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23 Abstract

24

25 Beside biotic interactions, habitat preference and dispersal ability of species play a prominent
26 role in the building of animal species assemblages. However, these traits are usually very poorly
27 documented for soil organisms. A soil transfer experiment was designed to study habitat preference
28 (including land-use and soil preference) and dispersal ability of soil springtail species living in a
29 meadow and in an adjoining deciduous forest. The study was performed in the Morvan Regional
30 Natural Park (Central France), using untreated or defaunated soil blocks, transferred to another land-
31 use or replaced in their original land-use. Land-use preference was quantified in untreated and
32 untransferred samples from meadow and forest. Dispersal ability was estimated from the time at which
33 species colonized defaunated samples in their own habitat. Soil preference was estimated from the
34 colonization rate of defaunated samples by comparing transferred and untransferred soil blocks.
35 Results showed that in the community, 6% of species were land-use generalists, 30% were soil
36 generalists and 36 % recolonized defaunated soil blocks within a week. Land-use preference, soil
37 preference and dispersal ability were largely independent components of species characteristics.
38 Although our experiment dealt only with small-scale colonization, comparisons between species
39 showed that the dispersal type based on anatomical features (legs, antenna, furcula, visual apparatus)
40 does not allow predicting the dispersal ability of these species. Discrepancies between land-use
41 preference and soil preference suggest that other habitat features must be relevant for Collembola, and
42 that a trade-off exists between eco-physiological and biotic interactions (including food requirements).

43

44 *Keywords:* Collembola; forest; meadow; transfer experiment; habitat preference; land-use preference;
45 soil preference; dispersal ability; morphological traits; response traits

46

47 1. Introduction

48

49 According to theories in community ecology (Drake, 1990; Hunter and Price, 1992; Clobert et
50 al., 2001; Weiher and Keddy, 2001; Tews et al., 2004), the composition of species assemblages can be
51 explained by three processes, the former two acting at the species level, the third one acting at the
52 community level: (1) habitat preference, (2) dispersal, (3) biotic interactions (positive and negative).
53 These interconnected processes filter regional biodiversity, shaping species assemblages at the local
54 level (Keddy, 1992; Zobel, 1997; Rajaniemi et al., 2006). Knowledge on habitat preference and
55 dispersal ability is necessary to understand the distribution of species both at local and regional scales.
56 Species belonging to the same community and thought to have similar or at least compatible
57 ecological requirements may disperse at varying rates, and thus may respond differently to
58 environmental change and heterogeneity (Ribera et al., 2001; Ponge et al., 2006). Indeed, dispersal
59 ability and habitat preference constrain species capability to reach and occupy different parts of an
60 ecosystem mosaics. Species with high dispersal ability are able to reach more easily all patches of the
61 landscape and will respond to environmental and land-use change, while species with low dispersal
62 ability might not reach some patches (depending on habitat connectivity) even those suitable in habitat
63 requirements (Dunning et al., 1992; Andr n et al., 1997). Similarly, species with narrow habitat
64 requirements are constrained to live in particular patches, which can also impede them to reach some
65 patches (again depending on landscape structure).

66

67 Springtails are an integral part of healthy soils and play a critical role in ecosystem services
68 such as dissemination and control of microbial communities (Rusek, 1998). They also influence litter
69 decomposition by the control they have on microbial diversity (H ttenschwiler et al., 2005; Lavelle
70 and Spain, 2005). Despite of their prominent role in structuring communities (see above), habitat
71 preferences and dispersal abilities are still imperfectly known in this group. Moreover, documenting
72 these traits could help understanding some features of Collembolan spatial distribution. For example,
73 as many other soil invertebrates, they are poorly sensitive to habitat fragmentation at local scale (1 m²)

74 (Rantalainen et al., 2008) even though they are sensitive to fragmentation at the landscape scale (1
75 km²) (Sousa et al., 2006) and they may suffer from land-use change due to poor active dispersal
76 (Ponge et al., 2006) even if some species are known for their high passive dispersal ability (Van der
77 Wurff et al. 2003). All these results show that (1) it is worth studying further the factors which shape
78 Collembolan species assemblages in mosaics of land-uses and (2) documenting species characteristics
79 such as dispersal and habitat preference would allow to better understand mechanisms hidden behind
80 patterns of species distribution.

81

82 To do so, in situ transfer of soil blocks between a forest and a nearby meadow was performed
83 to directly assess in the same experiment habitat preferences and dispersal abilities of all species of
84 Collembola found. With this in situ experiment we could also identify whether species preference for
85 meadow or forest is due to a preference for soil quality. As we documented different species
86 characteristics, we could also test for significant correlations between them. For example we tested
87 whether (1) land-use specialists (restricted to a given habitat) are also specialized in the soil type of
88 their land-use, (2) habitat generalists have higher dispersal ability than habitat specialists.

89

90 **2. Materials and methods**

91

92 This field experiment was established in the Morvan Regional Natural Park (Central France)
93 from December 2005 to June 2006 and was similar to the shorter-term and simpler experimental
94 approach by Ponge et al. (2008).

95

96 *2.1. Study site*

97

98 The Morvan Regional Natural Park (Central France) is under submontane-atlantic climate
99 with continental influence, with a mean annual rainfall of 1000 mm, and a mean temperature of 9°C.
100 The parent rock is granite (Adolphe and Desmanèges-Lorenz, 1977). Soils are weakly to strongly
101 acidic (Fédoroff & Arousseau, 1981), with a humus form sensu Brêthes et al. (1995) varying from
102 Eumull to Dysmoder (Ponge et al., 2003).

103

104 The forest contains hundred-year-old beeches (*Fagus sylvatica* L.) and oaks [*Quercus petraea*
105 (Matt.) Liebl]. The soil is an Acrisol and the humus form is a Dysmoder. The nearby meadow was
106 mowed each year at the end of spring and then grazed by cattle in autumn. The soil is a Cambisol and
107 the humus form is a Eumull. There is a sharp transition between the forest and the meadow.

108

109 2.2. *Experimental design*

110

111 On December 2005, 60 circular soil blocks (15 cm diameter ×10 cm depth) were dug in both
112 land-use plots along 10 evenly spaced transects (25 m between transects), with 6 blocks in each
113 transect (50 cm between blocks located in the same transect). Transects were perpendicular to the
114 forest edge and started 10 m from it both in the forest and the meadow. Sixty soil blocks among 120
115 were dug ten days before start of the experiment then kept frozen to -20° C in order to get rid of fauna,
116 the other 60 being let undisturbed until start of the experiment.

117

118 In each land-use plot 15 untreated and 15 defaunated blocks were transferred to the other site
119 while the remaining 15 untreated and 15 defaunated blocks were replaced in their original land-use
120 plot. Meadow blocks were transferred with their original grass, without any further pre-treatment. In
121 the same manner, forest blocks were transferred with their thick litter but with no ground vegetation
122 (except some mosses). Taken together, eight treatments were implemented (Fig. 1), according to the

123 initial presence or absence of fauna (W with fauna, O without fauna), land-use plots from which
124 blocks have been taken (F forest, M meadow), and land-use plots where blocks have been replaced (F
125 forest, M meadow). In each treatment (15 blocks), five blocks were sampled randomly one week after
126 start of the experiment (December 2005), five others after 1 month (January 2006) and the remaining
127 five after 6 months (June 2006). The following treatment codes were used in the experimental design:
128 OFF = blocks without fauna taken in the forest and replaced in the forest; OFM = blocks without
129 fauna taken in the forest and replaced in the meadow; OMM = blocks without fauna taken in the
130 meadow and replaced in the meadow; OMF = blocks without fauna taken in the meadow and replaced
131 in the forest; WFF = blocks with fauna taken in the forest and replaced in the forest; WFM = blocks
132 with fauna taken in the forest and replaced in the meadow; WMM = blocks with fauna taken in the
133 meadow and replaced in the meadow; WMF = blocks with fauna taken in the meadow and replaced in
134 the forest.

135

136 Samples were immediately taken to the laboratory to be extracted over 10 days in a Berlese-
137 Tullgren apparatus with a 15 W bulb lamp suspended over each sample. Extracted micro-arthropods
138 were preserved in 95% ethyl alcohol until sorting and identification. Springtails were identified to
139 species level under a binocular microscope (50×) and a light microscope (400×) using keys by Gisin
140 (1960), Zimdars and Dunger (1994), Potapow (2001), Thibaud et al. (2004) and Hopkin (2007).

141

142 *2.3. Characterization and statistical validation of classes of dispersal ability*

143

144 For each of the springtail species which were present in the 60 blocks replaced in their original
145 environment (WFF, WMM, OFF, OMM), dispersal ability was defined by the time at which the
146 species reappeared in the defaunated blocks (OFF, OMM). This allowed us to classify springtail
147 species in four classes of dispersal ability, either in the forest or the meadow. Indeed, the dispersal

148 ability of a species could well be different in the two land-use types (noted F in the forest and M in the
 149 meadow): species for which the first individuals colonized defaunated blocks (1) within a week (F1 or
 150 M1), (2) after a week and within a month (F2 or M2), (3) after a month and within six months (F3 or
 151 M3), (4) species which did not colonize defaunated blocks after six months but were found in
 152 untreated blocks (F4 or M4). When species were never found in the land-use under investigation, we
 153 noted them M0 in the meadow and F0 in the forest.

154

155 To test the relevance of our four classes of dispersal ability, we tested the effect of the
 156 interaction between time and dispersal ability on the presence/absence of species using Generalized
 157 Linear Models (GLM) with binomial models for presence/absence of species (Pinheiro and Bates,
 158 2000). We used OFF and OMM treatments for dispersal ability. All statistics were implemented using
 159 R software (Crawley, 2007).

160

161 *2.4. Characterization of species land-use preference and statistical validation of preference classes*

162

163 To define land-use preference we used the IndVal index (Dufrêne and Legendre, 1997) which
 164 combines the specificity of a species for a habitat type (a species is found only in a defined habitat)
 165 and its fidelity to this habitat (a species is found in all samples of a defined habitat):

166 $I_{ij} = A_{ij} \times B_{ij} \times 100$, where

167 A_{ij} = average abundance of species i in blocks of habitat j /average abundance of species i

168 B_{ij} = number of blocks of habitat j where species i is present/number of blocks of habitat j

169 I_{ij} reaches its maximum value (100) when species i is present in all soil blocks from habitat j and
 170 absent in blocks from all other habitats. Here only two land-uses (forest and meadow) were

171 considered. For the calculation of the IndVal index, we only used untreated blocks that were replaced
172 in their original land-use plot, i.e. WFF and WMM treatments.

173

174 For each species, we calculated forest and meadow IndVal indices using the ‘duleg’ function
175 of the ‘labdsv’ package from R software (Ihaka and Gentleman, 1996). Then we classified the species
176 in five groups according to their affinity for one or both land-uses: (1) forest specialists or strict-forest
177 species (F), (2) forest-preferring species (FP), (3) meadow specialists or strict-meadow species (M),
178 (4) meadow-preferring species (MP), (5) generalists (G).

179

180 To test the relevance of our classes of land-use preference, we tested the effect of the
181 interaction between land-use preference and land-use category on the abundance and on the
182 presence/absence of species using Generalized Linear Models (GLM) with approximate Poisson error
183 for species abundance or binomial models for presence/absence of species (Pinheiro and Bates, 2000).
184 We used WFF and WMM treatments to validate classes of land-use preference.

185

186 *2.5. Characterization of soil preference and statistical validation of preference classes*

187

188 To characterize the preference of species for soil types we compared defaunated or untreated
189 soil blocks from a land-use with defaunated or untreated blocks transferred from the other land-use.
190 For each species we run a Generalised Linear Model with approximate Poisson error to test for the
191 effect of block transfer on species abundances. When this test was significant, the block type in which
192 the species was the more abundant was considered as the preferred soil of the species. For strict forest,
193 forest-preferring and generalist species, we used OFF-OMF and WFF-WMF treatments and for strict
194 meadow, meadow-preferring and generalist species, we used OMM-OFM and WMM-WFM
195 treatments. Indeed, a meadow-soil-preferring species will be more abundant in OMM or OMF blocks,

196 while a forest-soil-preferring species will be more abundant in OFF or OFM blocks. When the type of
197 soil had no significant effect on the abundance of a species, the species was considered as soil-
198 generalist. Otherwise, the parameters estimated from the GLM model indicated the soil preference of
199 the species: (i) meadow-soil preferential species (MS), (ii) forest-soil preferential species (FS) and (iii)
200 soil generalist species (SG).

201

202 *2.6. Relationship between land-use preference, soil preference and dispersal ability*

203

204 The relationship between the land-use preference and the dispersal ability of species was
205 tested by a Fisher's exact test based on two-way contingency tables with classes of land-use
206 preference (forest-specialist or meadow-specialist species depending on the land-use where dispersal
207 was examined, forest- or meadow-preferring and generalist species) and classes of dispersal ability
208 (species colonizing defaunated blocks within a week, within a month, within six months or more than
209 six months) as entries. The relationships between soil preference and land-use preference or dispersal
210 ability were tested in the same way with all land-use preferences and all dispersal abilities for soil
211 preference modalities, except for the species for which there were not enough specimens to run the
212 model (NR, Table 1). Finally, the relationship between dispersal abilities in two land-uses (forest and
213 meadow) was also tested by the Fisher's exact test not taking into account species absent from the
214 land-uses tested (modality M0 in the meadow and F0 in the forest).

215

216 **3. Results**

217

218 In the 120 soil blocks a total of 80,119 springtails were identified to species; 57 species were
219 found in this study but only 49 species in untreated and untransferred blocks (WMM and WFF) for
220 which dispersal ability and land-use preference were established (Table 1, Figure 2).

221

222 Species could be classified according to their dispersal ability (Table 1). We found 18 species which
223 dispersed within a week (nine in the forest, four in the meadow and five in both land-uses), one which
224 dispersed after a week and within a month (in the forest), five which dispersed after a month and
225 within six months (two in the forest and three in the meadow) and seven which did not disperse after
226 six months (five in the forest and two in the meadow). However, as estimated from the colonization of
227 defaunated blocks, dispersal abilities varied with the land-use (Table 1) and forest-preferring and
228 meadow-preferring species could have different abilities to disperse depending on land-use (Table 2).

229

230 Species could be classified in decreasing affinity to the meadow and increasing affinity to the
231 forest, using respective Indval values (Fig. 2). Only three species did not exhibit any preference for
232 one habitat: *Mesaphorura macrochaeta* (Mes_mac), *Lepidocyrtus lignorum* (Lep_lig) and
233 *Lepidocyrtus lanuginosus* (Lep_lan). A total of 19 species were forest-specialists, ten were meadow-
234 specialists, nine were meadow-preferring and eight were forest-preferring species (Table 1).

235

236 Species could be classified according to their soil type preferences (Table 1). Five species
237 were forest-soil-preferring, twenty were meadow-soil-preferring species and fifteen had no preference
238 (i.e. soil generalists). For nine species, the total abundance of each species was too low to allow us
239 running the analysis to determine their soil preference (i.e. NR modality in Table 1).

240

241 Our classes of land-use preference were validated: there is a significant interaction between
242 sampling land-uses and land-use preference classes when taking into account the abundance of species
243 or their presence/absence in WFF and WMM soil blocks (GLM, ANOVA test $p < 0.01$). A similar
244 validation was achieved on classes of dispersal ability: there is a significant interaction between time
245 of sampling and classes of dispersal ability when taking into account the presence/absence of species

246 in OFF and OMM blocks (GLM, ANOVA test $p < 0.01$). Soil preference classes were directly validated
247 by the GLM procedure that was used to build these classes.

248

249 There was a significant relationship between land-use preference and dispersal ability of
250 species in the meadow (Table 3, Fig. 3a, Fisher's exact test, $p < 0.05$) but not in the forest (Table 3,
251 Figure 3b, Fisher's exact test, $p > 0.05$): the meadow soil was colonized more rapidly by meadow
252 species than by forest species. Among forest species (forest-specialist and forest-preferring species),
253 4.1% (two species among a total of 49) colonized the blocks within a week in the meadow and 26.5%
254 (13 species among 49) in the forest (Table 2), while among meadow species (meadow-specialist and
255 meadow-preferring species) 22.4% (11 species among 49) did so in the meadow and 10.2% (five
256 species among 49) in the forest. However, 47 % forest-specialist and 50% forest-preferring species
257 dispersed within a week in the forest while only 25% forest-preferring species did it in the meadow
258 and 40% meadow-specialist and 77% meadow-preferring species dispersed within a week in the
259 meadow while only 22 % meadow-preferring species did it in the forest (Table 2). This confirmed that
260 recolonization was more rapid in the meadow than in the forest.

261

262 There was no significant relationship between land-use preference and soil preference of
263 species (Figure 3c, Fisher's exact test, $p > 0.05$): when transferred into the other land-use, forest as
264 well as meadow species preferred the meadow soil. Only four among the 21 forest-specialist and
265 forest-preferring species that could be tested showed a preference for the forest soil, while nine
266 preferred the meadow soil and eight were indifferent (Table 1). Among the 16 meadow-specialist and
267 meadow-preferring species that could be tested, ten showed a preference for the meadow soil, only
268 one preferred the forest soil and five were indifferent. There was no significant relationship between
269 soil preference and dispersal ability of species in the meadow and in the forest (Table 3, Figs. 3d, 3e,
270 Fisher's exact test, $p > 0.05$) and there was no significant relationship between the dispersal abilities of
271 species in the meadow and in the forest (Table 3, Fig. 3f, Fisher's exact test, $p > 0.05$).

272

273 **4. Discussion and conclusion**

274

275 By transferring soil blocks with and without their fauna between a forest and a meadow, we
276 showed that habitat preference and dispersal ability of springtail species could be estimated, and that
277 soil preference could be distinguished from land-use preference. We found 19 forest-specialist, eight
278 forest-preferring, ten meadow-specialist, nine meadow-preferring and three generalist species.
279 Concerning soil preference, we found five forest-soil-preferring, 20 meadow-soil-preferring and 15
280 soil-generalist species (nine were not categorized as they were too scarce). Within a week 17 species
281 recolonized soil blocks in the meadow and 18 did it in the forest, while ten did not recolonize the
282 blocks after six months in the meadow and 13 did not it in the forest. Land-use preference, soil
283 preference and dispersal ability were largely independent from each other.

284

285 *4.1. Dispersal ability*

286

287 Given that they live in a dense and movement-impeding environment, litter- and soil-dwelling
288 springtail species could be suspected at first sight to have low dispersal abilities (Rantalainen et al.,
289 2008). However, our results showed that 37% of the species colonized 15 cm wide soil blocks in less
290 than a week. Ponge et al. (2006) estimated the dispersal ability of 88 springtail species of the Morvan
291 Natural Regional Park using several anatomical features: species with long legs and antennae, a
292 functional jumping apparatus (furcula) and complete eye spots (eight ommatidies) were considered as
293 able to disperse rapidly by their own means (Hopkin, 1997). Our results invalidate the overall
294 principle of these predictions as there was no link between anatomical features and dispersal ability
295 classes for half of the species (Table 1). For example, species such as *Mesaphorura macrochaeta*,
296 *Xenylla grisea* and *Friesea truncata*, which have short legs and do not possess any functional jumping

297 apparatus and thus were classified as slow-dispersal species by Ponge et al. (2006), were observed to
298 colonize defaunated blocks within a week. Vannier (1975) studied the colonisation rate of springtails
299 in soil columns of varying particle size distribution. Rapid colonization (less than a week) was mostly
300 observed for species with long legs and antennae, developed furcula and complete visual apparatus.
301 However, Neelidae (most probably *Megalothorax minimus*) were also shown to colonize rapidly soil
302 columns. *Megalothorax minimus* was classified by Ponge et al. (2006) as a poorly dispersing species
303 on the base of its anatomical features. In our experiment it was also shown to colonize the meadow
304 soil (which it preferred) within a week (Table 1). Ojala and Huhta (2001) performed a microcosm
305 experiment in which dispersal rates of springtail species could be measured at several distances of a
306 colonisation source. They found that springtail species with high dispersal rates belonged to very
307 different taxonomic groups: both Tullbergiinae (short legs and antennae, no furcula, no eyes) and
308 Sminthuridae (opposite features) were active migrants. Dunger et al. (2002) followed experimentally
309 over a year the colonisation of opencast mine dumps by Collembola. The first immigrant was a species
310 with long legs, antenna and furcula and complete visual apparatus, *Bourletiella pistillum*, but the
311 second immigrant was *Mesaphorura florum* a Tullbergiinae. In our study *Mesaphorura macrochaeta*
312 (Tullbergiinae) exhibited high dispersal ability (colonization in less than a week) in the forest habitat.
313 Discrepancies between aptitude for jump and walk and observed dispersal ability could be partially
314 explained by passive dispersal which, however, has never been measured directly but was inferred
315 from genetic exchange between distant populations of the epigeic springtail *Orchesella cincta* (Van
316 der Wurff et al., 2003). Rightly, Dunger et al. (2002) did not attribute to passive dispersal by wind a
317 prominent influence, except for the first immigrant, *B. pistillum*. We cannot rule out that other
318 mechanisms of passive dispersal such as phoresy or egg transport could help some poorly mobile
319 species to reach remote places, as this has been shown in aquatic invertebrates (Frisch et al., 2007),
320 which might explain discrepancies between predicted (on the base of anatomy) and observed
321 colonisation rates by springtail species.

322

323 *4.2. Land-use preference*

324

325 For 85 % of the species we sampled there was a fairly good correspondence between land-use
326 preferences estimated in our experiment and already published results (Table 1). However, some
327 species (*Arrhopalites principalis*, *Dicyrtomina minuta*, *Entomobrya multifasciata*, *Folsomia*
328 *manolachei*, *Friesea truncata*, *Isotomiella minor*, *Neanura muscorum*, *Orchesella cincta*,
329 *Paratullbergia callipygos*, *Pogonognathellus flavescens*, *Pseudachorutes parvulus*, *Sphaeridia*
330 *pumilis*, *Subisotoma pusilla*) were classified in our study as forest- or meadow- specialists while,
331 according to literature, they can be found in both habitats (Ponge, 1980; Rusek, 1989; Ponge, 1993;
332 Dombos, 2001; Ponge et al., 2003; Petersen et al., 2004; Kuznetsova, 2006; Ponge et al., 2006;
333 Chauvat et al., 2007) and should be classified as preferring or generalist but not specialist species. This
334 could be due to local environmental peculiarities that did not allow these species to live in both
335 habitats, such as differences in soil condition (humus form). It should also be noted that in the present
336 study land-use preferences were estimated from a limited set of IndVal values and thus cannot be
337 extrapolated to a variety of environments, contrary to studies cited above.

338

339 4.3. Soil preference

340

341 Species known for their strong affinity to acid soils, such as *Lipothrix lubbocki* and *Willemia*
342 *anophthalma* (Ponge, 1980; Hågvar and Abrahamsen, 1984; Ponge, 1993) exhibited a preference for
343 the forest soil, in accordance with its Dysmoder humus form. Conversely, species which are repelled
344 by soil acidity, such as *Sminthurinus aureus* and *Heteromurus nitidus* (Ponge, 1980, 1993; Salmon and
345 Ponge, 1999) preferred the meadow soil, in accordance with its Eumull humus form. However, the
346 preference for the forest soil exhibited by *Sphaeridia pumilis*, a species which we classified as
347 meadow-specialist according to its distribution in our sites (the present study), seems to be
348 contradictory. However, as this species, according to its distribution observed by Ponge et al. (2003) in
349 the same regional context, should be meadow-preferring rather than meadow-specialist, the result

350 obtained here is probably due to a stochastic effect of its lower abundance in the forest. Together with
351 our results on land-use preference (see above), this study points to other, still imperfectly explored,
352 environmental features that could be meaningful for Collembola. Microclimate, which differs to a
353 great extent between forest and meadow (Morecroft et al., 1998), has a decisive influence on the
354 survival of these moisture-sensitive tiny arthropods (Betsch and Vannier, 1977; Tsiafouli et al., 2005).
355 Biotic interactions such as competition are also thought to influence species distribution (Hågvar,
356 1990; Christiansen et al., 1992; Theenhaus et al., 1999; Salmon and Ponge, 2001; Krivtsov et al.,
357 2003; Salmon et al., 2005). Hågvar (1990) suggested that oribatid species living commonly in
358 Dysmoder (acid-tolerant species) dominate in forest soils, not because they are attracted to acidity, but
359 rather because they compete better with acid-intolerant species. Indeed, competition with resident
360 species can impede a local patch to be colonized by dispersing individuals of other species:
361 competition can thus decrease the realized niche of species (Shigesada and Kawasaki, 1997). Hints on
362 the effect of inter-specific competition could be given in the future by the comparison of our
363 defaunated and untreated blocks.

364

365 To the present state of our knowledge it is not possible to establish a link between habitat
366 preference (including soil preference) and morphological traits of Collembola, although Ponge (2000)
367 noted that extant springtail species or species groups with ancestral anatomical characters exhibited a
368 higher tolerance to soil acidity, as ascertained by their present-day distribution.

369

370 *4.4. Interactions between dispersal ability, land-use preference and soil preference*

371

372 The attractiveness of the meadow soil (Fig. 3c) for a majority of forest as well as meadow
373 specialist and preferring species needs to be interpreted. The meadow humus form was a Eumull,
374 which contrasts with the Dysmoder into which it was transferred in our experiment. It has been

375 demonstrated that soils with high earthworm activity, such as our meadow soil, are attractive for many
376 arthropod species and particularly for Collembolan species (Hamilton and Sillman, 1989; Loranger et
377 al., 1998; Salmon and Ponge, 1999; Maraun et al., 1999). Earthworm activity, which is usually high in
378 Eumull (Brêthes et al., 1995), provides food and habitat for many subterranean organisms, mainly
379 through bioturbation and redistribution of organic matter in the topsoil (Scheu, 1987), and protection
380 against predation offered by earthworm burrows (Salmon et al., 2005). That forest species could be
381 attracted to Eumull (with prominent earthworm activity) while they are commonly living in Dysmoder
382 with poor earthworm activity (Brêthes et al., 1995), and are absent from the nearby meadow, might
383 indicate that their achieved distribution is due to a trade-off between (i) their preference for soils with
384 more favourable biotic interactions (food included) and (ii) their eco-physiological constraints
385 (sensitivity to desiccation, waterlogging, frost) which can be easier fulfilled in sheltered woodland
386 microclimate conditions.

387

388 Although we did not detect any link between dispersal ability in the forest and the type of
389 land-use preference (Fig. 3b), there was a significant correlation between dispersal ability in the
390 meadow and the type of land-use preference (Fig. 3a): in the meadow, meadow-specialist and
391 meadow-preferring species disperse more quickly than forest-preferring species. This suggests that
392 dispersal in the meadow was easier than in the forest. An explanation could be that the meadow
393 represents a disturbed habitat for Collembola, so that meadow species need to be more mobile to
394 persist in this land-use. Indeed, forests are more stable habitats as the establishment of a mature forest
395 takes several decades (Ponge et al., 1998) whereas a meadow is usually ploughed and replanted each
396 ten years. Temperature range and soil compression due to cattle trampling are higher in meadow than
397 in forest (Friberg et al., 2008). Thus forest Collembolan species would not have evolved towards high
398 dispersal abilities because their environment was stable, thereby confirming previous results obtained
399 by Ponge et al. (2008). The absence of correlation between dispersal ability in the forest and land use
400 preference would be explained by the lack of attractiveness of the forest soil for most species (see
401 above). In the light of our results and according to Mysrerud and Ims (1998), it can be suggested that

402 (1) Collembolan species can be attracted to another soil than that of their current habitat, (2) this does
403 not impede them to persist in this habitat if food is abundant enough. In the example of *Vertagopus*
404 *arboreus*, tree trunks are known to be favoured temporary habitats, in both disturbed and undisturbed
405 environments (Ponge, 1993; Prinzing, 2001).

406

407 We did not detect any link between dispersal ability, either in the meadow or in the forest, and
408 soil preference. However, as noticed above, we found a link between land-use preference and dispersal
409 ability in the meadow. If we combine these results with the abovementioned attractiveness of the
410 meadow soil, and the fact that we did not detect any significant relationship between meadow- and
411 forest-dispersal abilities, this points to species-specific barriers to colonization, which do not
412 necessarily match soil preferences. The freezing procedure which was used to deprive the blocks from
413 their original fauna could make the forest soil somewhat distasteful for some species: it has been
414 shown that freezing, by splitting macromolecular assemblages, may increase the toxicity of carbon-
415 rich sediments (Geffard et al., 2004).

416

417 4.5. Working hypotheses and perspectives

418

419 Our results do not support the hypothesis that land-use-specialist species are also soil-
420 specialists of the corresponding soil. However the meadow soil was more attractive whatever the land-
421 use preference of the species, suggesting that food resources must be an important dispersal-triggering
422 stimulus. This is supported by Bengtsson et al. (1994) who experimentally showed that the dispersal
423 rate decreased as food resources increased in Collembolan populations. Our results do not fully
424 support our second hypothesis that land use generalists have higher dispersal ability than specialists.
425 This hypothesis was supported for dispersal in the meadow but the idea that dispersal is not counter-
426 selected for habitat specialists (and vice versa) is not supported. However, the selection of more

427 mobile species in the more disturbed land-use (the meadow) supports the hypothesis that dispersal and
428 habitat-preference strategies of species have been selected to allow them to recolonize quickly soil
429 patches after a disturbance. It would also be interesting to further investigate whether disturbed
430 habitats have led to the selection of species that can survive disturbances. Indeed, temperature
431 variability is stronger in meadows than in forests (Friberg et al., 2008) and Collembola are known to
432 be sensitive to temperature (Betsch and Vannier, 1977). Moreover, springtails have already been
433 shown to have evolved different eco-physiological strategies to resist disturbance by selecting species-
434 specific traits such as, among others, diapausing eggs (Leinaas and Bleken, 1983) and light avoidance
435 (Salmon and Ponge, 1998). More generally, the absence of relationship between species traits (i.e.
436 dispersal ability, land-use preference and soil preference), except in the case of land-use preference
437 and dispersal in the meadow, suggests that these species characteristics were selected mostly
438 independently. Because Collembolan life-history is probably constrained by many trade-offs (Tully et
439 al., 2006), this might also mean that more traits have to be documented to find a general pattern.

440

441 More investigations are needed to better understand the determinants and stimuli of active
442 dispersal for springtails. Indeed, there are still very few studies on dispersal in Collembola but existing
443 ones suggest that Collembolan movements influence their population dynamics (Bengtsson et al.,
444 1994, 2002). For example, dispersal can be a way to avoid intra-specific competition. Moreover, if the
445 role of facilitation or competitive exclusion is established as a mechanism structuring local species
446 assemblages (Connell & Slatyer, 1977), the role of inter-specific competition was never tested for
447 springtails. The design of our experimental protocol will allow us to investigate further these issues.

448

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450

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684

685 **Figure captions**

686

687 **Figure 1.** Experimental design of soil block transfer between a forest and a nearby meadow. Gray
688 arrows represent soil blocks transferred in the other land-use. Upper case letters indicate
689 treatment codes (refer to text in Section 2.2 for symbols)

690

691 **Figure 2.** Graphical representation of the distribution of Collembolan species between the forest and
692 the meadow according to IndVal values for meadow (light grey) and forest (black). Full light
693 grey lines indicate species specialist of the meadow and full black lines indicate species
694 specialist of the forest. Dotted and dashed light grey lines indicate species preferential of the
695 meadow and black ones the same for the forest. Full dark grey lines indicate generalist
696 species, i.e. species did not displaying any preference for one or the other land-use

697

698 **Figure 3.** Distribution of species according to different response traits. Trait classes in abscissa,
699 number of species in ordinate (refer to text or to Table 1 for symbols). (a) Land-use
700 preference. (b) Dispersal ability in the meadow. (c) Dispersal ability in the forest. (d) Soil
701 preference

702

Table 1. Land-use preference, dispersal ability and nature of soil preference for springtail species used in the soil transfer experiment. **Land use preference:** F = forest-specialist or strict forest species, FP = forest-preferring species, M = meadow-specialist or strict meadow species, MP = meadow-preferring species, G = land-use generalist species. **Dispersal ability in meadow:** M0 = species absent in the meadow, M1 = species which colonized meadow frozen blocks within a week, M2 = species which colonized meadow frozen blocks after a week and within a month, M3 = species which colonized meadow frozen blocks after a month and within six months, M4 = species which did not colonize meadow frozen blocks within six months. **Dispersal ability in forest:** F0 = species absent in the forest, F1 = species which colonized forest frozen blocks within a week, F2 = species which colonized forest frozen blocks after a week and within a month, F3 = species which colonized forest frozen blocks after a month and within six months, F4 = species which did not colonize forest frozen blocks within six months. **Soil preference:** FS = forest-soil-preferring species, MS = meadow-soil-preferring species, SG = soil-generalist species. NR: not enough specimens to run the model

Species name	Species code	Land use preference	Dispersal ability		Soil preference	Dispersal type (from Ponge et al., 2006)	Habitat preference (from Ponge et al., 2006)
			in the meadow	in the forest			
<i>Allacma fusca</i>	All_fus	F	M0	F4	NR	Fast	Woodland
<i>Arrhopalites principalis</i>	Arr_pri	F	M0	F4	MS		
<i>Arrhopalites sericus</i>	Arr_ser	FP	M4	F1	MS		
<i>Ceratophysella denticulata</i>	Cer_den	MP	M1	F4	MS		
<i>Ceratophysella recta</i>	Cer_rec	FP	M4	F3	MS		
<i>Deuteraphorura inermis</i>	Deu_ine	FP	M4	F1	MS		
<i>Deuterostminthurus sulphureus</i>	Deu_sul	M	M3	F0	MS	Fast	Agricultural land
<i>Dicyrtomina minuta</i>	Dic_min	F	M0	F1	FS	Fast	Agricultural land
<i>Entomobrya multifasciata</i>	Ent_mul	F	M3	F4	NR	Fast	Agricultural land
<i>Folsomia listeri</i>	Fol_lis	M	M4	F0	NR		
<i>Folsomia manolachei</i>	Fol_man	M	M1	F0	MS		
<i>Folsomia quadrioculata</i>	Fol_qua	FP	M1	F1	MS	Slow	Woodland
<i>Friesea truncata</i>	Fri_tru	F	M0	F1	SG	Slow	Woodland
<i>Gisinianus flammeolus</i>	Gis_fla	F	M0	F4	NR		
<i>Heteromurus nitidus</i>	Het_nit	M	M1	F0	MS	Slow	Agricultural land
<i>Isotoma anglicana</i>	Iso_ang	MP	M1	F4	MS		
<i>Isotomiella minor</i>	Iso_min	F	M0	F1	MS	Slow	Woodland
<i>Lepidocyrtus cyaneus</i>	Lep_cya	M	M1	F0	SG	Fast	Agricultural land
<i>Lepidocyrtus lanuginosus</i>	Lep_lan	G	M1	F1	SG	Fast	Woodland
<i>Lepidocyrtus lignorum</i>	Lep_lig	G	M1	F1	SG	Fast	Agricultural land
<i>Lipothrix lubbocki</i>	Lip_lub	F	M0	F2	FS	Fast	Woodland
<i>Megalothorax minimus</i>	Meg_min	MP	M1	F3	MS	Slow	Woodland
<i>Mesaphorura florum</i>	Mes_flo	M	M3	F0	MS		
<i>Mesaphorura macrochaeta</i>	Mes_mac	G	M2	F1	MS	Slow	Woodland
<i>Micranurida pygmaea</i>	Mic_pyg	MP	M4	F3	NR	Slow	Woodland
<i>Micraphorura absoloni</i>	Mic_abs	F	M0	F4	NR	Slow	Woodland
<i>Neanura muscorum</i>	Nea_mus	F	M0	F3	SG	Slow	Woodland
<i>Orchesella cincta</i>	Orc_cin	F	M0	F3	MS	Fast	Woodland
<i>Paratullbergia callipygos</i>	Par_cal	F	M0	F4	NR	Slow	Woodland
<i>Parisotoma notabilis</i>	Par_not	MP	M1	F1	SG	Slow	Agricultural land
<i>Pogonognathellus flavescens</i>	Pog_fla	F	M0	F1	SG	Fast	Woodland
<i>Protaphorura aurantiaca</i>	Pro_aur	MP	M1	F4	SG		
<i>Pseudachorutes parvulus</i>	Pse_par	F	M0	F1	SG	Slow	Woodland
<i>Pseudosinella alba</i>	Pse_alb	MP	M1	F4	SG	Slow	Agricultural land
<i>Pseudosinella terricola</i>	Pse_ter	F	M0	F1	SG		
<i>Sminthurides parvulus</i>	Smi_par	M	M3	F0	SG	Fast	Agricultural land
<i>Sminthurides schoetti</i>	Smi_sch	MP	M2	F4	MS	Fast	Agricultural land
<i>Sminthurinus aureus</i>	Smi_aur	MP	M1	F1	MS	Fast	Agricultural land
<i>Sminthurinus signatus</i>	Smi_sig	F	M0	F1	SG	Fast	Woodland
<i>Sminthurus viridis</i>	Smi_vir	M	M1	F0	MS	Fast	Agricultural land
<i>Sphaeridia pumilis</i>	Sph_pum	M	M4	F3	FS	Fast	Agricultural land
<i>Stenaphorura denisi</i>	Steph_de	M	M4	F0	NR	Slow	Agricultural land
<i>Stenognathellus denisi</i>	Stegn_de	F	M0	F1	FS		
<i>Subisotoma pusilla</i>	Sub_pus	F	M3	F4	NR		
<i>Vertagopus arboreus</i>	Ver_arb	FP	M1	F4	MS	Fast	Woodland
<i>Willemia anophthalma</i>	Wil_ano	FP	M4	F2	FS	Slow	Woodland
<i>Willemia denisi</i>	Wil_den	FP	M4	F3	MS	Slow	Woodland
<i>Xenylla grisea</i>	Xen_gri	F	M0	F1	SG	Slow	Woodland
<i>Xenylla tullbergi</i>	Xen_tul	FP	M4	F1	SG	Slow	Woodland

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Table 2. Crossed relationships between categories of land-use preference and dispersal ability. Data are numbers of species belonging to each crossed category. Marginal totals are indicated in italic type. Same codes for categories as in Fig. 3

Dispersal ability in the forest (F0 to F4) and in the meadow (M0 to M4)						
	M0	M1	M2	M3	M4	
F0	0	4	0	3	2	9
F1	9	5	1	0	3	18
F2	1	0	0	0	1	2
F3	2	1	0	0	4	7
F4	5	5	1	2	0	13
	<i>17</i>	<i>15</i>	<i>2</i>	<i>5</i>	<i>10</i>	<i>49</i>

Dispersal ability of land-use preference categories in the meadow						
	M0	M1	M2	M3	M4	
F	17	0	0	2	0	19
FP	0	2	0	0	6	8
M	0	4	0	3	3	10
MP	0	7	1	0	1	9
G	0	2	1	0	0	3
	<i>17</i>	<i>15</i>	<i>2</i>	<i>5</i>	<i>10</i>	<i>49</i>

Dispersal ability of land-use preference categories in the forest						
	F0	F1	F2	F3	F4	
F	0	9	1	2	7	19
FP	0	4	1	2	1	8
M	9	0	0	1	0	10
MP	0	2	0	2	5	9
G	0	3	0	0	0	3
	<i>9</i>	<i>18</i>	<i>2</i>	<i>7</i>	<i>13</i>	<i>49</i>

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Table 3. Links between land-use preference, dispersal ability and nature of soil-preference for springtail species tested by the Fisher's exact test.

LUP: Land-use preference. DAM: Dispersal ability in the meadow. DAF: Dispersal ability in the forest. SP: Soil preference. (1)

Modalities used: M = meadow-specialist species, MP = meadow-preferring species, G = land-use generalist species. (2) Modalities used: F = forest-specialist species, FP = forest-preferring species, G = habitat generalist species. (3) All modalities used except species for which there were not enough specimens to run the model. (4) All modalities used except M0 = species absent in the meadow and F0 = species absent in the forest. * = Significant at 0.05 level. NS = not significant

	LUP	DAM	DAF
DAM	* (1)		
DAF	NS (2)	NS (4)	
SP	NS (3)	NS (3)	NS (3)

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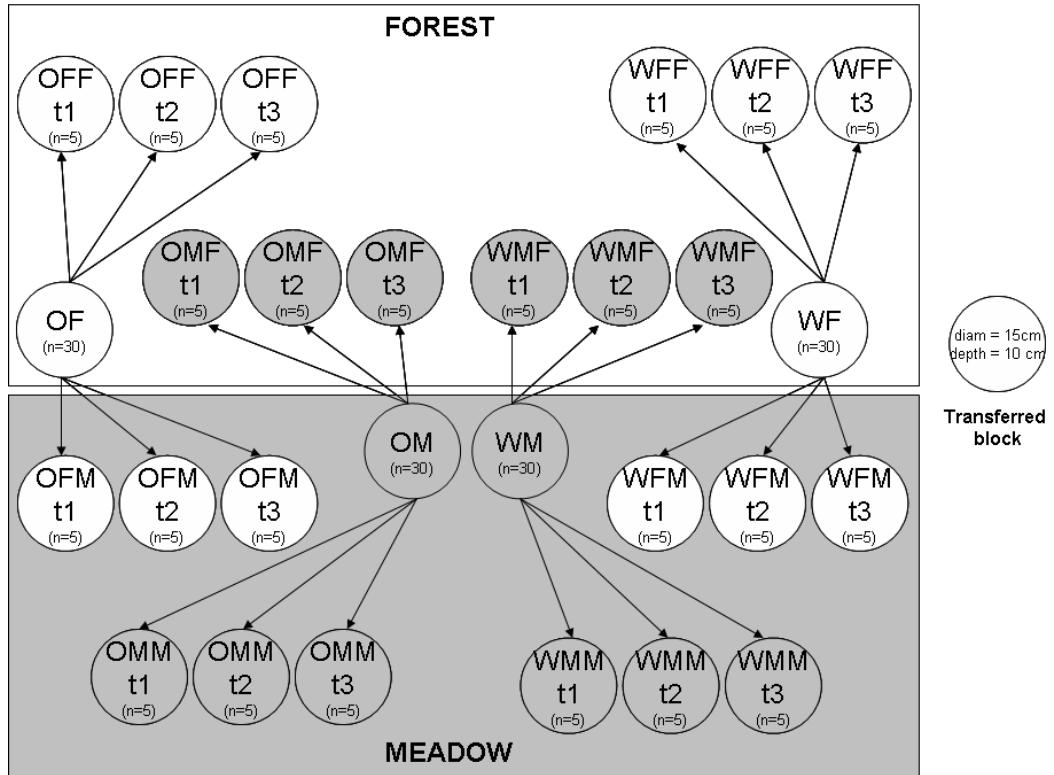
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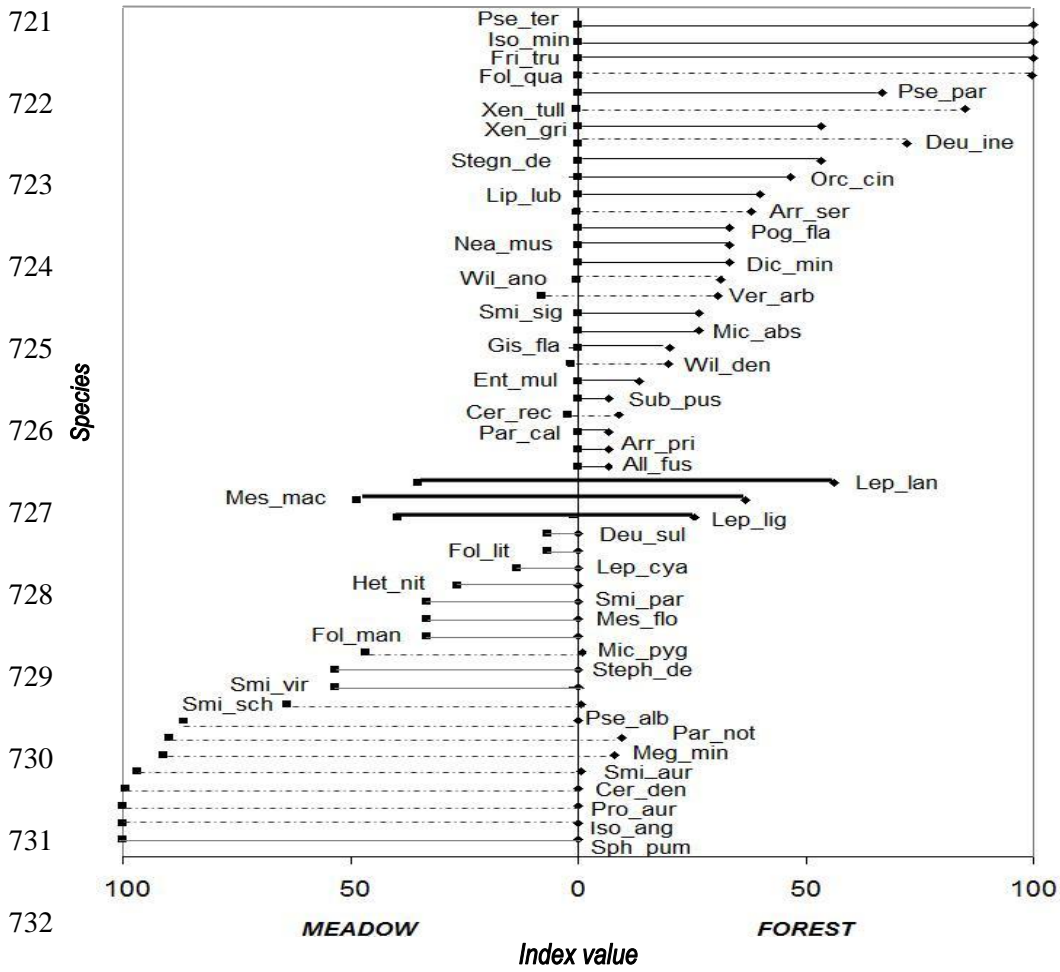
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719 **Figure 1**

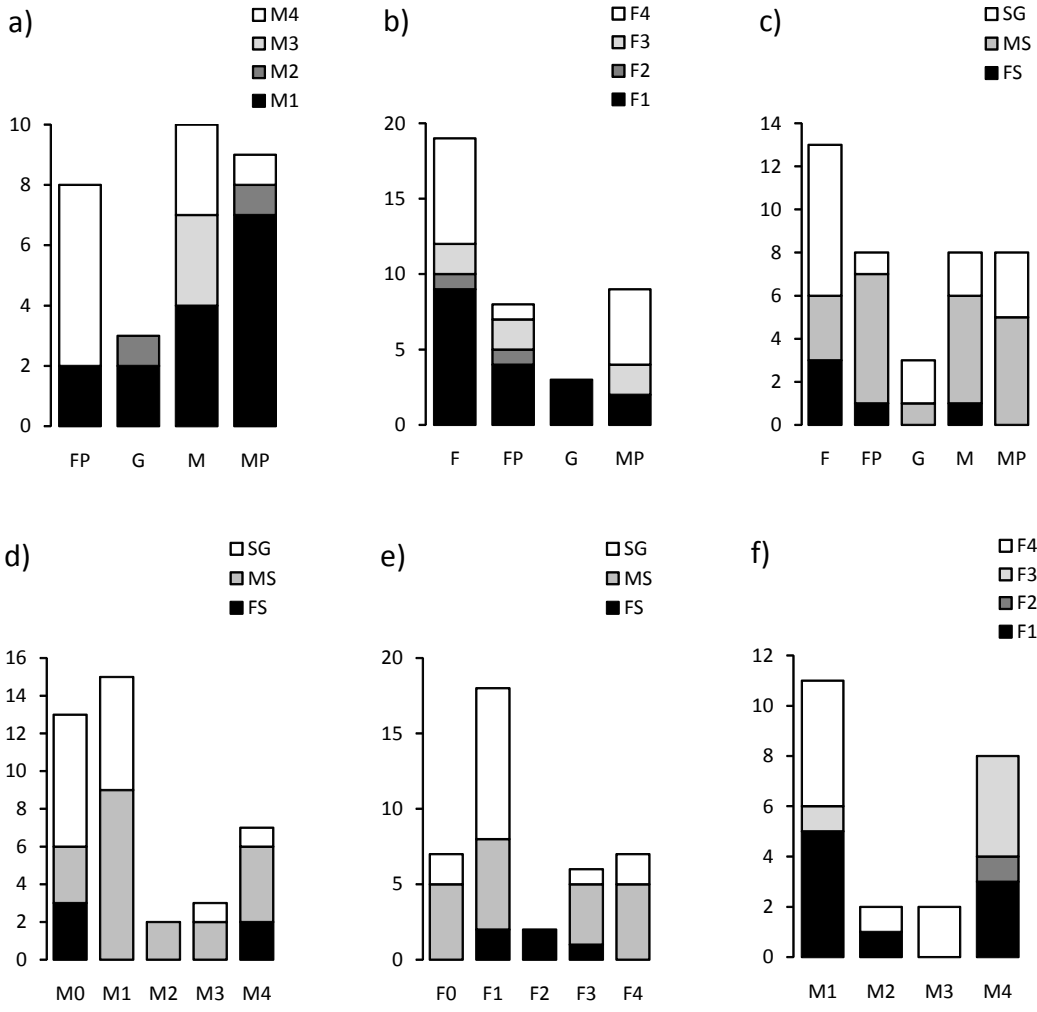
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734 **Figure 2**

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738 **Figure 3**

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