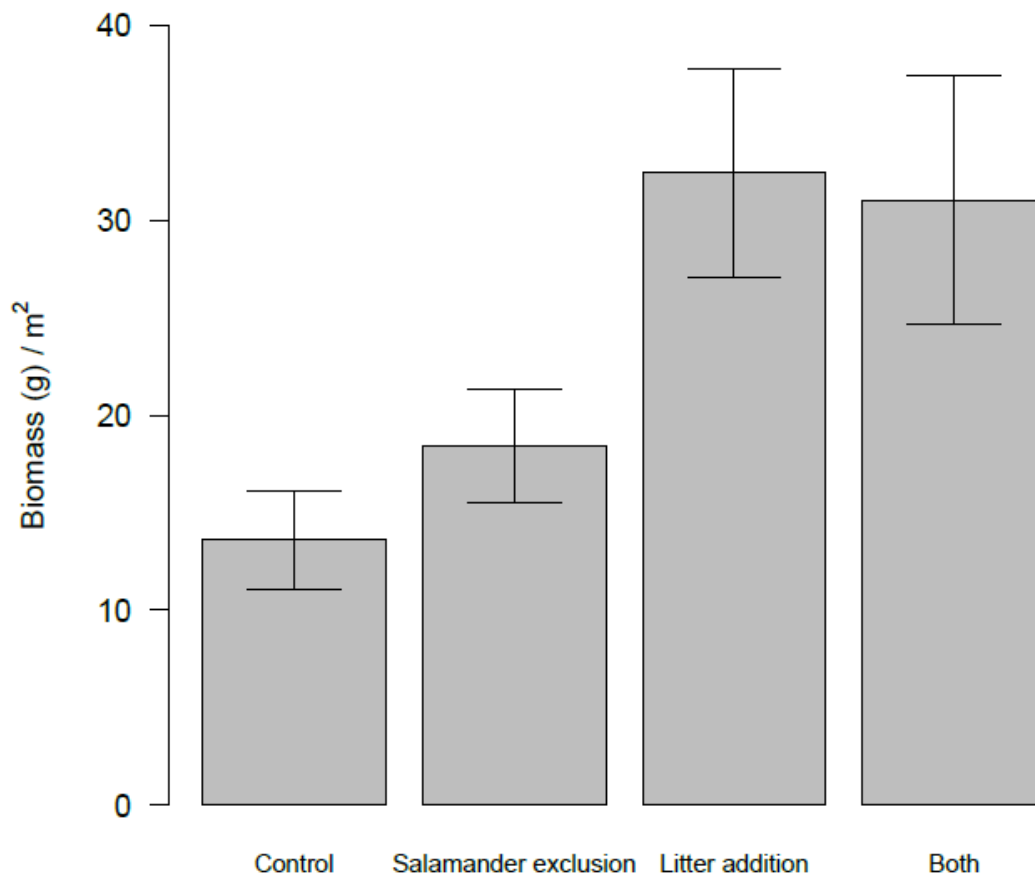
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539   Fig. 2: Distribution of macroinvertebrate biomass (g / m^2) among different treatments.

540   Bars show mean values while vertical lines standard errors.

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