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Relative effects of elevational and habitat constraints on alpine spring biodiversity

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Abstract:	<p>Global climatic changes and local disturbances may alter composition and distribution of spring invertebrates in mountains. In this study, we compared the effects of elevation, landscape and local characteristics on spring biodiversity. At 16 springs (from 570 to 1650m a.s.l.) in The Chartreuse Range (French Alps) benthic, vegetation, and interstitial habitats were sampled in summer for aquatic invertebrate assemblage structure (abundances, richness, reproduction and dispersal traits, functional feeding groups). Assemblages were related to geographic location (elevation), landscape characteristics and local variables. Elevation was the major driver of the fauna: taxonomic richness and the percentage of scrapers decreased with elevation, while the proportion of predators and species with an asexual reproduction increased with elevation. The landscape characteristics around the spring had a weak influence on the benthic taxonomic richness which increased with the percentage of forest and decreased with the proportion of grassland. Finally, the habitat characteristics had no effect on taxonomic richness, but partially control the abundances of benthic assemblages and sediment-feeder organisms that both decreased with increasing sediment grain size. Future changes in the temperature patterns would affect alpine spring fauna, but disturbance of the local characteristics of springs must not be neglected.</p>
Suggested Reviewers:	<p>Emmanuel Castella, Dr Prof, Université de Genève Emmanuel.Castella@unige.ch Prof Castella works on the effect of altitudinal gradients on aquatic fauna for a long time.</p> <p>Martin Pusch, Dr Prof, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, IGB pusch@igb-berlin.de Prof Martin Pusch works on the ecotone between groundwater and surface water</p>

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Dr G. Rossetti work on invertebrates living in small water bodies

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Relative effects of elevational and habitat constraints on alpine spring biodiversity

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ABSTRACT

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Global climatic changes and local disturbances may alter composition and distribution of spring invertebrates in mountains. In this study, we compared the effects of elevation, landscape and local characteristics on spring biodiversity. At 16 springs (from 570 to 1650m a.s.l.) in The Chartreuse Range (French Alps) benthic, vegetation, and interstitial habitats were sampled in summer for aquatic invertebrate assemblage structure (abundances, richness, reproduction and dispersal traits, functional feeding groups). Assemblages were related to geographic location (elevation), landscape characteristics and local variables. Elevation was the major driver of the fauna: taxonomic richness and the percentage of scrapers decreased with elevation, while the proportion of predators and species with an asexual reproduction increased with elevation. The landscape characteristics around the spring had a weak influence on the benthic taxonomic richness which increased with the percentage of forest and decreased with the proportion of grassland. Finally, the habitat characteristics had no effect on taxonomic richness, but partially control the abundances of benthic assemblages and sediment-feeder organisms that both decreased with increasing sediment grain size. Future changes in the temperature patterns would affect alpine spring fauna, but disturbance of the local characteristics of springs must not be neglected.

(194 word)

Key words: Alp Mountains, Ecotone, Groundwater, Landscape, Land-cover, Species traits.

58 INTRODUCTION

59

60 Ecosystems at high altitudes are particularly sensitive to climate change and
61 present thus particular challenges for biodiversity conservation (Walther et al., 2002;
62 Elsen & Tingley, 2015; Allen & Lendemer, 2016). Climate changes trigger species
63 distribution shifts in many parts of the world, but species from mountains are
64 disproportionately sensitive to these changes (Thuiller et al., 2005; Dullinger et al.,
65 2012). Range-restricted species, particularly mountaintop species, show severe range
66 contractions and have been the first group in which entire species have gone extinct
67 (Parmesan, 2006). Although not all climatic warming effects in mountain systems
68 necessarily involve area reductions (Peterson, 2003). Upward shifts of plant species
69 in high mountain systems are already observed. For example, the tree line and related
70 human activities linked to forestry advance in response to environmental change
71 (Grace et al., 2002) together with agriculture at lower elevations. The distribution of
72 species along the elevational gradient represents a stimulating model for the study of
73 global climatic change on biodiversity and its consequences for conservation (Gaston,
74 2000).

75 Species richness is generally supposed to decrease along elevational gradients
76 (Rapoport, 1982; Stevens, 1992) because the climatic constraints (temperature,
77 duration of sub-zero temperatures) progressively exclude species on the basis of their
78 biological and ecophysiological characteristics (e.g. for aquatic fauna Milner *et al.*,
79 2001). More recently, the generality of a decrease in species richness with elevation
80 was criticized (Kattan & Franco, 2004). In a review, Rahbek (1995) showed that
81 decrease in species richness was not the rule and approximately half of the studies
82 had a mid-elevation peak in species richness, because mountains may represent an
83 attractive ecosystem for organisms. In most cases, studies of biodiversity patterns
84 along elevation gradients focus on species richness or other global community
85 variables, whereas groups of species based on their biological traits may follow very
86 different elevation patterns (Gaston, 2000). Colwell and Lees (2000) insisted that
87 resistance to dispersal or survival may explain elevational patterns and may be
88 included in assemblage analyses. Biologic traits at the scale of the assemblages may
89 represent an innovative way to study the elevational patterns in fauna and flora.

90 However, elevation is not a simple variable. There are two categories of
91 environmental constraints that change with elevation (Kattan & Franco, 2004; Körner,

92 2007): 1) those directly linked to the physical elevation above the sea level, such as
93 atmospheric pressure, oxygen partial pressure, UV inputs, and temperature that
94 govern the large scale patterns that will be modified with global warming; and 2) those
95 influenced by local scale characteristics, such as rainfall heterogeneity, soil and
96 sediment characteristics, human activities and land-use (e.g. Castella *et al.*, 2001;
97 *Milner et al.*, 2001; *Forister et al.*, 2010; Death & Collier, 2010). Confounding the former
98 by the latter will introduce confusion in the studies of elevational gradients, and detailed
99 analysis of clines in local environmental variables needs to be combined with surveys
100 of large scale biodiversity distribution (Lomolino, 2001).

101 Alpine springs perfectly fit with this double scale interaction, because they are
102 ecotones between subterranean and superficial aquatic systems characterized by a
103 mix of epigeal and hypogean invertebrates (Vervier *et al.*, 1992; Plénet *et al.*, 1992;
104 Botosaneanu, 1998). The conservation of this fauna needs disentangling the relative
105 effects of global and local disturbances. In springs, ambient conditions, and especially
106 water temperature, are clearly controlled by the mean elevation and temperature of the
107 aquifer that fed the spring (Kamp, 1995), but the local geology and the surrounding
108 landscape strongly modify the basic ecological properties of the ecotone (Vervier *et al.*,
109 1992). The geological characteristics of the substratum for example controls the
110 porosity of the rocks and the hydrodynamic of the springs (Plénet and Gibert, 1995;
111 Zollhöfer *et al.*, 2000), their stochasticity in dry climate (Rosati *et al.*, 2017), whereas
112 the bottom sediment grain size, the land-cover and the vegetation surrounding the
113 spring may control the quantity and quality of the available organic matter (Stone &
114 Wallace, 1998; Death & Collier, 2010; von Fumetti & Blattner, 2017). In contrast with
115 rivers and streams, the colonization of alpine springs can only occur through upstream
116 migration or flying adults. The species traits of spring fauna, such as ability to dispersal
117 or reproduction strategies, may thus represent crucial characteristics that control the
118 assemblage composition (Murphy *et al.*, 2010; Rosati *et al.*, 2017).

119 The aim of the present study was to assess the effect of elevational gradient,
120 landscape, and local characteristics on the composition and structure of 16 spring
121 invertebrate assemblages in the Chartreuse Mountain Range (French Alps), extending
122 from 570 to 1650 m a.s.l. We examined abundance, taxonomic richness, diversity of
123 the invertebrates in three habitats (benthic, vegetation, interstitial) as well as the effect
124 of elevation on the proportion of three species traits in the assemblages: their ability to
125 dispersal, their reproductive strategies, and their feeding preferences (i.e. five

126 functional feeding groups). We hypothesised a strong effect of elevation on
127 invertebrate assemblages, because poorly mobile ectotherm invertebrates are limited
128 by the temperature (Claret et al., 1997; hypothesis 1). The colonization of isolated
129 springs after drought or catastrophic snow melt will be directly controlled by the
130 dispersal ability of species (Milner et al., 2001; Murphy et al., 2010) and their
131 reproduction strategies (i.e. asexual species may found a population with a single
132 individual; hypothesis 2). The vegetation characteristics of the surrounding landscape
133 may also control the assemblages (forest versus grassland, Stone & Wallace, 1998;
134 Moore & Palmer, 2005; hypothesis 3) together with the local characteristics of the
135 spring (grain size or water chemistry, Culp et al., 1983; Castella et al., 2001; hypothesis
136 4).

137

138 **METHODS**

139

140 The Chartreuse Range is a pre-alpine mountain chain located on the Western
141 side of the French Alps between the cities of Grenoble and Chambéry (Fig. 1). With an
142 elevation that ranges from 250 to 2086 m a.s.l., the climate is wet (≈ 2000 mm rainfall
143 a year) and cold, with a mean annual temperature of 9.1 °C (February mean = -4.4 °C;
144 August mean = 17.3 °C) at Saint Pierre de Chartreuse (900 m a.s.l.). The geological
145 substratum is essentially calcareous (from Oxfordian to Barremian) and medium-to-
146 highly karstified. The dominant vegetation is a mixed forest of oak (*Quercus* spp.) and
147 fir (*Abies alba*) at low elevation and of spruce (*Picea abies*) at intermediate and high
148 elevations. Agriculture is primarily milk and wood production, which results in a mix of
149 grasslands and forests in the landscape.

150 During July 1999, 16 springs were sampled (Table 1) from 570 to 1650 m a.s.l.
151 At each spring, temperature and electric conductance were measured using a thermo-
152 conductimeter (WTW LF 92) immersed directly in the spring water, with an additional
153 surface water sample collected in a 100 ml acidic-washed plastic bottle. At each spring,
154 we measured the diameter of 100 randomly chosen particles (± 1 mm, Kellerhals and
155 Bray, 1971). Mean particle sizes, with sand noted as 0.1 mm (Table 1) were calculated
156 for each spring.

157 Fauna samples were collected from three different habitats. Benthic and
158 vegetation habitats were sampled at three points in each using a mini-Surber net (200
159 μm mesh-net) on a surface of 0.033 m² (total surface 0.1 m²). Interstitial fauna was

160 sampled using the Karaman-Chapuis pit method: three pits of 15–20 cm deep and 20–
161 30 cm width were dug in the emerged sediment on the border of the spring and a total
162 of 5 L were sampled randomly combining the water of the three pits. Samples were
163 preserved in the field in a 5 % formaldehyde solution and stained with Bengal Pink.

164 In the laboratory, water samples were measured for chloride, nitrate, and
165 sulphate concentrations ($\pm 0.1 \text{ mg.L}^{-1}$) using a Capillary Ion Analyser (Waters, Milford,
166 MA, U.S.A.). Land-cover of the landscape surrounding each spring was estimated from
167 aerial photographs, with the area of six landscape units (built area, roads, cultivated
168 fields, grassland, forest, and rocks without vegetation) measured in a 1 km radial circle
169 and expressed in percentage.

170 Invertebrates were sorted using sieves, identified to species, group of species,
171 or genus level when allowed by individual size and available keys (Planaria, Acheta,
172 Gastropoda, Bivalvia, Ostracoda, Cladocera, Amphipoda, Isopoda, Ephemeroptera,
173 Trichoptera, Plecoptera, Coleoptera). Diptera were identified to the family level, the
174 Copepoda were separated between Cyclopids and Harpacticids, the Nematoda, the
175 Clitellata (Oligocheta), and the Hydracarian groups were not identified further. Three
176 descriptors were calculated for each spring and each habitat: total abundance,
177 taxonomic richness, Shannon diversity index (H'). Three biological traits were
178 documented for the invertebrate assemblages: (1) dispersal ability, divided in low or
179 high dispersal (without or with flying adults); (2) reproduction strategy, divided in
180 exclusively sexual (separated sex) or potentially asexual (through body division or
181 parthenogenesis); and (3) functional feeding groups, divided in shredders (chew
182 conditioned litter or live vascular plant tissue or gouge wood), filtering collectors
183 (suspension feeders - filter particles from the water column), deposit feeders (gathering
184 collectors - ingest sediment or gather loose particles in depositional area), predators
185 (capture and engulf prey or tissue, ingest body fluids) and scrapers (graze rock and
186 wood surface or stems of rooted aquatic plants). Ecological traits of species were
187 documented using the works of Usseglio-Polatera *et al.* (2000) and synthetic tables
188 from Tachet *et al.* (2000). All percentages of feeding groups were calculated on
189 abundances, when one taxon was affiliated to 2 or more functional groups, we applied
190 a percentage of functional affinity in the abundance table according to its affinity to the
191 different groups quoted in Tachet *et al.* (2000).

192 Patterns in the relationships between physical, chemical and landscape
193 variables were revealed using Principal Components Analysis (PCA). The

194 relationships between environmental variables and the assemblage characteristics
195 (defined here above) were then examined by (1) including these assemblage
196 characteristics as supplementary variables in a PCA performed on the environmental
197 variables and (2) using linear correlation with the physical and landscape variables
198 (following Log_{x+1} transformation when necessary). The probability thresholds used in
199 linear correlation and ANOVA were (as noted in the text): *, $P<0.05$; **, $P<0.01$; ***,
200 $P<0.001$. All tests were calculated using Statistica (8.0, Statsoft Inc., 2009, Tulsa, USA)
201 or Excel 2016.

202

203 RESULTS

204 A total of 13,931 invertebrate specimens, representing 46 taxa, were collected
205 from benthic habitats, 10,036 individuals (41 taxa) from vegetation habitats, and
206 11,289 individuals (43 taxa) from interstitial habitats. Only two stygobite species (the
207 Amphipoda *Niphargus rhenorhodanensis* (Schellenberg) and the Ostracoda
208 *Cavernocypris subterranea* (Wolf)) were observed, having been collected at rather
209 high elevation (until 1250m for *N. rhenorhodanensis* and 1650m a.s.l. for *C.*
210 *subterranea*). The most diversified groups in these alpine springs were the Diptera
211 (nine taxa), the Plecoptera (eight taxa), the Trichoptera (eight taxa), and the Ostracoda
212 (six species), while the Ephemeroptera (four taxa), the Amphipoda (three species), and
213 the Coleoptera (four taxa) poorly contributed to the total biodiversity. The most
214 abundant organisms (Table 2) were all sampled in the three habitats, but showed
215 contrasted elevational ranges.

216 *Elevation gradient and environmental parameters*

217 Elevation gradient dominated the first principal component axis (PC1), which
218 accounted for 27.8% of the variation (Fig. 2), encompassing the following variables:
219 percentage of rocks, mean diameter of the particles, temperature, electric
220 conductance, percentages of build area and cultivated fields. The low elevation sites
221 (C1, C2, C3) have negative ordination scores, whereas high elevation sites (C14, C15,
222 C16) have positive scores. Whereas, PC2, which accounted for 23.6% of the variation,
223 represents the human practice in the landscape surrounding the springs, including, the
224 percentages of grassland (positive ordination scores) and of forest, roads, nitrate
225 concentrations, and to a lesser extent mean diameter of the spring particles (negative
226 scores). PC2 distinguishes the mid-elevation site (site C9), located in grazed
227 grassland, from those in managed forests with several unpaved roads for wood

228 extraction (sites C4, C5, C6, C11). The dominance of elevation is apparent (Table 1),
229 as it correlates positively with spring water temperature ($r^2 = 0.38$, $P < 0.01$) and the
230 percentage rocks ($r^2 = 0.60$, $P < 0.001$), and negatively with the percentages of built
231 area ($r^2 = 0.31$, $P < 0.05$) and cultivated fields ($r^2 = 0.40$, $P < 0.01$). There are clear
232 differences between areas devoted to milk or wood production, with the percentage of
233 grassland negatively correlated to the percentage of forest ($r^2 = 0.94$, $P < 0.001$). Micro-
234 habitat characteristics also contribute to PC2, sediment grain size and nitrate
235 concentration have both negative ordination scores and are significantly correlated (r^2
236 = 0.55, $P < 0.001$), because nitrate concentrations is low in station with fine sediment
237 (sites C8 and C10).

238 *Elevation and invertebrate assemblages*

239 When assemblage characteristics were added as supplementary variables in
240 the PCA performed on environmental variables (Fig. 2c) or plotted with elevation (Fig.
241 3), significant changes with elevation were observed but with contrasted trends. The
242 abundances did not significantly change with elevation, but the taxonomic richness
243 was clearly associated to the temperature (Fig. 2c) and negatively correlated with
244 elevation in all three habitats (in all cases $P < 0.05$; Fig. 3). The Shannon diversity
245 index H' decreased significantly with elevation in the vegetation habitat ($r^2 = 0.33$, P
246 < 0.05), but not in the benthic and interstitial habitats (data not shown).

247 Similarly, the changes in the biological traits with elevation show contrasted
248 trends. While dispersal characteristic did not change with elevation ($P > 0.05$), the
249 percentage of species with potential asexual reproduction were clearly associated to
250 the elevation (positive ordination scores, Fig. 2c and significant correlations in all three
251 habitats, $P < 0.01$; Fig. 3). The species driving these trends (Table 2) were the
252 parthenogenic microcrustaceans (e.g. *Cavernocypris subterranean*, *Potamocypris*
253 *zschokkei*) or the flatworm *Crenobia alpina* that can multiply asexually using body
254 division.

255 The abundances of three feeding groups changed with altitude. The percentage
256 of predators (mainly *Crenobia alpina*) increased with altitude ($P < 0.05$; Fig.3), while the
257 percentage of scrapers decreased significantly with elevation in the benthic habitat (r^2
258 = 0.44, $P < 0.01$) and in the interstices ($r^2 = 0.56$, $P < 0.001$; Fig. 3). These scarpers
259 consisted in insect larvae (e.g. *Baetis* sp., *Agapetus* sp.), micro-crustaceans (mostly
260 Cladocera) or large crustaceans that use both coarse organic matter and microphytes
261 (*Gammarus fossarum* Koch and *G. wautieri* Roux; Gayte & Fontvieille, 1997).

262

263 *Landscape and habitat characteristics*

264 The surrounding landscape had a weak effect on the taxonomic richness and
265 diversity of spring invertebrates for vegetation and interstitial habitat. Benthic richness
266 slightly increased with increasing proportions of forest ($r^2=0.22$, $P < 0.05$; Fig. 4) and
267 decreasing proportions of grassland around the spring ($r^2=0.28$, $P < 0.05$; Fig 4). Six
268 species of Plecoptera and 4 species of Ostracoda occurred together in stations C11,
269 C12 and C13 surrounded by more than 80% of forest.

270 The local characteristics of springs also had no effect on assemblage richness
271 and Shannon diversity, but partially explained the abundances of the assemblages,
272 especially in the benthic habitat. Benthic abundances (log transformed) decreased with
273 the sediment grain size ($r^2=0.60$, $P < 0.001$; Fig. 5) because of deposit feeder
274 abundances that were high in fine sediment ($r^2=0.65$, $P < 0.001$; Fig. 5). The chemical
275 characteristics of the spring water had no effect on species richness and diversity, but
276 slightly influenced faunal abundances: nitrate concentrations were significantly
277 correlated with benthic abundances ($r^2=0.234$, $P < 0.05$) and deposit feeder
278 abundances ($r^2=0.301$, $P < 0.05$).

279

280 **DISCUSSION**

281 *The effect of elevation on fauna diversity (hypothesis 1)*

282 In the alpine springs examined, species richness (in the three types of habitat)
283 and the H' diversity index (in the vegetation) decreased with elevation, whereas
284 invertebrate abundances did not change with elevation. Our first hypothesis was thus
285 only partially supported. This weak change in abundances may be explained by a
286 progressive replacement of a large number of low-elevation species (e.g. *Nemoura*
287 spp., *Gammarus* spp.) by few species with a wide elevational range (e.g. *Crenobia*
288 *alpina*), while the abundances of Clitellata and Chironomidae changed little. The
289 resulting decreasing pattern in species richness with elevation lend support to
290 Rapoport's study (1982) where species average range size increases with increasing
291 elevation, thus species with a narrow range are more likely to be found at lower
292 elevations (Stevens, 1992).

293 The mountain springs are very small systems, the distance between them (and
294 the resulting difficulties in colonization) may reinforce this decreasing gradient of
295 taxonomic richness with elevation. In the present study, this observed elevational

296 pattern in taxonomic richness was not influenced by human activities. In contrast,
297 Chawla et al. (2008) observed that human impacts at lower elevations result in low
298 plant diversity towards the bottom of the valley in western Himalaya. In our case, the
299 very low surfaces occupied by villages and cultivated fields at low elevations explained
300 the poor impact of agriculture on spring fauna.

301 The environmental constraints that explain these changes with elevation need
302 to be considered. The temperature of the spring water and other related variables (e.g.
303 duration of the frozen period) was certainly the most important constraints for the
304 invertebrates. Several studies have highlighted the importance of temperature for
305 population survival: for example, the reproduction of *Gammarus roeseli* Gervais is
306 limited by thermal characteristics and the species is restricted to low elevations in the
307 Austrian Alps (Pöckl, 1992). The occurrence of the hypogean Amphipoda, *Niphargus*
308 *rhenorhodanensis*, in a spring at 1250m a.s.l. may be surprising; these springs
309 certainly froze during winter, and the subterranean organisms were supposed to live
310 in thermally buffered biotopes. However, laboratory trials have demonstrated that *N.*
311 *rhenorhodanensis* reared at sub-zero temperatures possess great thermal plasticity,
312 which resulted in extended survival times (Issartel et al., 2005). These unexpected
313 results can be explained by a large accumulation of cryoprotective molecules during
314 cold acclimation, mainly membrane and protein protectants (Issartel et al., 2005). Their
315 high tolerance to cold might be a relict adaptation which enabled their survival during
316 glaciations and the nowadays colonization of high elevation springs (Colson-Proch et
317 al., 2009).

318

319 *Species traits and elevation* (hypothesis 2)

320 Connection between springs decreases with elevation. Above 1500 m a.s.l.,
321 spring catchments are strongly isolated by deep valleys, but the predicted increased
322 in invertebrate dispersal ability with elevation was not observed in this study (the
323 hypothesis 2 is partially rejected). Abundances of organisms with winged adults
324 decreased with elevation (Plecoptera, Ephemeroptera) or remained similar
325 (Chironomidae). Similarly, abundances of taxa with low dispersal decreased
326 (*Gammarus fossarum*) or increased (*Crenobia alpina*) with elevation.

327 In contrast, the mode of reproduction clearly changed with elevation, with an
328 increase in the percentage of species with potentially asexual reproduction (hypothesis
329 2 partly verified). The stygobite Ostracoda *Cavernocypris subterranea* is a good

330 example of the constraint represented by the colonization of isolated springs at high
331 elevation. This tiny crustacean is restricted to ground waters (in caves or porous
332 aquifers) and the hyporheic zone of valley streams, and therefore unlikely to be
333 translocated by birds or mammals. In springs, *C. subterranea* occurs in the benthic and
334 vegetation habitats, sustained by the groundwater flux, which induces the drift of this
335 animal outside the subterranean habitat and minimizes variations in surface water
336 temperature and chemical composition. In these two superficial habitats, the probability
337 of a transport of a single individual by a bird or a mammal strongly increased compared
338 to groundwater habitat (Rogulj et al., 1994). For this species, the ability for an isolated
339 individual to found a new population by asexual reproduction represents an important
340 advantage, even with a reduced genetic diversity (e.g. for parthenogenetic Ostracoda,
341 Butlin et al., 1998).

342 Predicted changes in the trophic groups with elevation was only verified for
343 scrapers and predators. The relative abundances of scrapers decreased with
344 elevation probably because algal growth is reduced at low temperature (Bothwell,
345 1988; Larras et al., 2013) even if insolation increases at high altitude. The percentage
346 of predators was found to increase at high elevation in all three habitats. This latter
347 pattern may be explained by the increase of a very few number of species. For
348 example, *Crenobia alpina* represented 10–25 % of individuals in springs between 1000
349 and 1500 m a.s.l. and 50–60 % of individuals above 1500 m. The study of the trophic
350 links and the long term stability of such assemblage with 60 % of predators may
351 represent a stimulating topic for future research.

352

353 *The effects of landscape and local characteristics*

354 In contrast to the elevational gradient, the landscape characteristics of the
355 springs had relatively little influence on invertebrate assemblage structure. For the
356 landscape around the springs, we did not measure any significant decrease of
357 shredder abundance or diversity with the decrease of forest or an increase of scrapers
358 with the proportion of grassland as observed by Stone & Wallace (1998) in springs
359 after clearcutting. The only trend observed concerned the benthic taxonomic richness
360 that increased with the percentage of forest and decreased with the percentage of
361 grassland. More than a stimulation of a single trophic group (e.g. the shredders), the
362 increase in forest litter inputs may represent a resource for all taxa (as food, habitat or
363 refuge) resulting in an increase of spring invertebrate richness.

364 The local characteristics of the spring had no influence on taxonomic richness
365 nor assemblage diversity, but sediment grain size and the nitrate concentrations
366 controlled the number of individuals present in the spring. The abundance of the
367 benthic fauna increased with the proportion of thin sediment because of an increase in
368 deposit feeder abundances. Sandy bottom sediment of these springs was densely
369 colonized by Clitellata and micro-crustaceans, a trend already observed in several
370 small streams (Sarriquet et al., 2006; Jones et al., 2012). In the same way, water
371 characteristics (electric conductivity, chloride and sulphate concentrations) had no
372 effect on species richness, but nitrate concentrations were correlated to grains size
373 and thus to total and deposit feeder abundances. In springs with fine sediment,
374 abundances were high, but nitrate concentrations were low certainly because of
375 denitrification that occurs frequently in sand and silt (Lefebvre et al., 2004). The link
376 between nitrate and abundances was thus indirect and weak compared to grain size.
377 In this case, the superficial processes control spring benthic assemblages more
378 efficiently than groundwater characteristics (Plénet & Gibert, 1995) and must be
379 documented in more detail (e.g. light intensity inside the spring, organic matter content
380 of the sediment, denitrification, net primary productivity; Gaston, 2000) to understand
381 the complex effects of local characteristics on invertebrate densities.

382

383 *Importance for biodiversity conservation*

384 In conclusion, the community composition of spring invertebrates is more
385 strongly influenced by the elevational gradient than by the local and landscape
386 characteristics of the springs. Future changes in the temperature patterns over
387 mountainous regions are, therefore, likely to have a much greater effect on spring
388 fauna than local management actions to protect spring biodiversity.

389 The protection of alpine spring (e.g. with a fenced area around the spring) is a
390 frequent proposed management, because it prevents the direct access of cattle to the
391 spring and resulting bottom sediment disturbance (e.g. inputs organic matter). The role
392 of sediment grain size in the control of invertebrate assemblages was highlighted by
393 several studies in a large range of aquatic systems (e.g. Culp et al., 1983), certainly
394 because grain size is a synthetic variable that accounts for the habitability of the bottom
395 sediment (Boulton et al., 1998), the type of organic matter stored (fine detritus *versus*
396 algae; Corkum, 1996), and the maximum velocity of water that shapes grain size
397 profiles. The link between sediment grain size and benthic abundances observed in

398 this study highlights the potential role of local disturbance in spring biodiversity
399 dynamics and supports that local management must be carefully considered.

400 The observed predominance of elevation over other local constraints illustrates
401 the importance of temperature and related variables in determining spring biodiversity.
402 Future climatic changes will induce modifications in mean aquifer temperature and thus
403 in the distribution of invertebrate species along elevation gradients. Some range-
404 restricted species (such as *Crenobia alpina*) may be endangered with upward shift of
405 mobile and aggressive species (e.g. *Gammarus* spp.) now restricted to lower
406 elevations. Climate changes may also induce modifications in mountain human
407 activities at low elevations that may induce in turn changes in the diversity of spring
408 assemblages.

409

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416

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560

561

Table 1. Characteristics of the springs sampled in the Chartreuse range.

Station	Altitude	T	Electric conduct	Cl	NO ₃	SO ₄	Sediment mean diameter	Built	Roads	Fields	Grass land	Forest	Rocks
		°C	μS/cm	mg/l	mg/l	mg/l	mm	%	%	%	%	%	%
C1	570	12.3	330	0.7	0.6	1.5	2	6.2	0.2	12.6	36.3	45.4	0.3
C2	620	10.7	498	1	1.5	5.9	2.7	2.6	0.1	10.6	50.5	36.2	
C3	710	9.6	605	3.4	3.9	14.3	2.2	1.3	0.1	8.1	71.7	18.8	
C4	725	16.3	355	0.2	1.9	21.5	3		9.8		6	88.6	4.5
C5	830	8.2	308	0.6	2.4	3.5	2.2		0.1		1.8	97.2	0.9
C6	930	5.5	195	0.4	3.6	1.3	5		0.1		8.7	91.1	
C7	950	7.7	395	1.5	3.9	2.5	1.5		0.1		21.1	78.5	0.3
C8	1000	6.9	698	0.1	0	1.2	0.5		0.1		0.8	97.7	1.3
C9	1070	5.9	263	0.7	1.4	4.7	1.5	1.3	0.1	2.4	80.9	15.3	
C10	1155	12.9	340	0.4	0.2	0.9	0.1				14	86	
C11	1250	5.4	218	1.5	6.6	4.1	10.5		0.8			95.7	3.5
C12	1285	5.7	270	1	2.3	0.9	4.5				0.5	96.4	3.1
C13	1340	6	261	2	0.8	5.4	1.7		0.8		7.4	80.4	11.4
C14	1550	3.5	224	3.2	1.4	2.5	5.2				76.8	4.4	18.8
C15	1650	6	341	0.5	1.1	4.3	2.7				75.1	9.2	15.7
C16	1650	5.3	350	0.9	1.4	2.5	2				40.7	26.2	39.1

Table 2. Characteristics of the assemblages sampled in the studied springs. Mean abundances (\pm DS, n=16). The midpoint altitude corresponds to the altitude where 50% of the individuals were caught (calculated from a cumulative curve).

	Mean densities			Altitudinal range		
	Benthic (ind./ 0.1m ²)	Vegetation (ind./ 0.1m ²)	Interstitial (ind./5l)	Minimum	Midpoint (50%)	Maximum
<i>Baetis</i> sp. ⁴	71 \pm 198	36.5 \pm 72.6	9.4 \pm 24.2	570	575	1550
Simuliidae div. sp. ⁷	2.8 \pm 5.9	15.8 \pm 31.2	1.6 \pm 4.9	570	620	1000
<i>Nemoura</i> cf <i>mortoni</i> ⁵	12 \pm 43	3.6 \pm 9.9	2.9 \pm 5.3	620	620	1070
<i>Gammarus</i> <i>fossarum</i> ³	82 \pm 128	52.9 \pm 112.5	52.4 \pm 94.0	570	700	1340
<i>Nemoura</i> cf <i>sinuata</i> ⁵	23 \pm 39	15.1 \pm 22.8	19.3 \pm 27.6	570	720	1550
Limnephilidae div. sp. ⁶	16 \pm 22	5.9 \pm 10.2	7.4 \pm 23.7	570	940	1650
<i>Protonemura</i> sp. ⁵	20 \pm 35.4	18.5 \pm 35.7	0.8 \pm 2.0	620	1020	1650
Chironomidae div sp. ⁷	127 \pm 111	212.8 \pm 254.6	154.1 \pm 178.0	570	1100	1650
<i>Candona</i> <i>neglecta</i> ²	23 \pm 79.5	1.4 \pm 2.9	6.1 \pm 12.7	570	1155	1650
<i>Cavernocypris</i> <i>subterranea</i> ²	5 \pm 17.9	0.3 \pm 0.6	3.4 \pm 6.4	725	1340	1650
<i>Crenobia</i> <i>alpina</i> ¹	72 \pm 115	31 \pm 41.8	20.3 \pm 28.6	725	1590	1650
Mean abundances	870.7 \pm 685.4	627.3 \pm 560.5	705.6 \pm 622.0			
Mean taxonomic richness	14.3 \pm 3.9	14.2 \pm 4.6	14.4 \pm 3.7			

Taxonomic status: ¹Planaria; ²Crustacea Ostracoda; ³Crustacea Amphipoda; ⁴Hexapoda Ephereroptera; ⁵Hexapoda Plecoptera; ⁶Hexapoda Trichoptera; ⁷Hexapoda Diptera.

Legends of the figures:

Fig. 1: Location of sampling sites in the Chartreuse Range, ranked according to their elevation.

Fig. 2: Principal Component Analysis performed on the landscape and habitat characteristics of springs. (a) Relationships between the environmental variables (see Table 1 for abbreviation codes). (b) Location of sites in the C1xC2 plan. (c) Invertebrate assemblage characteristics added as supplementary material (Abund = abundances, Asex = percentage of species with a potential asexual reproduction, DF = deposit feeders, H' = Shannon diversity index, HD = percentage of species with a high dispersal ability, PDR = predators, Rich = taxonomic richness, SCR = scrappers that fed on microphytes, Sex = species with an obligate sexual reproduction, SHR = shredders, WD = percentage of species with a weak dispersal ability).

Fig. 3. Variation with elevation of taxonomic richness (a), with the proportion (%) of species with potential asexual reproduction (b), and with the relative abundance of predators (c) and scrappers (d) in the benthic (upper panel), vegetation (middle panel), and interstitial habitats (lower panel).

Fig. 4. Variation of benthic taxonomic richness with the percentage of forest (a) and the percentage of grassland (b) in a circular buffer of 1 km diameter around the spring. Linear regression models are $y = 0.051x + 10.49$ for forest and $y = -0.067x + 15.58$ for grassland.

Fig. 5. Variation of benthic abundances (a) and benthic deposit feeder abundances (b) with sediment grain size. Regression models are $y = -505.7 \ln(x) + 1228.8$ for the total benthic abundances and $y = -406.1 \ln(x) + 733.34$ for deposit feeders.

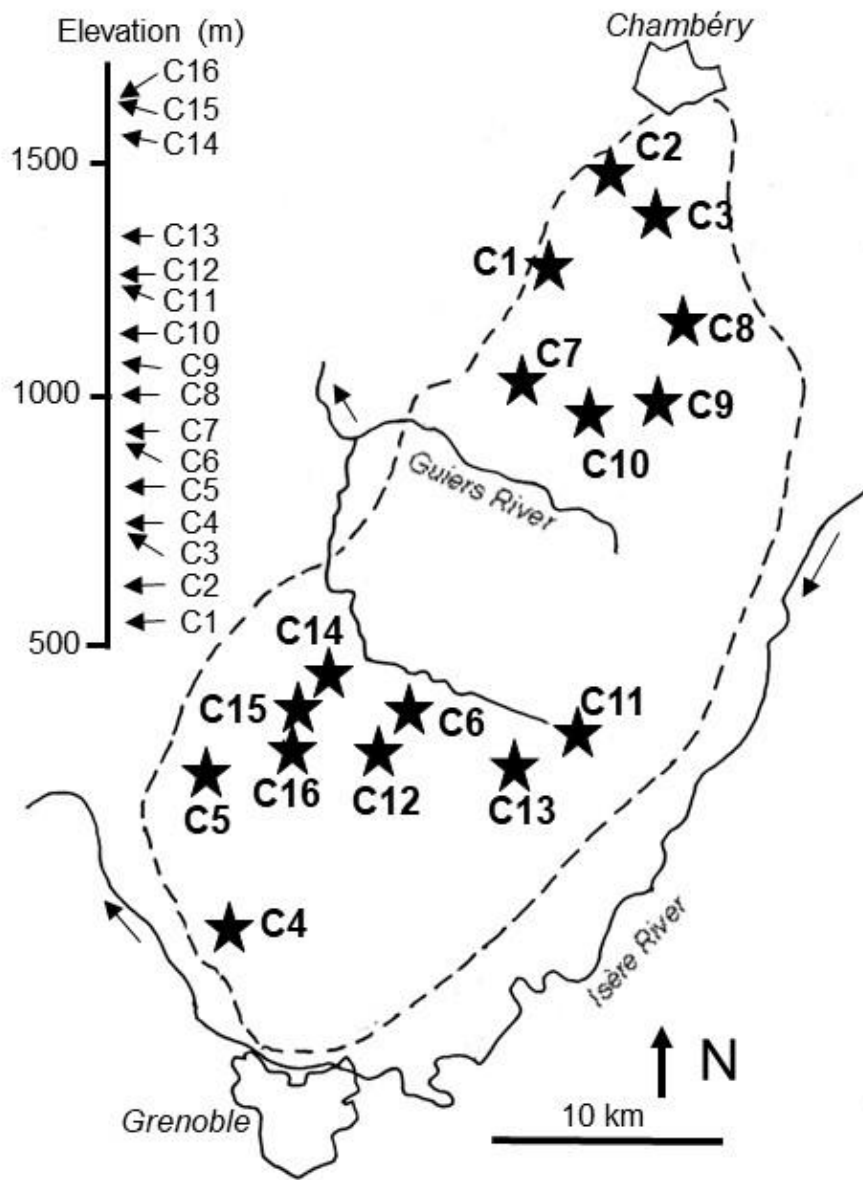


Fig. 1

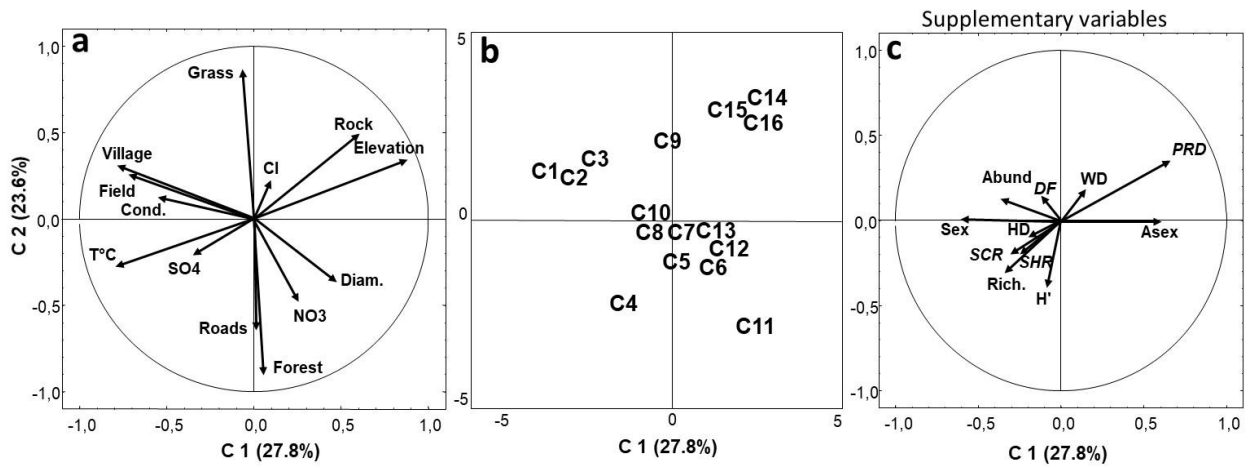


Fig. 2a, b, c

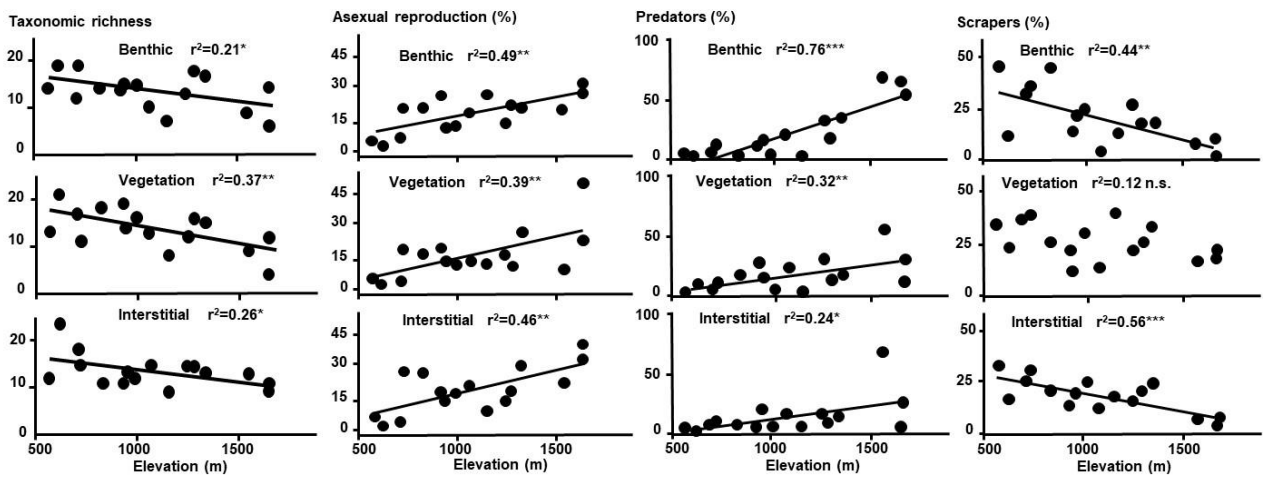


Fig. 3

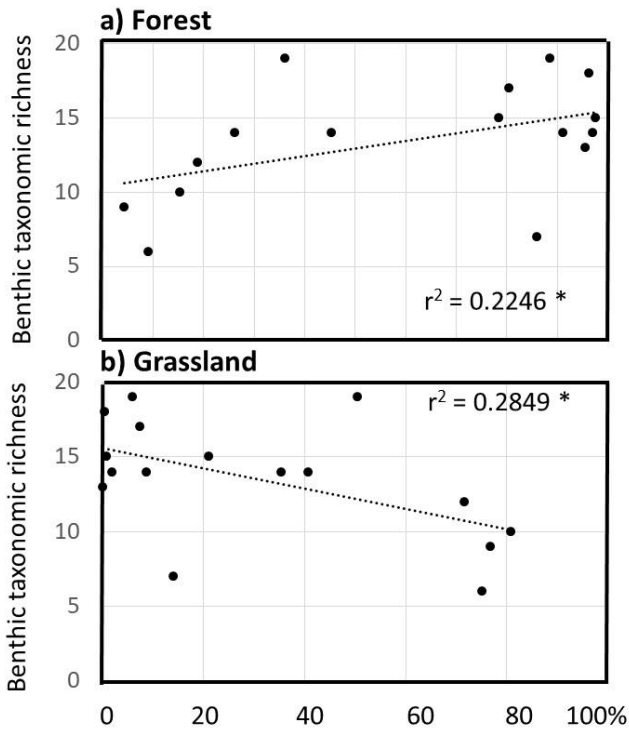


Fig. 4

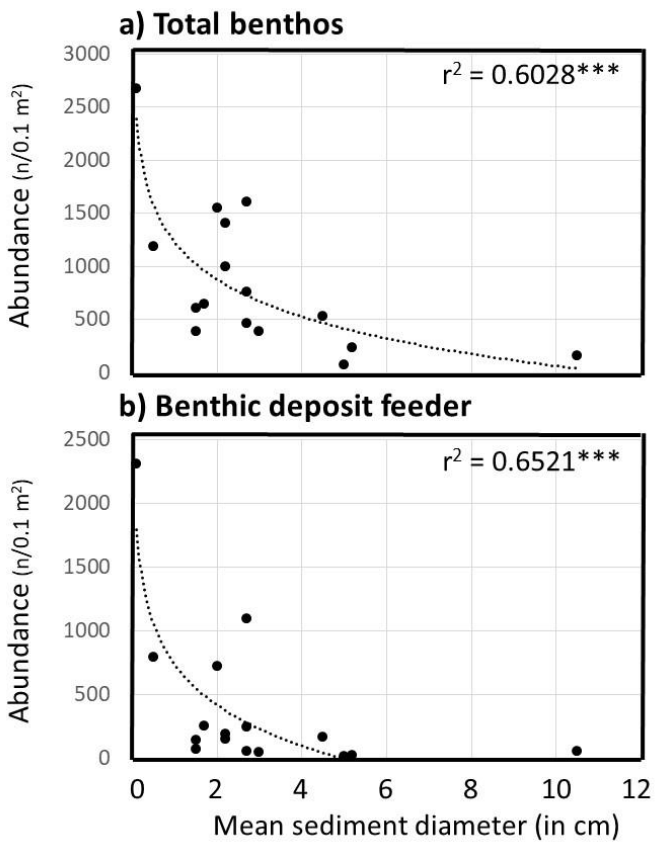


Fig. 5



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Dear Editor,

Please find as online submission for Hydrobiologia the manuscript entitled 'Relative effects of elevational and habitat constraints on alpine spring biodiversity' authored by Cécile Claret and me (as corresponding author).

This manuscript deals with the effect of environmental constraints on biodiversity in alpine springs. Biodiversity was considered at the species level (using taxonomic richness and diversity index) and at the functional group level (using biological traits and trophic groups). The environmental constraints studied were the elevation (from 570 to 1650 m a.s.l.), the landscape (land cover around the springs) and the local characteristics of springs (water chemistry and sediment grain size).

We thus included variables that vary over a long period (elevational gradient as a model for temperature changes) or with rapid changes in human activities (landscape changes or sediment modifications). This combination of long term and short term constraints explains why our research was funded by the Regional Natural Park of the Chartreuse and the resulting manuscript may concern both scientists working on biodiversity dynamics and nature managers.

I state that all authors agree to the submission of the manuscript and as corresponding author I have been authorized by my co-author. I affirm that this article has not been published before and is not concurrently being considered for publication elsewhere. I assert that this article does not violate any copyright or other personal proprietary right of any person or entity and contains no abusive, defamatory, or fraudulent statements, nor any other statements that are unlawful in any way.

I inform you that the manuscript was edited for the English language by G.H. Copp, senior scientist at the CEFAS (Lowestoft, UK) and I am at your disposal for any further questions.

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