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Abstract

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

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

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

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

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

Introduction

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

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

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

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

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

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

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

2. Material and methods

2.1. Study sites and sampling design

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

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

Lowland site is located in the Orléans forest, centre France (47° 51' – 47° 47’ N, 2° 24' – 2° 31’ E). The climate is temperate continental with an oceanic influence: mean annual temperature is 11.1 °C and the mean annual rainfall is 729 mm (1970–2014 data from the weather station at Nogent-sur-Vernisson, France). Altitudes of the sampled stands do not exceed 150 m and slopes are less than 3%. Throughout the forest the soil is deep, relatively poor and acidic with a sandy clay-loam texture, and is classified as a planosol (IUSS Working Group WRB 2006). Superimposed layers of clay and sand lead to a temporary perched water table in winter. Pure stands are composed of either oak trees (*Quercus petraea* Liebl.) for deciduous stands or pine trees (*Pinus sylvestris* L.) for coniferous stands. Mixed stands are composed of both oak and pine trees in a close proportion (Suppl. 1).

2.2. Data collection

Soil fauna sampling took place between the 17^{th} and 24^{th} of November 2013. Two samples, one meter away from each other were collected in each stand using a soil corer (4.7 cm diameter x 7 cm depth). Hologanic and organo-mineral horizons were collected, and brought back to the laboratory within at most two days. Mesofauna was extracted using a Berlese dry-funnel device for 8 days and stored in ethyl-alcohol (70%). Collembola were identified using a light microscope (400x magnification). Identification to species level followed several keys (Schlitt and Dunger 1994, Bretfeld 1999, Potapov 2001, Thibaud et al. 2004, Dunger and Schlitt 2011, Jordana 2012). Collembola of both fauna samples of each stand were pooled for further data analyses, and expressed in m^2.

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

Humus forms were described, classified according to Brêthes et al. (1995) numerically transformed into the Humus index according to Ponge et al. (2002). Furthermore, litter of each stand were collected between September to November. For the lowland site, litterfall collectors were installed (6 per sites) and spread over the plot to collect pine litter (September) and oak litter (October-November). In the Moutain site, some branches were cut using a pole pruners, then shaked to collect fallen senescent leaves and needles (October-November). Litter samples were dried out during 48H at 35°C. The biochemical composition of litter was assessed by stepwise chemical digestion in a Fiber analyzer (FIWE 6, VELP Scientifica, Italy) (Van Soest 1994). This method quantifies four different biochemical fractions: cell solubles-like substances, hemicellulose-like substances, cellulose-like substances, and lignin. These compounds are further abbreviated in the text as: soluble; hemicellulose; cellulose and lignin, respectively. Each type of litter in each stand was analysed separatly. To obtain a average value of litter in mixed stands, we used the mean values of coniferous and deciduous litters from the mixed stands.

2.3. Statistical analyses

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

$$H' = \Sigma \, p_i \, . \ln (p_i)$$

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

E_H = H' / ln (S)

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

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

The influence of soil/environmental properties and litter quality on Collembola communities was assessed using Partial Least Square Regression models (PLSR). The PLSR is used to identify the variables responsible for the variance observed in abundance and species richness. We tested abundance and species richness of all species, or by functional groups (euedaphic, hemiedaphic, epedaphic). Eight alternative models were tested with two dependent variables (abundance and richness of total Collembola and for each life-forms in both sites) and 12 predictor variables (soil moisture, Humus index, carbon to nitrogen ratio (C/N), CEC, pH_{H2O}, thickness of the OL + OF soil layers, thickness of the OL soil layer, Lignin to N ratio (Lignin:N) and litter biochemical quality (i.e. solubles, hemicellulose, cellulose and lignin). PLSR combines predicting variables (x) in one or more independent components to explicitly describe the dependent variable (y). Partial least square regression models and the number of components were tested by cross-validation (Wold 1978); PLSR model were considered significant when the cross-validated coefficient of determination (Q^2) exceeds a critical value Q^2_{limit} = 0.097 (Eriksson et al. 2006). Variable Importance in the Projection (VIP) was used to rank predicting variables (Eriksson et al. 2006). For each predictor, the percentage of explained variance (EV) was estimated by the following equation: EV = (VIP^2/p) x (R^2Y/100), with "p" corresponding to the number of predictors included in the PLSR model and R^2Y correspond to the part of variance (in %) of dependent variables explained by predictor variables (Tenenhaus 1998).

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

3. Results

3.1. Species identification

In total, 1490 individuals were identified out of 41 species (Suppl 2). In the lowland site, among the 32 species identified in total, 12 species were present in all stand types, 13 were present only in one type of stand (deciduous: *Pygmarrhopalites pygmaeus*, *Isotoma riparia*, *Protaphorura armata*, *Pseudosinella alba*, *Pseudachorutes parvulus* and *Smithurides* *schoetti* ; coniferous: *Ceratophysella denticulata*, *Pseudisotoma sensibilis* and *Sminthurinus aureus* ; mixed: *Ceratophysella armata*, *Entomobrya nivalis*, *Lepidocyrtus cyaneus* and *Willemia intermedia*) and 7 species were absent in only one type of stand (absent in deciduous stand: *Dicyrtomina ornata* and *Folsomia manolachei* ; absent in coniferous stand: *Dicyrtomina minuta* and *Paratullbergia callipygos* ; absent in mixed stand: *Dicyrtoma fusca*, *Neanura muscorum* and *Proisotoma minima*). In the mountain site, among the 27 species identified, 9 species were present in all stand types, 14 were present in only one type of stand (deciduous: *Ceratophysella denticulata*, *Folsomia penicula*, *Megalothorax minimus* and *Tomocerina minuta;* coniferous: *Oligaphorura absoloni*, *Superodontella lamellifera*, *Pseudosinella alba*, *Pseudanophorus binoculatus*, *Tomocerus minor* and *Xenylla tullbergi* ; mixed: *Ceratophysella armata*, *Folsomia manolachei*, *Sminthurinus elegans* and *Sphaeridia pumilis)* and 4 species were absent in only one type of stand (absent in deciduous stand: *Pseudachorutes parvulus* ; absent in coniferous stand: *Kalaphorura burgmeisteri* and *Neanura muscorum* absent in mixed stand: *Folsomia inocula*).

3.2. Effects on the species richness and abundance

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

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

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

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

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

3.3. Effects on the Collembola community

The BGA on the Collembola abundances explained 16% and 18% of the total variance for the mountain (BGAm, Fig. 4a) and the lowland sites (BGAl, Fig. 4b), respectively. Axis 1 represented 62% and 70% and axis 2 37% and 29% of the extracted variance, respectively for the mountain and the lowland sites. The simulated p-value obtained using Monte-Carlo permutation test was not significant for the mountain site (p=0.204), but highly significant for the lowland site (p=0.004). Nevertheless, for both sites, the three stand types were highly discriminated with these two axes (Fig. 4).

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

3.4. Soil and litter characteristics

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

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

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

4. Discussion

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

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

Likewise, most studies comparing pure to mixed litter or stands found an intermediate diversity and abundance of Collembola in mixed stands or equal to one of the pure stands (Scheu et al. 2003, Wardle et al. 2006b, Jacob et al. 2009, Cavard et al. 2011, Korboulewsky et al. 2016). Nevertheless, and similar to our result in the mountain site, several studies did not find any significant effect of litter mixture on diversity of Collembola (Scheu et al, 2003; Jiang et al, 2013, Salamon et al, 2008). Concomitantly, few authors found a significant positive response of microarthopods (i.e. Collembola and Oribatid mites) to increasing litter diversity (Kaneko et Salamanca 1999). Therefore, the variety of responses and the resulting absence of any general pattern of increasing litter diversity, suggest that soil organism responses are idiosyncratic, so driven by litter species identity (Scherer-Lorenzen et al. 2007, Korboulewsky et al. 2016).

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

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

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

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

The effect on the community structure was mainly driven by the litter chemical composition (lignin:N, cell solubles, hemicellulose, lignin) and soil C/N. Indeed, these parameters were major predictors for community structures in both mountain and lowland sites (Tab. 2). It is well known that the higher the lignin/N ratios, C/N or polyphenol content in litter, the lower the abundance and activity of soil organisms, which leads to lower organic matter decomposition rates (Harbone, 1997; Hansen and Coleman, 1998; Berg and McClaugherty, 2003; Hattenschwiler et al., 2005; Cesco et al., 2012). It is interesting to point out that although both sites showed almost the same patterns in terms of effect of mixture on Collembola community, some factors explaining the variability were different. Indeed, the soil pH and humus form were important predictors only in lowland site, and the CEC only in the mountain site (Models M1 and L1 for abundance and richness of all Collenbola).

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

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

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

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

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

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

Figure 1

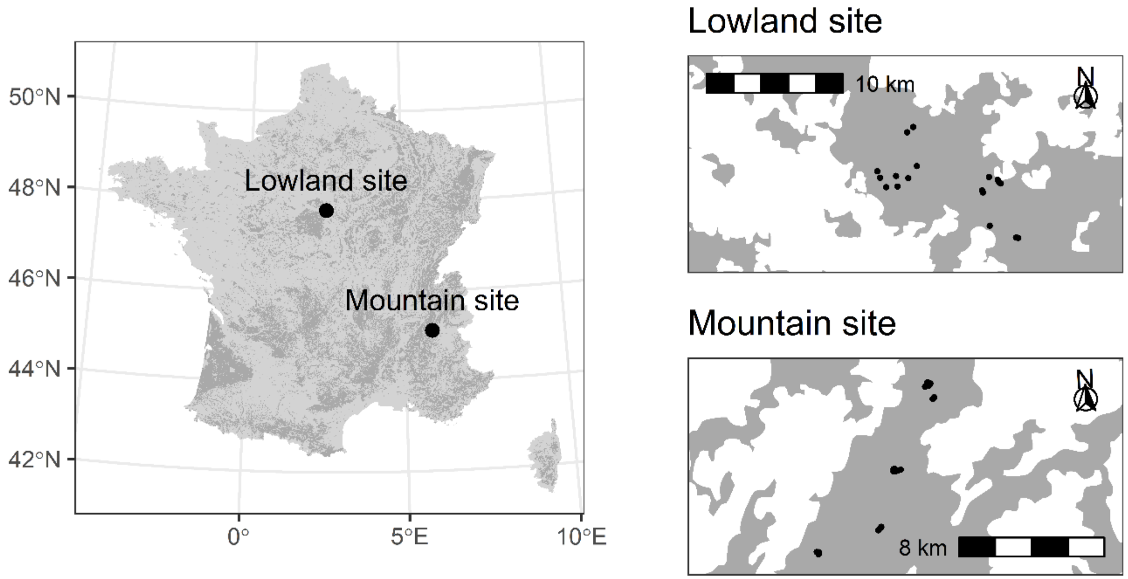
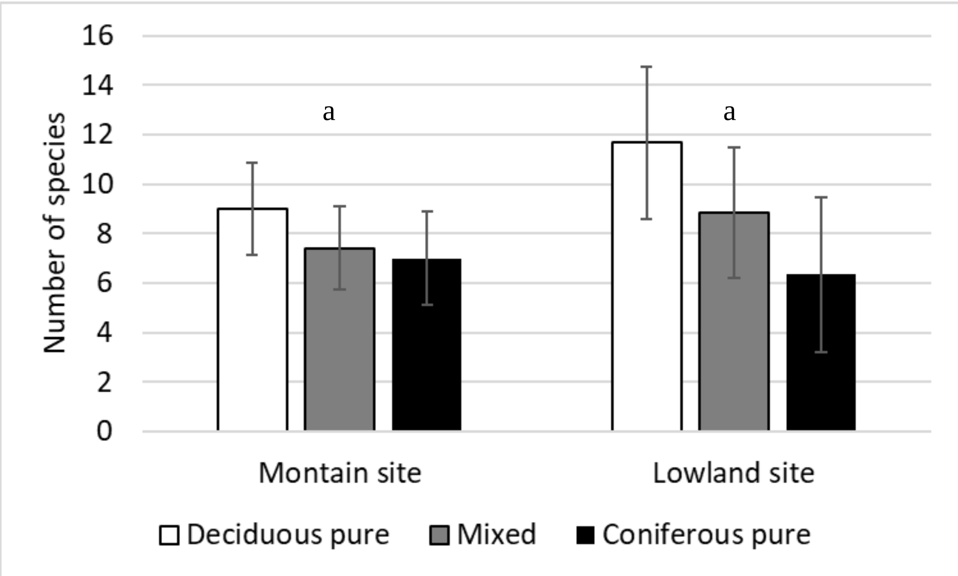

Lowland site
Mountain site
50°N
48°N
46°N
44°N
42°N
0°
5°E
10°E
Lowland site
10 km
N
Mountain site
N
8 km

Figure 2

	df	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	

	df	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	



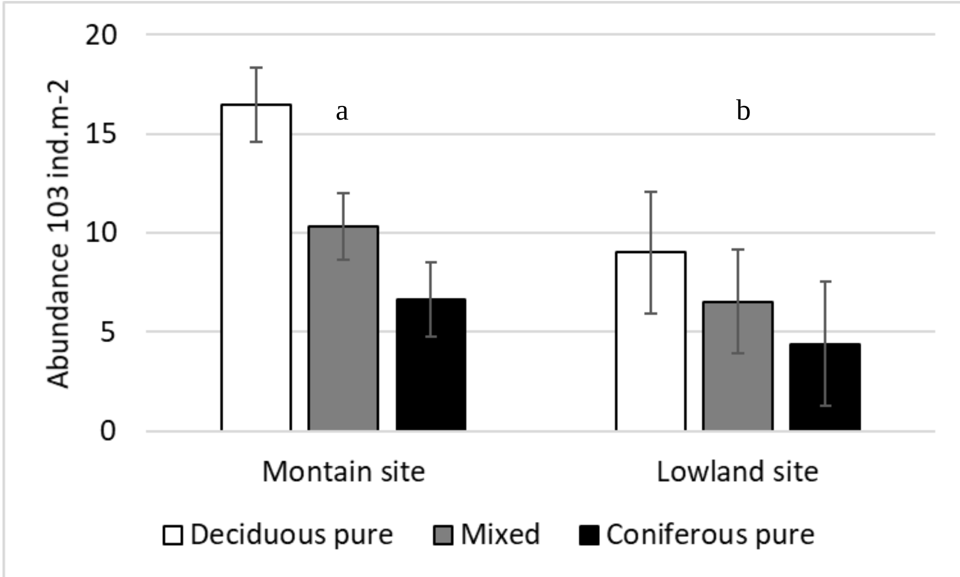
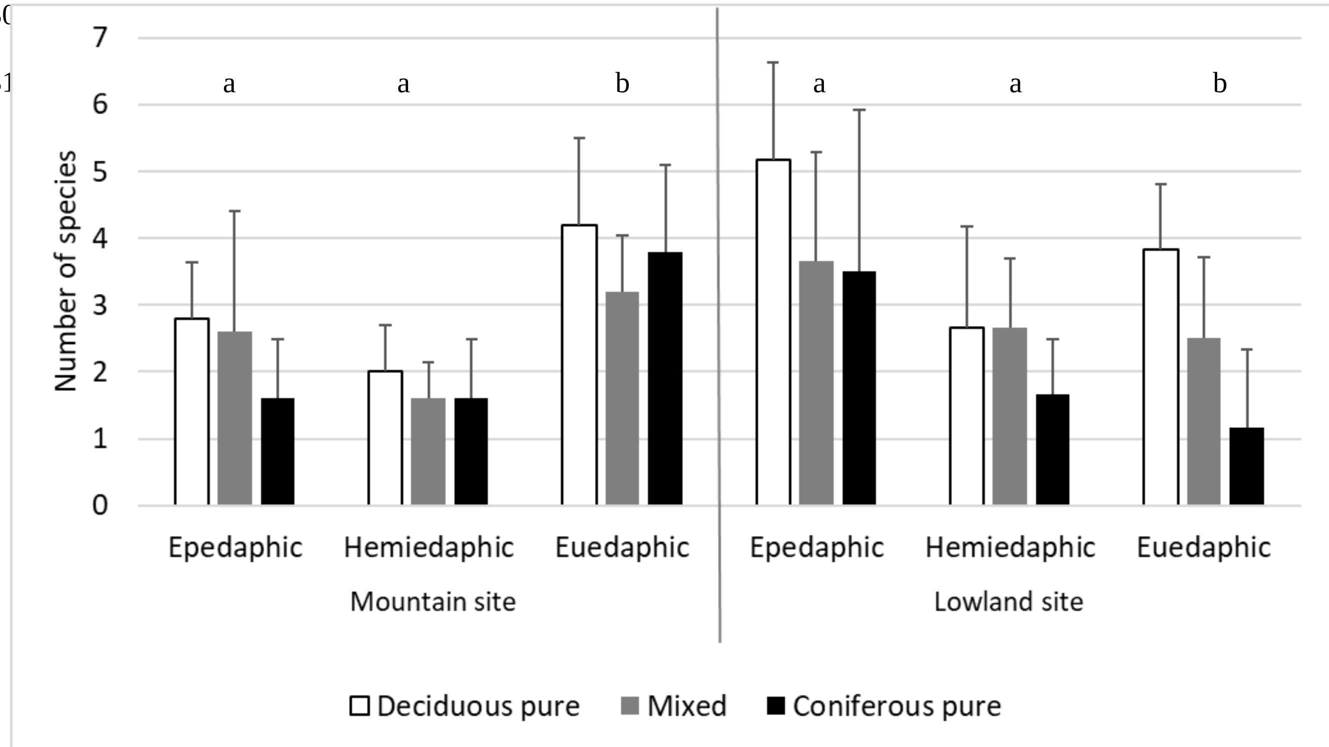


Figure 3

(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 ≥ M ≥ 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	

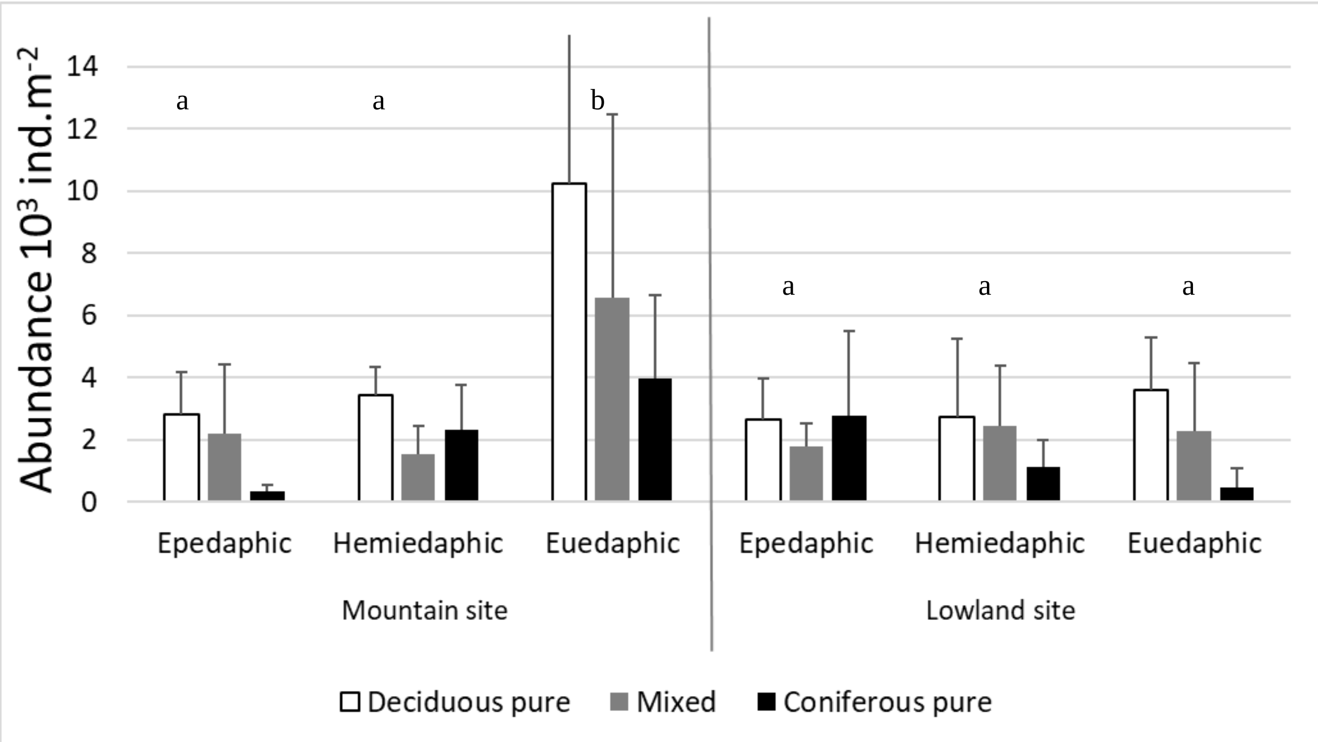


Figure 4

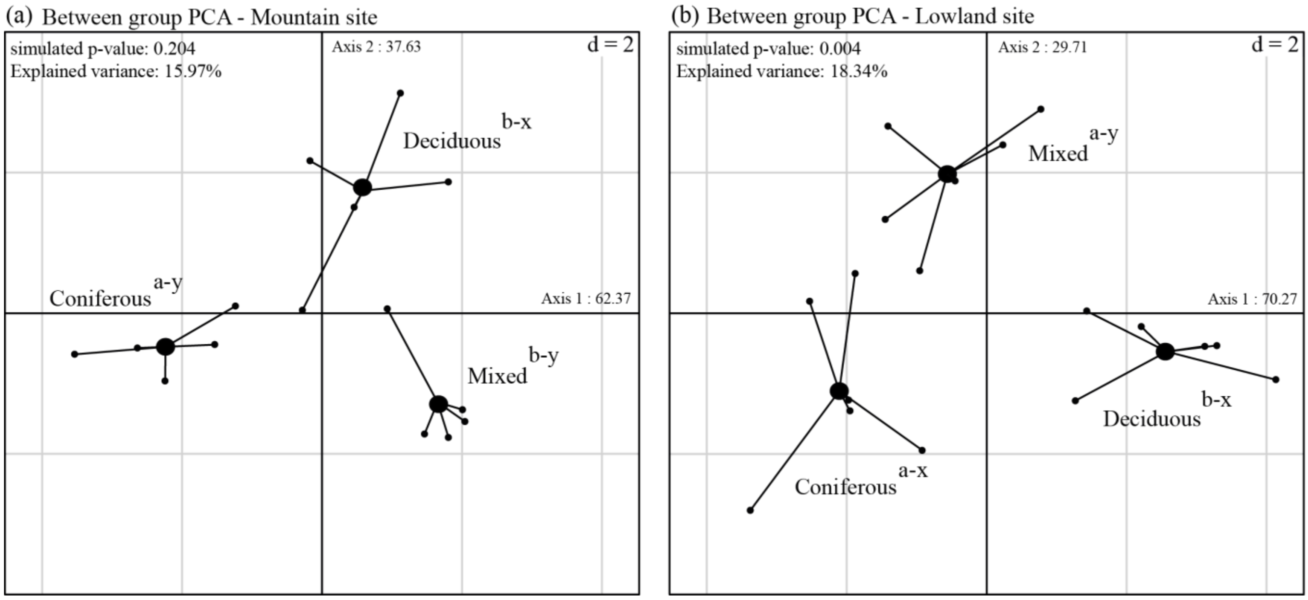

(a) Between group PCA - Mountain site
simulated p-value: 0.204
Explained variance: 15.97%
Axis 2 : 37.63
d = 2
Deciduous b-x
Coniferous a-y
Axis 1 : 62.37
Mixed b-y
(b) Between group PCA - Lowland site
simulated p-value: 0.004
Explained variance: 18.34%
Axis 2 : 29.71
d = 2
Mixed a-y
Axis 1 : 70.27
Deciduous b-x
Coniferous a-x

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

		Deciduous	Mixed	Coniferous	*p-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*

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

		Epedaphic		Hemiedaphic		Euedaphic	
	df	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

Table 3: Soil and litter characteristics (mean ± SD) of three stand types (coniferous pure, deciduous pure and mixed) in two different sites (mountain and 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 stand type (c). Signicicant statistical results are indicated in the tables with different letters. Means litter chemical characteristics of mixed stands were calculated as the mean (±SD) of coniferous and deciduous values from litter analyzed in mixed stands.

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

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*	**

(II)	Montain										
	Deciduous			Mixed			Coniferous			*p-value*	
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*	*

(c)	Overall model		Site		Stand		Site * Stand	
	F-value	*p-value*	F-value	*p-value*	F-value	*p-value*	F-value	*p-value*
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	*0.16*	1.64	*0.22*	2.52	*0.11*	0.69	*0.51*
Litter Lignin	15.49	***<0.0001***	24.52	***0.0001***	5.34	*0.0151*	16.22	***0.0001***
Litter phenols	4.47	***0.0080***	6.00	***0.0248***	1.24	*0.3124*	6.97	***0.0057***
Litter Solubles	5.54	***0.0029***	1.09	*0.31*	2.45	*0.11*	10.73	***0.0009***
Litter Tanins	7.96	*0.0004*	19.73	*0.0003*	3.71	*0.0448*	5.76	*0.0116*

Table 4 : (a) General model parameters of Partial Least Square (PLS) regression with number of significant PLS-components. R²Y correspond to the part of variance (in %) of dependent variables explained by predictor variables, and Q² is the coefficient of determination which indicates that the model is significant 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 each model projection. Indication of the Variable Importance in the Projection (VIP) was used to rank predicting variables.

(a)

N° Model	Dependants variables	PLS-components	R²Y(%)	Q² (%)
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

(b)

N° Model		WC	Humus	pH	OLOF	OL	C/N	CEC	Lignin/N	SOl	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}	-	$10.8^{-1.5}$	-	-	-	-	-	-	$10.3^{+1.5}$	$7.4^{+1.2}$	$10.7^{-1.5}$	$8.6^{-1.3}$

Variable Importance for the Projection (VIP) added in subscript to EV. Trend of standardized Regression Parameters (by target variable) was represented (+) or (-). “-”: parameter included in the model but not significant, i.e. VIP < 1. EV: explained variance; WC: water content; CEC: cation exchange capacity; OLOF: OL+OF soil layers thickness; OL soil layer thickness; SOL.: cell solubles; HEM.: hemicellulose; CEL.: cellulose; LIC.: lignin