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1 **Collembolan preferences for soil and microclimate in forest and** 2 **pasture communities**

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9 *Key words: collembolan communities, habitat preference, forest and pasture soil, microclimate effect,*
10 *field experiment*

11 **Abstract**

12 The goal of the present study was to determine whether the habitat preference of collembolan species
13 is more influenced by soil properties or by microclimate and whether the preference for a given soil
14 matches the preference for the corresponding microclimate. To answer these questions, we set up a
15 soil core transfer experiment between a forest and an adjacent pasture. We first eliminated the entire
16 soil fauna from forest and pasture soil cores and inoculated them with a new community originated
17 from forest or pasture. After enclosing them, in order to prevent exchanges of soil animals between
18 treated soil and surrounding environment, soil cores were transplanted back to the field for four
19 months and a half. The experimental design comprises every combination of three factors (community
20 origin, soil nature and microclimate) for a total of 8 treatments. Twenty-two species were present in
21 the experiment, 16 of which were present in more than 10 % of the experimental soil cores. We
22 determined habitat preference for these 16 species using a large dataset comprised of field
23 observations in the same region. Results showed that most forest species did not withstand pasture

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24 microclimate, although some of them preferred pasture soil. Likewise several pasture species were
25 favoured by the forest microclimate, some of them also preferring forest soil. We concluded that forest
26 species were absent (or less abundant) in pastures because they are not resistant enough to drought,
27 while pasture species were absent (or less abundant) in forests because of food requirements, and/or
28 soil physicochemical properties such as soil pH and organic carbon content, and/or were less
29 competitive. Moreover, when selecting their habitat, some species are submitted to a trade-off between
30 preferences for different habitat features.

31 **1. Introduction**

32 The search for unifying principles in community ecology led to the identification of three
33 processes that interact to shape species assemblages: 1) habitat selection, 2) dispersal and 3) biotic
34 interactions (Weiher and Keddy, 2001; Wardle, 2006; Mayfield et al., 2009). Understanding the
35 factors that determine the preference of a species for a given habitat is thus essential to predict species
36 distribution and local community composition. In most habitats, many different factors (biotic and
37 abiotic) interact, creating environmental conditions that allow or impede species persistence and
38 reproduction (Bull et al., 2007). Furthermore, different species show different levels of specialization
39 for a given habitat, from specialists which are only found in a restricted array of environmental
40 conditions to generalists which are found in a wide array of environmental conditions (Egas et al.,
41 2004; Julliard et al., 2006). The extent to which a species is specialist of a given habitat probably
42 depends on how much it is adapted to the different habitat features and the level of specialization is
43 likely to differ between habitat features.

44 For invertebrate species inhabiting soil and litter layers, habitat is at least twofold. First, the nature
45 of the soil and the humus form are very influential: (1) they determine the availability and quality of
46 resources such as organic matter, which in turn determines the composition and activity of microbial
47 communities, one of the main food sources of soil invertebrates (Ponge, 1991; Murray et al., 2009;
48 Sabais et al., 2011); (2) soil and humus through several physicochemical properties, such as pH,
49 moisture, structure, carbon content, etc., are critical parameters for collembolan survival (Ponge, 1993;
50 Berg et al., 1998; Loranger et al., 2001). Second, the type of vegetation is also influential: (1) it

51 influences the quality and quantity of organic matter inputs; (2) it influences the local microclimate
52 and interacts with soil and humus to determine temperature and moisture levels which prevail within
53 the soil (Chen et al., 2008; Ponge, 2013). For example tree canopy cover in forests prevents most UV
54 radiation from reaching the ground surface and creates lower soil temperatures in forests compared to
55 pastures (Scott et al., 2006).

56 Collembolan communities have been shown to vary according to vegetation types, e.g. open vs
57 closed vegetation (Ponge et al., 2003; Vanbergen et al., 2007). Forests (closed vegetation) benefit from
58 high inputs of litter which create thick organic (and organic-mineral) layers. High soil carbon content
59 induces both low pH and high soil moisture and creates conditions favouring overall collembolan
60 abundance and diversity (Hopkin, 1997). In addition, high organic inputs in forests provide abundant
61 trophic resources. In contrast, open vegetation (e.g. any habitat without trees such as pastures or
62 meadows) is characterized by intense export through mowing, grazing, or harvesting, and more active
63 decomposition, which induces lower organic contents and reduced or absent organic layers (Compton
64 and Boone, 2000). Additionally, the absence of tree cover induces higher temperatures in summer and
65 lower soil moisture than in forests (Batlle-Aguilar et al., 2011). Thus, in collembolan communities,
66 specialists of a given habitat should be intolerant to at least one feature of non-preferred habitats
67 (microclimate, resource quality and/or availability, physicochemical factors): for example, forest
68 specialists should be intolerant either to soil properties or microclimate of open habitats. In contrast,
69 generalist species should be generalist for both soil and microclimate.

70 In their experiment, Auclerc et al. (2009) determined habitat preference and dispersal ability of a
71 large set of collembolan species. Using a soil transplant experiment between a forest and a meadow,
72 they showed that several forest-preferring and forest-strict species actually colonized more efficiently
73 meadow soil transferred to forest than non-transferred forest soil. They suggested that certain forest
74 species, more abundant in the transplanted meadow soil, could not survive in the meadow because of
75 its microclimate. However, in their study the effect of species ability to colonize both soil types
76 through dispersal was difficult to distinguish from the effects of actual preferences for a given habitat.
77 Moreover, Auclerc et al. (2009) only transplanted soil cores from one type of habitat to another but did
78 not submit collembolan communities to a different microclimate. This did not allow a full

79 disentanglement of the effects of soil and humus nature from the effects of microclimate determined
80 by plant cover.

81 The present experiment thus aimed at addressing the two following questions. Are forest or
82 pasture species excluded from (or less abundant in) pastures and forests, respectively, because they do
83 not withstand differences in temperature and related soil moisture (microclimate) in these habitats, or
84 because they do not find appropriate trophic resources and suitable physicochemical conditions (soil
85 nature)? Are generalist species tolerant to both soil and microclimate? We hypothesize that forest and
86 pasture species are not primarily influenced by the same habitat features. Forest species would be
87 absent (or less abundant) in pastures because of physiological requirements for forest microclimate
88 (i.e. higher humidity and lower temperature) whereas pasture species would be absent (or less
89 abundant) in forests because they do not find appropriate trophic resources in them.

90 Given our choice of a transfer experiment in which animals cannot freely move to find suitable
91 conditions for their growth and reproduction, preferences will be only inferred from their ability to
92 survive and multiply better under certain conditions than others. This is also the sense given to the
93 word “affinity” in similar experiments (Huhta, 1996) but we here refer to the definition given by Pey
94 et al. (2014) of “ecological preference” as “the optimum and/or the breadth of distribution of a trait on
95 an environmental gradient”, considering “ecological preference” as the result of multiple interacting
96 ecophysiological traits each species display and “habitat preference” as a subset of “ecological
97 preference.

98 **2. Material and methods**

99 *2.1. Study site*

100 The study was set up in a forest and an adjacent pasture in the Morvan Regional Natural Park
101 at the same location as the experiment reported in Auclerc et al. (2009). The Morvan Natural Park is
102 located in the centre of France (Burgundy) and has a submontane-atlantic climate with continental
103 influence (mean annual rainfall 1000 mm and mean temperature 9 C). The bedrock is granite and soils
104 are moderately to strongly acidic (pH < 5). The forest canopy is comprised of deciduous trees (*Fagus*
105 *sylvatica* and *Quercus petraea*) and has been in place over at least a century, according to stand

106 structure. The forest soil is an Acrisol and the humus form is a dysmoder sensu Brêthes et al. (1995).
107 The nearby pasture used to be mowed every year in spring and then grazed by cattle in summer and
108 autumn, but mowing had been abandoned for several years because of poor forage production due to
109 several consecutive drought years. The pasture soil is a Cambisol and the humus form is an eumull.
110 The transition between forest and pasture is sharp.

111 *2.2. Experimental design and soil core manipulation*

112 We designed a soil core transplantation experiment between forest and pasture (closed vs.
113 open vegetation, respectively) coupled with a manipulation of invertebrate communities. Eight
114 treatments (five replicates each) corresponded to all possible combinations of three factors:
115 community origin, COM (forest vs. pasture), soil origin, S (forest vs. pasture) and microclimate,
116 CLIM (forest vs. pasture) (Fig. 1, see also Fig. 2 for a global view of manipulation steps). The setup
117 took place between March and June 2011 (fauna removal, inoculation and transplantation) and the
118 experiment ended in the beginning of November 2011.

119 *2.2.1. Fauna removal and re-inoculation*

120 In order to control the communities present in both soils (forest and pasture), we first removed
121 the fauna and re-inoculated it with a new community extracted from a fresh soil core. This allowed us
122 to have a forest community in the pasture soil and conversely a pasture community in the forest soil.
123 Thirty soil cores (20 cm diameter x 10 cm depth) were taken in both forest and pasture (60 soil cores
124 in total, i. e. the soil, including the soil biota, was sampled by taking of soil samples) and brought back
125 to the laboratory. Soil fauna was then eliminated by repeatedly freezing soil cores. Each soil core was
126 dipped in liquid nitrogen for 45 min. This was repeated after a week interval, in order to eliminate
127 possible resistant eggs that could have been stimulated to hatch by the first freezing. In between, soil
128 cores were stored in a cold chamber at 15 °C.

129 We then inoculated each soil core with a new community. To do so, 48 soil cores (24 for each
130 soil) of the same volume (20 cm diameter x 10 cm depth) were taken at the same site. These cores
131 were split into four equal parts in the field, packed into semi waterproof bags (plastic bags with holes

132 allowing gas exchanges) and brought back to the lab within two days. They were immediately stored
133 in a cold chamber at 15 °C before being used as a new community source for re-inoculation. Fourteen
134 defaunated pasture soil cores were inoculated with a community originating from the pasture (4 of
135 which were used as controls, see following section) and 10 pasture soil cores were inoculated with a
136 community originating from the forest. Likewise, 14 defaunated forest soil cores were inoculated with
137 a community originating from the forest (4 of which were used as controls, see following section) and
138 10 forest soil cores were inoculated with a community originating from the pasture. To re-inoculate
139 communities, we used a Berlese dry-funnel extractor. We placed the fresh soil on the extractor sieve
140 and the soil core which had been previously defaunated under it. This procedure allowed transferring
141 the new community from the fresh to the defaunated soil core. Each quarter of the fresh cores was left
142 one week on the extractor sieve. Re-inoculation thus lasted 4 weeks. Each week, one quarter of the soil
143 cores used for re-inoculation was placed on the extractor sieve after the previous quarter was removed.
144 Soil cores were watered every week with 100 mL distilled water. After fauna removal and before re-
145 inoculation, we watered all soil cores with a soil suspension (10 g of soil sampled the same day per
146 litre distilled water) sieved to 20 µm. Pasture and forest soil cores were watered with a soil suspension
147 prepared with pasture and forest soils, respectively. This procedure was performed in order to re-
148 establish the microbial community in soil cores after fauna removal (freezing).

149 *2.2.2. Soil core enclosure and transplantation to the field*

150 In order to prevent as much as possible exchanges of soil animals between treated soils and the
151 surrounding environment, soil cores were enclosed in PVC pipes covered with a 350 µm mesh at their
152 top and a 20 µm mesh at their bottom. We finally brought the 46 manipulated soil cores back to the
153 field. Each soil-community treatment was transplanted both in the forest and in the pasture and was
154 left in the field from June 15 to November 2, 2011 (four and a half months).

155 The experimental design thus comprised every combination of three factors (community
156 origin, soil and microclimate) for a total of 8 treatments with 5 replicates each (Fig 1). Additionally, it
157 included 3 types of manipulation controls and 2 types of natural references (3 to 5 replicates
158 depending on the type of control, see next section).

159 2.2.3. *Experimental controls and natural references*

160 At each stage of the experimental setup, controls were implemented. This allowed us to assess
161 the efficiency of: 1) fauna removal, 2) community re-inoculation, 3) enclosure, and allowed us to
162 determine the composition of forest and pasture communities in a non-manipulated situation.

163 To check for the efficiency of fauna removal, we randomly selected 3 soil cores of each soil
164 directly after fauna removal and we performed fauna extraction (fauna removal controls).

165 To check for the efficiency of community re-inoculation, 8 soil cores (4 forest and 4 pasture
166 cores inoculated with their own community) were randomly selected directly after re-inoculation and
167 placed in a Berlese dry-funnel extractor (inoculation controls).

168 To check for the efficiency of enclosure, 6 soil cores (3 for each soil) were randomly selected
169 and directly enclosed after fauna removal (i. e. without inoculation with a fresh community) and
170 brought back to the field for transplantation (enclosure controls).

171 In order to determine the composition of both communities in the undisturbed (i.e. non-
172 manipulated) situation, 3 samples (5 cm diameter x 10 cm depth) were taken at the same time in each
173 habitat (forest and pasture) when sampling for the soil material used to re-inoculate experimental soil
174 cores (natural control t_0). They were brought back to the laboratory on the same day for fauna
175 extraction. Likewise, 5 samples (5 cm diameter x 10 cm depth) were taken in each habitat (forest and
176 pasture) at the end of the experiment and brought back to the laboratory within three days for fauna
177 extraction (natural controls t_{end}).

178 All fauna extractions were performed using a Berlese dry-funnel apparatus and lasted 12 days.

179 2.3. *Soil sample treatments*

180 At the end of the experiment, we sampled each core according to three methods. First, a
181 sample 6.3 x 6.3 x 10 (depth) cm was taken at the centre of each core for fauna extraction (fauna
182 samples). Second, a 300-g sample was taken in each core, air dried and sieved (2 mm) for soil analysis
183 (soil pH_{water} , total carbon, and total nitrogen content by gas chromatography). And third, another 300-g
184 sample was taken in each core and immediately packed in waterproof bags for soil moisture
185 measurements.

186 Fauna samples were brought back to the lab within three days and placed in a Berlese dry-
 187 funnel extractor for 12 days. Animals were collected and stored in 70 % ethyl alcohol until
 188 identification. Collembola were mounted, cleared in chloral-lactophenol and identified to species level
 189 under a light microscope (magnification x 400), according to Hopkin (2007), Potapov (2001), Thibaud
 190 et al. (2004) and Bretfeld (1999). Due to the very large number of individuals belonging to this species
 191 group, we pooled the two species *Folsomia quadrioculata* and *F. manolachei* together.

192 2.4. Calculation of species overall habitat preference

193 The two ecological traits describing the habitat preference (IndF and IndA, see below) of each
 194 species were calculated using the IndVal index (Dufrêne and Legendre, 1997) adapted to the
 195 measurement of preference for a given habitat type by Auclerc et al. (2009). For this calculation, we
 196 used the data set produced in Ponge et al. (2003), who worked in exactly the same region. One species
 197 present in our study (*Detriturus jubilarius*) was absent from the study by Ponge et al. (2003). The
 198 habitat preference of this species was assessed according to expert knowledge (Salmon, unpublished
 199 data).

200 The IndVal index combines the specificity of a species for a habitat type (maximized when the
 201 species is found only in a given habitat) and its fidelity to this habitat (maximized when the species is
 202 found in all samples of a given habitat):

203
$$\text{Ind}_{ij} = A_{ij} * B_{ij} * 100, \text{ where}$$

204 A_{ij} = average abundance of species *i* in samples of habitat *j* divided by the average abundance
 205 of species *i* in all samples.

206 B_{ij} = number of samples of habitat *j* where the species is present divided by the total number
 207 of samples of habitat *j*.

208 Ind_{ij} ranges from 0, when species *i* is absent from habitat *j*, to 100 (its maximum value), when species
 209 *i* is present in all samples of habitat *j* and absent in all other habitat samples. We thus obtained two

210 IndVal values for each species, one for forest (IndF) and one for agricultural land (IndA). Classes of
211 habitat preference were then determined using the IndVal values IndF and IndA for each species.
212 Species present in both habitat types and having a ratio IndF/IndA (or the reverse) higher or equal to
213 0.25 were classified as “generalists”. Species having a ratio IndA/IndF lower than 0.25 were classified
214 as “forest-preferring” and species having a ratio IndA/IndF = 0 were classified as “strict forest”
215 species. Species having a ratio IndF/IndA lower than 0.25 were classified as “agricultural-preferring”
216 and species having a ratio IndF/IndA = 0 were classified as “strict agricultural” species (sensu Auclerc
217 et al., 2009).

218 2.5. Data analyses

219 2.5.1. Assessing the effect of experimental manipulation

220 In order to detect possible effects of soil manipulation, inoculation, and enclosure on species
221 abundance, we implemented linear models testing the effect of control type (natural controls t_0 and t_{end} ,
222 inoculation control, enclosure control, and experimental control, i.e. treated soil cores transplanted in
223 their own microclimate with their own community), habitat type (forest vs. pasture) and the interaction
224 between these factors, on total abundance (type III sum of squares used for unbalanced design). As the
225 soil volumes sampled for natural controls (t_0 and t_{end}) and experimental controls were different, we
226 transformed the total abundance into areal density (number of individuals per m^2). To fulfil linear
227 model assumptions, areal density was log-transformed. In order to compare community structure and
228 composition of all types of controls (natural controls t_0 and t_{end} , inoculation control, enclosure control,
229 and experimental control), we performed a principal component analysis using abundances of
230 common species (i.e. present in at least 10 % of the experimental cores).

231 In order to detect the effects of experimental treatments on soil properties (total carbon and
232 nitrogen content, soil pH and moisture) we implemented linear and generalized linear models (Gamma
233 link function) testing the effect of soil nature (forest vs. pasture) and microclimate (forest vs. pasture)
234 on soil properties. Data for total carbon and nitrogen content and for soil moisture were log-
235 transformed to fulfil linear model assumptions.

236 *2.5.2. Effect of experimental treatments on collembolan diversity and abundance*

237 In order to detect the effects of experimental treatments on collembolan diversity and
238 abundance, we tested the effect of the three experimental factors (origin of the community, soil nature
239 and microclimate) and the interaction between these factors on species richness, Shannon diversity
240 index, and total abundance using linear models. Abundances were log-transformed to fulfil linear
241 model assumptions. Models were tested after a procedure of automatic model selection based on AIC
242 criterion (stepwise procedure). Combinations of experimental treatments were compared using least
243 square means and associated multiple comparisons of means (Tukey).

244 *2.5.3. Effect of experimental treatments on collembolan community structure and species abundance*

245 In order to detect the effect of experimental treatments on community structure, we
246 implemented a between-group multivariate analysis (Baty et al., 2006) on abundances of common
247 species in each treatment. Between-group analysis is a particular case of instrumental variables
248 methods where a single qualitative variable is accounted for (Baty et al., 2006), providing the best
249 linear combination of variables maximizing between-group variance. Between-group analysis was
250 performed using a combination of the three experimental factors (origin of the community COM, soil
251 nature S and microclimate CLIM, 8 combinations) as the explanatory variable. The significance of the
252 composite factor COM/S/CLIM was tested using a Monte-Carlo permutation test (999 permutations).

253 The effects of experimental factors (COM, S, CLIM and all possible interactions) on the
254 abundance of each common species (i.e. species present in at least 10 % of the experimental cores)
255 were tested using generalized linear models (poisson link function) after a procedure of automatic
256 model selection based on AIC criterion (stepwise procedure). Combinations of experimental
257 treatments were compared using least square means and associated multiple comparisons of means
258 (Tukey). Based on the results of these models, we classified species according to their response to
259 experimental factors. Species being significantly more abundant in a given soil and/or microclimate
260 were considered as preferring this soil and/or microclimate. Species showing similar preferences for
261 soil nature and microclimate were grouped together.

262 All statistical analyses were performed using vegan, ade4, car, and lsmeans packages of R
263 software (R Development Core Team, 2010).

264 3. Results

265 3.1. Experimental controls

266 In total, 28 species were found (controls included), of which 22 species were present in the
267 experimental treatments (controls excluded). Among these 22 species, 6 were present in less than
268 10 % of the experimental soil cores (< 4 cores) and were thus excluded from the analysis for
269 improving robustness of the conclusions. Among the 16 species kept for the analysis, 9 were also
270 present in enclosure controls. Among these 9 species, four were present in both pasture and forest
271 enclosure controls (*Lepidocyrtus lanuginosus*, *Mesaphorura macrochaeta*, *Parisotoma notabilis* and
272 *Sphaeridia pumilis*), four were present in pasture enclosure controls only (*Brachystomella parvula*,
273 *Isotoma viridis*, *Protaphorura armata* and *Sminthurides schoetti*) and one species was present in forest
274 enclosure controls only (*Xenylla tullbergi*) (Table 1). Thirteen species were successfully inoculated in
275 the experimental soil cores, among them four species were successfully inoculated in both forest and
276 pasture soils, seven were inoculated in forest soil only and two were successfully inoculated in pasture
277 soil only (Table 1). No Collembola were found in the fauna removal control either in pasture or forest
278 soil.

279 The linear model testing the effect of treatments on collembolan density showed that the type
280 of control (natural controls t_0 and t_{end} , inoculation control, enclosure control, and experimental control)
281 and the interaction between control type and soil nature exerted an influence on collembolan density
282 ($p < 0.001$ and $p < 0.01$, respectively). Collembolan density was significantly higher in inoculation
283 controls and in experimental controls than in natural controls taken at the end of the experiment (t_{end})
284 (Fig. 3). Additionally, post-hoc tests (Tukey) showed that the natural control taken at the end of the
285 experiment (t_{end}) in the pasture showed a lower collembolan density than both forest and pasture
286 experimental controls. It also showed a lower density than the natural controls taken at the end of the
287 experiment in the forest and than enclosure and inoculation controls in the pasture (Fig 3). The first
288 two axes of principal component analysis (PCA) implemented on species abundances of controls (Fig.

289 4) extracted 34.5 % of the total variance (29.4 % and 15.1 %, respectively). PCA showed that
290 communities were distinguished according to community origin on axis 1, pasture communities
291 standing on the positive side and forest communities standing on the negative side of axis 1. However,
292 the enclosure control in the forest (TexF) displayed communities closer to the pasture on axis 1. The
293 community in the forest experimental control (FFF) lay close to the community of forest natural
294 reference both at the beginning and at the end of the experiment. In contrast, the community of the
295 pasture experimental control (PPP) lay close to the community of the pasture natural reference at the
296 end of the experiment but far from the one present at beginning of the experiment.

297 *3.2. Effects of experimental treatments on soil physicochemical properties*

298 Linear and generalized linear models (Table 2) testing the effect of soil nature (forest vs.
299 pasture) and microclimate (forest vs. pasture) on soil properties (total carbon and nitrogen content, soil
300 pH and moisture) showed that the total carbon content was higher in forest than in pasture soil. In
301 contrast, the total nitrogen content did not differ with soil nature or microclimate. Soil pH was higher
302 in pasture than in forest soil ($p < 0.001$) and soil pH in pasture soil was higher under forest than under
303 pasture microclimate ($p < 0.001$, Fig. 5a). Soil moisture was significantly affected both by soil nature
304 and microclimate ($p < 0.001$, and $p < 0.01$ respectively). Soil moisture was higher in forest than in
305 pasture soil and soil moisture in pasture soil was higher under forest than under pasture microclimate
306 (Fig. 5b).

307 *3.3. Effects of experimental treatments on collembolan diversity and abundance*

308 Linear models testing the effect of the three experimental factors (origin of the community,
309 soil nature and microclimate) on species richness, Shannon index, and total abundance (Table 3)
310 showed that the three factors (community origin, soil nature and microclimate) had an effect on total
311 abundance ($p < 0.01$, $p < 0.05$, and $p < 0.001$, respectively). Collembola were more abundant in the
312 pasture than in the forest community (community origin), they were also more abundant in the pasture
313 than in the forest soil, but they were more abundant under forest than under pasture microclimate (Fig.
314 6a). Only the origin of the community exerted an effect on species richness ($p < 0.001$). The community

315 originating from the forest displayed higher species richness than the community originating from the
316 pasture, whatever the microclimate or the soil in which they were inoculated (Fig. 6b). Finally, these
317 models showed that community origin, soil nature, and the interaction between community origin and
318 microclimate had a significant effect on the Shannon index ($p < 0.001$, $p < 0.01$, and $p < 0.01$
319 respectively). The Shannon index was higher in forest than in pasture community and was also higher
320 in forest than in pasture soil. Post-hoc tests (Tukey) showed that the interaction between community
321 origin and microclimate was due to the fact that the Shannon index was higher under forest than under
322 pasture microclimate, but only for the community originating from the pasture (Fig. 6c).

323 3.4. Effects of experimental treatments on collembolan community structure and species abundance

324 The individual response to experimental treatments of the 16 most common species is shown
325 in the Appendix. Between-group analysis (Fig. 7) performed on species abundances taking a
326 combination of community origin, soil nature, and microclimate as the explanatory variable extracted
327 56 % of the total variance. Axes 1 and 2 accounted for 44 % and 23 % of the variance extracted,
328 respectively. Nine species contributed to the formation of axis 1, four on the positive side
329 (*Protaphorura armata*, *Parisotoma notabilis*, *Mesaphorura macrochaeta* and *Pseudosinella alba*) and
330 five on the negative side (*Folsomia* spp., *Isotomiella minor*, *Detriturus jubilarius*, *Megalothorax*
331 *minimus* and *Friesea truncata*). Axis 1 discriminated communities according to their origin, pasture on
332 the positive side and forest on the negative side. Only three species mostly contributed to the
333 formation of axis 2, all of them negatively (*Sminthurides schoetti*, *Isotoma viridis* and *Xenylla*
334 *tullbergi*). Axis 2 discriminated forest communities according to the microclimate in which they were
335 transplanted, forest microclimate on positive side and pasture microclimate on negative side. For the
336 pasture community, treatments were much less discriminative on axis 2 than for the forest community.
337 A Monte-Carlo permutation test showed that the composite factor COM/S/CLIM significantly affected
338 the community ($p = 0.001$).

339 3.5. Species classification based on the effect of experimental treatments on species abundance

340 Using generalized linear models testing the effect of the three factors COM, S, and CLIM on
341 species abundance, we classified species into six groups according to their response to the factors
342 (Table 1). Group A was comprised of three species (*Isotomiella minor*, *Megalothorax minimus*, and
343 *Pseudosinella mauli*) that were more abundant in forest community, soil and microclimate. They were
344 labeled “true forest species” (Fig 8a). Group B was comprised of three species (*Folsomia* spp., *Friesea*
345 *truncata* and *Detriturus jubilarius*), that were more abundant in both forest community and
346 microclimate, but were more abundant in pasture soil (Fig. 8b). They were labeled “forest species
347 preferring pasture soil”. Species of groups A and B were classified as forest species except *Folsomia*
348 spp. that were classified as generalists using the IndVal index calculated with the data set produced in
349 Ponge et al. (2003) (Table 1). Group C was comprised of two species (*Protaphorura armata* and
350 *Pseudosinella alba*) that were more abundant in the pasture community but more abundant in the
351 forest soil. Additionally, while *Protaphorura armata* was also more abundant in the forest
352 microclimate (Fig. 8c), microclimate did not exert an effect on the abundance of *Pseudosinella alba*.
353 Group C was labeled “pasture species preferring forest soil”. Group D was comprised of two species
354 (*Mesaphorura macrochaeta* and *Parisotoma notabilis*) which were more abundant both in pasture
355 community and soil but were more abundant in forest microclimate (Fig 8d). They were labeled
356 “pasture species preferring forest microclimate”. Group E was comprised of three species
357 (*Brachystomella parvula*, *Lepidocyrtus lanuginosus*, and *Sphaeridia pumilis*) that were more abundant
358 in pasture microclimate. However, in this group, all three species showed a preference for a different
359 component of the forest habitat, either for soil (*Lepidocyrtus lanuginosus*) or forest community, i.e.
360 were more abundant in cores inoculated with a forest community (*Sphaeridia pumilis*), or both
361 components (*Brachystomella parvula*). Group E was labeled “species preferring pasture
362 microclimate”. And finally, group F was comprised of three species (*Xenylla tullbergi*, *Isotoma viridis*
363 and *Sminthurides schoetti*), that were more abundant in both pasture soil and microclimate. *Isotoma*
364 *viridis* (Fig. 8e) and *Sminthurides schoetti* were as abundant in cores inoculated with a pasture
365 community as in cores inoculated with a forest community whereas *Xenylla tullbergi* (Fig. 8f) was
366 more abundant in cores inoculated with a forest community. This group was labeled “pasture species”.

367 Most species of groups C, D, E and F were classified as agricultural and generalist species except for
368 *Xenylla tullbergi* that was classified as a forest species according to the IndVal index calculated with
369 the data set produced in Ponge et al. (2003) (Table 1).

370 **4. Discussion**

371 *4.1. Effect of soil nature and microclimate on collembolan total abundance and community structure*

372 Our results show that collembolan abundance was higher in forest than in pasture
373 microclimate for both forest and pasture communities. Transplantation decreased the moisture content
374 of forest cores when transplanted in the pasture and it increased the soil moisture of pasture cores
375 transplanted in the forest (Fig. 5b, Table 2). Collembola are known to be sensitive to drought (Vannier,
376 1987). We thus attribute to this physiological trait the overall abundance increase in forest
377 microclimate and decrease in pasture microclimate. It means that forest species are likely to be absent
378 (or less abundant) in pasture mainly because they survive poorly in pasture climate conditions. This
379 may concern only some stages of collembolan life, such as the moisture-sensitive first stadium,
380 stemming in the incapacity of some species to endure moisture and temperature fluctuations which
381 characterize open environments as opposed to closed environments (Betsch and Vannier, 1977).
382 Additionally, we showed that forest communities were different under pasture and forest microclimate
383 whatever the nature of the soil. This means that microclimate conditions are the first driver shaping
384 collembolan communities in the forest. We thus suggest that forest species display physiological traits
385 (namely poor resistance to drought) that prevent them from surviving or growing larger populations in
386 open habitats. The pasture community did not show such a trend, suggesting that microclimate change
387 (pasture to forest) did not affect its species composition. Thus, microclimate conditions are not likely
388 to be the most important constraint shaping the pasture community.

389 *4.2. Species preferences for soil and microclimate*

390 Our experimental design enabled us to unravel species responses to soil nature and
391 microclimate. We showed that some species, classified as forest species according to field occurrence
392 data, are more abundant in forest soil and microclimate and that these species are also more abundant

393 in the communities originating from the forest (Group A). These species can thus be regarded as “true
394 forest species” because they need both forest microclimate (moisture, temperature) and soil (food
395 resources and physicochemical properties) to fully develop, at least in the studied region. This is
396 supported by previous experiments showing that *I. minor* and *M. minimus*, two out of the three “true
397 forest species” (Group A), are particularly sensitive to drought (Makkonen et al., 2011). However,
398 some other species, also classified as forest species using the large data set from Ponge et al. (2003),
399 are shown to prefer the pasture soil when transplanted to the forest microclimate (Group B). Hence,
400 for these species, preferences for soil and microclimate are not tuned. It means that although they
401 prefer the forest microclimate (temperature and moisture) they prefer trophic resources or
402 physicochemical properties of the pasture soil. Their confinement to forest habitats is thus the result of
403 climate requirements overwhelming soil quality requirements, i.e. least-worst strategy (Berger et al.,
404 2012).

405 Some authors have already underlined the strong influence of microclimate on Collembola
406 (Lindberg and Bengtsson, 2005; Makkonen et al., 2011; Petersen, 2011). In their experiment, Krab et
407 al. (2010) showed that most species found in a subarctic community tended to select microclimate
408 over substrate quality. Here, we go further and show that some forest species survive better in pasture
409 soil (of mull type) if they can find forest climate conditions. Such conditions (forest microclimate and
410 pasture soil quality) are fulfilled in not or poorly acidic forest soils, as already shown on census basis
411 (but not experimentally demonstrated) by Ponge (1993).

412 Likewise, we showed that some pasture and generalist species benefit from the forest
413 microclimate (Group D plus *Protaphorura armata*) but that the abundance of some species decreases
414 when they are transferred to the forest soil (Group D). These species are thus also favoured by higher
415 soil moisture and lower temperature but probably do not find in forest habitat appropriate resources
416 and/or physicochemical features, or are too poorly competitive to maintain populations as large as in
417 the pasture soil. However, pasture species of Group C are more abundant in the forest soil indicating
418 that this soil fulfils their trophic and/or physicochemical requirements. We can thus genuinely ask why
419 these species are more abundant in pasture, given that they seem to be favoured by forest microclimate
420 and soil. Since we eliminated environmental filters (microclimate, soil quality) and dispersal limitation

421 (eliminated in our experimental design) the answer probably relies in species interactions. Although
422 suspected to explain cases of species richness deficit or species turnover at the local scale (Hågvar,
423 1990; Winkler and Kampichler, 2000), competition within soil communities is still a too scarcely
424 investigated topic (Bardgett, 2002; Decaëns, 2010). Despite being primarily carried out in laboratory
425 conditions and with a reduced number of species, the few studies trying to shed light on the
426 importance of competition in structuring soil communities suggest that competition occurs and is an
427 important mechanism (Christiansen, 1967; Christiansen et al., 1992; Theenhaus et al., 1999; Postma-
428 Blaauw et al., 2005). Our experiment does not allow directly testing this hypothesis, but our results
429 show that some pasture and generalist species would perfectly withstand and even benefit from forest
430 climate conditions and/or soil quality. This suggests that they are prevented from developing larger
431 populations in forests by forest collembolan species that might be more efficient in exploiting forest
432 resources. To these effects of other members of the collembolan community must be added those of
433 members of a much wider community, the complete trophic network in which Collembola are
434 included, still imperfectly known up to present (Brose and Scheu, 2014). Biotic interactions in which
435 Collembola are dynamically involved include negative interactions such as predation (Lawrence and
436 Wise, 2000), but also positive interactions such as earthworm attraction (Salmon, 2001).

437 Finally, several species are more abundant under pasture microclimate (Groups E and F). They
438 were all classified as agricultural or generalist species with a single exception: *Xenylla tullbergi* is the
439 only forest species (present in the original forest community only) that is more abundant in pasture soil
440 and under pasture microclimate. This result may be explained by the fact that *Xenylla tullbergi* is
441 mostly found in corticolous habitats (Ponge, 1993). It is thus drought tolerant but found more
442 abundantly in trees (absent from agricultural plots such as pasture). Its absence in the pasture
443 community may also result from competition with pasture species. All other species of Groups E and
444 F are agricultural or generalist species that prefer pasture microclimate (Group E) or pasture
445 microclimate and soil (Group F). In Group E, two species were more abundant in the forest soil, which
446 suggests that they either prefer resources found in forest soil or are favoured by higher soil moisture
447 (or other physicochemical properties linked to forest soil) as we showed that under pasture
448 microclimate, soil moisture was higher in the forest than in the pasture soil. We only found two

449 species classified as agricultural species that were actually more abundant in pasture soil and under
450 pasture microclimate as supported by previous observations in agricultural habitats (Fratello et al.,
451 1985; Dittmer and Schrader, 2000; Frampton et al., 2001). These two “pasture species” are thus likely
452 to be primarily influenced by microclimate, resources, and soil physicochemical properties rather than
453 by interspecific competition. However, conclusions about *Sminthurides schoetti* (one of the two
454 abovementioned species) must be drawn with caution. Indeed, this species is the only one that did not
455 succeed in re-inoculated samples but was present in the enclosure controls in the pasture. It is thus
456 present in the experimental soil cores as a pure “invader”. Therefore, the preference of this species for
457 pasture or forest microclimate could not be ascertained. However we can be fairly certain that this
458 species preferred the pasture soil as it was more abundant than in the forest soil independently of the
459 community that was present in the soil beforehand.

460 Our results show that all forest species are better represented under forest microclimate, but
461 that some of them prefer the pasture soil. It means that the most important factor constraining forest
462 species is actually the microclimate. This is probably explained by physiological intolerance of forest
463 species to summer drought. Thus, for some forest species (Group B) habitat preference seems to be the
464 result of a trade-off between physiological requirements and requirements for resources and/or the
465 physicochemical environment.

466 4.3. Methodological limitations

467 We were not able to fully prevent exchanges between experimental cores and their
468 surroundings. More than half of the species present in more than four experimental soil cores (i.e.
469 common species) invaded the mesocosms. All these species but one were agricultural or generalist
470 species. This means that agricultural and generalist species have a greater mobility than forest species,
471 as they had to climb or jump over the mesocosms in order to penetrate them. This is also partly why
472 forest communities transplanted to pasture microclimate largely differed from forest communities
473 transplanted to forest microclimate. The latter communities were not influenced by species invading
474 from the surrounding pasture. Additionally, soil moisture in pasture soil cores was higher under forest
475 than under pasture microclimate and we showed that total collembolan abundance was also higher in

476 pasture experimental control than in natural controls. Thus, microclimate conditions created in the
477 mesocosms seem to overall favour species abundance of the pasture community. Hence some of our
478 results must be interpreted cautiously. First we showed that species richness was not affected by any
479 experimental treatment. Species richness was only lower in the original pasture than in the original
480 forest community. However, the invasion of the forest community by pasture species in microcosms
481 transplanted to the pasture artificially increased species richness. Second, we cannot totally refute that
482 the decrease in the abundance of some forest species under pasture microclimate was due to
483 competitive exclusion from species invading from the surrounding pasture. Besides, we do not know
484 what effects experimental manipulations had on microbial communities. Nevertheless, we were able to
485 successfully re-inoculate most common species despite a long-lasting experimental procedure and to
486 provide responses about soil and microclimate preferences of several collembolan species. This is very
487 encouraging for future experiments dealing with Collembola as more studies are still needed to fully
488 understand mechanisms responsible for patterns of species distribution.

489 Changes in species composition are known to occur over the year in collembolan communities
490 (Chagnon et al., 2000). Thus in our transfer experiment starting in spring and ending in autumn
491 temporal variability accompanied the effects of microclimate and soil change, and thus could have
492 blurred these effects. This cannot avoided, because expected effects take necessarily some time to
493 appear at community level, through the combination of growth, reproduction, dispersal and species
494 interactions, adding their effects to immediate mortality. However, natural controls, sampled at the
495 beginning and at the end of our transfer experiment, allowed discerning changes in species
496 composition in the meadow while no discernible change occurred in the forest (Fig. 4). Data collected
497 on the same sites in the abovementioned experiment by Auclerc et al. (2009) can be used to support
498 this assessment. A sign-test done on the 16 more common species (unpublished data) showed that over
499 the six months of this experiment (from December to June) the species composition did not change in
500 the forest (exact P value = 0.454) while it significantly changed in the meadow (exact P value =
501 0.021). Thus temporal changes of collembolan populations are probably included in the observed
502 effects of transfer from forest to pasture but not in the reverse case, to the possible exception of species
503 with genetically coded cycles of egg diapause (Leinaas and Bleken, 1983).

504 5. Conclusion

505 We showed that habitat preference depends on responses to microclimate and soil quality and
506 that environmental constraints have a different importance depending on the overall habitat preference
507 of species. We conclude that an anthropogenic-induced stress, such as habitat conversion
508 (deforestation or afforestation), modifies collembolan communities to a large extent, and that species
509 show different levels of resistance to perturbations and respond to different constraints (e.g.
510 microclimate, soil, interspecific competition). Generally, forest species seem to be primarily
511 influenced by microclimate, whereas pasture species seem more influenced by trophic resources and
512 competition. This suggests that trade-offs between several habitat constraints are at play and structure
513 collembolan communities in open vs. closed vegetation. More insights into the importance of
514 competition and predation in structuring collembolan communities are still needed at community
515 level.

516

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527

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- 654

655 **Figure captions**

656 **Figure 1.** Schematic representation of the experimental design. Soils cores are represented by squares
 657 (dark grey for the forest and light grey for the pasture). Letters on squares summarize the treatments:
 658 the first letter refers to the origin of the community (“F” for forest and “P” for pasture); the second
 659 letter refers to the origin of the soil (“F” for forest and “P” for pasture) and the third letter refers to the
 660 habitat (microclimate) in which the core has been transplanted (“F” for forest and “P” for pasture). For
 661 species codes see Table 1.

662 **Figure 2.** Summary of manipulation steps.

663 **Figure 3.** Mean collembolan density in 5 types of controls (experimental, inoculation, natural at the
 664 beginning (t_0) and at the end (t_{end}) of the experiment, exclosure) in forest (grey bars) and pasture (white
 665 bars) soils (see text for details). Letters indicate significant differences among means. Error bars
 666 represent standard errors.

667 **Figure 4.** Principal component analysis using abundances of common collembolan species (i.e.
 668 present in at least 10 % of the samples) in the 5 types of controls (3 manipulation controls e.g.
 669 inoculation, exclosure, and experimental controls and 2 natural references e.g. t_0 and t_{end} controls).
 670 Left: Projection of dataset variability plotted on a factorial map of the first two principal components.
 671 Labels on the gravity centers correspond to each treatment. TF0: natural reference in forest at
 672 beginning of the experiment, TFend: natural reference in forest at end of the experiment, FFF: control
 673 experiment for forest community, TeF: inoculation control for forest community in forest soil, TexF:
 674 fauna removal control for forest community, TP0: natural reference in pasture at beginning of the
 675 experiment, TPend: natural reference in pasture at end of the experiment, PPP: control experiment for
 676 pasture community, TeP: inoculation control for pasture community in pasture soil, TexP: fauna
 677 removal control for pasture community. Right: Correlation circle plot with species vectors (vector
 678 labels correspond to species codes in Table 1).

679 **Figure 5.** Mean soil pH (a) and mean soil moisture (b) in experimental forest (left) and pasture (right)
 680 soil cores, placed in forest (grey bars) and pasture (white bars) microclimates and in natural references
 681 (dashed bars). Letters indicate significant differences among means. Error bars represent standard
 682 errors.

683 **Figure 6:** Mean collembolan abundance (a), species richness (b) and Shannon index (c) in
 684 experimental soil cores. From the left to right: forest community in forest soil, forest community in
 685 pasture soil, pasture community in forest soil, and pasture community in pasture soil. Grey bars: forest
 686 microclimate and white bars: pasture microclimate. Letters indicate significant differences among
 687 means. Error bars represent standard errors.

688 **Figure 7:** Between-group analysis on the abundance of common species, with the composite factor
 689 COM/S/CLIM as explanatory variable. Left: Projection of dataset variability plotted on a factorial map
 690 of the first two discriminating axes according to a combination of COM, S and CLIM. Labels on the
 691 gravity centers correspond to each treatment (treatment codes according to Fig. 1). Right: Correlation
 692 circle plot with species vectors (vector labels correspond to species codes in Table 1). Eigen values
 693 0.44, 0.24, 0.16 for axes 1 to 3, respectively; Randtest: simulated p-value: 0.001; Explained variance:
 694 0.56.

695 **Figure 8:** Abundance of six species in the experimental treatments. (a) *Isotomiella minor* (Group A);
 696 (b) *Detriturus jubilarius* (Group B); (c) *Protaphorura armata* (Group C); (d) *Mesaphorura*
 697 *macrochaeta* (Group D); (e) *Isotoma viridis* (Group E); (f) *Xenylla tullbergi* (Group E); Upper right:
 698 correlation circle of the between-group analysis (Fig. 7). For group codes see Table 1. Letters on bars
 699 indicate significant differences among means. Labels under bars correspond to each treatment (for
 700 treatment codes see Fig. 1). Error bars represent standard errors.

701

702 **Table 1.** Presence/absence in inoculation and exclosure controls of the 16 species which were
 703 common in experimental soil cores (X = not present in controls; F = present in forest control only; P =
 704 present in pasture control only; FP = present in both forest and pasture controls). Results of
 705 generalized linear models testing the effect of three factors (community origin, soil nature and
 706 microclimate) on each species abundance (* = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$; / = not
 707 significant; F = species more abundant in forest community, soil or microclimate; P = species more
 708 abundant in pasture community, soil or microclimate). Habitat preference was calculated using IndVal
 709 index with the data set produced in Ponge et al. (2003): g = generalist species; f = strict-forest species;
 710 fp = forest-preferring species; a = strict agricultural species; ap = agricultural-preferring species.
 711 Response groups correspond to the six groups formed using species responses to the three factors
 712 community origin, soil, and microclimate. Group A = true forest species; Group B = forest species
 713 preferring pasture soil; Group C = pasture species preferring forest soil; Group D = pasture species
 714 preferring forest microclimate; Group E = species preferring pasture microclimate; Group F = pasture
 715 species.

	Species codes	Exclosure	Inoculation	Community	Soil	Microclimate	Habitat preference	Response group
<i>Isotomiella minor</i>	Iso.min	X	F	F ***	F ***	F ***	fp	A
<i>Megalothorax minimus</i>	Meg.min	X	F	F ***	F ***	F ***	fp	A
<i>Pseudosinella maui</i>	Pse.mau	X	F	F ***	F ***	/	f	A
<i>Folsomia quadrioculata/manolachei</i>	Fol	X	FP	F ***	P ***	F ***	g	B
<i>Friesea truncata</i>	Fri.tru	X	F	F ***	P **	F **	fp	B
<i>Detriturus jubilarius</i>	Det.jub	X	F	F ***	P ***	F ***	f	B
<i>Protaphorura armata</i>	Pro.arm	P	P	P ***	F *	F ***	ap	C
<i>Pseudosinella alba</i>	Pse.alb	X	X	P ***	F ***	/	a	C
<i>Mesaphorura macrochaeta</i>	Mes.mac	FP	FP	P ***	P ***	F ***	g	D
<i>Parisotoma notabilis</i>	Par.not	FP	FP	P ***	P ***	F ***	ap	D
<i>Brachystomella parvula</i>	Bra.par	P	X	F ***	F **	P ***	ap	E
<i>Lepidocyrtus lanuginosus</i>	Lep.lan	FP	FP	/	F *	P *	g	E
<i>Sphaeridia pumilis</i>	Sph.Pum	FP	F	F *	/	P *	ap	E
<i>Xenylla tullbergi</i>	Xen.tul	F	F	F ***	P ***	P ***	f	F
<i>Isotoma viridis</i>	Iso.vir	P	P	/	P ***	P ***	ap	F
<i>Sminthurides schoetti</i>	Smi.sch	P	X	/	P ***	P **	ap	F

716

717

718 **Table 2.** Effect of soil nature and microclimate (and interaction between both factors) on total carbon
 719 (Ctot) and nitrogen (Ntot) content, soil pH and soil moisture of experimental soil cores. Results of
 720 linear and generalized linear models (F value/Chi square and degrees of freedom df). Significance
 721 levels: ** = $p < 0.01$; *** = $p < 0.001$; NS = not significant.

722

	F values/Chi square									
	df	Ctot		pH		Moisture		Ntot		
Soil (S)	1	48.7	***	30.49	***	105.2	***	1.52	NS	
Climate (Cli)	1	0.14	NS	20.35	***	9.56	**	0.3	NS	
S : Cli	1	0.07	NS	2.4	NS	0.03	NS	0.36	NS	
model type		Normal		Gamma		Normal		Normal		
transformation		log ₁₀		none		log ₁₀		log ₁₀		

723

724

725

726 **Table 3.** Effect of community origin, soil nature and microclimate on total abundance, species
 727 richness and Shannon index. Results of linear models (F values and degrees of freedom df) tested after
 728 a procedure of automatic selection based on AIC criterion. NT = not tested. * = $p < 0.05$; ** = $p <$
 729 0.01 ; *** = $p < 0.001$; NS = not significant.

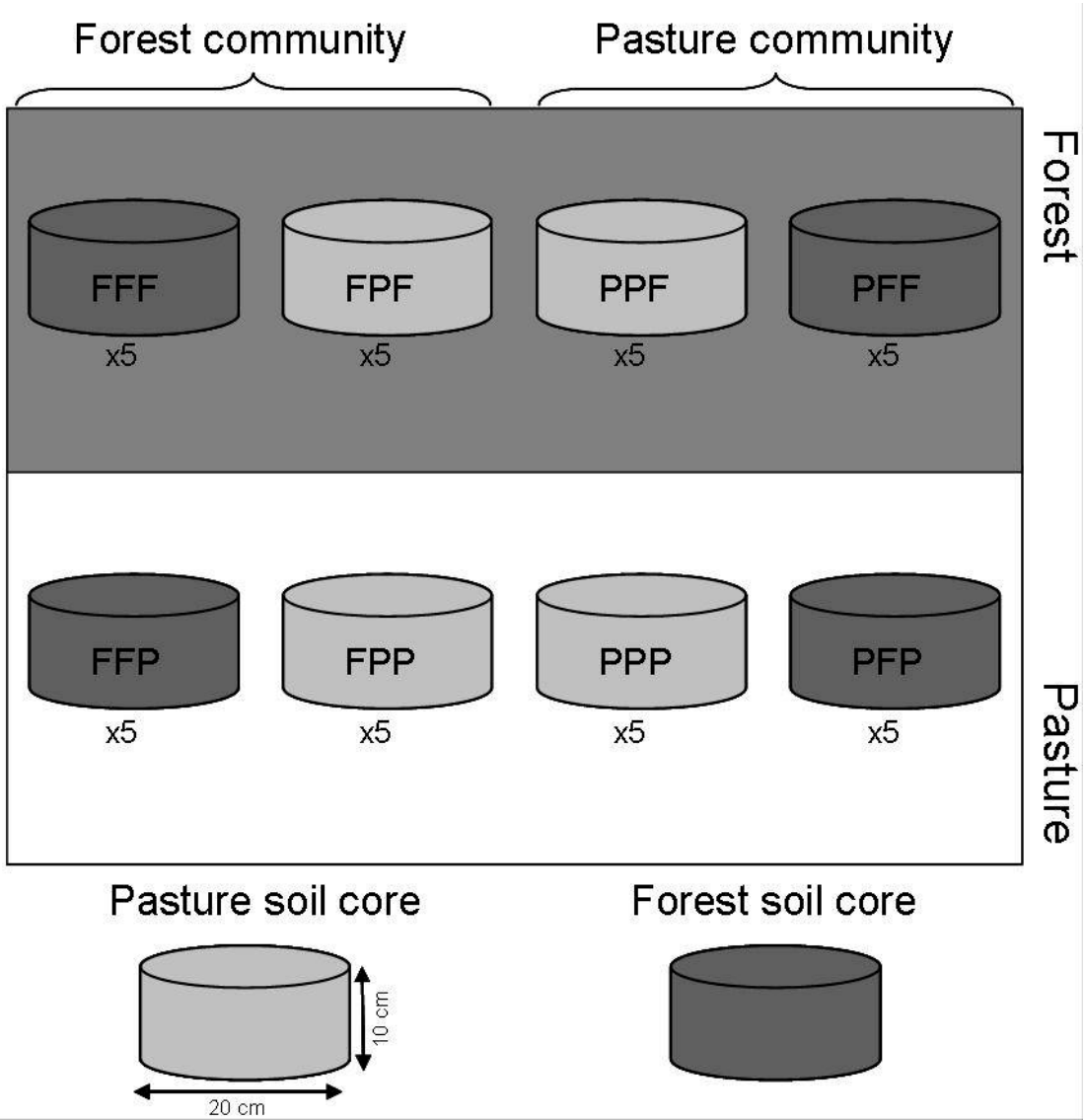
	F values								
	df	Abundance		df	Species richness		df	Shannon index	
Community (Co)	1	10.98	**	1	15.8	***	1	33.85	***
Soil (S)	1	5.29	*	1	1.9	NS	1	9.33	**
Climate (Cli)	1	50.02	***	1	0.06	NS	1	0.88	NS
Co : S	NT			1	0.8	NS	NT		
Co : Cli	NT			1	0.007	NS	1	11.04	**
S : Cli	NT			1	0.007	NS	NT		
Co : S : Cli	NT			1	0.16	NS	NT		
model type		Normal			Normal			Normal	
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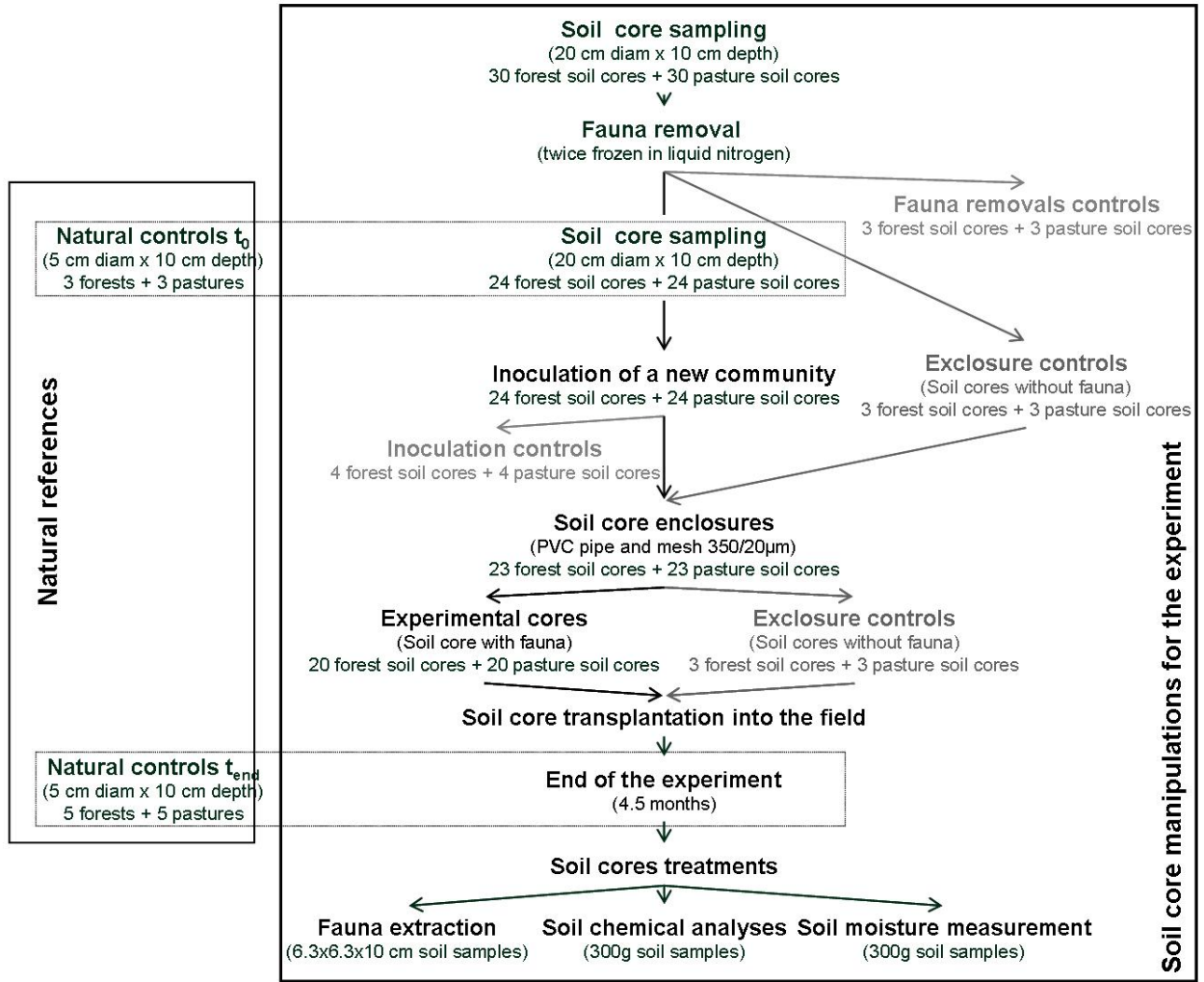
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734

735 **Fig. 1**

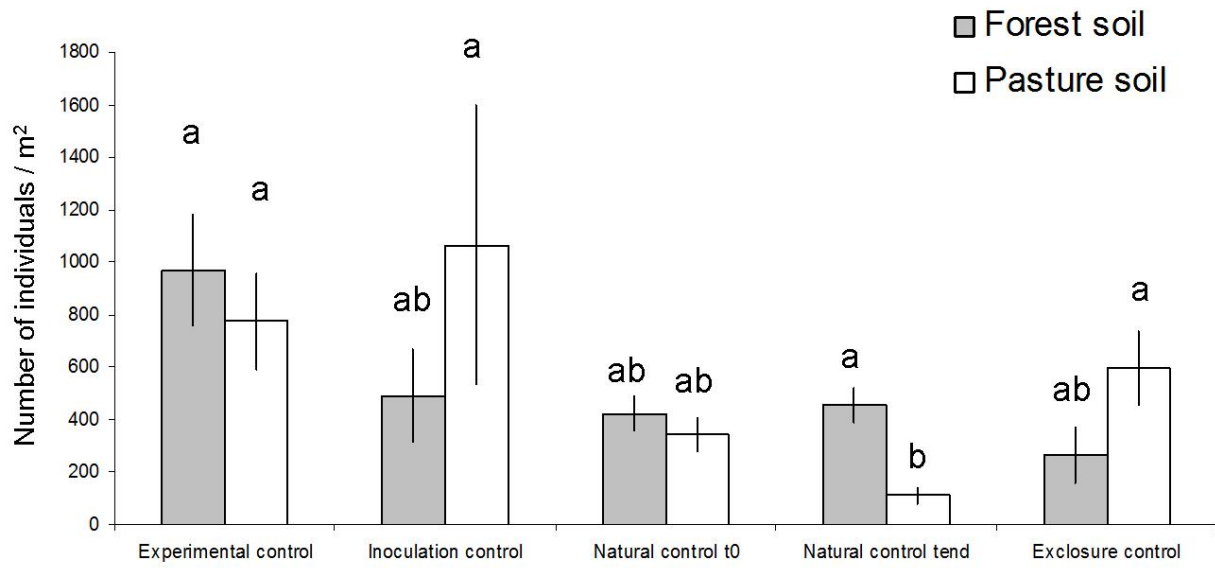
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738 **Fig. 2**

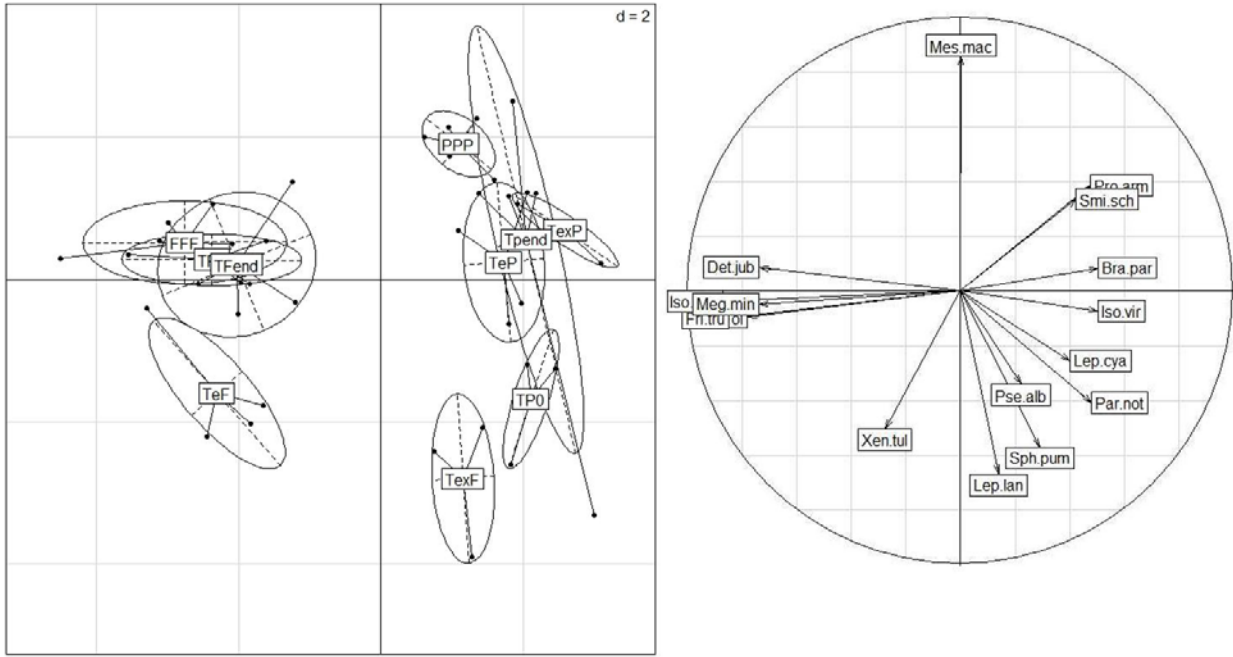
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741 **Fig. 3**

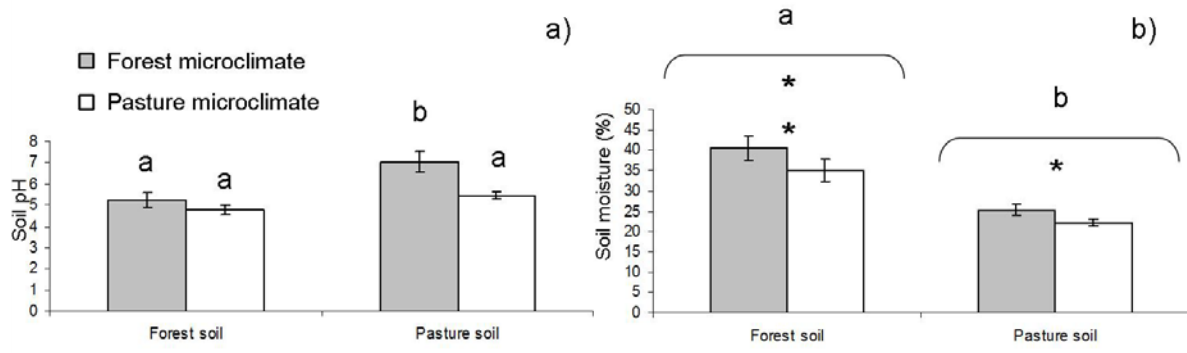
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744 **Fig. 4**

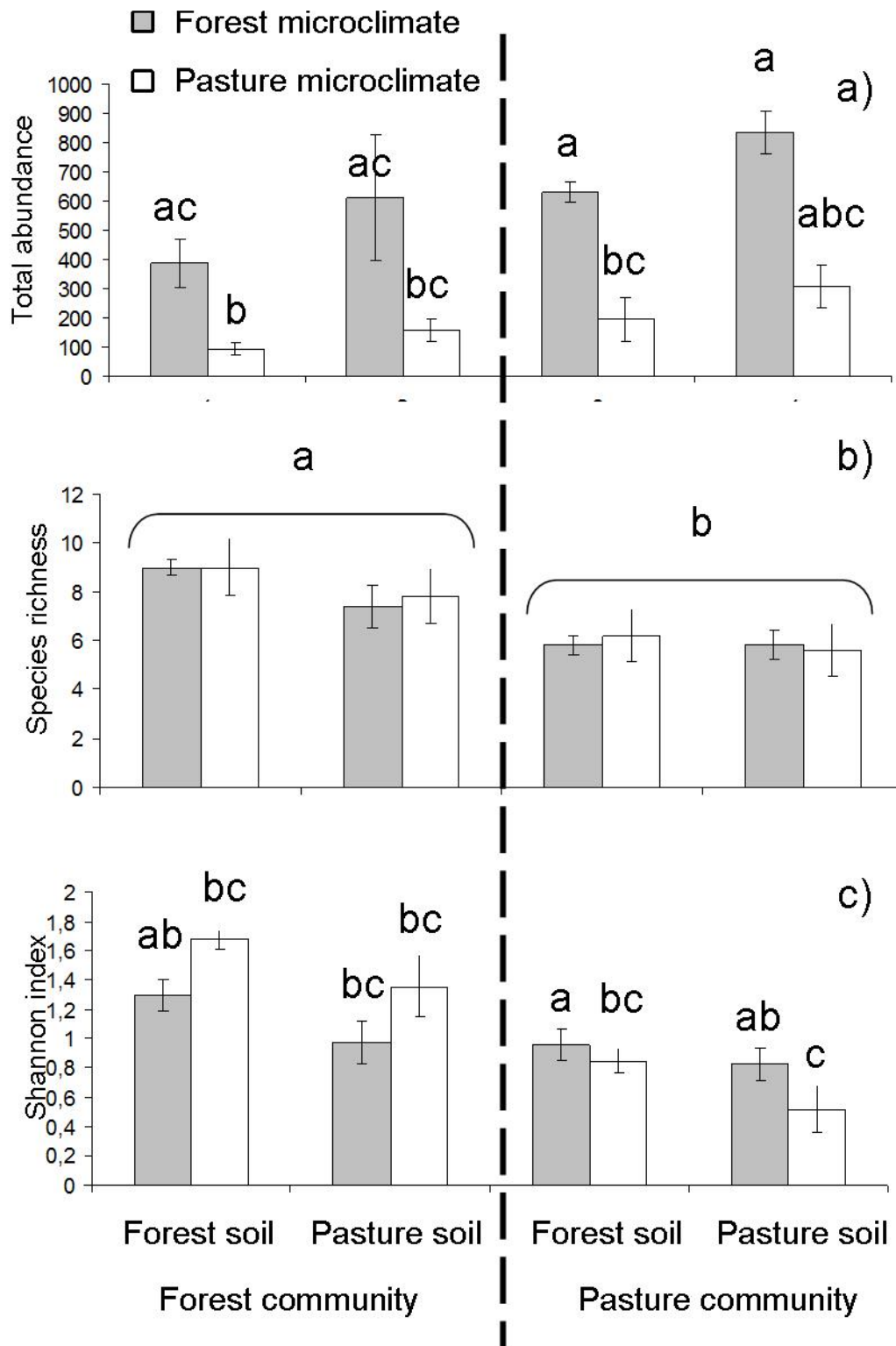
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746

747 **Fig. 5**

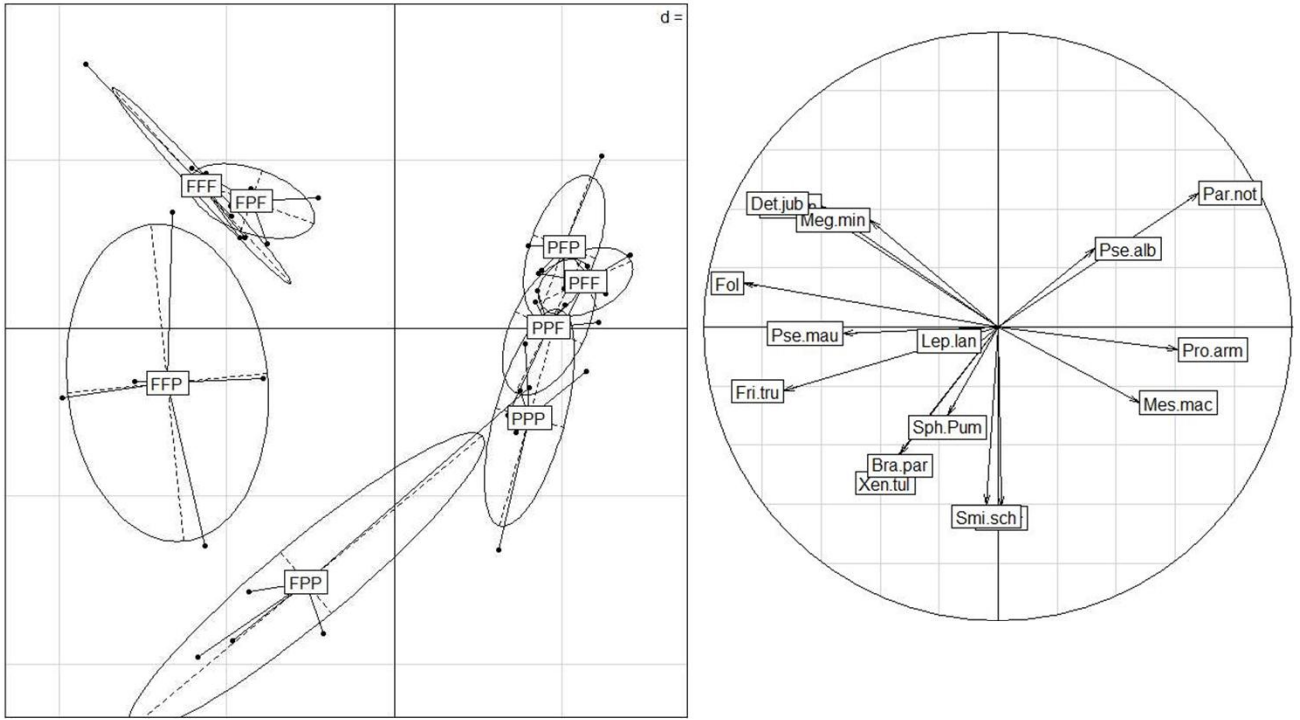
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749

750 **Fig. 6**

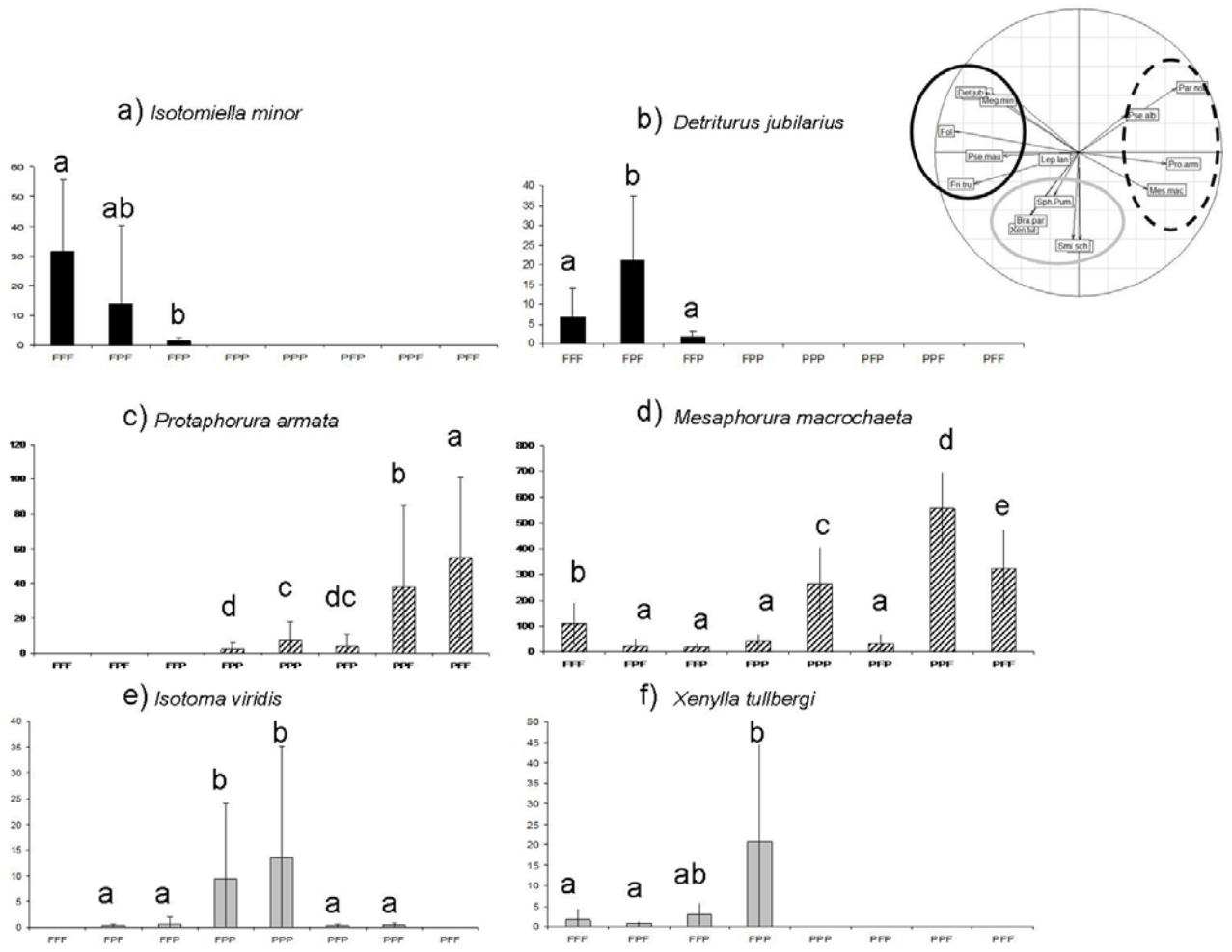
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752

753 **Fig. 7**

754

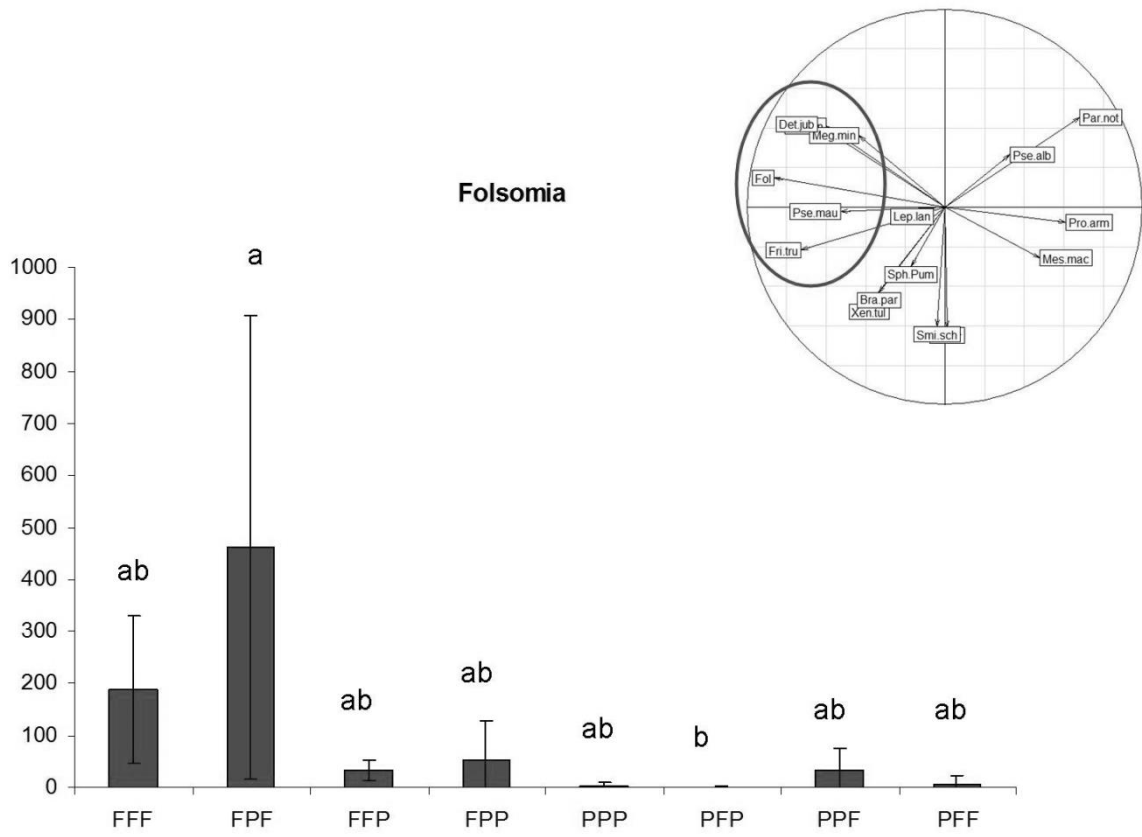


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756 **Fig. 8**

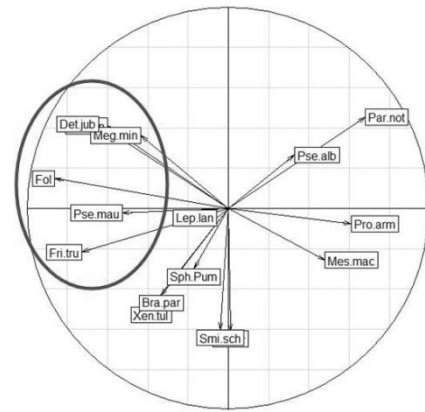
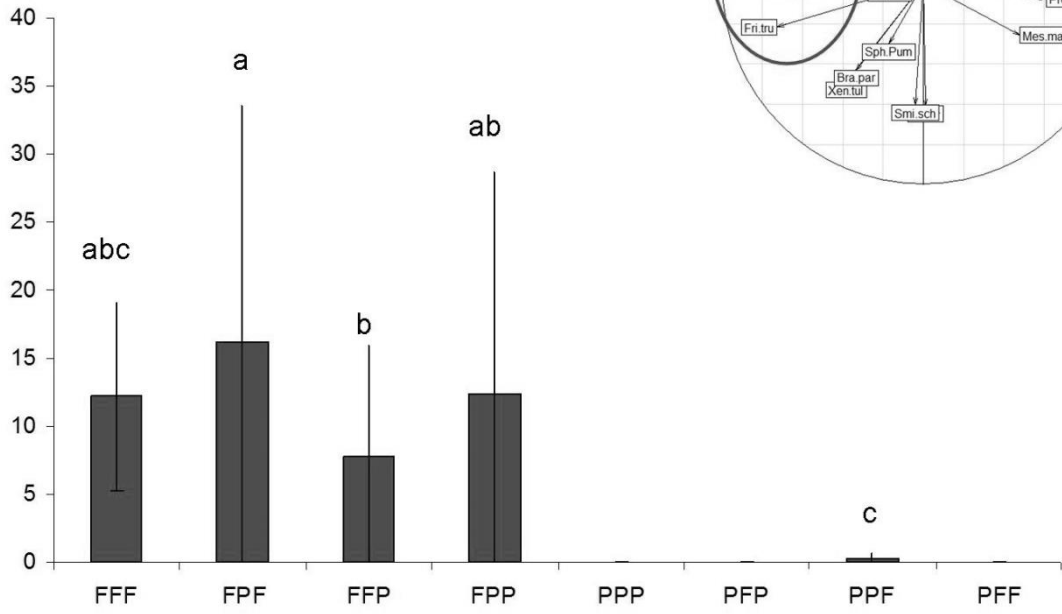
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758 **Appendix.** Abundances of the 16 common species in the eight experimental treatments together with
 759 the correlation circle of between-group analysis performed on the abundances of the 16 common
 760 species using a combination of community origin, soil, and microclimate as explanatory variable.
 761 Letters on bars indicate significant differences. Labels under bars correspond to each treatment (codes
 762 according to Figure 1).



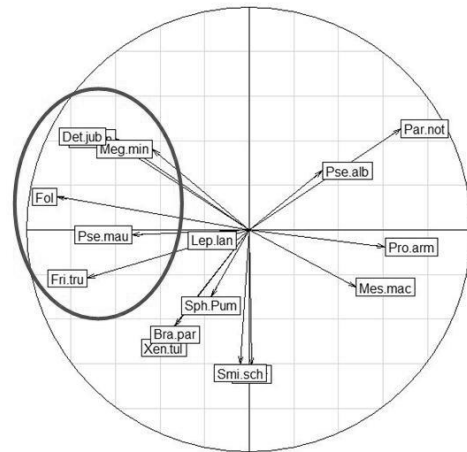
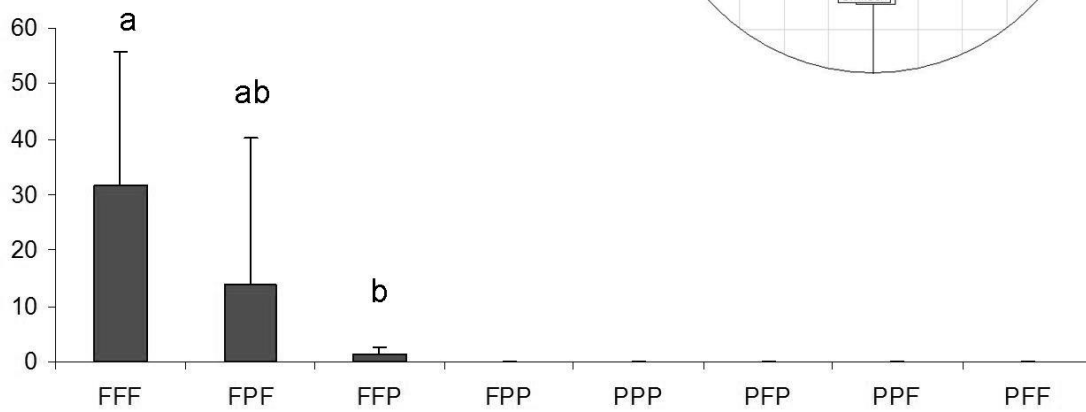
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Friesea truncata



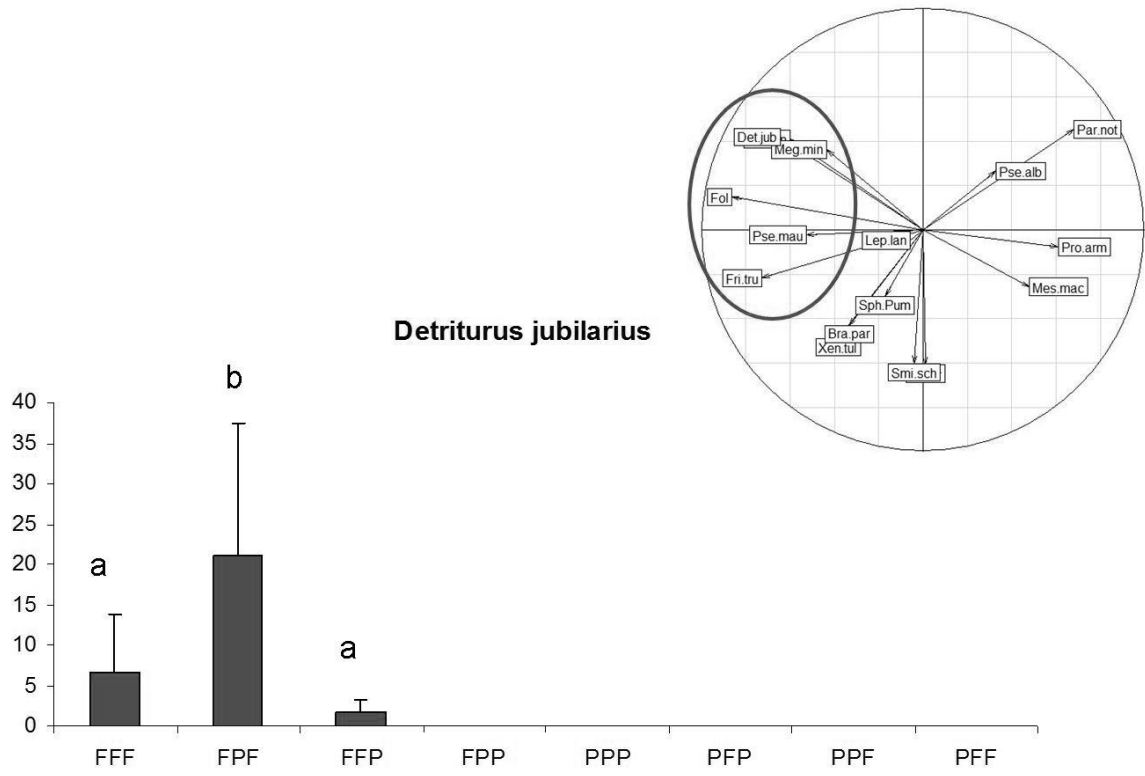
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Isotomiella minor

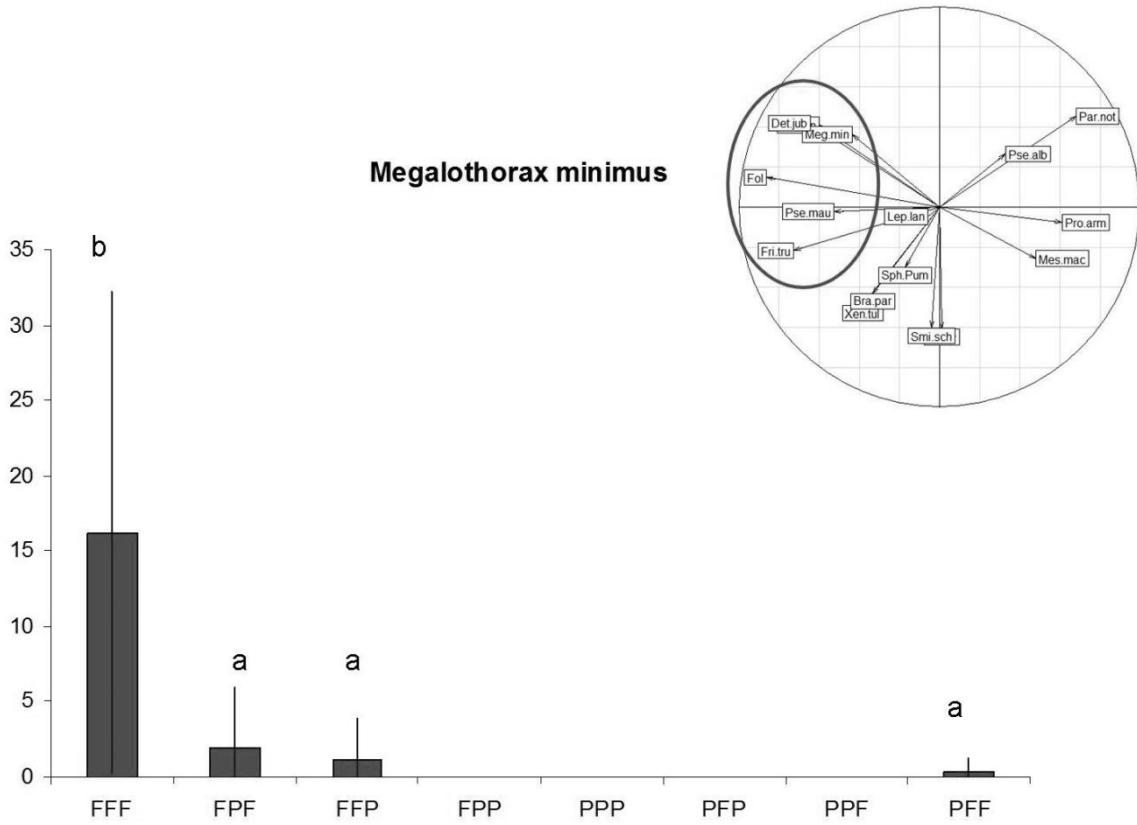


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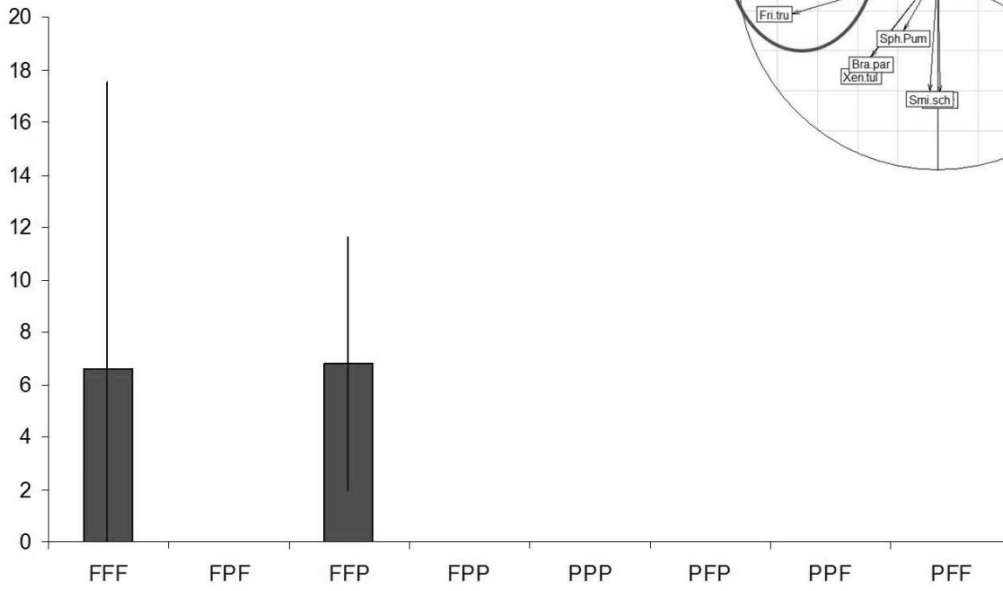
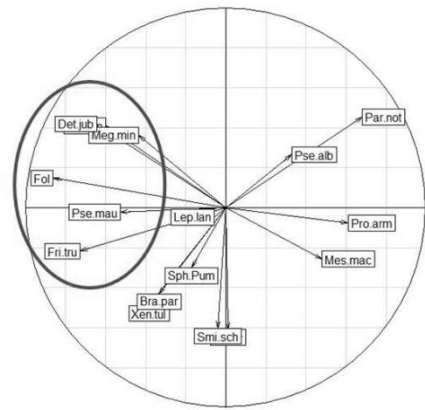
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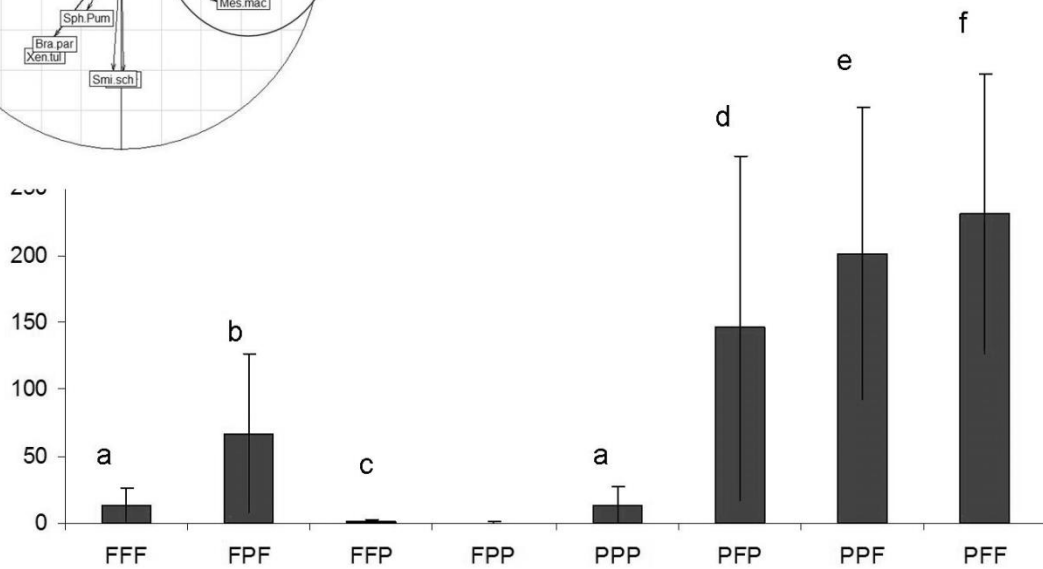
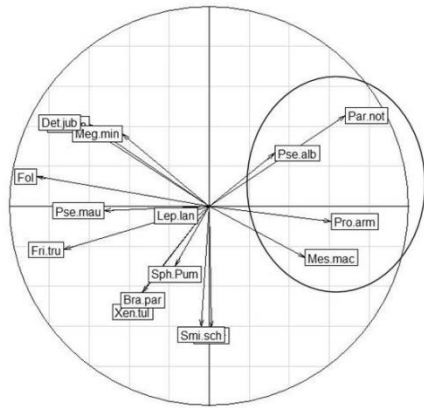


Pseudosinella mauli

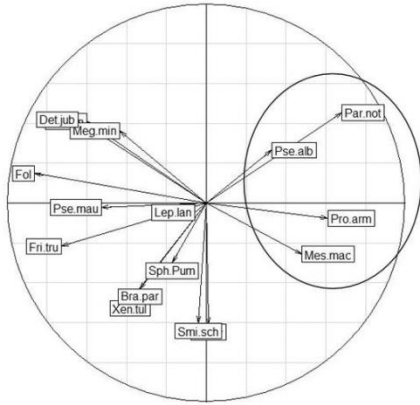


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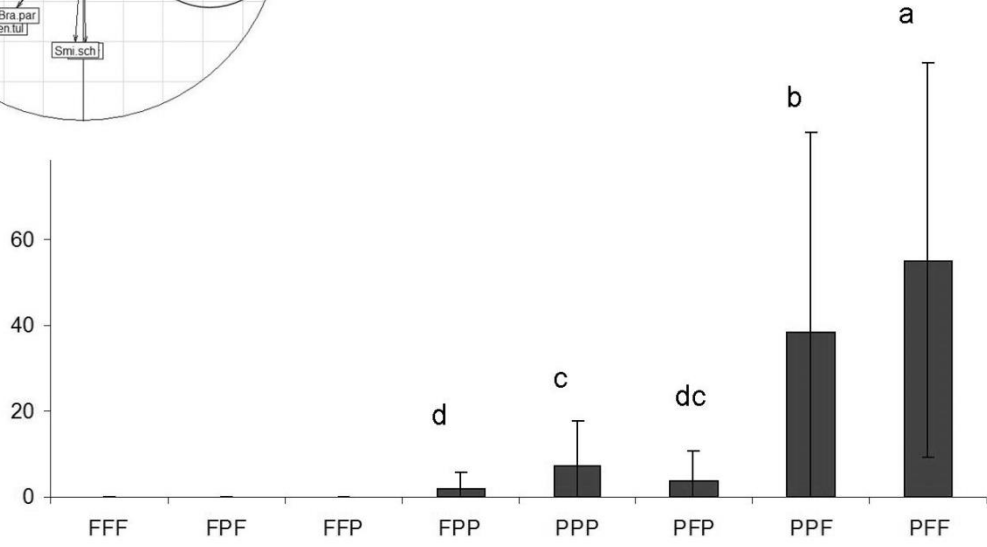
Parisotoma notabilis



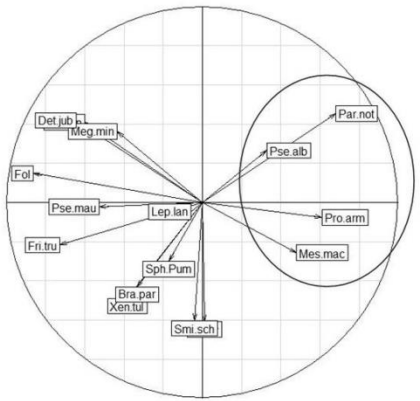
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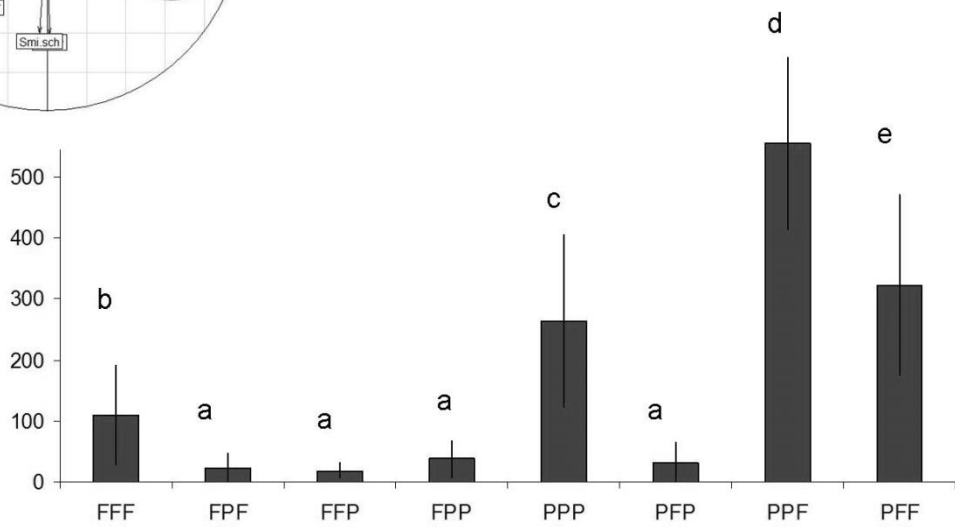
Protaphorura armata



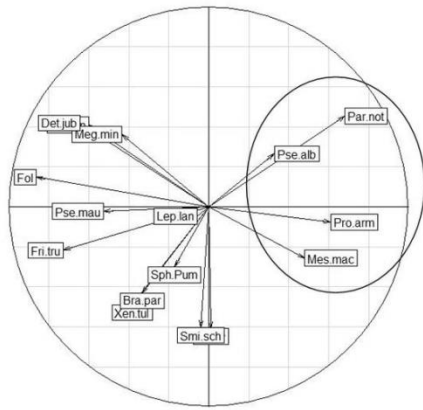
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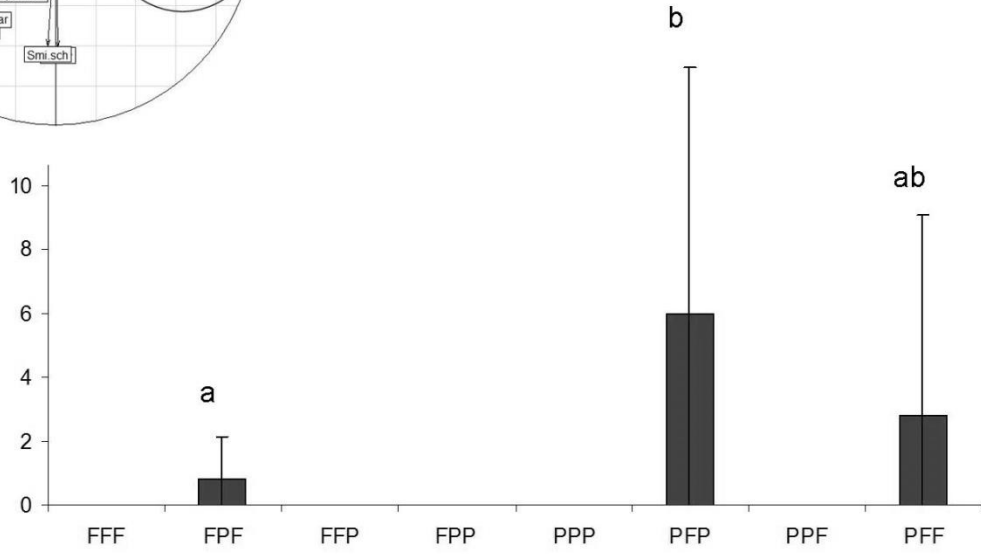
Mesaphorura macrochaeta



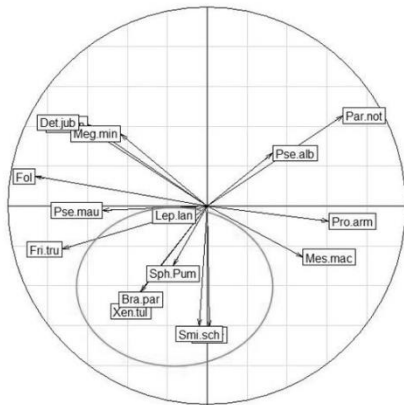
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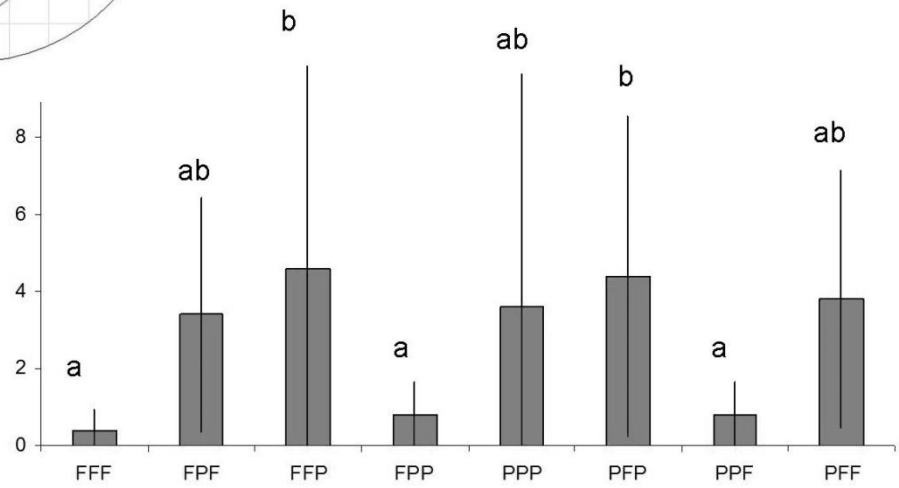
Pseudosinella alba



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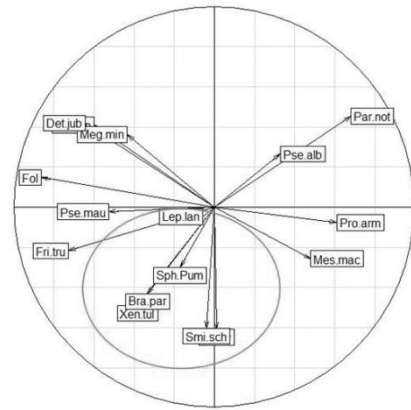
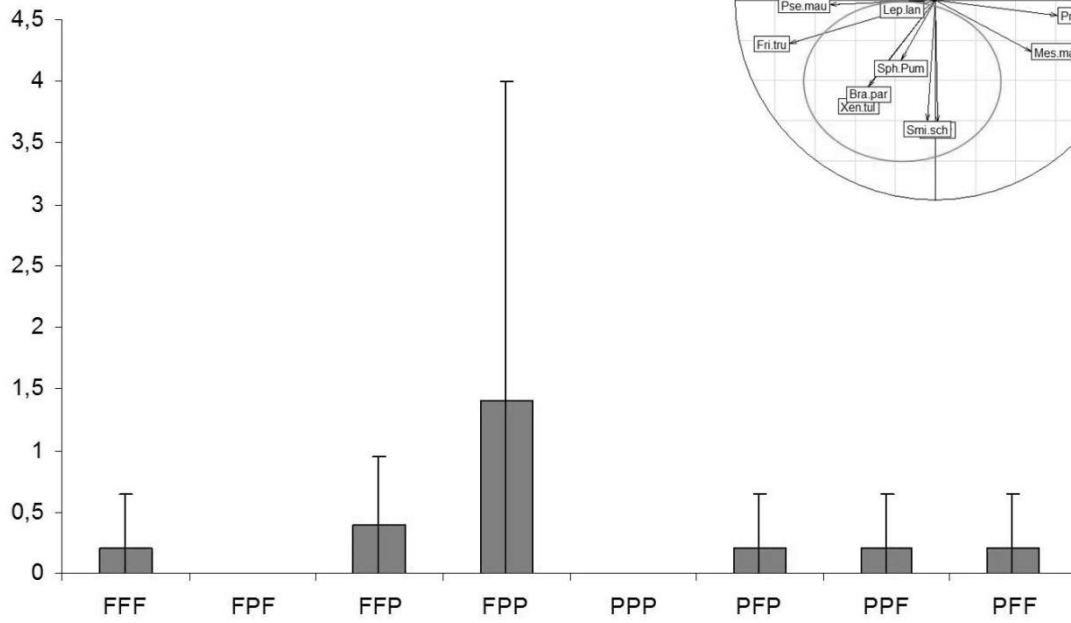


Lepidocyrtus lanuginosus



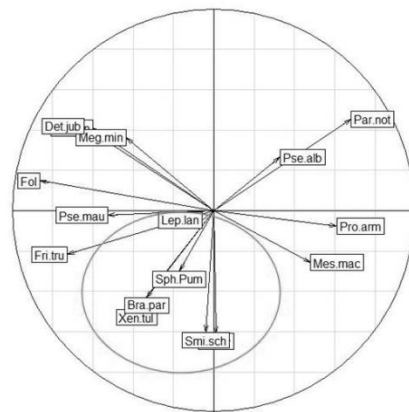
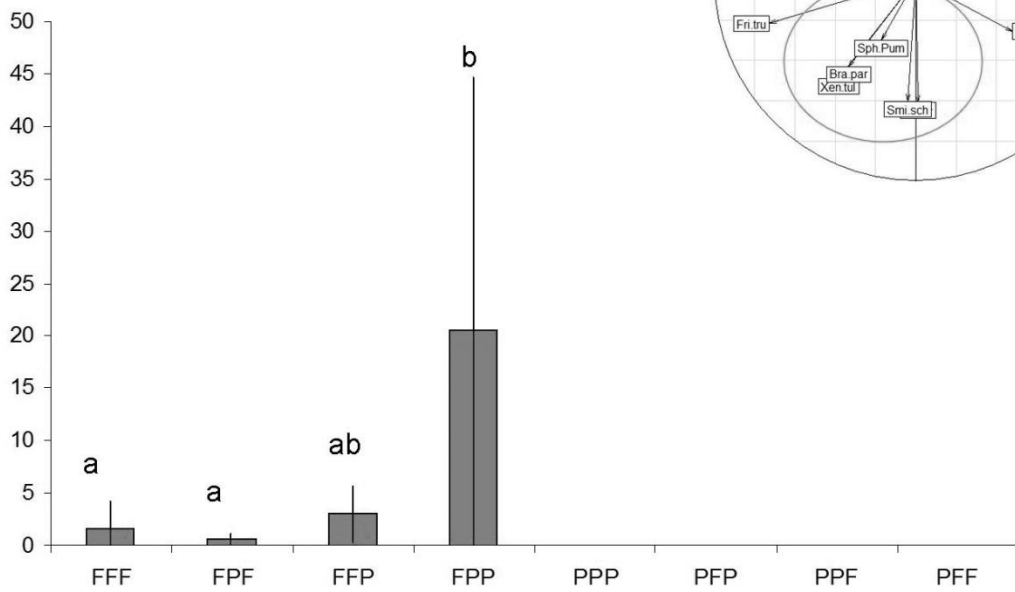
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Sphaeridia pumilis

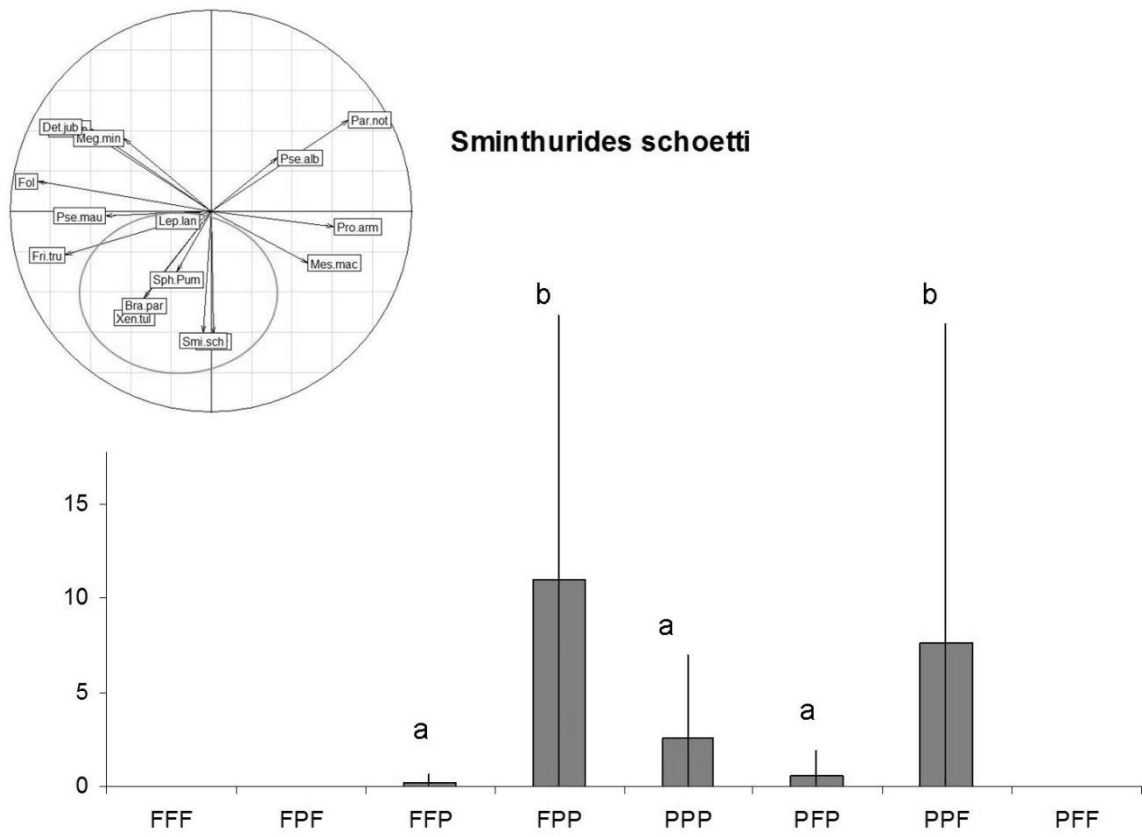


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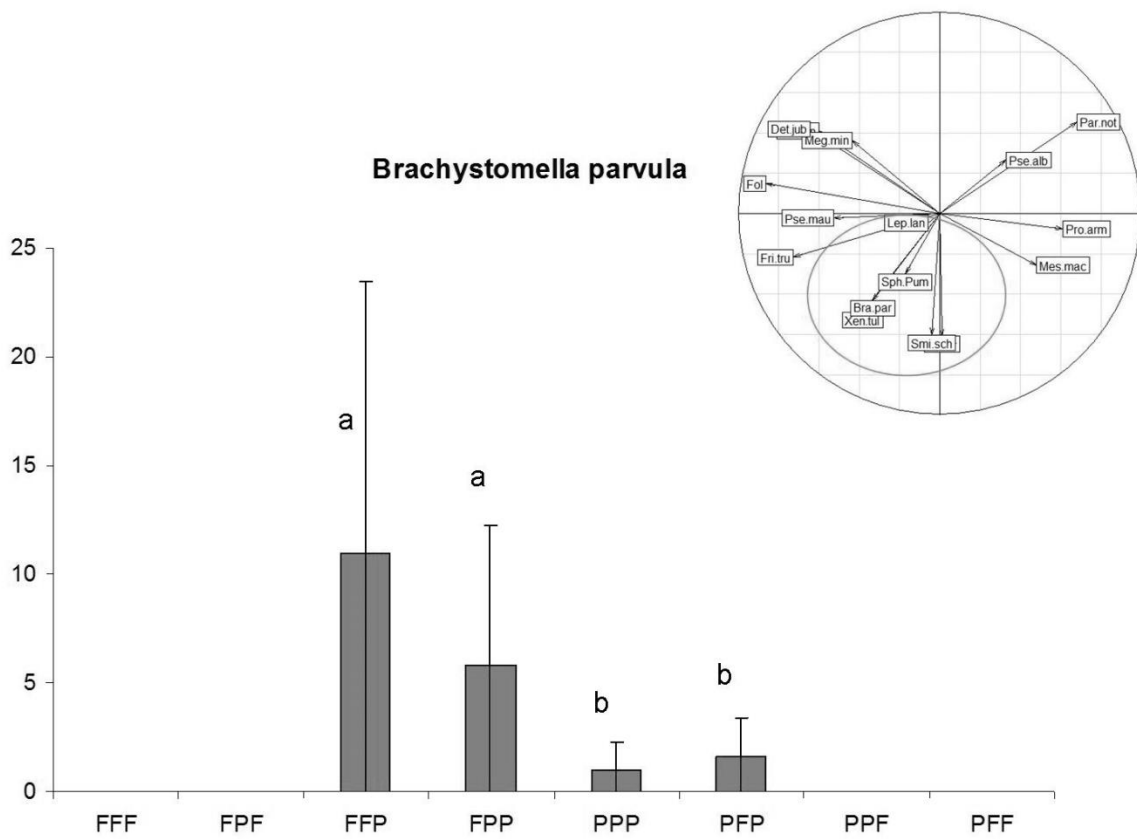
Xenylla tullbergi



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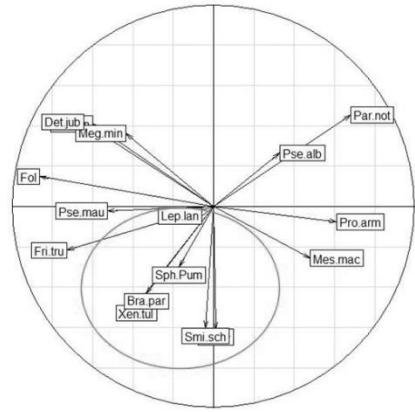
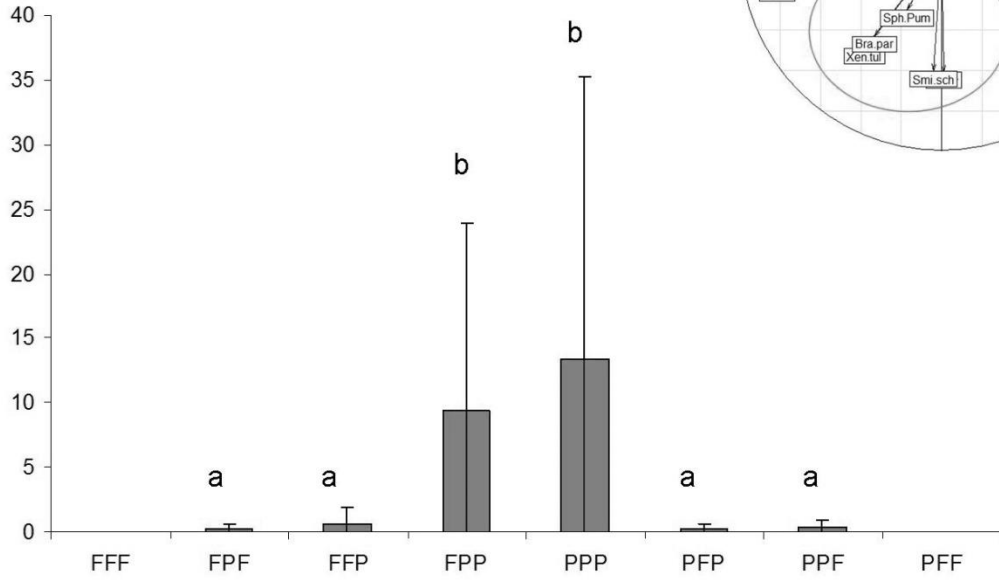


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Isotoma viridis



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