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1 **Effect of tree mixture on Collembola diversity and community structure in**
2 **temperate broadleaf and coniferous forests**

3

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15 **Keywords**

16 Soil fauna; life-forms, sessile oak (*Quercus petraea*); Scot pine (*Pinus sylvestris*); beech (*Fagus*
17 *sylvatica*); silver fir (*Abies alba*)

18

19

20 Abstract

21 Springtails (Collembola) are the most abundant arthropods in terrestrial ecosystems and, are
22 considered as key indicators of organic matter turnover and soil functioning. Mixture of tree
23 species are often regarded as a mean to improve tree growth, soil fertility and biodiversity.
24 We compared α -diversity, taxonomic β -diversity and functional diversity of Collembola of
25 mixed forest stands to pure stands in two forest sites, a mountain and a lowland site composed
26 of a coniferous and a deciduous species for effect on. We choose sessile oak (*Quercus*
27 *petraea*) and Scot pine (*Pinus sylvestris*) in lowland, and beech (*Fagus sylvatica*) and silver
28 fir (*Abies alba*) in mountain stands.

29 In total 41 species Collembola were identified. We showed that richness and abundance in
30 mixed stands were in between those found in the pure stands, with a more pronounced
31 response of the soil fauna in lowland compared to mountain. In the lowland, Shannon
32 diversity index followed the same pattern, and we found species richness from 6.3 to 11.7
33 mean species, and 4400 to 9000 ind.m⁻², dominated by epedaphic group. In the mountain, we
34 found species richness from 7 to 9 mean species, and 6600 to 103000 ind.m⁻², dominated by
35 euedaphic group.

36 Among the 12 soil and litter characteristics, many differs between sites and/or stand type. The
37 best predictors of the model explaining differences in mean Collembola were litter chemical
38 composition including the lignin to N ratio and C to N ratio. Soil characteristics, such as
39 humus index, organic layer thickness or pH, was also a good predictors for some life-forms
40 and one or the other site.

41 In addition, mixture modified Collembola community structure with some species found only
42 in the pure stands. Jaccard similarity index showed that mixture, even composed of different
43 tree species, homogenized Collembola community structure.

44 We conclude that mixture of tree species in temperate forests can locally increase Collembola
45 diversity, but this management should not be generalized to maximize the β -diversity.

46

47

48 Introduction

49 During the last decades, many studies investigated the effects of biodiversity on ecosystem
50 functioning (Chapin et al. 2000, Hooper et al. 2005). First studies focused on the effect of
51 small plants (grasses, legumes, herbs), on several taxa and ecosystems functions (Zak et al.
52 2003, Hooper et al. 2005, Milcu et al. 2006), and much lesser studies concerned forest
53 ecosystems. Studies on tree diversity were first conducted on mixed stand of few species (2-
54 3). Overall, mixed forest stands present stronger resistance to disturbances (Jactel and
55 Brockerhoff 2007, Vallet and Pérot 2011), and can have higher productivity depending on the
56 tree species in the mixtures, the site fertility or water stress (Vallet and Perot 2011, Condés et
57 al. 2013, Grossiord et al. 2014, Toigo et al. 2015, Lu et al. 2016, Toïgo et al. 2018). These
58 results lead to an increasing interest of forest managers for mixed forest stand, and mixture of
59 tree species is often proposed to favour mixture to adapt forestry management to climate
60 change and to the increasing needs for wood and for ecosystem services released by forest to
61 human societies (Gamfeldt et al. 2013).

62 Although, it is known that management practices, such as stand composition, affect
63 biodiversity of vascular plants (Scherer-Lorenzen et al. 2005, Barbier et al. 2008, Cavard et al.
64 2011), and on other taxa such as spiders, micro-organisms, earthworms, pathogens, and
65 insects (Ampoorter et al. 2020), much less is known on soil biota. This lack of knowledge
66 limits our understanding and the cascading effect of tree diversity on associated taxa, though
67 it would be useful for biodiversity conservation.

68 Soil fauna diversity and functioning is affected by forest management (Farska et al. 2014)
69 through both direct (litter quality) and indirect effects (microhabitats, environmental factors
70 such as pH, radiation, soil humidity). However, correlations between diversity of
71 aboveground and belowground organisms does not show a general pattern, both locally and
72 across larger biogeographical scales (Chapin et al. 2000, Hooper et al. 2000, Hooper et al.

73 2005). Some studies highlighted a positive response of α -diversity and abundance of soil
74 fauna to mixed tree species (Hansen and Coleman 1998, Cesarz et al. 2007, Jacob et al. 2009)
75 and others show weaker or opposite effects (Aubert et al. 2003, Scheu et al. 2003, Wardle et
76 al. 2006a). Increased tree diversity affects the richness and quality of the litter and thus the
77 resources dispatched throughout soil food webs (Hansen and Coleman 1998, Rusek 2001,
78 Cavard et al. 2011). Nevertheless, the difference between pure and mixed stands in terms of
79 soil fauna diversity and abundance seems idiosyncratic and strongly depends on the studied
80 group (Korboulewsky et al. 2016).

81 The major distinction can be made between deciduous and coniferous litter. Basically, the
82 higher the C/N or lignin/N ratios and the higher the polyphenol content, the lower the
83 abundance and activity of soil organisms (Harbone 1997, Hansen and Coleman 1998, Berg
84 and McClaugherty 2003, Hattenschwiler et al. 2005, Cesco et al. 2012). Litter traits also
85 include physical characteristics, and it has been shown that litter diversity in mixed stands
86 favours soil microhabitat heterogeneity (Hansen and Coleman, 1998). Different litter types
87 affect directly and indirectly soil community structure, through bottom-up and top-down
88 forces (Polis and Strong 1996, Chen and Wise 1999). Therefore, it can be thought that diverse
89 litter types would allow different decomposer species to coexist and share the resources
90 (Wardle et al. 2006b). In other word, it can be hypothesized that soil fauna diversity would be
91 increased under mixed forest stand composed of tree species with very different litter traits. In
92 temperate forests, this has been verified for earthworm communities, whose density and
93 diversity increased after broadleaf litter was added to coniferous stands (Tian et al. 1993,
94 Cesarz et al. 2007). For other taxa of soil organisms, no general pattern can be drawn
95 concerning mixture effects on their α -diversity and abundance. The absence of general pattern
96 can come from the lack of studies conducted on triplet (pure stands of two species and the
97 mixture), or from the species in the mixture which had similar litter traits.

98 We set up an experiment based on triplet composed of a deciduous and a coniferous
99 species on Collembola. Among soil fauna, Collembola represent the dominant group of soil
100 organisms with oribatid mites in terms of abundance. They are known to respond to changes
101 in soil conditions and vegetation cover (Hopkin 1997, Ponge et al. 2003). They affect litter
102 decomposition due to their trophic regimes, i.e. detritus fragmentation activities, grazing on
103 microflora (Verhoef and Brussaard 1990, Filser 2002), but also because they form nutrient
104 rich patches through fecal pellets deposition (Petersen 2000). Collembola species can be
105 subdivided into three life forms based on morphological, ecological and habitat criteria: (i)
106 epedaphic species live on top of the litter, present a high metabolic activity; (ii) euedaphic are
107 soil dwelling species and have a low metabolic activity; (iii) hemiedaphics includes species
108 with intermediate attributes (Gisin 1943, Rusek 1998). Collembola group is also often used as
109 a bioindicator to assess soil quality (ISO).

110 We studied the mixture effect on α -diversity, taxonomic β -diversity and functional
111 diversity on Collembola. We compared mixed forest stands to pure stands in two forest sites,
112 a mountain and a lowland site composed of a coniferous and a deciduous species. We tested
113 the following hypotheses: 1) Mixed stands host a higher Collembola diversity compared to the
114 pure stands; 2) The communities is different in mixed stands compared to the pure stands but
115 composed of species from both pure stands 3) The mixture effect is similar in both regions, as
116 the plant traits would be the major factor, 4) Litter chemistry is the major factor affecting
117 Collembola community.

118

119 2. Material and methods

120 2.1. Study sites and sampling design

121 We compare 33 plots for their Collembola diversity and community structures in two
122 regions, lowland and mountain selected for their contrasted altitudes (Fig. 1). Plots were
123 equally established on three stand types: pure deciduous, pure coniferous and mixed. Our
124 sampling design comprised for each stand type, 5 stands in the mountain region, and 6 in the
125 lowland, in general several kilometre apart and at least 100 m away from each other, so as to
126 avoid spatial autocorrelation. All plots were established on an even-aged mature forest (tree
127 age >50 yr) managed by the French National Forest Office (ONF).

128 The mountain site was located in the centre-west part of the French Alps (45° 09' –
129 45° 04' N, 5° 47' – 5° 53' E), in the Belledonne massif (Chamrousse, Isère). The climate is
130 alpine-continental: mean annual rainfall 1530 mm and mean annual temperature 8.9 C° at
131 1000 m. Soil type is a Cambisols (Hyperdystric)(IUSS Working Group WRB 2006), above
132 green schist (Joud 2006). Elevation of sampled stands ranges from 970 to 1400 m. All stands
133 were exposed NW except for two deciduous stands that were exposed S. Slopes ranged from
134 0 to 69 %. Pure stands were composed of either beech trees (*Fagus sylvatica* L.) for
135 deciduous stands or silver fir trees (*Abies alba* Mill.) with some inclusion of *Picea abies* L.
136 for coniferous stands. Mixed stands are composed of both beech and fir trees in a close
137 proportion, with some other trees of *Picea abies* L. (Suppl. 1).

138 Lowland site is located in the Orléans forest, centre France (47° 51' – 47° 47' N, 2° 24'
139 – 2° 31' E). The climate is temperate continental with an oceanic influence: mean annual
140 temperature is 11.1 °C and the mean annual rainfall is 729 mm (1970–2014 data from the
141 weather station at Nogent-sur-Vernisson, France). Altitudes of the sampled stands do not
142 exceed 150 m and slopes are less than 3%. Throughout the forest the soil is deep, relatively

143 poor and acidic with a sandy clay-loam texture, and is classified as a planosol (IUSS Working
144 Group WRB 2006). Superimposed layers of clay and sand lead to a temporary perched water
145 table in winter. Pure stands are composed of either oak trees (*Quercus petraea* Liebl.) for
146 deciduous stands or pine trees (*Pinus sylvestris* L.) for coniferous stands. Mixed stands are
147 composed of both oak and pine trees in a close proportion (Suppl. 1).

148 2.2. Data collection

149 Soil fauna sampling took place between the 17th and 24th of November 2013. Two
150 samples, one meter away from each other were collected in each stand using a soil corer
151 (4.7 cm diameter x 7 cm depth). Holorganic and organo-mineral horizons were collected, and
152 brought back to the laboratory within at most two days. Mesofauna was extracted using a
153 Berlese dry-funnel device for 8 days and stored in ethyl-alcohol (70%). Collembola were
154 identified using a light microscope (400x magnification). Identification to species level
155 followed several keys (Schlitt and Dunger 1994, Bretfeld 1999, Potapov 2001, Thibaud et al.
156 2004, Dunger and Schlitt 2011, Jordana 2012). Collembola of both fauna samples of each
157 stand were pooled for further data analyses, and expressed in m².

158 One soil sample (0-7 cm depth) was collected in each stand the same day as fauna
159 samples and immediately packed in waterproof bags in order to measure soil moisture.
160 Additional soil samples were collected, the A horizon (roughly 0–5 cm depth) in order to
161 measure soil parameters. Content of total C and N were determined by gas chromatography
162 using a CHN pyrolysis microanalyser (Flash 2000 Series, CHNS/O Analysers Thermo
163 Scientific). Additionally, we measured pH_{H2O} (soil-to-solvent ratio= 1/2.5) and cation
164 exchange capacity (Ciesielski and Sterckeman 1997, Baize 2000).

165 Humus forms were described, classified according to Brêthes et al. (1995) numerically
166 transformed into the Humus index according to Ponge et al. (2002). Furthermore, litter of

167 each stand were collected between September to November. For the lowland site, litterfall
168 collectors were installed (6 per sites) and spread over the plot to collect pine litter (September)
169 and oak litter (October-November). In the Mountain site, some branches were cut using a pole
170 pruners, then shaken to collect fallen senescent leaves and needles (October-November).
171 Litter samples were dried out during 48H at 35°C. The biochemical composition of litter was
172 assessed by stepwise chemical digestion in a Fiber analyzer (FIWE 6, VELP Scientifica, Italy)
173 (Van Soest 1994). This method quantifies four different biochemical fractions: cell solubles-
174 like substances, hemicellulose-like substances, cellulose-like substances, and lignin. These
175 compounds are further abbreviated in the text as: soluble; hemicellulose; cellulose and lignin,
176 respectively. Each type of litter in each stand was analysed separately. To obtain a average
177 value of litter in mixed stands, we used the mean values of coniferous and deciduous litters
178 from the mixed stands.

179 *2.3. Statistical analyses*

180 Differences between the three stand types in both regions in Collembola abundance
181 and richness, in total and per life-forms, and soils and litter characteristics were all tested at
182 the 5% probability level using two-way ANOVAs (site x stand type) and Tukey HSD post-
183 hoc tests. When necessary, logarithmic transformations were applied to ensure normal
184 distribution and homogeneity of variances (Shapiro-Wilk test; $P > 0.05$; Bartlett test; $P >$
185 0.05). When interactions between the two factors were observed, meaning that mixing tree
186 species affect differently the soil community, one-way ANOVA was performed on each sites
187 to test the stand effect. We further explored the effect of stand type and site on Shannon
188 diversity (H') (Shannon 1948, Shannon and Weaver 1963) and evenness (E_H , Pielou index)
189 (Pielou 1966).

$$190 H' = \sum p_i \cdot \ln(p_i)$$

191 p_i is the proportion of the I species, and is the ratio between the number of individual
192 of the species i by the total number of individual ($p_i = N_i/N$)

193 $E_H = H' / \ln(S)$

194 S is the species richness (total number of species).

195 Collembola community structure was defined as the assemblage of every species for each
196 plot. Differences on Collembola communities was assessed with the Jaccard similarity index
197 (J) (Jaccard 1912) and tested with non-parametric tests (Kruskal-Wallis and Mann-Whitney
198 tests) performed on Statgraphics Centurion version XVII. In addition, we performed between-
199 group multivariate analysis (BGA) on all species abundances for both sites to highlight
200 differences in Collembola community structures between stand types. The BGA was
201 performed using the stand type as single factor. Between-group analysis (BGA) is an
202 instrumental variable method that provides the best linear combination of variables so as to
203 maximize between-group variance. It enables testing the significance of a single qualitative
204 factor (Baty et al. 2006). Prior to analysis, species abundances were transformed using the
205 Hellinger transformation. BGA was performed using stand type as single factor. In order to
206 detect differences in community structure according to stand type, we performed BGA on
207 species abundances in the lowland (BGAl) and in the mountain (BGAm) sites separately,
208 using the type of stand as single factor. Significance of the single factors in the lowland BGA
209 (BGAl) and the mountain BGA (BGAm) were tested using Monte Carlo permutation test (999
210 permutations).

211 The influence of soil/environmental properties and litter quality on Collembola
212 communities was assessed using Partial Least Square Regression models (PLSR). The PLSR
213 is used to identify the variables responsible for the variance observed in abundance and
214 species richness. We tested abundance and species richness of all species, or by functional
215 groups (euedaphic, hemiedaphic, epedaphic). Eight alternative models were tested with two

216 dependent variables (abundance and richness of total Collembola and for each life-forms in
217 both sites) and 12 predictor variables (soil moisture, Humus index, carbon to nitrogen ratio
218 (C/N), CEC, $\text{pH}_{\text{H}_2\text{O}}$, thickness of the OL + OF soil layers, thickness of the OL soil layer,
219 Lignin to N ratio (Lignin:N) and litter biochemical quality (i.e. solubles, hemicellulose,
220 cellulose and lignin). PLSR combines predicting variables (x) in one or more independent
221 components to explicitly describe the dependent variable (y). Partial least square regression
222 models and the number of components were tested by cross-validation (Wold 1978); PLSR
223 model were considered significant when the cross-validated coefficient of determination (Q^2)
224 exceeds a critical value $Q^2_{\text{limit}} = 0.097$ (Eriksson et al. 2006). Variable Importance in the
225 Projection (VIP) was used to rank predicting variables (Eriksson et al. 2006). For each
226 predictor, the percentage of explained variance (EV) was estimated by the following equation:
227 $\text{EV} = (\text{VIP}^2/p) \times (\text{R}^2\text{Y}/100)$, with “p” corresponding to the number of predictors included in
228 the PLSR model and R^2Y correspond to the part of variance (in %) of dependent variables
229 explained by predictor variables (Tenenhaus 1998).

230 All statistical analyses were performed using packages car, vegan and ade4 of R
231 software (R Development Core Team, 2014). PLS-regression was performed using
232 TANAGRA 1.4.40 program (Rakotomalala 2005).

233

234 **3. Results**

235 3.1. Species identification

236 In total, 1490 individuals were identified out of 41 species (Suppl 2). In the lowland
237 site, among the 32 species identified in total, 12 species were present in all stand types, 13
238 were present only in one type of stand (deciduous: *Pygmarrhopalites pygmaeus*, *Isotoma*
239 *riparia*, *Protaphorura armata*, *Pseudosinella alba*, *Pseudachorutes parvulus* and *Smithurides*

240 *schoetti* ; coniferous: *Ceratophysella denticulata*, *Pseudisotoma sensibilis* and *Sminthurinus*
241 *aureus* ; mixed: *Ceratophysella armata*, *Entomobrya nivalis*, *Lepidocyrtus cyaneus* and
242 *Willemia intermedia*) and 7 species were absent in only one type of stand (absent in deciduous
243 stand: *Dicyrtomina ornata* and *Folsomia manolachei* ; absent in coniferous stand:
244 *Dicyrtomina minuta* and *Paratullbergia callipygos* ; absent in mixed stand: *Dicyrtoma fusca*,
245 *Neanura muscorum* and *Proisotoma minima*). In the mountain site, among the 27 species
246 identified, 9 species were present in all stand types, 14 were present in only one type of stand
247 (deciduous: *Ceratophysella denticulata*, *Folsomia penicula*, *Megalothorax minimus* and
248 *Tomocerina minuta*; coniferous: *Oligaphorura absoloni*, *Superodontella lamellifera*,
249 *Pseudosinella alba*, *Pseudanophorus binoculatus*, *Tomocerus minor* and *Xenylla tullbergi* ;
250 mixed: *Ceratophysella armata*, *Folsomia manolachei*, *Sminthurinus elegans* and *Sphaeridia*
251 *pumilis*) and 4 species were absent in only one type of stand (absent in deciduous stand:
252 *Pseudachorutes parvulus* ; absent in coniferous stand: *Kalaphorura burgmeisteri* and
253 *Neanura muscorum* absent in mixed stand: *Folsomia inocula*).

254

255 3.2. Effects on the species richness and abundance

256 For both site, we found the highest total richness and abundance in the deciduous
257 stands and intermediate in the mixture. We found no significant interaction between factors
258 site x stand, but an effect of the factor site (mountain vs lowland), and the stand type
259 (coniferous pure, mixed, deciduous pure) on total Collembola diversity and abundance
260 (Fig.2).

261 Overall for the site effect, we found no significant difference in total richness, but a
262 higher abundance in the mountain site, principally due to abundant two species (*Isotomiella*
263 *minor*, *Protaphorura armata*). For the stand effect in the lowland site, total Collembola
264 species richness and abundance were the lowest in coniferous pure stands with an average of

265 6.3 species and 4387 ind.m⁻², intermediate in mixed stands with 8.6 mean species and 6532
266 ind.m⁻², and the highest in deciduous pure stands with 11.7 mean species and 8998 ind.m⁻²
267 (Fig.2). In the mountain site, we observed the same pattern: 7 mean species and 6609 ind.m⁻²
268 in coniferous stands, 7.4 mean species and 10298 ind.m⁻² in mixed stands, and 9.0 mean
269 species and 16446 ind.m⁻² in deciduous stands.

270 Shannon diversity index (H') ranged from 1.37 to 2.04. The stand type was significant
271 only in the lowland site (Tab. 1) with H' the lowest in coniferous stands, intermediate in
272 mixed stands, and the highest in deciduous stands. Evenness was high for all stands as it
273 ranged from 0.79 to 0.84, and no difference was noticed. As this index is close to the maximal
274 value (which is 1), it means that a little number of species dominated the total number of
275 individual collected. Indeed, the two main species in samples represented from 40 to 93% of
276 the total Collembola per plots (mean per stand type: from 49 to 71%).

277 Both abundance and richness of Collembola life-forms showed some differences
278 between the two sites (Tab. 2). In the mountain site, the euedaphic group showed the higher
279 richness and abundance, while in the lowland it was the epedaphic group (Fig. 3). In the
280 lowland, there was a significant stand effect on richness and abundance on each life-form
281 groups, with richness and abundance in the following order: coniferous, mixture, deciduous
282 stands (Fig. 3). Though no significative in the mountain site, we found the same tendency.

283

284 3.3. Effects on the Collembola community

285 The BGA on the Collembola abundances explained 16% and 18% of the total variance
286 for the mountain (BGAm, Fig. 4a) and the lowland sites (BGAl, Fig. 4b), respectively. Axis 1
287 represented 62% and 70% and axis 2 37% and 29% of the extracted variance, respectively for
288 the mountain and the lowland sites. The simulated p-value obtained using Monte-Carlo
289 permutation test was not significant for the mountain site (p=0.204), but highly significant for

290 the lowland site ($p=0.004$). Nevertheless, for both sites, the three stand types were highly
291 discriminated with these two axes (Fig. 4).

292 Jaccard similarity index (J) is used to gauge the similarity and diversity of
293 communities. J were above 0.6 when comparing communities of the same site from different
294 stand types (coniferous vs deciduous, coniferous vs mixed, mixed vs deciduous). More
295 precisely, J ranged from 0.61 to 0.74 in the lowland, and from 0.63 to 0.65 in the mountain
296 site. On the contrary, J was very different when used to compare communities from the two
297 sites (lowland vs mountain) of the same type of stand (coniferous, mixed or deciduous).
298 Indeed, J was low for communities in the two coniferous type of stands (lowland vs mountain,
299 $J=0.35$), medium for the deciduous type of stands ($J=0.53$), and the highest between mixed
300 stands ($J=0.69$). It can be noted that J for mixed stands was also higher than J between sites of
301 coniferous vs deciduous stands (0.44 for mountain deciduous vs lowland coniferous, and 0.59
302 for mountain coniferous vs lowland deciduous).

303

304 3.4. Soil and litter characteristics

305 Among the 12 soil and litter characteristics, almost all responded significantly to the
306 factor site, or stand, or the interaction site*stand (Tab. 3c, Suppl 3 and 4). The two sites were
307 different (Site effect p -value <0.05 , and no interaction site*stand) according to four of the
308 tested characteristics (soil pH, OLOF and OL thickness, litter C/N). The effect of the stand
309 type on the soil pH was similar in both sites (p -value=0.039, and no interaction site*stand)
310 (Tab. 3c). On the contrary, we found an interaction site x stand for the humus index. Humus
311 index was higher in the Coniferous stands. (Tab. 3a and b). The significant interaction site
312 *stand is due to the fact that mixed stand humus index is either similar to the one of deciduous
313 stand (mountain site), or to the one of coniferous stand (lowland site). In addition and only in

314 the lowland, soil water content was the lowest in the deciduous stands compared to the two
315 others. Mixed stands presented intermediated values.

316 Some litter characteristics showed differences between stands, both in lowland and
317 mountain sites but in different ways. In the lowland, coniferous litter contained more lignin,
318 while deciduous litter contained more solubles and tanins. In the mountain, it was the
319 opposite: deciduous litter contained more lignin, while coniferous litter contained more tanins,
320 solubles and cellulose.

321 Among the 8 partial least square regressions tested, only 5 were significant ($Q^2 >$
322 0.097, models M1, M3, L1, L2, L4) (Tab. 4). For both sites, the model with abundance and
323 richness of all Collembola (i.e. model M1 and L1) as dependent variables was significant and
324 predictors explained 25.58% and 50.05% of the variance of dependent variables for mountain
325 and lowland site, respectively. In addition, the model with hemiedaphic life-form (model M3
326 and L3) as dependent variable (both abundance and richness) was significant only at the
327 mountain site with an explained variance of 24.72%. Conversely, the models with epedaphic
328 (M4 and L4) and euedaphic (M2 and L2) as dependent variables were significant only in the
329 lowland site, with 26.93% and 58.28% of the variance explained, respectively (Tab. 4). For
330 each significant models, litter biochemical chemistry (fiber content) including the lignin to N
331 ratio and C to N ratio were among the best predictors. The Humus index was a good predictor
332 for hemiedaphic and euedaphic species of mountain and lowland sites, respectively (3% and
333 11% of explained variance). Three predictors were specific to a site: the thickness of OLOF
334 soil layers and pH was an interesting predictor for epedaphic species only for lowland site
335 (6.3% and 2.7% of explained variance, respectively), and CEC for mountain (4.5% of
336 explained variance).

337

338

339 4. Discussion

340 Our study aimed to determine first whether there is a mixture effect on Collembola
341 communities by comparing coniferous-broadleaf mixed stands to pure coniferous and
342 broadleaf stands, second if the site (lowland vs mountain) affects this effect, and third which
343 are the environmental factors responsible.

344 Collembola richness, abundance of the whole community were affected by the stand
345 type, with the mixed stands showing intermediate richness and abundance compared to the
346 two pure stands. Shannon diversity index was significantly different only for the lowland site:
347 the index was the highest in the deciduous and the lowest in the coniferous, intermediate in
348 the mixture. Most studies showing a beneficial effect on soil fauna richness was in the case of
349 an admixture of broad-leaved species into coniferous stands, especially when beech was
350 introduced into a spruce stand (Korboulewsky et al. 2016). Our results corroborate these
351 observations as in the lowland, oak-pine mixture harbours a higher richness than in pure pine.
352 In the mountain site, we found the same tendency, though not statistically significant, for
353 beech and fir species. The lack of significance may be due to the beech litter that contained
354 more lignin, so was more recalcitrant to decomposition than fir. This low litter quality of both
355 species, may partly explain our results because a poor litter quality affects negatively soil
356 fauna abundance and diversity (Chauvat et al. 2011). Therefore, the potential benefit to soil
357 fauna of admixture with this broadleaf species was highly reduced in that case.

358 Likewise, most studies comparing pure to mixed litter or stands found an intermediate
359 diversity and abundance of Collembola in mixed stands or equal to one of the pure stands
360 (Scheu et al. 2003, Wardle et al. 2006b, Jacob et al. 2009, Cavard et al. 2011, Korboulewsky
361 et al. 2016). Nevertheless, and similar to our result in the mountain site, several studies did
362 not find any significant effect of litter mixture on diversity of Collembola (Scheu et al, 2003;
363 Jiang et al, 2013, Salamon et al, 2008). Concomitantly, few authors found a significant

364 positive response of microarthropods (i.e. Collembola and Oribatid mites) to increasing litter
365 diversity (Kaneko et Salamanca 1999). Therefore, the variety of responses and the resulting
366 absence of any general pattern of increasing litter diversity, suggest that soil organism
367 responses are idiosyncratic, so driven by litter species identity (Scherer-Lorenzen et al. 2007,
368 Korboulevsky et al. 2016).

369 Functional diversity responded in the same way as total species richness. Based on
370 Collembola life-forms, we showed that deciduous stands tend to have the highest, the
371 coniferous the lowest, and mixed stands intermediate abundances and richness. Stand effect
372 was though significant only in lowland site. It can be expected that the epedaphic group
373 would be the most responsible group to mixture, as this group is directly in contact with the
374 litter, but the greatest differences were observed for the euedaphic group (Fig. 3). This result
375 shows the multifactorial drivers of Collembola structure. Similarly, other authors highlighted
376 an influence of litter mixture on Collembola life-forms structure. For example, Chauvat et al.
377 (2011) reported that the mean species richness of both hemiedaphic and euedaphic groups
378 dramatically dropped in pure spruce stands compared to mixed spruce-birch-fir stands. They
379 added that euedaphic species (i.e. soil-dwelling species) were the most responsive to mixed
380 litter. Nevertheless, mixture effect highly depends on the taxa (Scheu et al 2003) and the tree
381 species studied (Korboulevsky et al. 2016).

382 Community structure was also affected by stand types (Fig 4). Nevertheless, our study
383 revealed that 28% and 38 % of species, in mountain and lowland respectively, were present in
384 all stand types, while few Collembola species were present only in one stand type and only 4
385 species were found only in mixed stands (not the same species between sites). This result is
386 also revealed by the Jaccard similarity index which was high (>0.63) between the three stand
387 types of the same site. This index can range from 0 to 1; the higher the index the more similar
388 are the communities. We also compared the Jaccard similarity index between the two sites.

389 The lowest values were found between the two coniferous stand types: fir versus pine
390 ($J=0.35$), and the highest between the two mixed stands: fir-beech versus pine-oak ($J=0.68$).
391 All other comparisons (coniferous-deciduous, mixed-coniferous...) presented intermediate
392 values. These results indicates that Collambola communities are more similar between two
393 mixed stands composed of different species than between two pure stands also composed of
394 different species. Our results echo the review of Korboulewsky et al. 2016 who found the
395 highest Jaccard similarity index for mixed stands with $J= 0.74$. Soil community structure
396 (taxonomic β -diversity) is known to be affected by tree species and stand composition, but its
397 homogenization with mixture is less intuitive.

398 Our results on Collembola communities suggests that (i) the distinction between
399 coniferous and deciduous plant trait is not enough to predict community structure, and (ii)
400 mixing tree species tend to homogenised Collembola communities (iii) pure stands host a few
401 species not found in the mixture. Therefore, on a management perspective, it is important to
402 maintain a diversity of type of stand to increase microarthropod biodiversity at a larger scale,
403 as it was observed on a meta-analysis conducted by Korboulewsky et al. 2016.

404

405 The effect on the community structure was mainly driven by the litter chemical
406 composition (lignin:N, cell solubles, hemicellulose, lignin) and soil C/N. Indeed, these
407 parameters were major predictors for community structures in both mountain and lowland
408 sites (Tab. 2). It is well known that the higher the lignin/N ratios, C/N or polyphenol content
409 in litter, the lower the abundance and activity of soil organisms, which leads to lower organic
410 matter decomposition rates (Harbone, 1997; Hansen and Coleman, 1998; Berg and
411 McLaugherty, 2003; Hattenschwiler et al., 2005; Cesco et al., 2012). It is interesting to point
412 out that although both sites showed almost the same patterns in terms of effect of mixture on
413 Collembola community, some factors explaining the variability were different. Indeed, the

414 soil pH and humus form were important predictors only in lowland site, and the CEC only in
415 the mountain site (Models M1 and L1 for abundance and richness of all Collembola).

416 Similarly, for Collembola structure based on life-forms, only some predictors were
417 common for both sites such as litter fibre quality. It appeared that pH and thickness of OLOF
418 soil layer were significant predictors only for lowland sites. Our results and these of other
419 studies support the fact that litter mixing affects soil fauna community if this creates new
420 microhabitats, provides new food resources, or if it significantly modifies soil and/or humus
421 characteristics (Korboulewsky et al., 2016). Litter traits, such as physical characteristics
422 which promoted microhabitat heterogeneity, may be important for decomposers community
423 (Hansen and Coleman 1998). The heterogeneity of architecture induced by plurispecific litter
424 could be an important explicative factor of soil organisms communities, especially for soil
425 biota inhabiting litter (Sulkava and Huhta 1998, Gartner and Cardon 2004). Therefore, abiotic
426 parameters and litter species identity are the main parameters driving soil Collembola
427 community structure (Scheu et al. 2003, Jacob et al. 2009, Jiang et al. 2013).

428

429 Overall, we showed that richness and abundance were intermediate in mixed
430 compared to the pure stands, with a more pronounced response of the soil fauna in lowland
431 compared to mountain. In addition, Collembola community structure responded to tree
432 mixture. Our results highlighted that total Collembola communities and their life-forms were
433 not only impacted by litter quality, but also by other factors specific to each studied sites.
434 Finally, we found that mixture tends to homogenize Collembola community. Our results
435 therefore confirm that mixed stands in temperate forests can increase Collembola diversity
436 locally, but mixture of tree species should not be generalized to preserve the taxa specific to
437 pure stands.

438

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440

441

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446

447 References

- 448 Ampoorter, E., L. Barbaro, H. Jactel, L. Baeten, J. Boberg, M. Carnol, B. Castagneyrol, Y. Charbonnier,
449 S. M. Dawud, M. Deconchat, P. De Smedt, H. De Wandeler, V. Guyot, S. Hattenschwiler, F. X.
450 Joly, J. Koricheva, H. Milligan, B. Muys, D. Nguyen, S. Ratcliffe, K. Raulund-Rasmussen, M.
451 Scherer-Lorenzen, F. van der Plas, J. Van Keer, K. Verheyen, L. Vesterdal, and E. Allan. 2020.
452 Tree diversity is key for promoting the diversity and abundance of forest-associated taxa in
453 Europe. *Oikos* **129**:133-146.
- 454 Aubert, M., M. Hedde, T. Decaëns, F. Bureau, P. Margerie, and D. Alard. 2003. Effects of tree canopy
455 composition on earthworms and other macro-invertebrates in beech forests of Upper
456 Normandy (France): The 7th international symposium on earthworm ecology · Cardiff · Wales
457 · 2002. *Pedobiologia* **47**:904-912.
- 458 Baize, B. 2000. Guide des analyses en pédologie. INRA Editions, Paris.
- 459 Barbier, S., F. Gosselin, and P. Balandier. 2008. Influence of tree species on understory vegetation
460 diversity and mechanisms involved - A critical review for temperate and boreal forests.
461 *Forest Ecology and Management* **254**:1-15.
- 462 Baty, F., M. Facompre, J. Wiegand, J. Schwager, and M. H. Brutsche. 2006. Analysis with respect to
463 instrumental variables for the exploration of microarray data structures. *Bmc Bioinformatics*
464 **7**.
- 465 Berg, B., and C. McClaugherty. 2003. Plant litter, decomposition, humus formation, carbon
466 sequestration, Berlin.
- 467 Bretfeld, G. 1999. Synopses on Palearctic Collembola, II Syphypleona. , Görlitz.
- 468 Brêthes, A., M. Bonneau, and B. Jabiol. 1995. RENECOFOR. Manuel de référence n°9 pour la
469 description des sols. ONF, Département des Recherches techniques, Fontainebleau.
- 470 Cavard, X., S. E. Macdonald, Y. Bergeron, and H. Y. H. Chen. 2011. Importance of mixedwoods for
471 biodiversity conservation: Evidence for understory plants, songbirds, soil fauna, and
472 ectomycorrhizae in northern forests. *Environmental Reviews* **19**:142-161.

473 Cesarz, S., N. Fahrenholz, S. Migge-Kleian, C. Platner, and M. Schaefer. 2007. Earthworm
474 communities in relation to tree diversity in a deciduous forest. *European Journal of Soil*
475 *Biology* **43**:S61-S67.

476 Cesco, S., T. Mimmo, G. Tonon, N. Tomasi, R. Pinton, R. Terzano, G. Neumann, L. Weisskopf, G.
477 Renella, L. Landi, and P. Nannipieri. 2012. Plant-borne flavonoids released into the
478 rhizosphere: impact on soil bio-activities related to plant nutrition. A review. *Biology and*
479 *Fertility of Soils* **48**:123-149.

480 Chapin, F. S. I., E. S. Zavaleta, V. T. Eviner, R. L. Naylor, P. M. Vitousek, H. L. Reynolds, D. U. Hooper, S.
481 Lavorel, O. E. Sala, S. E. Hobbie, M. C. Mack, and S. Diaz. 2000. Consequences of changing
482 biodiversity. *Nature* **405**:234-242.

483 Chauvat, M., D. Titsch, A. S. Zaytsev, and V. Wolters. 2011. Changes in soil faunal assemblages during
484 conversion from pure to mixed forest stands. *Forest Ecology and Management* **262**:317-324.

485 Chen, B., and D. H. Wise. 1999. Bottom-up limitation of predaceous arthropods in a detritus-based
486 terrestrial food web. *Ecology*. *Ecology* **80**:761-772.

487 Ciesielski, H., and T. Sterckeman. 1997. Determination of cation exchange capacity and exchangeable
488 cations in soils by means of cobalt hexamine trichloride. Effects of experimental conditions.
489 *Agronomie* **17**:1-7.

490 Condés, S., M. Del Rio, and H. Sterba. 2013. Mixing effect on volume growth of *Fagus sylvatica* and
491 *Pinus sylvestris* is modulated by stand density. *Forest Ecology and Management* **292**:86-95.

492 Dunger, W., and B. Schlitt. 2011. Synopses on Palaearctic Collembola Pt 6/1: Onychiuroidea:
493 Tullbergiidae, Görlitz.

494 Eriksson, L., E. Johansson, N. Kettaneh-Wold, J. Trygg, C. Wikström, and S. Wold. 2006. Multi- and
495 Megavariate Data Analysis: Advanced Applications and Method Extensions. Umetrics, Umeå.

496 Farska, J., K. Prejzkova, and J. Rusek. 2014. Management intensity affects traits of soil
497 microarthropod community in montane spruce forest. *Applied Soil Ecology* **75**:71-79.

498 Filser, J. 2002. The role of Collembola in carbon and nitrogen cycling in soil. *Pedobiologia* **46**:234-245.

499 Gamfeldt, L., T. Snäll, R. Bagchi, M. Jonsson, L. Gustafsson, P. Kjellander, M. C. Ruiz-Jaen, M. Froberg,
 500 J. Stendahl, C. D. Philipson, G. Mikusinski, E. Andersson, B. Westerlund, H. Andren, F.
 501 Moberg, J. Moen, and J. Bengtsson. 2013. Higher levels of multiple ecosystem services are
 502 found in forests with more tree species. *Nat Commun* **4**:1340.

503 Gartner, T. B., and Z. G. Cardon. 2004. Decomposition dynamics in mixed-species leaf litter. *Oikos*
 504 **104**:230-246.

505 Gisin, H. 1943. Ökologie und Lebengemeinschaften der Collembolen im schweizerischen
 506 Exkursionsgebiet Basels. *Revue Suisse de Zoologie*.

507 Grossiord, C., A. Granier, S. Ratcliffe, O. Bouriaud, H. Bruelheide, E. Chećko, D. I. Forrester, S. M.
 508 Dawud, L. Finér, M. Pollastrini, M. Scherer-Lorenzen, F. Valladares, D. Bonal, A. Gessler, and
 509 W. H. Schlesinger. 2014. Tree diversity does not always improve resistance of forest
 510 ecosystems to drought. *Proceedings of the National Academy of Sciences of the United*
 511 *States of America* **111**:14812-14815.

512 Hansen, R. A., and D. C. Coleman. 1998. Litter complexity and composition are determinants of the
 513 diversity and species composition of oribatid mites (Acari : Oribatida) in litterbags. *Applied*
 514 *Soil Ecology* **9**:17-23.

515 Harbone, J. B. 1997. Role of phenolic secondary metabolites in plants, and their degradation in
 516 nature. *Driven by nature: plant litter quality and decomposition*. Eds. G. Gadish & K.E. Giller,
 517 University Press, Cambridge.

518 Hattenschwiler, S., A. V. Tiunov, and S. Scheu. 2005. Biodiversity and litter decomposition
 519 interrestrial ecosystems. Pages 191-218 *Annual Review of Ecology Evolution and*
 520 *Systematics*. Annual Reviews, Palo Alto.

521 Hooper, D. U., D. E. Bignell, V. K. Brown, L. Brussaard, J. M. Dangerfield, D. H. Wall, D. A. Wardle, D. C.
 522 Coleman, K. E. Giller, P. Lavelle, W. H. Van der Putten, P. C. De Ruiter, J. Rusek, W. L. Silver, J.
 523 M. Tiedje, and V. Wolters. 2000. Interactions between aboveground and belowground

524 biodiversity in terrestrial ecosystems: Patterns, mechanisms, and feedbacks. *Bioscience*
525 **50**:1049-1061.

526 Hooper, D. U., F. S. Chapin, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D. M. Lodge, M.
527 Loreau, S. Naeem, B. Schmid, H. Setälä, A. J. Symstad, J. Vandermeer, and D. A. Wardle. 2005.
528 Effects of biodiversity on ecosystem functioning: A consensus of current knowledge.
529 *Ecological Monographs* **75**:3-35.

530 Hopkin, S. P. 1997. *Biology of the springtails*. Oxford Univ. Press., New York.

531 IUSS Working Group WRB. 2006. *World reference base for soil resources 2006*. FAO, Rome.

532 Jaccard, P. 1912. The distribution of the flora in the alpine zone. *New Phytologist* **11**:37-50.

533 Jacob, M., N. Weland, C. Platner, M. Schaefer, C. Leuschner, and F. M. Thomas. 2009. Nutrient
534 release from decomposing leaf litter of temperate deciduous forest trees along a gradient of
535 increasing tree species diversity. *Soil Biology & Biochemistry* **41**:2122-2130.

536 Jactel, H., and E. G. Brockerhoff. 2007. Tree diversity reduces herbivory by forest insects. *Ecology*
537 *Letters* **10**:835-848.

538 Jordana, R. 2012. *Synopses on Palaearctic Collembola Pt 7/1: Capbryinae & Entomobryini*, Görlitz.

539 Joud, D. 2006. *Guide pour identifier les stations forestières de Rhône-Alpes - Synthèse pour les Alpes*
540 *du Nord et les montagnes de l'Ain*.

541 Korboulewsky, N., G. Perez, and M. Chauvat. 2016. How tree diversity affects soil fauna diversity: A
542 review. *Soil Biology and Biochemistry* **94**:94-106.

543 Lu, H. C., G. M. J. Mohren, J. den Ouden, V. Goudiaby, and F. J. Sterck. 2016. Overyielding of
544 temperate mixed forests occurs in evergreen-deciduous but not in deciduous-deciduous
545 species mixtures over time in the Netherlands. *Forest Ecology and Management* **376**:321-
546 332.

547 Milcu, A., S. Partsch, R. Langel, and S. Scheu. 2006. The response of decomposers (earthworms,
548 springtails and microorganisms) to variations in species and functional group diversity of
549 plants. *Oikos* **112**:513-524.

550 Petersen, H. 2000. Collembola populations in an organic crop rotation: Population dynamics and
551 metabolism after conversion from clover-grass ley to spring barley. *Pedobiologia* **44**:502-515.

552 Pielou, E. C. 1966. The measurement of diversity in different types of biological collections. *Journal of*
553 *Theoretical Biology* **13**:131-144.

554 Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. *American*
555 *Naturalist* **147**:813-846.

556 Ponge, J. F., R. Chevalier, and P. Lousot. 2002. Humus index: An integrated tool for the assessment
557 of forest floor and topsoil properties. *Soil Science Society of America Journal* **66**:1996-2001.

558 Ponge, J. F., S. Gillet, F. Dubs, E. Fedoroff, L. Haese, J. P. Sousa, and P. Lavelle. 2003. Collembolan
559 communities as bioindicators of land use intensification. *Soil Biology and Biochemistry*
560 **35**:813-826.

561 Potapov, M. 2001. Synopses of Palearctic Collembola, III Isotomidae, Görlitz.

562 R.Development.Core.Team. 2014. R : A language and environment for statistical computing. R
563 Foundation for Statistical Computing, Vienna.

564 Rakotomalala, R. 2005. TANAGRA : un logiciel gratuit pour l'enseignement et la recherche, in Actes
565 de EGC'2005, RNTI-E-3, vol. 2.

566 Rusek, J. 1998. Biodiversity of Collembola and their functional role in the ecosystem. *Biodiversity and*
567 *Conservation* **7**:1207-1219.

568 Rusek, J. 2001. Microhabitats of Collembola (Insecta : Entognatha) in beech and spruce forests and
569 their influence on biodiversity. *European Journal of Soil Biology* **37**:237-244.

570 Scherer-Lorenzen, M., J. L. Bonilla, and C. Potvin. 2007. Tree species richness affects litter production
571 and decomposition rates in a tropical biodiversity experiment. *Oikos* **116**:2108-2124.

572 Scherer-Lorenzen, M., C. Körner, and E.-D. Schulze. 2005. *Forest Diversity and Function: Temperate*
573 *and Boreal Systems*. Springer-Verlag, Berlin Heidelberg.

574 Scheu, S., D. Albers, J. Alpehi, R. Buryan, U. Klages, S. Migge, C. Platner, and J. A. Salamon. 2003. The
575 soil fauna community in pure and mixed stands of beech and spruce of different age: trophic
576 structure and structuring forces. *Oikos* **101**:225-238.

577 Schlitt, B., and W. Dunger. 1994. Synopses on Palaearctic Collembola Pt 1: Introduction,
578 Tullbergiinae, Görlitz.

579 Shannon, C. E. 1948. A Mathematical Theory of Communication. The Bell System Technical Journal
580 **27**:379-423, 623-656.

581 Shannon, C. E., and W. Weaver. 1963. The Mathematical Theory of Communication. University of
582 Illinois Press.

583 Sulkava, P., and V. Huhta. 1998. Habitat patchiness affects decomposition and faunal diversity: a
584 microcosm experiment on forest floor. *Oecologia* **116**:390-396.

585 Tenenhaus, M. 1998. La Régression PLS: Théorie et Pratique. Technip, Paris.

586 Thibaud, J. M., H. J. Schultz, and M. M. da Gamma. 2004. Synopses on Palearctic Collembola, IV.
587 Hypogastruridae, Görlitz.

588 Tian, G., L. Brussaard, and B. T. Kang. 1993. Biological effects of plant residues with contrasting
589 chemical - compositions under humid tropical conditions - effects on soil fauna. *Soil Biology*
590 *& Biochemistry* **25**:731-737.

591 Toigo, M., T. Perot, B. Courbaud, B. Castagnyrol, J. C. Gégout, F. Longuetaud, H. Jactel, and P. Vallet.
592 2018. Difference in shade tolerance drives the mixture effect on oak productivity. *Journal of*
593 *Ecology* **106**:1073-1082.

594 Toigo, M., P. Vallet, T. Perot, J. D. Bontemps, C. Piedallu, and B. Courbaud. 2015. Overyielding in
595 mixed forests decreases with site productivity. *Journal of Ecology* **103**:502-512.

596 Vallet, P., and T. Perot. 2011. Silver fir stand productivity is enhanced when mixed with Norway
597 spruce: evidence based on large-scale inventory data and a generic modelling approach.
598 *Journal of Vegetation Science* **22**:932-942.

599 Vallet, P., and T. Pérot. 2011. Silver fir stand productivity is enhanced when mixed with Norway
600 spruce: evidence based on large-scale inventory data and a generic modelling approach.
601 *Journal of Vegetation Science* **22**:932-942.

602 Van Soest, P. J. 1994. *Nutritional ecology of the ruminant*. Second edition. Cornell University Press,
603 Ithaca.

604 Verhoef, H. A., and L. Brussaard. 1990. Decomposition and nitrogen mineralization in natural and
605 agroecosystems - the contribution of soil animals. *Biogeochemistry* **11**:175-211.

606 Wardle, D. A., G. W. Yeates, G. M. Barker, and K. I. Bonner. 2006a. The influence of plant litter
607 diversity on decomposer abundance and diversity. *Soil Biology and Biochemistry* **38**:1052-
608 1062.

609 Wardle, D. A., G. W. Yeates, G. M. Barker, and K. I. Bonner. 2006b. The influence of plant litter
610 diversity on decomposer abundance and diversity. *Soil Biology & Biochemistry* **38**:1052-1062.

611 Wold, S. 1978. Cross-Validatory Estimation of the Number of Components in Factor and Principal
612 Components Models. *Technometrics* **20**:397-405.

613 Zak, D. R., W. E. Holmes, D. C. White, D. P. Aaron, and D. Tilman. 2003. Plant Diversity, Soil Microbial
614 Communities, and Ecosystem Function: Are There Any Links? *Ecology* **84**:2042-2050.

615

616

1 Figure 1: Location of the two studied sites and the forest plots for each. Plots were established on adult
2 stands on forests managed by the French Forest National Office.

3

4 Figure 2: (a) Mean species richness and (b) mean abundances of Collembola in the two sites
5 (mountain and lowland) and three stand types (C: coniferous pure, M: mixed, D: deciduous pure).
6 Error bars represent standard deviation. Results of two-way ANOVA were resumed above the figure.
7 Results of post-hoc tests are represented by letters in the figure for site effect (different letters indicate
8 significant differences), and in the table for stand effect when there are no interaction.

9

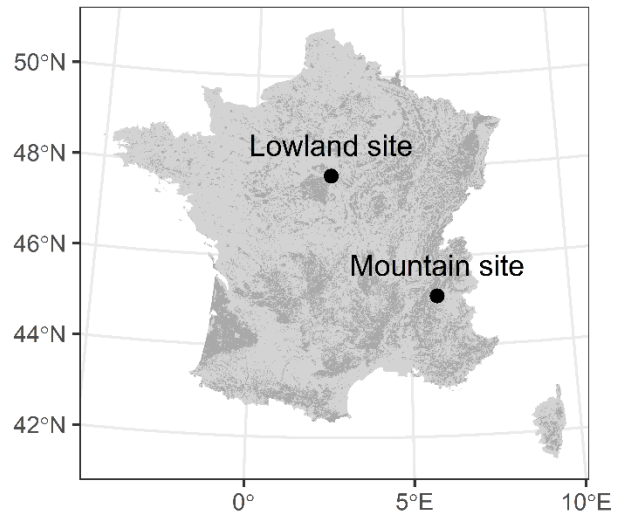
10 Figure 3: (a) Mean species richness and (b) mean abundances of each Collembola life-forms in the
11 two sites (mountain and lowland) and three stand types (C: coniferous pure, M: mixed, D:
12 deciduous pure). Error bars represent standard deviation. Results of two-way ANOVA were
13 resumed above the figure. Results of post-hoc tests are represented by letters in the figure for
14 differences between life-forms (different letter indicate significant differences), and in the
15 table for stand effect when there were no interaction.

16

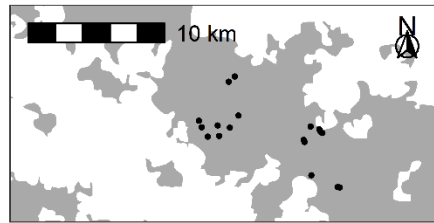
17 Figure 4: Between-group analysis (BGA) based on PCA of Collembola communities of both regions,
18 (a) in mountain (BGAm) and (b) lowland site (BGA1), with the factor stand type as explanatory
19 variable. BGA was performed on all species abundances for both sites. Each small dot represents the
20 centroid of a plot (5 plots for the Mountain and 6 plots for the Lowland), and each bigger dot the
21 centroids of a stand type (Mixed, Pure deciduous, Pure coniferous).

22 Figure 1

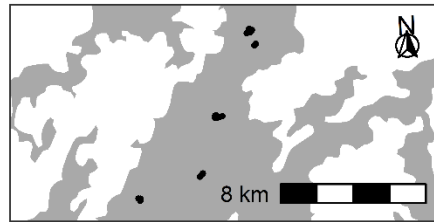
23



Lowland site



Mountain site



24

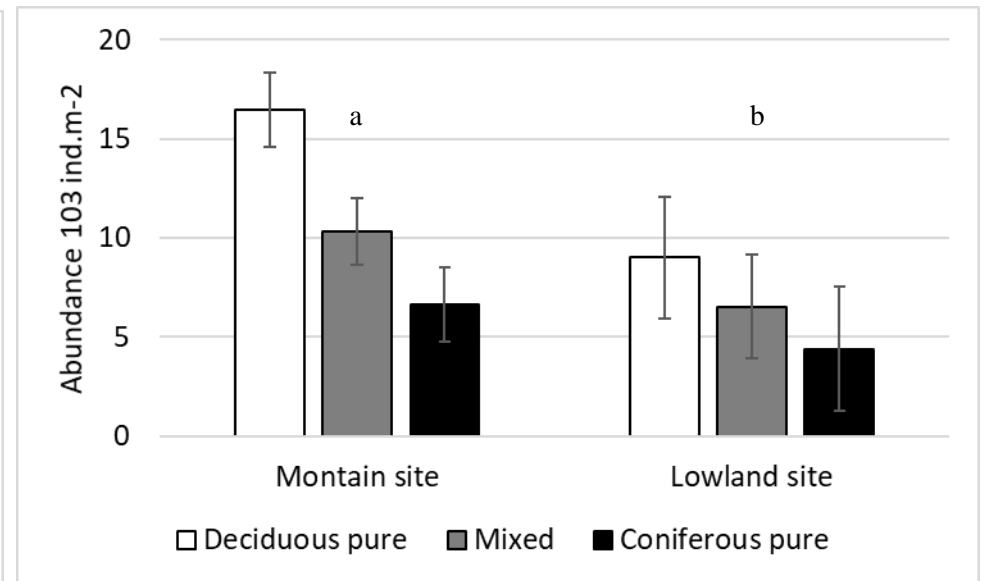
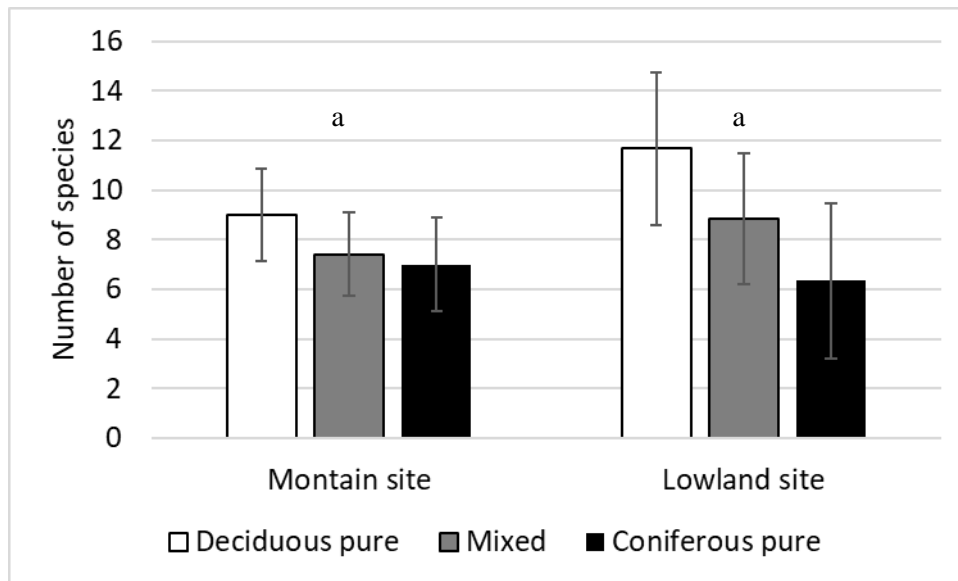
25 Figure 2

26

	d f	F	p-value
site	1	10,72	0,2
stand type	2	37,20	0,008** D ≥ M ≥ C
site * stand type	2	7,75	0,31

	d f	F	p-value
site	1	4,76	0,038*
stand type	2	4,18	0,026* D ≥ M ≥ C
site * stand type	2	0,57	0,57

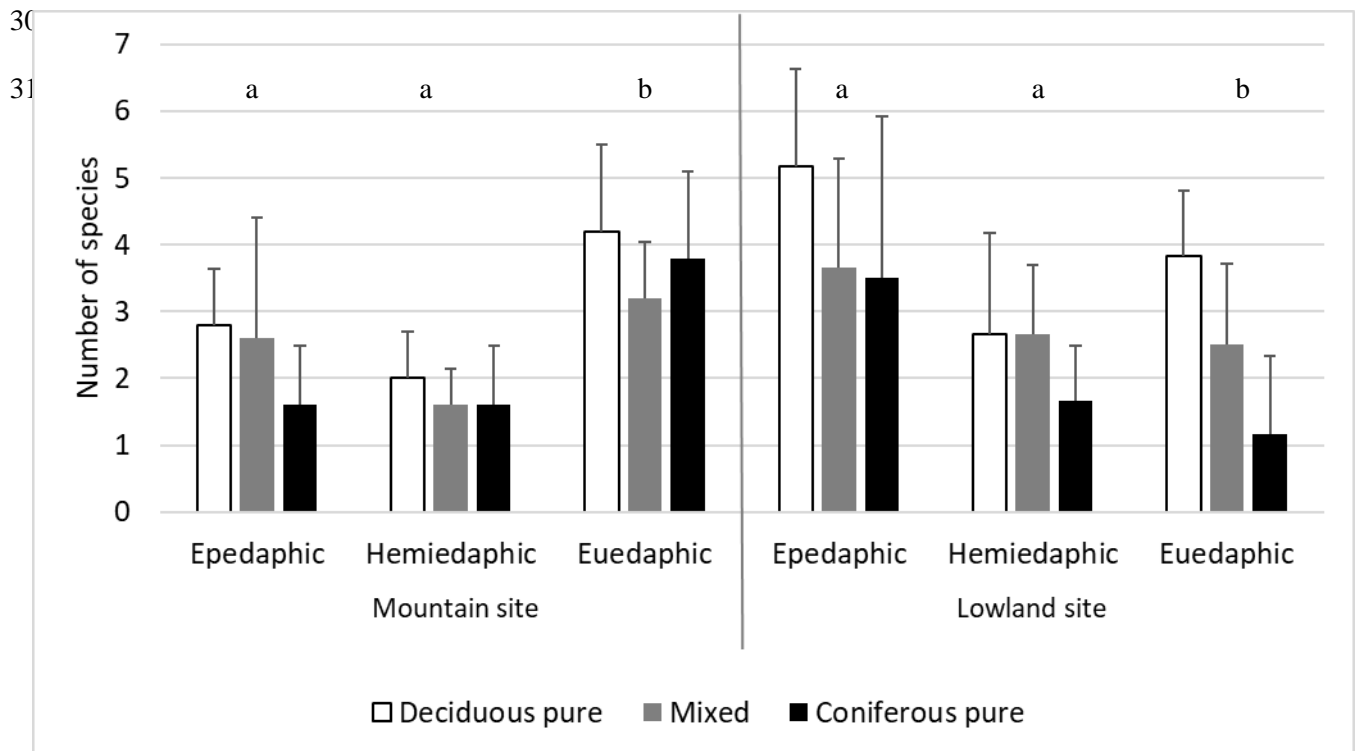
27



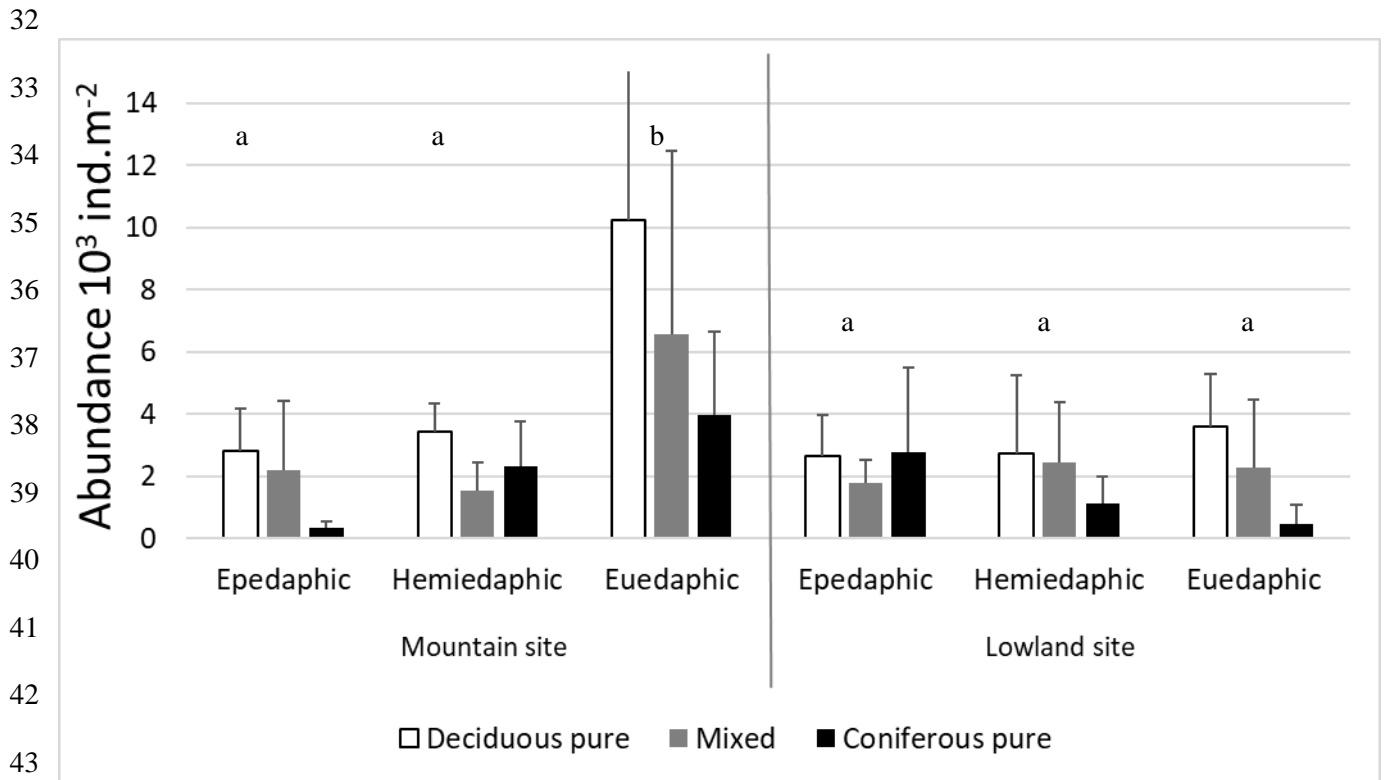
28 Figure 3

29

(a) Species richness	Mountain			Lowland		
	df	F	p-value	F	p-value	
stand type	1	1,6	0,22	6,9	0,0024**	D ≥ M ≥ C
Functional group	2	13,54	<0.0001***	8,41	0,0008***	
stand type* fct group	2	0,74	0,57	0,84	0,50	



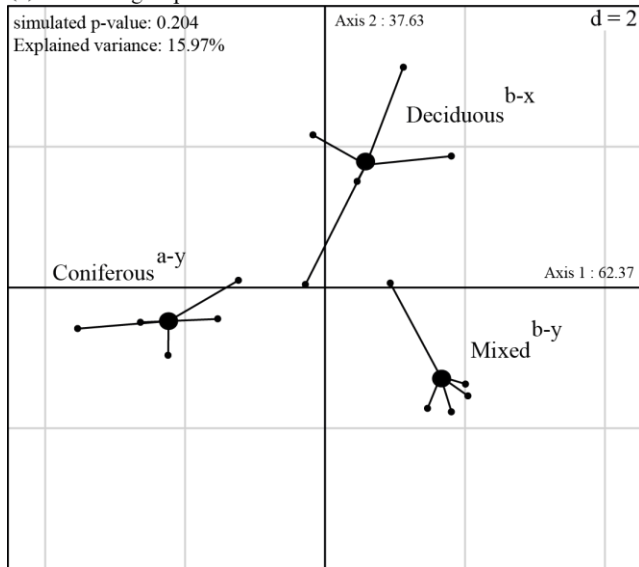
(b) Abundance	Mountain			Lowland		
	df	F	p-value	F	p-value	
stand type	1	2,02	0,15	3,37	0,04*	$D \geq M \geq C$
Functional group	2	5,76	0,007*	0,17	0,84	
stand type* fct group	2	0,51	0,72	1,62	0,18	



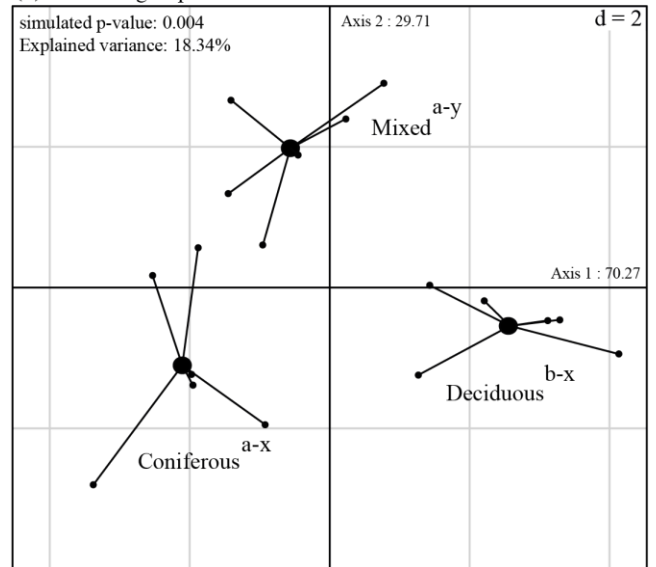
47 Figure 4

48

(a) Between group PCA - Mountain site



(b) Between group PCA - Lowland site



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53

54 Table 1. Shannon diversity index (H') and evenness index (E_H) for the different sites and stands types.
 55 Statistical differences between stand type of a same site occurs when p -value < 0.05 (Kruskal-Wallis
 56 test, $n=6$ in the Lowland and 5 in the Mountain site), and when significant different groups are
 57 indicated by a different letter.

58

59

	Deciduous	Mixed	Coniferous	<i>p</i> -value
Lowland				
H'	2.04a	1.77ab	1.37b	0.03
E_H	0.84	0.83	0.82	0.93
Mountain				
H'	1.63	1.57	1.53	0.93
E_H	0.74	0.79	0.79	0.88

60

61 Table 2: Results of two-way ANOVA on the species richness (a) and mean abundances (b) of each
 62 Collembola life-forms in the two sites (mountain and lowland).

63

	df	Epedaphic		Hemiedaphic		Euedaphic	
		F	p-value	F	p-value	F	p-value
(a) Species richness							
site	1	9,58	0,0045**	3,01	0,09	9,45	0,0048*
stand type	2	2,1	0,14	1,45	0,25	5,31	0,0114*
site * stand type	2	0,44	0,65	0,71	0,50	3,1	0,06
(b) Abundance							
site	1	1,17	0,29	0,31	0,58	6,96	0,0137*
stand type	2	1,35	0,28	2,27	0,12	2,21	0,13
site * stand type	2	2,4	0,11	1,31	0,29	0,27	0,77

64

65 Table 3: Soil and litter characteristics (mean \pm SD) of three stand types (coniferous pure, deciduous pure and mixed) in two different sites (mountain and
66 lowland). Figures and statistical results for the lowland site (I), for the mountain site (II). Results of two-way ANOVA testing the effect of the factors site and
67 stand type (c). Significant statistical results are indicated in the tables with different letters. Means litter chemical characteristics of mixed stands were
68 calculated as the mean (\pm SD) of coniferous and deciduous values from litter analyzed in mixed stands.

69

(I)	Lowland										
	Deciduous			Mixed			Coniferous			<i>p-value</i>	
Water content (% DW)	32.2	\pm 10.9	a	50.3	\pm 8.6	b	53.6	\pm 10.3	b	<i>0.0046</i>	**
Humus index	5.8	\pm 1.0	a	7.2	\pm 0.4	b	8.0	\pm 0.0	b	<i>0.0001</i>	***
pH _{H2O}	4.1	\pm 0.1	b	4.0	\pm 0.2	ab	3.8	\pm 0.2	a	<i>0.037</i>	*
OLOF thickness (mm)	13.7	\pm 5.1	a	23.0	\pm 10.3	a	15.4	\pm 18.2	a	<i>0.4</i>	<i>ns</i>
OL thickness (mm)	12.1	\pm 4.3	a	14.2	\pm 5.7	a	9.6	\pm 6.9	a	<i>0.4</i>	<i>ns</i>
Soil N (% DW)	0.50	\pm 0.27	a	0.36	\pm 0.28	a	0.56	\pm 0.27	a	<i>0.31</i>	<i>ns</i>
Soil C/N	15.6	\pm 5.7	a	19.7	\pm 8.0	a	14.6	\pm 5.9	a	<i>0.24</i>	<i>ns</i>
Soil OM (%)	11.0	\pm 3.1	a	9.0	\pm 3.3	a	11.8	\pm 2.9	a	<i>0.17</i>	<i>ns</i>
Soil CEC (meq/100 g)	8.5	\pm 5.1	a	8.7	\pm 7.1	a	15.1	\pm 8.8	a	<i>0.11</i>	<i>ns</i>
Litter C/N	48.4	\pm 0.9	a	72.4	\pm 27.0	a	87.9	\pm 7.7	a	<i>0.11</i>	<i>ns</i>

Litter Cellulose (%)	18.6	±0.5	a	22.7	±4.0	a	25.1	±0.1	a	0.07	ns
Litter Hemi-cellulose (%)	15.1	±0.03	a	14.5	±2.1	a	13.2	±0.05	a	0.38	ns
Litter Lignin	15.9	±0.2	a	15.1	±0.4	b	18.8	±0.1	c	<0.0001	***
Litter phenols	21.9	±1.7	a	19.3	±1.2	a	6.3	±1.2	a	0.06	ns
Litter Solubles	50.4	±0.4	c	47.6	±1.7	b	42.9	±0.2	a	0.0002	***
Litter Tanins	8.1	±0.9	b	9.6	±2.0	ab	4.6	±1.2	a	0.0069	**

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71

(II)	Montain										
	Deciduous			Mixed			Coniferous			<i>p-value</i>	
Water content (% DW)	31.3	±5.5	a	37.2	±14.5	a	31.9	±8.5	a	0.6	ns
Humus index	2.8	±0.4	a	2.0	±0.7	a	4.2	±0.8	b	0.0009	***
pH _{H2O}	4.7	±0.3	a	4.5	±0.4	a	4.3	±0.4	a	0.35	ns
OLOF thickness (mm)	2.7	±1.0	a	1.5	±0.7	a	2.3	±0.8	a	0.098	ns
OL thickness (mm)	2.7	±1.0	b	1.4	±0.7	ab	1.5	±0.5	a	0.03	*
Litter C/N	48.4	±4.1	a	48.1	±4.2	a	49.1	±2.8	a	0.9	ns
Litter Cellulose (%)	23.6	±0.4	b	20.4	±2.2	a	18.3	±0.3	a	0.01	**

Litter Hemi-cellulose (%)	15.4	±0.6	a	12.2	±3.6	a	11.4	±2.1	a	0.2	ns
Litter Lignin	27.0	±0.3	b	22.6	±4.3	b	15.3	±1.8	a	0.0058	*
Litter phenols	10.4	±1.1	a	29.2	±20.2	ab	45.8	±0.6	b	0.052	ns
Litter Solubles	33.9	±1.3	a	44.8	±10.0	ab	54.9	±0.2	b	0.022	*
Litter Tanins	8.5	±0.4	a	23.7	±15.4	ab	37.0	±0.8	b	0.041	*

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(c)	Overall model		Site		Stand		Site * Stand	
	F-value	<i>p-value</i>	F-value	<i>p-value</i>	F-value	<i>p-value</i>	F-value	<i>p-value</i>
Water content (% DW)	5.60	0.0011	11.51	0.0021	4.72	0.0175	2.88	0.073
Humus index	75.56	<0.0001	313.72	<0.0001	24.19	<0.0001	7.63	0.0024
pH _{H2O}	7.70	0.0001	31.19	<0.0001	3.66	0.0392	0.03	0.97
OLOF thickness (mm)	5.06	0.0021	21.90	0.0001	0.59	0.56	0.97	0.39
OL thickness (mm)	9.76	<0.0001	45.02	<0.0001	0.86	0.43	0.88	0.42
Litter C/N	4.81	0.0057	10.92	0.0039	2.82	0.086	2.67	0.096
Litter Cellulose (%)	4.21	0.0104	1.70	0.2090	0.09	0.91	9.12	0.0018

Litter Hemi-cellulose (%)	1.82	<i>0.16</i>	1.64	<i>0.22</i>	2.52	<i>0.11</i>	0.69	<i>0.51</i>
Litter Lignin	15.49	<0.0001	24.52	0.0001	5.34	<i>0.0151</i>	16.22	0.0001
Litter phenols	4.47	0.0080	6.00	0.0248	1.24	<i>0.3124</i>	6.97	0.0057
Litter Solubles	5.54	0.0029	1.09	<i>0.31</i>	2.45	<i>0.11</i>	10.73	0.0009
Litter Tanins	7.96	<i>0.0004</i>	19.73	<i>0.0003</i>	3.71	<i>0.0448</i>	5.76	<i>0.0116</i>

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76 Table 4 : (a) General model parameters of Partial Least Square (PLS) regression with number of significant PLS-components. R²Y correspond to the part of
 77 variance (in %) of dependent variables explained by predictor variables, and Q² is the coefficient of determination which indicates that the model is significant
 78 when it exceeds a critical value of 0.097. (b) Partial Least Square (PLS) regression results showing the explained variance (EV, %) of different variables in
 79 each model projection. Indication of the Variable Importance in the Projection (VIP) was used to rank predicting variables.

80

81 (a)

N° Model	Dependants variables	PLS-components	R ² Y(%)	Q ² (%)
Mountain site				
M1	Abd & SP all collembola	1	25.58	0.16
M2	Abd & SP euedaphic	ns	ns	Ns
M3	Abd & SP hemiedaphic	1	24.72	0.12
M4	Abd & SP epedaphic	ns	ns	ns
Lowland site				
L1	Abd & SP all collembola	1	50.05	0.42
L2	Abd & SP euedaphic	1	58.28	0.42
L3	Abd & SP hemiedaphic	ns		
L4	Abd & SP epedaphic	1	12.98	0.68

2 13.95 26.93

82 (b)

N° Model		WC	Humus	pH	OLOF	OL	C/N	CEC	Lignin/N	SOI	HEM	CEL	LIC
Mountain site													
M1	EV (%) ^{VIP}	-	-	-	-	-	2.2 ^{-1.0}	4.5 ^{-1.5}	4.3 ^{+1.4}	2.6 ^{-1.1}	2.4 ^{+1.1}	2.6 ^{+1.1}	2.6 ^{+1.1}
M3	EV (%) ^{VIP}	2.9 ^{-1.2}	-	-	-	-	4.1 ^{-1.4}	-	2.7 ^{+1.2}	2.6 ^{-1.1}	2.5 ^{+1.1}	2.6 ^{+1.1}	2.5 ^{+1.1}
Lowland site													
L1	EV (%) ^{VIP}	6.5 ^{-1.25}	6.1 ^{+1.2}	-	-	-	-	-	4.6 ^{-1.0}	7.0 ^{+1.3}	4.8 ^{+1.1}	7.3 ^{-1.3}	5.7 ^{-1.2}
L2	EV (%) ^{VIP}	-	-	2.7 ^{+1.1}	6.3 ⁻⁷	-	3.0 ^{-1.2}	-	2.3 ^{-1.0}	-	2.3 ^{-1.0}	-	-
L4	EV (%) ^{VIP}	-	10.8 ^{-1.5}	-	-	-	-	-	-	10.3 ^{+1.5}	7.4 ^{+1.2}	10.7 ^{-1.5}	8.6 ^{-1.3}

83

84

85 Variable Importance for the Projection (VIP) added in subscript to EV. Trend of standardized Regression Parameters (by target variable) was represented (+)

86 or (-). “-”: parameter included in the model but not significant, i.e. VIP < 1. EV: explained variance; WC: water content; CEC: cation exchange capacity;

87 OLOF: OL+OF soil layers thickness; OL soil layer thickness; SOL.: cell solubles; HEM.: hemicellulose; CEL.: cellulose; LIC.: lignin