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► **To cite this version:**

Nathalie Korboulewsky, C. Heiniger, S. de Danieli, Jean-Jacques Brun. Effect of tree mixture on Collembola diversity and community structure in temperate broadleaf and coniferous forests. *Forest Ecology and Management*, 2021, 482, pp.1-42. 10.1016/j.foreco.2020.118876 . hal-03449716

**HAL Id: hal-03449716**

**<https://hal.inrae.fr/hal-03449716>**

Submitted on 2 Jan 2023

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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  $\alpha$ -diversity, taxonomic  $\beta$ -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<sup>-2</sup>, dominated by epedaphic group. In the mountain, we  
34 found species richness from 7 to 9 mean species, and 6600 to 103000 ind.m<sup>-2</sup>, 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  $\beta$ -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  $\alpha$ -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  $\alpha$ -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  $\alpha$ -diversity, taxonomic  $\beta$ -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 17<sup>th</sup> and 24<sup>th</sup> 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 m<sup>2</sup>.

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<sub>H2O</sub> (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  $\text{R}^2\text{Y}$  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<sup>-2</sup>, intermediate in mixed stands with 8.6 mean species and 6532  
266 ind.m<sup>-2</sup>, and the highest in deciduous pure stands with 11.7 mean species and 8998 ind.m<sup>-2</sup>  
267 (Fig.2). In the mountain site, we observed the same pattern: 7 mean species and 6609 ind.m<sup>-2</sup>  
268 in coniferous stands, 7.4 mean species and 10298 ind.m<sup>-2</sup> in mixed stands, and 9.0 mean  
269 species and 16446 ind.m<sup>-2</sup> 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  $\beta$ -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

442 **Acknowledgments**

443 This study was supported by French Ministry in charge of environmental issues (Ministère de  
444 l'Ecologie, du Développement Durable et de l'Energie, programme 113 action 8 – n°2100858785). We  
445 thank Victoria Moore for reviewing the English.

446

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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

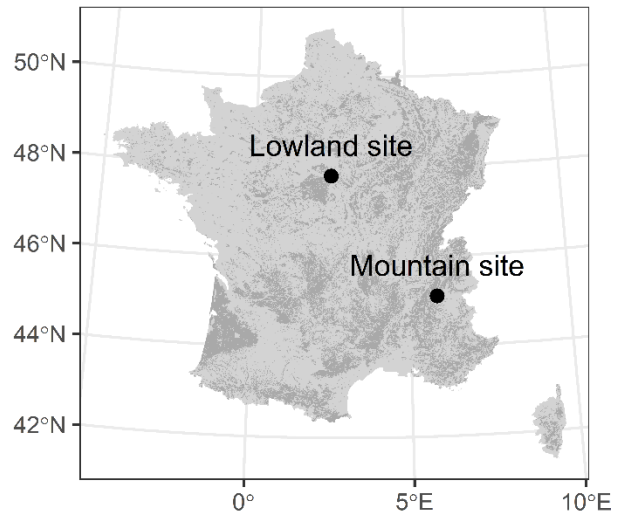
10 Figure 3: (a) Mean species richness and (b) mean abundances of each Collembola life-forms in the  
11 two sites (mountain and lowland) and three stand types (C: coniferous pure, M: mixed, D:  
12 deciduous pure). Error bars represent standard deviation. Results of two-way ANOVA were  
13 resumed above 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

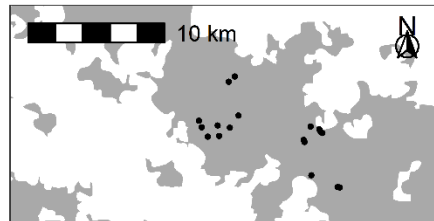
17 Figure 4: Between-group analysis (BGA) based on PCA of Collembola communities of both regions,  
18 (a) in mountain (BGAm) and (b) lowland site (BGAl), with the factor stand type as explanatory  
19 variable. BGA was performed on all species abundances for both sites. Each small dot represents the  
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

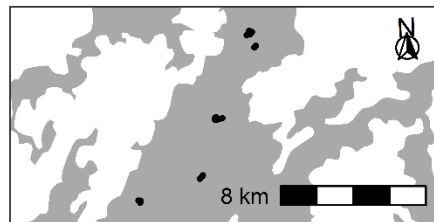
23



Lowland site



Mountain site



24

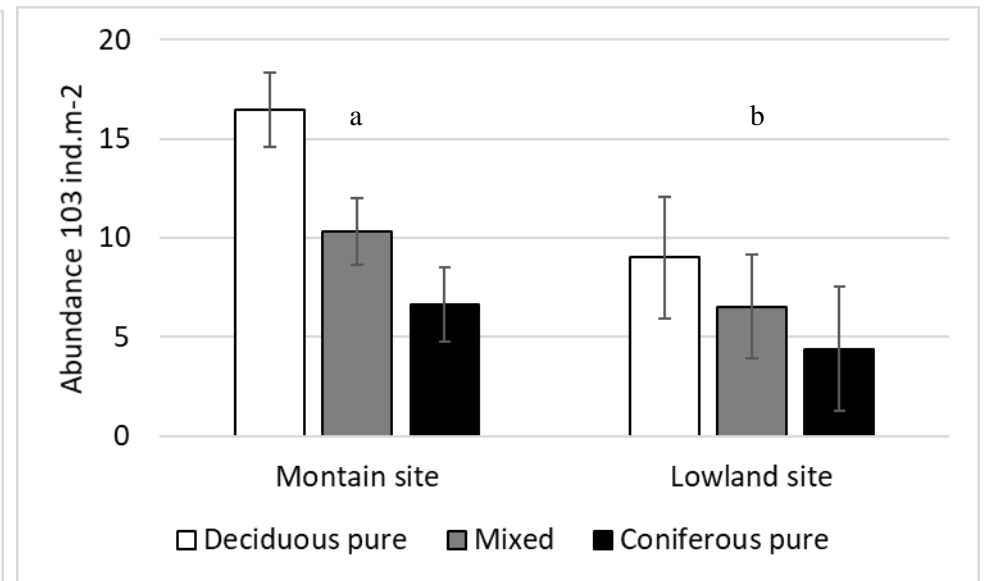
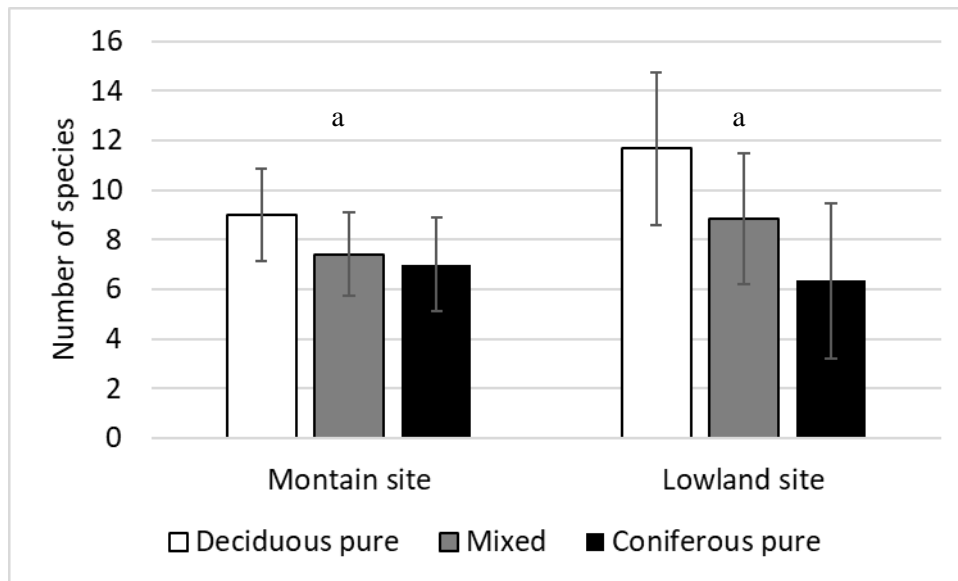
25 Figure 2

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

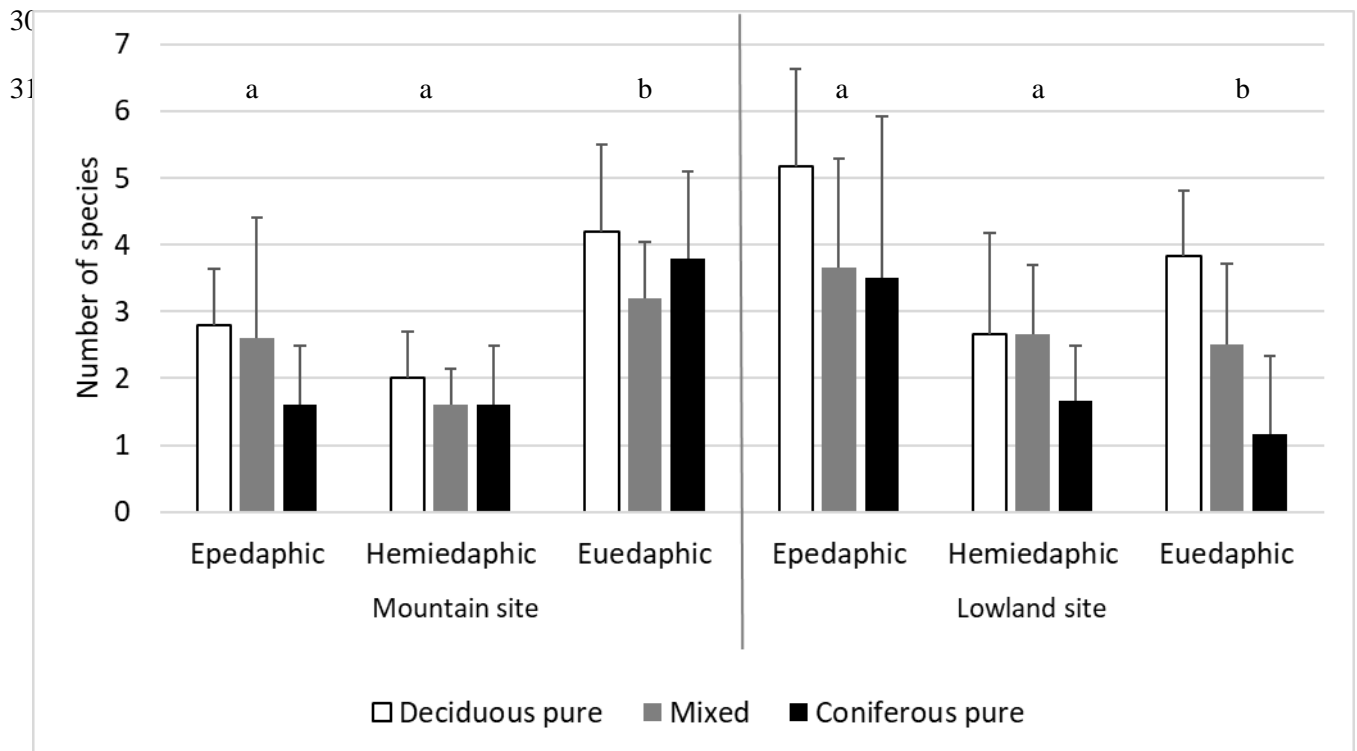
27



28 Figure 3

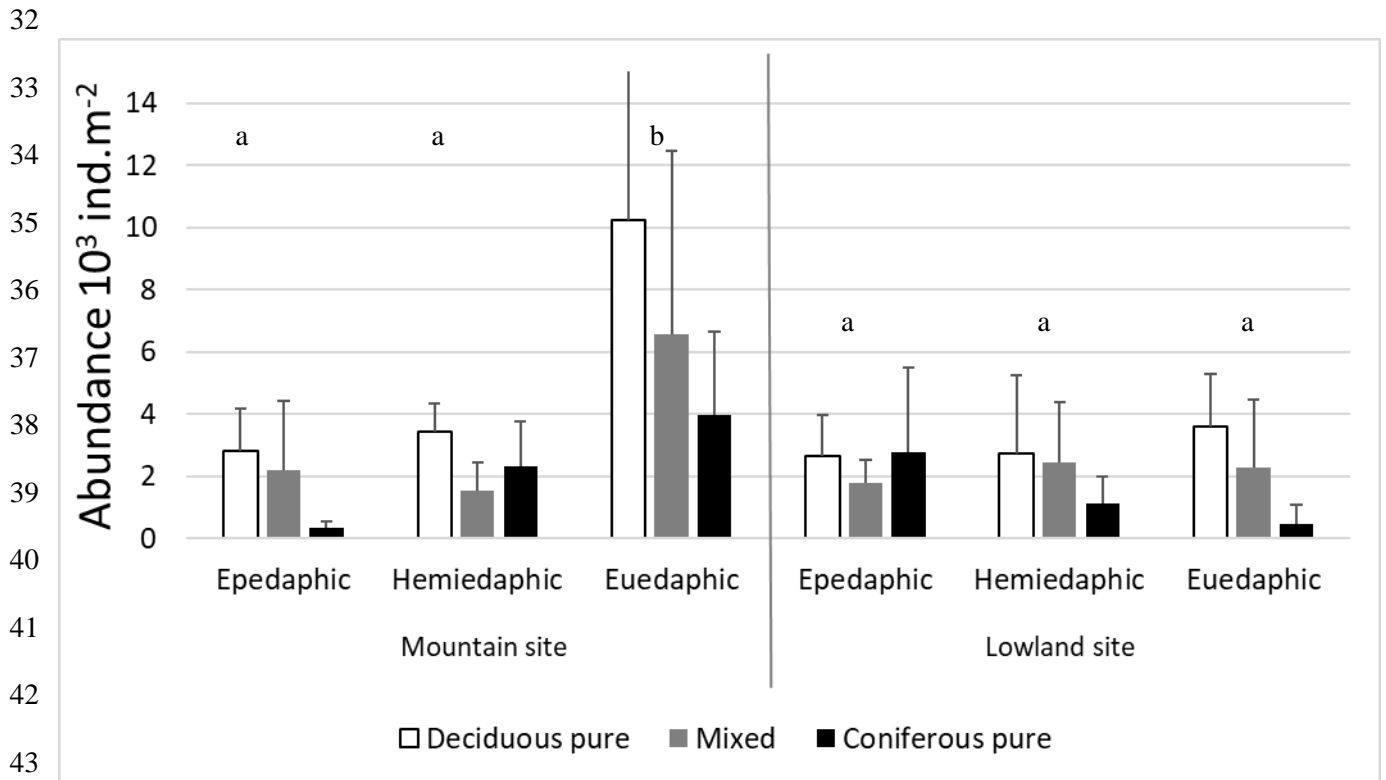
29

(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	





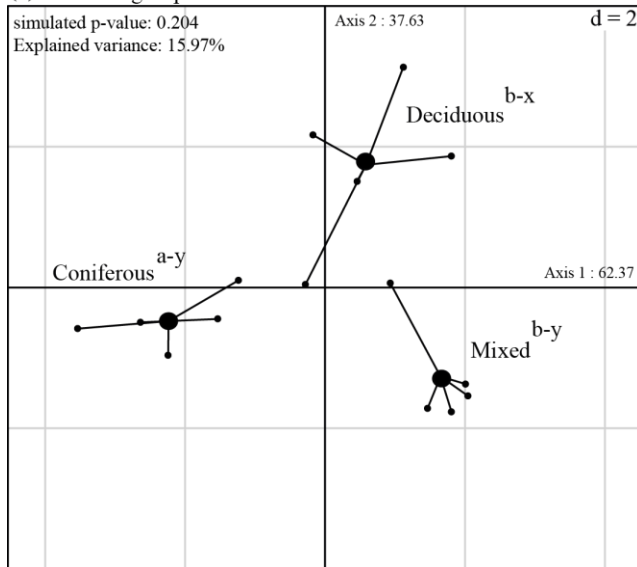
(b) Abundance	Mountain			Lowland		
	df	F	p-value	F	p-value	
stand type	1	2,02	0,15	3,37	0,04*	$D \geq M \geq C$
Functional group	2	5,76	0,007*	0,17	0,84	
stand type* fct group	2	0,51	0,72	1,62	0,18	



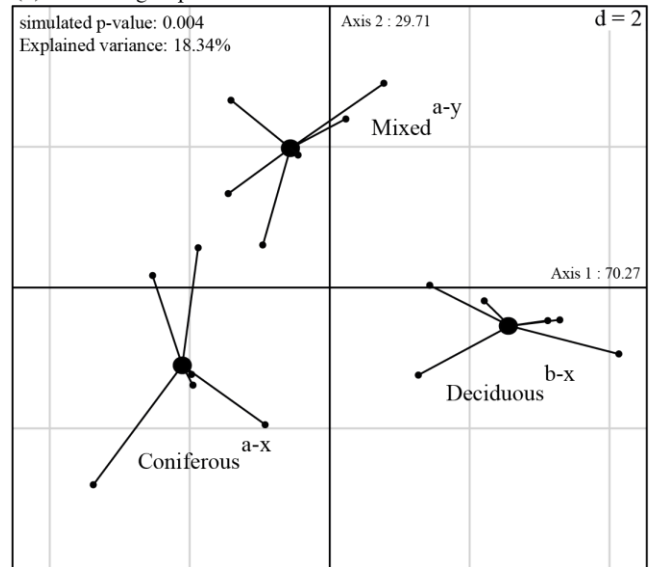
47 Figure 4

48

(a) Between group PCA - Mountain site



(b) Between group PCA - Lowland site



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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-value</i>
<b>Lowland</b>				
$H'$	2.04a	1.77ab	1.37b	0.03
$E_H$	0.84	0.83	0.82	0.93
<b>Mountain</b>				
$H'$	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
<b>(a) Species richness</b>							
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>(b) Abundance</b>							
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										<i>p-value</i>	
	Deciduous			Mixed			Coniferous					
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 <sub>H2O</sub>	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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(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 <sub>H2O</sub>	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	*

72

(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	<b>0.0011</b>	11.51	<b>0.0021</b>	4.72	<b>0.0175</b>	2.88	0.073
Humus index	75.56	<b>&lt;0.0001</b>	313.72	<b>&lt;0.0001</b>	24.19	<b>&lt;0.0001</b>	7.63	<b>0.0024</b>
pH <sub>H2O</sub>	7.70	<b>0.0001</b>	31.19	<b>&lt;0.0001</b>	3.66	<b>0.0392</b>	0.03	0.97
OLOF thickness (mm)	5.06	<b>0.0021</b>	21.90	<b>0.0001</b>	0.59	0.56	0.97	0.39
OL thickness (mm)	9.76	<b>&lt;0.0001</b>	45.02	<b>&lt;0.0001</b>	0.86	0.43	0.88	0.42
Litter C/N	4.81	<b>0.0057</b>	10.92	<b>0.0039</b>	2.82	0.086	2.67	0.096
Litter Cellulose (%)	4.21	<b>0.0104</b>	1.70	0.2090	0.09	0.91	9.12	<b>0.0018</b>

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	<b>&lt;0.0001</b>	24.52	<b>0.0001</b>	5.34	<i>0.0151</i>	16.22	<b>0.0001</b>
Litter phenols	4.47	<b>0.0080</b>	6.00	<b>0.0248</b>	1.24	<i>0.3124</i>	6.97	<b>0.0057</b>
Litter Solubles	5.54	<b>0.0029</b>	1.09	<i>0.31</i>	2.45	<i>0.11</i>	10.73	<b>0.0009</b>
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. R<sup>2</sup>Y correspond to the part of  
 77 variance (in %) of dependent variables explained by predictor variables, and Q<sup>2</sup> 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 <sup>2</sup> Y(%)	Q <sup>2</sup> (%)
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

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2                      13.95                      26.93

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82 (b)

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

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