

Structural relationships among vegetation, soil fauna and humus form in a subalpine forest ecosystem: a Hierarchical Multiple Factor Analysis (HMFA)

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ABSTRACT

Aboveground vegetation, four belowground fauna groups and humus composition have been analyzed in order to investigate the links between autotrophic and heterotrophic communities in a Norway-spruce mountain forest in Tours-en-Savoie (France). The aboveground plant community was recorded in small patches corresponding to contrasting microhabitats. Animal communities and humus layers were sampled within the same patches. The relationships between humus profile, faunistic and floristic compositional gradients were investigated by Multiple Factor Analysis (MFA) and, for the first time in ecology, a Hierarchical Multiple Factor Analysis (HMFA) was used to interpret differences among humus layers. The analysis revealed a pattern with three main groups of microhabitats. The thorough study of separate humus layers could explain this result. The interplay of plant–animal–soil interactions is likely to drive the ecosystem toward three alternative states supporting humus traditional classification between mull–mor–moder. HMFA revealed the importance of depth to explain this contrast among humus forms, using humus layers as diagnostic tools in both inert and living components. HMFA also showed contrast between unexploited and exploited parts of the forest, but the study of soil and vegetation indicate that this contrast does not only hold in forest management but also in geomorphology. RV-coefficients among the six groups of variables showed significant fauna–fauna relationships in almost all humus layers except Actinedida. Plant–soil interactions are not as strong as expected and are even weaker when the soil in question is deep. In addition, HMFA failed to show direct interactions between plant and soil fauna but, paradoxically, HMFA does suggest that indirect plant–fauna interactions are at the focus of the ecosystem strategy that leads to the differentiation of ecological niches within the forest mosaic.

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Introduction

One of the main ecological challenges since the end of the last century has been to connect biodiversity with ecosystem processes such productivity (Kareiva 1994; Tilman et al. 1997), stability (Bardgett and Cook 1998), dynamics (Siemann et al. 1999; Marra and Edmonds 2005; Salmon et al. 2008), biogeochemical cycling (Beare et al. 1995), and forest regeneration (Nagaike et al. 1999). On the one hand, the soil food web is fundamental to plant growth (Wardle 1999). On the other, plant debris is essential in the organization of humus communities (Lavelle et al. 1993; Berg et al. 1998). Most studies have examined either the effect of plant diversity on soil processes (Spehn et al. 2000; Zimmer 2002) or the effect of soil biotic diversity on soil fertility and plant productivity (King et al. 2002; Scherer-Lorenzen et al. 2003) without having confirmed

any correlation between the diversity of the soil biota and plants (Hooper et al. 2000; Porazinska et al. 2003; Coleman and Whiteman 2005).

The purpose of this work is to search for some connections between soil fauna and plant communities, and to discern processes that explain these correlations, if any exist. Our working hypothesis was that variations in the local composition of plant communities will influence the soil fauna through differences in litter composition (Ball et al. 2009). In turn, the soil fauna will regulate humus processes by controlling the rate of litter decomposition, the nature and chemical activity of soil organic matter and thus, will influence the conditions for fine-scale vegetation structure and dynamics (De Deyn et al. 2003; Crow et al. 2009; Laganière et al. 2009; Mathieu et al. 2009). Humus composition is the meeting point of animal and plant communities: the long-lasting effect of humus properties is able to influence plant and animal community composition, which then again influence humus composition and properties. These feedback loops are supposed to result in a spatial segregation of closely linked communities and humus forms.

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This hypothesis will be tested by comparing a set of microhabitats within a single forest. One major concern in investigating relationships among biotic communities is the question of appropriate scale (Huston 1999; Loreau 2000). In our case, the vegetation has to be described at a scale of homogeneous units sufficiently small to allow soil fauna to discriminate (Tilman 2000; Mathieu et al. 2009; Doblás-Miranda et al. 2009). In forest ecosystems, the herb layer can be described as a mosaic of plant synusia that are linked to contrasting microhabitats, indicating differences in edaphic and microclimatic conditions (Barkman 1978; Gillet and Gallandat 1996). Within the forest phytocoenosis, we can thus delimit multi-layered microcoenoses (Barkman 1978), each including a distinct herb synusia and the superposed vegetation layers (shrubs and trees). Given the small-scale organization of humus components, the scale of plant microcoenosis is still large for soil fauna but it represented the appropriate level of description to determine a shared structure between flora, fauna and humus compartments.

Materials and methods

Study site

The subalpine forest under study covers 15 ha in the Tours-en-Savoie commune (western northern Alps, France: 45°40'40"N; 6°27'57"E). Altitude ranges between 1575 and 1750 m a.s.l., with a south-west facing aspect. The bedrock is a mixture of micaceous schists and albitic gneisses, the soil type is a Leptosol (IUSS Working Group 2006) and the vegetation belongs to *Piceetum subalpinum myrtilletosum* David 1979 according to traditional phytosociological classification. The total annual rainfall varies between 1200 and 1600 mm with half this amount falling in the form of snow.

The western part of the forest (8.5 ha) is more intensively and regularly exploited than the eastern part (6.5 ha). Thus we will call the western area E (exploited) and the eastern area U (unmanaged). Both parts of the forest were described as high-altitude coniferous forests in 1729 according to land registry and map of the Sardinian kingdom (<http://www.savoie-archives.fr/index.php?id=1233>). From 1729 to 1891, logging was frequent. The U area was entirely clear-cut in 1830–35 (Eynard-Nachet, personal communication). The E area was probably partially clear-cut during the same period. Landslides creating hollows crossing the slope and denuding little cliffs are common in the U area but rare in the E area. The slope of the U area is consistently steep (35°) compared to E area (20–30°).

Vegetation sampling

To investigate the fine-scale plant–fauna–humus interactions we selected three phytocoenoses within the Tours-en-Savoie forest, with homogeneous conditions for tree-age structure, slope, and geomorphology.

Phytocoenosis E2 is under silviculture regime. It shows contrasts between spruce-shaded *Prenanthes purpurea* and *Oxalis acetosella* synusia (microcoenosis E2-PO) and spruce-shaded *Vaccinium myrtillus* synusia (microcoenosis E2-PV). This phytocoenosis also exhibits a contrast between moist *O. acetosella* synusia shaded by maple (microcoenosis E2-AO), sunny dry, species-poor or species-rich *V. myrtillus* heath (microcoenoses E2-Vp and E2-Vr, respectively) and sunny moist microhabitats with *Athyrium filix-femina* and *Rubus idaeus* as dominant plant species (microcoenosis E2-R).

Phytocoenosis U8 developed under unmanaged conditions and shows a simple forest mosaic of tree and ericaceous heath elements (microcoenoses U8-P and U8-Vp, respectively).

Phytocoenosis U10 (unmanaged conditions) exhibits complex interactions between *Luzula nivea* synusia shaded by spruce (microcoenosis U10-PL), *O. acetosella* synusia shaded by maple (microcoenosis U10-AO) and sunny microhabitats dominated by *Agrostis agrostiflora* and *R. idaeus* (microcoenosis U10-AgR).

In a given phytocoenosis, each component of the forest mosaic (i.e., each microcoenosis) was sampled using a list of plant species with their cover ratio code according to Braun–Blanquet's 6-level dominance scale (classes +, 1, 2, 3, 4, 5, based on visual estimation of the percentage cover through all vegetation layers). The vegetation survey was carried out in a 20-m² area inside each of the 11 microcoenotic forest units during the 1999 summer season. The semi-quantitative dominance code was replaced by the central percentage cover of the corresponding class for further statistical analyses.

Ecological preferences of plant species with respect to pH, soil water and light were recorded according to a 3-level scale. For example: a strict acidophilic species was reported as acidophilic=2 and basophilic=0; a plant species more frequent in acidic condition is quoted as acidophilic=2 and basophilic=1. The plant database was taken from Aeschmann et al. (2004). In a given forest microcoenosis, the mean ecological preference of the plant species, weighted by dominance, provides an ecological indicator of microhabitat condition.

Humus profile and soil fauna

The eleven microcoenotic forest units were sampled for humus layers and soil fauna. Humus layer sampling followed the microstratified method of Ponge (1984) and Bernier and Ponge (1994). First, a column of undisturbed humus material, with an area of 25 cm² and a maximum depth of 15 cm, was isolated from the surroundings by progressively excavating the material around it using a sharp knife, scissors and pruning shears. Second, humus layers were separated manually with scissors from top to bottom; the humus layers were immediately fixed in 95% (v/v) ethyl alcohol. We measured the depth of each layer with an accuracy of 0.5 cm and a short, visual description was done. The sampling process was complete once the bedrock was reached given that Leptosols were very shallow. Humus composition was estimated at 40× magnification under a dissecting microscope using a seven-level ordinal scale. Each eleven humus profile showed layers with different thickness. For statistical reasons, 4 depth limits were chosen (1, 2, 3 and 5 cm below surface) regardless of layer composition. As a consequence, reference to the nature of layer was only considered a posteriori for interpretation needs. Humus typology follows Baize et al. (2009).

Soil animals were separated by hand under the dissecting microscope within the same humus material. It was often necessary to dissect plant fragments and humus aggregates that could possibly enclose animals. Among the fauna, only Nematodes and Protozoa were not counted given their small size and transparency. All specimens were identified to species for springtails (Collembola), to genera for Oribatid mites, to family for Actinedida mites and to supra-family taxonomical levels for the rest of the fauna.

Data analysis

Multiple Factor Analysis (MFA) (Escofier and Pagès 1994) was used to link symmetrically six different groups of descriptors, that is the four soil fauna groups, flora and humus components, and a passive supplementary group of data (diversity indices, forest management and plant ecology). Moreover, Hierarchical Multiple Factor Analysis (HMFA) was used to explore interactions between habitats and depths (Le Dien and Pagès 2003).

Popular asymmetric constrained ordination methods, such as CCA (Canonical Correspondence Analysis) or RDA (Redundancy

Analysis), were not applicable here since hypotheses were drawn on the relationship between soil fauna, flora and humus form without assuming a priori any causal relationship, and because the number of objects was very low compared to the number of descriptors in each group (Dray et al. 2003). Among the variety of symmetric ordination methods that are available for the linking of ecological data tables, MFA was chosen because it allows the simultaneous coupling of several groups or subsets of variables defined for the same objects (Escofier and Pagès 1994; Borcard et al. 2011). MFA is a simple variant of co-inertia analysis, which seeks the common structures present in all or some of these subsets. As this method, to date mainly used in sensory evaluation and chemistry, is not familiar to ecologists, we provide the following summary of its principles.

If all variables are numerical (as it is the case for all active data in our study), then MFA is basically a Principal Component Analysis (PCA) applied to the whole set of variables in which each subset is weighted. Qualitative variables may be used in MFA but need to weight the proportions between modalities. The use of weights balances inertia between the different groups and thus balances their influences. Each group of variables can get the status 'active' or 'passive': a passive (or illustrative) group does not contribute to the construction of axes.

MFA is performed in two steps. First, a PCA is performed on each subset, which is then normalized by dividing all of its elements by the first eigenvalue obtained from its PCA. Second, the normalized subsets are merged to form a unique matrix, which is subjected to a global PCA. The individual subsets are then projected onto the global analysis to analyze commonalities and discrepancies.

Various graphical displays are available for MFA: objects, variables, groups or PCA axes. The interpretation of objects (point position) and variables (arrow length and angle) is the same in PCA. In the superimposed display of objects, each object appears as a cloud of several points: one 'partial' point for each active group, which gives the position of the object from the point of view of this group, and one average point, which is the center of gravity of the partial ones.

The similarity between the geometrical representations derived from each group of variables is measured by the RV-coefficient, ranging from 0 to 1 (Robert and Escoufier 1976). RV-coefficients can be tested by permutations (Josse et al. 2008).

Prior to MFA, raw dominance or abundance of taxa and humus components were transformed by $\ln(y+1)$ to avoid placing too much importance to extreme values. Contrary to site profiles, species or double profiles commonly used in community ecology (Legendre and Gallagher 2001; Dray et al. 2003), this simple log-transformation does not remove important information about absence and relative quantities among objects or descriptors. For this reason, no standardization was applied to any subset of active variables in the MFA. However, quantitative and binary variables of the passive group were centered and scaled since they were not dimensionally homogeneous.

HMFA is a generalization of MFA integrating several hierarchical levels (Le Dien and Pagès 2003). This method is of high potential interest in ecology given the complexity of the systems under study.

All computations were performed with R 2.10.1 (R Development Core Team 2009) and the FactoMineR package (Lê et al. 2008; Husson et al. 2009).

Results

Plant and soil fauna communities

Plant species richness in the eleven studied microcoenoses ranged between 3 and 29 species (Appendix A).

We identified 28,608 animals from the eleven humus cores encompassing 116 taxa (Appendix B). The mean density was slightly more than 10^6 m^{-2} . The highest animal density was reached in the U8-P spruce unit ($3.6 \times 10^6 \text{ m}^{-2}$) and the lowest in the U10-AO Acer/Oxalis unit ($0.4 \times 10^6 \text{ m}^{-2}$). Oribatida were the most numerous fauna (56%), followed by Collembola (14%), Enchytraeidae (10%), Actinedida (9%) and Protura (3%). We distinguished four soil fauna groups: Collembola, Oribatida mites, Actinedida mites and supra-family fauna taxa. They were considered independent active groups in MFA and HMFA since each describes a distinct and homogeneous taxonomical level (Appendix B).

Humus composition

We identified 41 humus components encompassing plant fragments (spruce, bilberry, moss, herb or fern litter remains), animal feces (organic or a mixture of organic and minerals) and soil material (Appendix C). Humus form varied from mor and dysmoder (abundance of both litter and holorganic feces) to mull (low litter abundance together with high content of earthworm organo-mineral feces).

MFA

We first performed five MFAs on separate humus layers and one MFA combining all layers, each with the six independent groups of variables including a total of 55 plant species, 37 supra-family fauna taxa, 37 Collembola species, 43 Oribatida mite genera or morphotypes, 33 Actinedida families or morphotypes and 41 humus components. Taxonomic richness and Shannon diversity of each community (using abundance for fauna and cover for plant species), forest regime and plant ecology were added as supplementary variables in a passive group. Variance associated with the three first axes of separate PCAs ranged from 75.2 to 79.7% for Collembola, 75.7 to 87.9% for Oribatida mites, 68 to 85.9% for Actinedida mites, 66.4 to 87.7% for supra-family fauna, 51.9 to 71.6% for humus components and 62 to 69.9% for the passive supplementary variables. The unique flora matrix used for the six MFAs showed a cumulative percentage of variance of 62.4%. The three first axes of the six MFAs accounted for 54.4–59.2% of the total variance, with axis 1 alone accounting for 24.3–31.5%.

RV-coefficients among the six groups of variables (Table 1) ranged between 0.3 and 0.9. Animal groups showed significant relationships with other groups in almost all humus layers except Actinedida notably in the top layer. In contrast flora showed only significant links with humus variables in the two uppermost layers. Humus descriptors were well correlated to Oribatida and supra-family fauna taxa, but to a lesser degree to Collembola and Actinedida.

The six MFAs were closely related (Table 2). Axis 1 of the four uppermost layers showed contrast between spruce and herb habitats, whereas heath habitats were often discriminated along axis 2. Contrast between the E and U part of the forest was evident for the whole humus profile (along axis 2) and for various depths: 0–1 cm (axis 4), 3–5 cm (axis 2) and below 5 cm (axis 2). In the six MFAs, E2-Vr (species-rich *Vaccinium* vegetation) positioned itself between herb and heath habitats but closer to herb habitats, whereas E2-PV (*Vaccinium* habitat shaded by spruce) was closer to heath than to spruce habitats.

Passive data explained the contrast between spruce and herb habitats by both light and acidity levels as depicted by plant ecology (Appendix C). When focusing on plant species, MFA axis 1 showed a strong correlation with species richness and diversity (in the direction of the herb branch) (Appendix A). In contrast, spruce and heath branches were mainly correlated with *Picea abies* and *V. myrtillus*, respectively. Additional passive data indicated that heath branches

Table 1
Pairwise RV coefficients ($\times 10$) (down-leftward) between groups of variables and the corresponding *P*-values (up-rightward) (1: $P \leq 0.05$; 2: $P \leq 0.01$; 3: $P \leq 0.001$) for the six MFAs (MFA 0: 0–1 cm depth; MFA 1: 1–2 cm; MFA 2: 2–3 cm; MFA 3: 3–5 cm; MFA 5: >5 cm; MFA *t*: total).

MFA	Collembola						Oribatida						Actinedida						Fauna						Flora						Humus											
	0	1	2	3	5	<i>t</i>	0	1	2	3	5	<i>t</i>	0	1	2	3	5	<i>t</i>	0	1	2	3	5	<i>t</i>	0	1	2	3	5	<i>t</i>	0	1	2	3	5	<i>t</i>						
Collembola							3	2	2	1		2							3	1	1	2			3	3	3	2	1	3							1		2	2	1	2
Oribatida	7	7	8	6	5	7													1		2	1			3	3	2	1	2	2							2	2	3	2	2	3
Actinedida	3	5	8	6	7	8	3	5	6	4	6	6													1	1	1	2	2									1	1	2	2	
Fauna	7	7	7	7	6	8	9	9	7	6	6	7	4	5	7	7	8	7															2	3	1	1	2	3	1	1	2	3
Flora	4	4	5	4	5	5	4	5	5	4	4	4	4	5	6	5	5	5	4	5	6	7	6	6							2	2					2	2				2
Humus	6	6	7	7	6	7	7	7	7	7	7	7	4	6	7	5	7	7	6	7	7	7	7	8	8	8	7	6	6	7												

Table 2
Mean of site scores grouped by vegetation type and part of the forest for the six MFAs (spruce: E2-PO+U8-P+U10-PL; heath: E2-PV+E2-Vp+U8-Vp; herb: E2-AO+E2-Vr+E2-R+U10-AO+U10-AgR). Only mean values farthest from the axis origin are shown.

Depth	0–1 cm				1–2 cm				2–3 cm				3–5 cm				Below 5 cm				All layers			
	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
Mean																								
Spruce	3.0				2.2	–1.8			2.8	–1.2			2.7				2.4		–0.9		2.9			
Heath		1.6				1.3	1.0			1.8					–1.7			–1.2	0.9	–0.8				1.4
Herb	–1.9				–2.0				–1.9				–1.7							0.8	–1.7			
E				0.7										–1				–1.0				–1.0		
U				–0.9		1.1		–0.7						1.1				1.2						1.2

discriminate both dry and sunny conditions for these bilberry communities (Appendix C). Management (positive side of MFA axis 2) promotes a few heliophilous species such as *V. myrtillus*, *Anthoxanthum odoratum*, *Knautia dipsacifolia*, *P. purpurea* and *Phyteuma betonicifolium*. The unmanaged part of the forest promotes *Agrostis schraderiana*, *A. filix-femina*, *Calamintha grandiflora*, *Dryopteris filix-mas*, *Rosa pendulina* and *R. idaeus*, which are known to be frequent in rock-slide and moist habitats (Aeschmann et al. 2004). Those preferences suggest that the difference between the U and E part of the forest not only holds for forest management but also for geomorphology.

In contrast to what was observed with plant species, fauna dispersion along the three first MFA axes was not strongly unbalanced (Appendix B). Thirty-seven taxa among the 99 shown in Appendix B were placed on the spruce side of axis 1, 14 taxa on the herb side of axis 1 and 20 taxa toward the heath branch of axis 3. Those results could not be explained by the grouping of fauna abundance by main taxa, which was significantly higher in spruce habitat, but only in terms of richness and diversity. Spruce habitat only had higher Collembola richness whereas herb habitat had higher levels of Oribatida and supra-family fauna diversity. On the other hand, heath habitat (positive side of MFA axis 3) promoted Oribatida and Actinedida richness as well as Actinedida diversity.

HMFA

The similarity between the six MFAs justified the need to perform HMFA with two hierarchical levels. On the one hand, interactions within fauna groups and between fauna and humus components may be independent of depth but on the other hand, depth exerts an influence on every humus component. This asymmetry defined hierarchy. The upper level involved five sets of variables, one for each depth of belowground humus layers and one additional set for aboveground vegetation. The lower level consisted of the six groups of variables previously used for the six MFAs. The five depth-specific matrices (four for fauna and one for humus components) were used for the belowground data sets. The clouds of 352 dots (32 sets and groups × 11 habitats) in the plane of HMFA axes 1 and 2 showed 3 elongation axes matching with spruce, herb and heath habitats (Fig. 1). The three first axes of HMFA accounted for 51.7% of the total variance, axis 1 alone accounting for 24.9%, similar to MFA results. Discrepancies between vegetation and the barycentre were partially confirmed with the weak

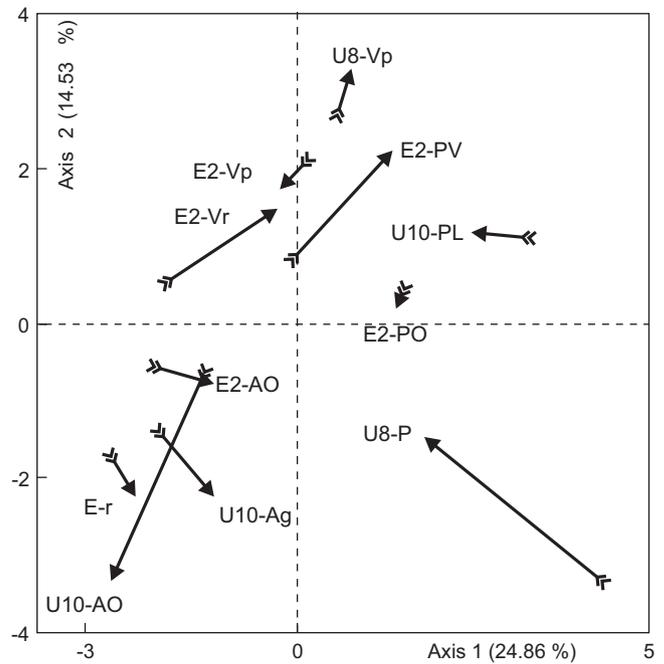


Fig. 2. Position of plant groups (arrow head) compared to the barycentre (arrow basis) for the 11 habitats in the two first axes of HMFA.

discrimination of U8-P and the high discrimination of E2-PV and U10-AO by vegetation data (Fig. 2). This result has to be reconciled with the low RV coefficients for vegetation in the six MFAs (Table 1).

The three spruce habitats showed three different interactions among fauna, humus composition and depth for the eleven habitats in the plane of HMFA axes 1 and 2; U8-P (pure spruce habitat, unexploited forest) was the furthest (Fig. 3). Every subset followed loops in the plane of axes 1 and 2 except Actinedida whose influence increased constantly with depth. Spruce direction was characterized by large amounts of leaf material and feces (Appendix C). For the U8-P habitat, these latter features were emphasized in both superficial and deep layers. This abundance of litter and feces in deep layers is consistent with the dysmoder humus form (Baize et al. 2009). *Oxalis* shaded in the spruce habitat (E2-PO) also showed a significant but different interaction with depth (Fig. 3). Shallow layers were placed in the moder area of HMFA, but with increasing depth, habitats and animals converged progressively toward those found in mull side. This trend was repeated itself regardless of the animal subset. Thus, E2-PO consisted of a typical moder habitat near ground level, but a mull habitat with depth. This also happens to be the description of the amphimull humus form (Baize et al. 2009). Lastly, *Luzula* shaded by spruce (U10-PL) only showed a poor interaction with depth.

Heath habitats had a poor dispersion around the barycentre (i.e., a weak interaction with depth; data not shown). E2-Vr (heath habitat rich in plant species) was found considerably left of the barycentre near the herb position, which is in agreement with the six MFAs analysis. This humus form was the only one among ericaceous habitats to show interactions with depth, being similar to what was observed for heath at layers below 3 cm and for herbs at the ground-level layer. HMFA placed E2-PV (bilberry heath shaded by spruce) in the heath area, just slightly closer to origin along axis 2.

The *Acer-Oxalis* habitats showed poor dispersion around the barycentre, confirming the lack of interactions with depth (data not shown). In contrast, *Rubus* and *Agrostis* habitats showed interactions with depth. Fig. 4 suggests that despite plant discrimination

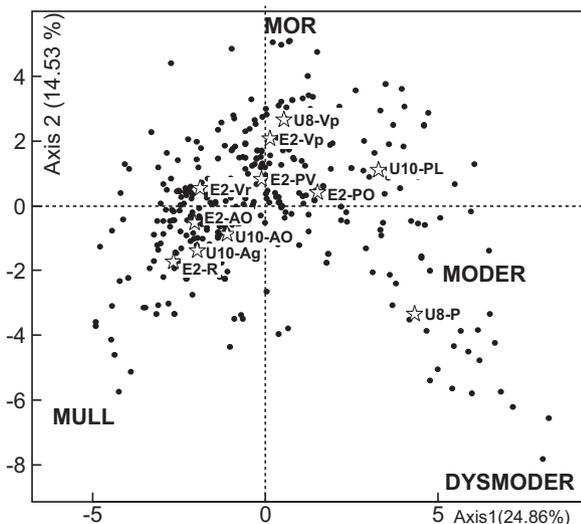


Fig. 1. Scatter plot of the 352 sampling points in the two first axes of HMFA for the 11 habitats.

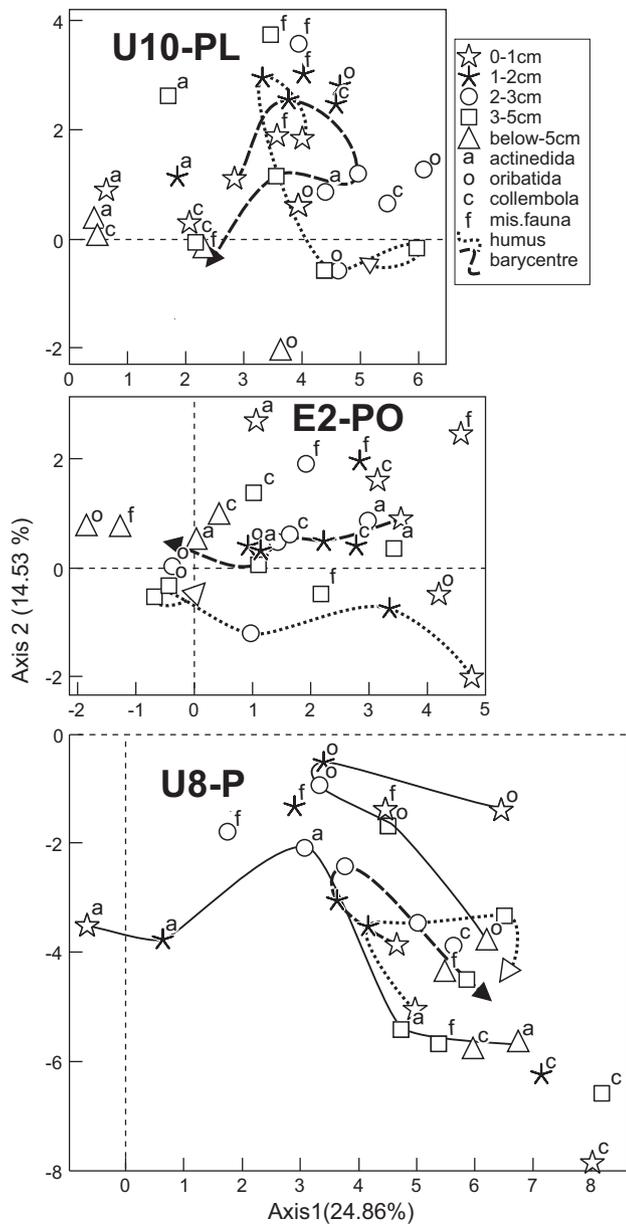


Fig. 3. Position of spruce habitats in the two first axes of HMFA according to depth and animal or humus groups.

(Fig. 2), *Rubus* and *Agrostis* habitats had the same humus characteristics. Near-ground-level samples were furthest in the herb direction and with increasing depth samples fell closer to the origin. Similarity between *Rubus* and *Agrostis* underground habitats was very high for Collembola and Oribatida even though the spreading around the barycentre was low for Collembola. For Actinedida and supra-family groups, similarity between the two habitats was high for the uppermost humus layers but weaker for deeper layers. This trend was also observed for humus composition but with depth the contrast was higher for U10-Ag than for E2-R.

As for several MFAs, the third HMFA axis showed contrast between unexploited and exploited parts of the forest (Fig. 5). For both humus and fauna, the contrast was higher on the herb side of axis 1 compared to the spruce side. Fig. 5 also shows that interactions between humus or animals groups and depth varied. For humus components, the contrast between U and E is highest at the 1 and 2 cm depth. For fauna, the contrast between E U and E was greatest for habitats below 3 cm.

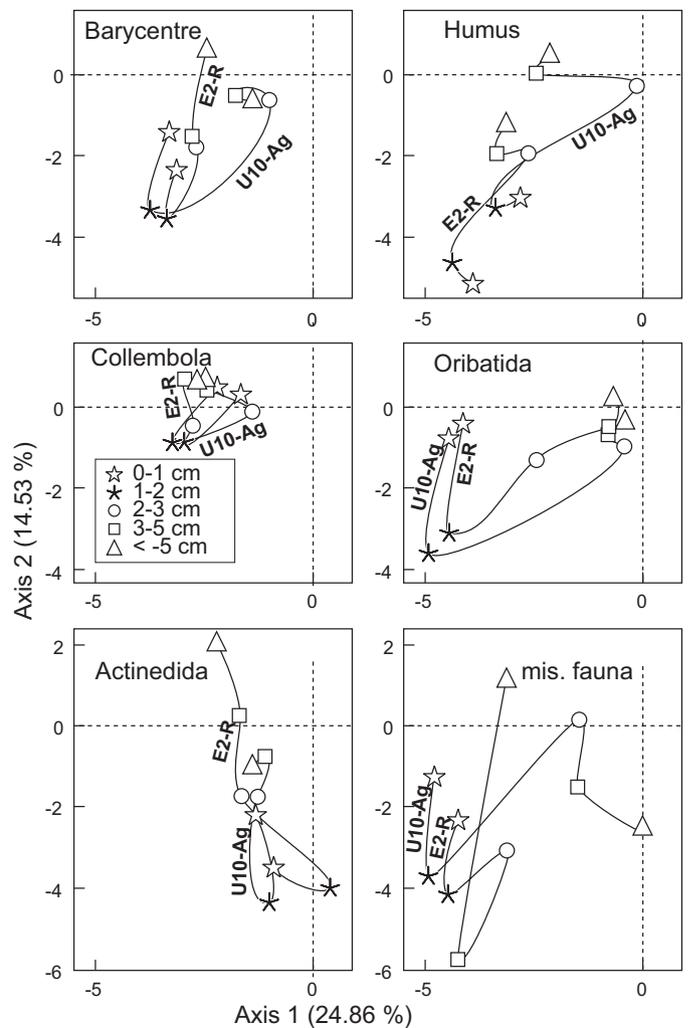


Fig. 4. Comparison of depth differentiation of *Rubus* habitat (E2-R) and *Agrostis* habitat (U10-Ag) in the two first axes of HMFA.

Animal taxa distribution showed two different trends. Animal taxa may be exclusive of a given habitat regardless of depth or may vary with depth (Fig. 6). *Achipteria*, *Mesaphorura tenuisensilata* and *Sciaridae* larvae are examples of dysmoder specific taxa. *Isoptoma saltans* is a moder specific taxa while *Tectocephus* illustrates a mor specific taxa (except in the deepest layers). The herb side of HMFA exhibited some nearly exclusive taxa such as *Oncopodura crassicornis*, *Malaconothrus* or *Chironomidae* larvae. For numerous taxa, animals discern mull from other humus forms, but only in the deepest humus layers (e.g., *Paurodora*, *Copepoda*, *Tardigrada*). HMFA showed differences on the mull side between humus layers (Fig. 4) and animals (Fig. 6). Near-ground humus layers were the furthest in the herb direction, but this mull branch is better characterized by deep-soil living fauna. The contrast between U and E parts of the forest corroborates this result. HMFA showed that mull was both characterized by its richness in minerals in upper layers and by the high level of biological activity in deeper layers. Except for the mull branch, interactions between humus form and depth were complex and mostly taxa specific. The optimum range moved toward dysmoder with increasing depth for *Oppiella*, but moved away from dysmoder for *Phyllhermania*. Several taxa, such as *Ceratozetes* mites, showed a complex relationship between depth and habitat. Lastly, some taxa like *Enchytraeidae* worms formed a curve from moder (ground level) by mor (at middle depth) to mull (below 5 cm depth).

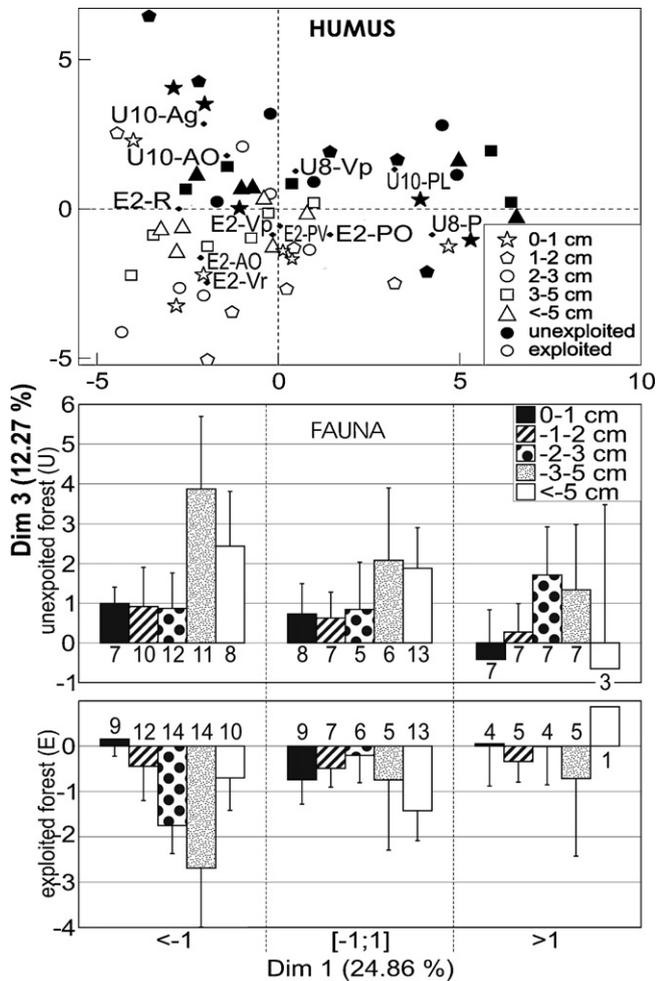


Fig. 5. Top: position of humus group in the plane of axes 1 and 3 of HMFA (same legend as Fig. 3). Bottom: mean and confidence interval of scores of the four animal groups in the third axis of HMFA grouped by first axis (3 classes) and forest parts (U or E). Numbers are size of each class.

Discussion

Among the various ordination methods available in the literature, MFA has rarely been used in ecology and the present study is the first application of HMFA to analyze structural relationships within complex ecological data. In contrast with frequently used multivariate methods, HMFA is concerned with both the symmetric relationship among homogeneous groups of variables and structural hierarchy among samples. This approach is motivated by the need to encompass the high number of interacting components within an ecosystem. The complexity of belowground subsystems is present in several ways such as scale, horizontal and vertical structure, diversity, and time relationships (Wardle 2002). In HMFA, variable groups provide an opportunity to be analyzed with coexisting components of the ecosystem but at individual scales or taxonomic groups. Hierarchy among sets recognizes the relative importance of the structural forces of the ecosystem such as depth gradient and spatial patterning. We demonstrate that, because of this type of resolution, HMFA simultaneously shows a broad and detailed view of interactions within an ecosystem using a low number of samples and a high number of descriptors. Indeed, given the low number of samples, our study is not adequate to study spatial heterogeneity, but our purpose was only to seek a common structure among matrices using HMFA. Combining HMFA with Fisherian methods such as spatially explicit sampling and structural equation modeling could help explain spatial structure.

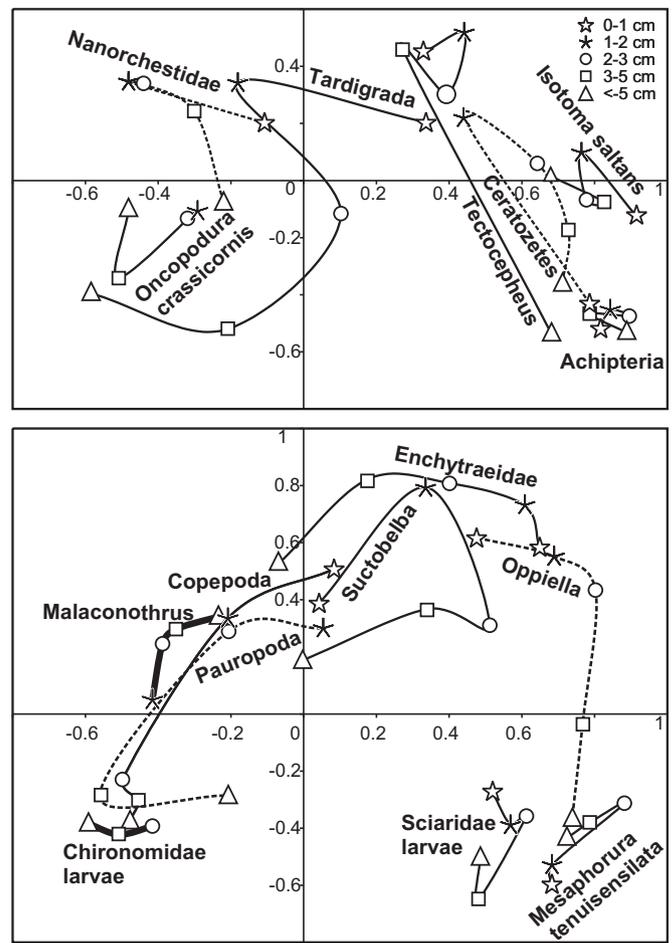


Fig. 6. Position of some animal taxa chosen among the most meaningful (cf. Appendix B) on the correlation circle to illustrate the variety of interactions with depth.

Very few studies reported such high soil animal density as we did – $3.6 \times 10^6 \text{ m}^{-2}$ (Forsslund 1948 in Ducarme et al. 2004: $2.9 \times 10^6 \text{ m}^{-2}$; Ducarme et al. 2004: $0.9 \times 10^6 \text{ m}^{-2}$). In agreement with Ducarme et al. (2004), we found that the density of arthropods is underrated by Berleze-Tullgren funnels, the technique used in most studies. MFA and HMFA show substantial consistency among plant community, soil fauna community and humus form that supports classical humus classification by Müller (1889), and confirmed by Hartmann (1944), Kubiens (1953), Klinka et al. (1981), Bernier and Ponge (1994) and Ponge (2003), namely, mull, moder and mor. For both plants and soil animals, mor humus does not represent the traditionally-held “extreme” humus form beyond moder, instead as suggested by Ponge et al. (2000), the “extreme” beyond moder is dysmoder. Although HMFA lends support to the mull–moder–mor model, our study also shows that plant–soil interactions are not as strong as expected compared to soil–soil interactions. Plant–soil interactions are even weaker when the soil component in question is deep. In addition, no evidence for plant–animal interaction was found (see RV coefficients, Table 1). The inconsistency between plant communities and humus habitats found in this study may be explained by the short-term variability of plant cover compared to belowground processes. The contrast that HMFA found between herb and spruce humus forms supports Ponge’s (2003) point of view concerning “the pattern (strategies) for capture and use of resources by ecosystems”. The richness in secondary metabolites (e.g., lignin, tannins, terpenes) is tightly linked to the life span of a plant or organ (Grime et al. 1997; Grime

1998; Aerts 1999; Aerts and Chapin 2000; Preston and Trofymow 2000). Mull is the habitat for a high number of plant species that are short-lived such as individuals or organs either present alive or as debris (Appel 1993; Schimel et al. 1996; Aerts and Chapin 2000). A consequence of the softness and high palatability of herb tissues is the high mineralization rate and the rapid incorporation of the humified fraction within hemioorganic casts (via earthworm or Enchytraeidae). Herbs and broadleaved trees produce an “improvable” litter (Fassnacht and Gower 1999; Preston and Trofymow 2000) and the humus form is typically a mull. In contrast, plant species (or organs) with extended turnover time such as spruce, accumulate secondary metabolites in their tissues (Aerts 1997) and produce a “detrimental” litter and a moder or dysmoder humus form. Rate and richness in plant secondary metabolites rather than plant diversity drives underground processes (De Bruyne et al. 1999). Single-species plant litter is able to support a food web as complex as mixed litter, which does not support the idea of an additive effect of litter on soil biodiversity (Hansen and Coleman 1998; Ball et al. 2009). Confirming the review by Schneider et al. (2004), we notice that Oribatida promoted in spruce litter are mostly primary decomposers (e.g., *Adoristes*, *Liacarus*, *Achipteria*, *Carabodes*, *Hoplophthyracarus*). In contrast, herbs promote inhabitants belonging to the organo-mineral food web such as Tardigrada, Copepoda, and Paupoda that mostly feed on microfauna and bacteria. Despite observations by Ducarme et al. (2004) that in forest ecosystems few taxa are exclusive to mineral horizons, mull habitat is not species poor. We hypothesize that animals are frequently enclosed within hemioorganic microporosity in mull humus, their extraction efficiency using Berleze-Tullgren method is lower compared to animals extracted from moder or mor humus types. This ultimately results in distortion.

In contrast to previous studies (Ponge 1993; Sadaka and Ponge 2003) and probably because of hierarchy, HMFA did not devote an axis to depth gradient. Nevertheless, careful examination of results shows that depth is a key criterion in distinguishing among humus forms (axis 1 and 2) and in understanding the factors involved in differentiating between exploited and preserved part of the forest. Indeed, HMFA is not a tool to describe the vertical structure of a single humus profile. Using U10PI as an example, HMFA considered, with a limited distinction of depths, that OL, OF, OH and OA layers are characteristic of eumoder irrespective of the difference between layers and sharpness of transitions. However, at closer investigation, the relative rightward position of the 2–3 cm depth layer (see U10PI humus profile, Fig. 3) highlights that the OF layer exhibits a higher diagnostic value. Regarding this result, HMFA supports findings of Green et al. (1993) who proposed the OF layer as a major diagnostic layer for moder because it is the place of litter transformation into animal fecal pellets. The diagnostic ability of HMFA may be refined focusing on one among the multiple factor of the analysis. For example, dysmoder litter (U8P) is specific in terms of both habitat and inhabitants except for Actinieda that partially shared populations with mull humus forms. With respect to mull humus forms, we suggest that diagnostic horizons could distinguish between habitats (the 1–2 cm layers) and inhabitants (the 3–5 cm layers for most of them) (Figs. 4–6). The discrepancy between fauna and humus groups indicates that the deepest humus layers were only minimally described.

Ponge et al. (2002) put forward a one-dimensional index to assess humus biological activity: the humus index. It focuses on the mull–moder contrast only. The mor humus form was discarded from this dichotomous perspective. In our study, we foresee numerous connections between the three humus forms. Thus, mor humus form is not a “dead-end.” HMFA showed that few soil fauna taxa are exclusively confined to a single humus form: most taxa are involved in several humus forms. The distinction between

humus forms applies mostly in the vertical amplitude of habitat. For example, Enchytraeidae worms are abundant in moder humus but most are near the surface; they are restricted to the middle depths in mor humus and only thrive in the lower depths of mull humus. Changes in humus form may bring both modification of habitat and in the food regime for a given taxa as confirmed by feces composition. Those modifications may or not be species specific.

Our study documents that the mull–moder–mor strategies of ecosystem may coexist at the small scale. A similar small-scale pattern was already found in mountain and subalpine forests (Bernier and Ponge 1994; Sagot et al. 1999) and also to a lesser extent in temperate forests (Ponge and Delhaye 1995; Aubert et al. 2006; Chauvat et al. 2007). We confirm the finding of Kallimanis et al. (2002), which shows that forest regional biodiversity stems largely from mechanisms of patch coexistence. Our results suggest that a high proportion of below- and above-ground diversity may depend on the variability of humus conditions within a forest mosaic (51.7% of the variance in our study) compared either to the variability below a single 25 cm² soil area (Giller 1996) or to the variability between two forests one kilometer away. Given its fine-scale structure, local diversity must be reallocated in the course of forest development (Christensen and Emborg 1996; Dufour et al. 2006). Our study strongly suggests that habitats are more continuous than expected for many animal taxa despite contrasting humus forms. Immigration-emigration fluxes among elements of the forest mosaic (Bernier and Ponge 1994; Bernier 1996; Ponge et al. 1998; Meiners et al. 2004) could still be key processes but this all-or-nothing perspective is likely neither the only nor the most frequent response in the face of forest dynamics.

In conclusion, HMFA demonstrates strong structural relationships between the six forest floor components investigated in this study. However, this result, supported by a small-size sample, now needs to be confirmed considering forest variability. HMFA did not show direct interactions between plant and soil fauna. However, paradoxically, HMFA also supported conclusions made by Wardle (2002) that indirect plant–fauna interactions are at the focal point of the ecosystem strategy that leads to the differentiation of ecological niches within the forest mosaic. Although limited, our analysis supports that among determinisms, humus form is central. Soil animals are known to be crucial for humus profile build-up, feeding either on litter and excreting hemioorganic fecal pellets (epigeic fauna) or feeding on soil and excreting mineral fecal pellets (endogeic fauna) (Zachariae 1965; Bernier and Ponge 1994). Vegetation also controls the humus form and the soil fauna via litter deposition and root absorption and exudation (Handley 1954; Northup et al. 1995; Hobbie 2000). Moreover, plants produce secondary metabolites (Robbins et al. 1987; Appel 1993) or shorten their biological cycle (Grime et al. 1997) to face interspecific competition or herbivory. In addition, soil animals have to cope with such an aggressive phytochemical environment (Provenza et al. 2003). The key question is whether or not the same set of molecules (i.e., the products of the secondary plant metabolism) governs plant–plant, plant–fauna and also fauna–fauna interactions (Ponge et al. 1998). Our work suggests that humus form may be at the center of all these interactions as suspected by Ponge (2003). Consequently, humus form is a key component of the ecosystem and should be considered to a greater extent in future studies on the fundamentals of diversity.

Acknowledgments

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Appendix A. Floristic composition of the sampled sites and correlations between MFA axes (i.e., all humus layers together) and species or supplementary variables (only correlations farthest from the axis origin are shown). Dominance codes are given according to Braun–Blanquet’s scale. All data are active in MFA with all humus layers together, except plant species richness and Shannon diversity.

	Dominance code										Correlation (×10)					
	U8-P	E2-PO	U10-PL	E2-PV	E2-AO	U8-Vp	E2-Vp	E2-Vr	U10-Ag	U10-AO	E2-R	Spruce (axis 1+)	Herb (axis 1–)	Heath (axis 3+)	Exploited (axis 2–)	Unmanaged (axis 2+)
<i>Abies alba</i>	+		+	+	+			1							5	
<i>Acer pseudoplatanus</i>			+	+	4					4			4			
<i>Adenostyles alliariae</i>		+		+												
<i>Agrostis schraderiana</i>			1						5					4		7
<i>Ajuga reptans</i>				+	2			+		2	1		5			
<i>Anthoxanthum odoratum</i>					+			1		+	1		5		3	
<i>Athyrium filix-femina</i>							+	+		2	4		4			3
<i>Blechnum spicant</i>		+	+	+		+										
<i>Calamintha grandiflora</i>		+							1	+						6
<i>Campanula rhomboidalis</i>		+		+	1			+			+		4			
<i>Deschampsia flexuosa</i>	1		2	1	1	2	1	1			1			4	4	
<i>Dryopteris carthusiana</i>		+	+	+	+											
<i>Dryopteris dilatata</i>		+				1					+					
<i>Dryopteris filix-mas</i>		+							+	3						5
<i>Epilobium angustifolium</i>							1	1	1					7		
<i>Fragaria vesca</i>					+			+					4			
<i>Galeopsis tetrahit</i>				+	+				+				4			
<i>Gentiana purpurea</i>			+			2								4		
<i>Geranium sylvaticum</i>				+	+			1	+	+	2		5			
<i>Gymnocarpium dryopteris</i>		+		+							+					
<i>Hieracium murorum</i>		+	+	1	1			1			1		6		5	
<i>Homogyne alpina</i>			1	2	1	1										
<i>Hypericum maculatum</i>					1			+			1		5			
<i>Knautia dipsacifolia</i>					1			1	+		+		4		5	
<i>Lotus corniculatus</i>					+						1		4			
<i>Luzula luzulina</i>				1		+	1			+	+			4	3	
<i>Luzula nivea</i>		+	1			+			+			5				3
<i>Luzula sylvatica</i>		+	4	1	+	1				+						
<i>Maianthemum bifolium</i>				+	+			+			+		4		4	
<i>Melampyrum sylvaticum</i>						+					+		3			
<i>Melica nutans</i>					+					+	+		6			
<i>Oxalis acetosella</i>		2	1	+	4					2	1		3			
<i>Phyteuma betonicifolium</i>			+	+				1			+				5	
<i>Picea abies</i>	5	5	5	2	1		+	1			1	6			3	
<i>Prenanthes purpurea</i>		3	2	2	2	+	+	1		+	1				4	
<i>Ranunculus nemorosus</i>								+			1		4			
<i>Ranunculus platanifolius</i>		1		+	1				1	+	1		5			
<i>Rosa pendulina</i>									2	2						8
<i>Rubus fruticosus</i>								1	1					6		
<i>Rubus idaeus</i>					+		1	+	2	2	4		4			5
<i>Rumex acetosa</i>		+			+											
<i>Sorbus aucuparia</i>				+					+							
<i>Vaccinium myrtillus</i>	+	2	1	4	1	5	5	5			1			5	7	
<i>Viola riviniana</i>		+		+	1								3			
Species richness	3	19	16	24	26	12	10	21	16	17	29		6			
Shannon diversity	1.0	4.1	5.0	5.6	7.9	3.3	2.5	5.6	4.2	7.2	8.0		8			

Appendix B. Mean fauna density and correlations between MFA (i.e., all humus layers together) and taxa or supplementary variables (only correlations farthest from the axis origin are shown). Taxa with density <200 m⁻² and detail for each sampled site are not shown. All data are active in MFA-total except total density, species richness and Shannon diversity.

	Density (1000 m ⁻²)	Confidence interval	Correlation (×10)					
			Spruce (axis 1+)	Herb (axis 1–)	Heath (axis 3+)	Unmanaged (axis 2+)	Exploited (axis 2–)	
Hexapoda, Collembola								
<i>Ceratophysella denticulata</i>	1.7	1.2						7
<i>Entomobrya quinquelineata</i>	0.6	0.4			8			
<i>Folsomia sensibilis</i>	8.7	11.0	9					
<i>Friesea mirabilis</i>	3.1	6.0	7					
<i>Isotoma saltans</i>	8.3	8.8	8					
<i>Isotomiella minor</i>	45.3	21.7				8		
<i>Lepidocyrtus lanuginosus</i>	1.8	1.0		7		3		
<i>Megalothorax minimus</i>	3.5	2.0			4			
<i>Mesaphorura hylophyla</i>	5.2	7.0						4
<i>Mesaphorura italica</i>	3.6	4.9	5					4
<i>Mesaphorura macrochaeta</i>	15.2	11.3						7
<i>Mesaphorura tenuisensilata</i>	21.9	30.8	8					
<i>Micranuridae pigmea</i>	2.7	2.2						
<i>Oncopodura crassicornis</i>	1.1	1.3		5				3
<i>Oligaphorura absoloni</i>	1.5	2.0	7					
<i>Parisotoma notabilis</i>	5.4	2.9				5		
<i>Protaphorura cancelata</i>	9.3	6.8	5					
<i>Pseudanurophorus binoculatus</i>	2.1	1.4			3			
<i>Sminthuridae</i> spp.1	0.3	0.4			5			
<i>Vergatopus montana</i>	0.8	1.0				5		
<i>Willemia anolphthalma</i>	4.3	4.5	9					
<i>Willemia aspinata</i>	1.2	0.9						
<i>Xenylla boernerii</i>	0.5	0.9						
Collembola: total density	149.3	81.9	8					
Collembola: richness	15.9	1.4	5					7
Collembola: diversity	6.7	1.4						8
Acarina, Actinedida								
<i>Alicorhagiidae</i>	18.6	19.0	8					
<i>Anystidae</i> spp.1	0.3	0.3	5					
<i>Anystidae</i> spp.2	0.3	0.4			5			
<i>Anystidae</i> spp.3	0.7	1.3			3	6		
<i>Bimichaeliidae</i>	2.9	1.7	5					4
<i>Ereynetidae</i>	0.3	0.2						
<i>Eupodidae</i> spp.1	6.2	3.6	9					
<i>Eupodidae</i> spp.2	0.3	0.3			5	5		
<i>Eupodidae</i> spp.3	4.3	2.9	5					
<i>Nanorchestidae</i>	5.7	3.8		5				5
<i>Rhagidiidae</i> spp.1	7.2	5.2	10					
<i>Rhagidiidae</i> spp.2	4.0	3.1	9					
<i>Scutacaridae</i>	0.9	0.8						
<i>Tarsonemidae</i>	0.2	0.3		3		5		
<i>Tetranychidae</i>	1.0	1.0			5	6		
<i>Tydeidae</i> spp.1	16.1	21.1	6					4
<i>Tydeidae</i> spp.2	5.1	3.3				7		
<i>Tydeidae</i> spp.3	0.7	0.6						
<i>Tydeidae</i> spp.4	0.3	0.4			6			
<i>Tydeidae</i> spp.5	13.1	17.4	6					5
Actinedida: total density	89.3	67.2	9					
Actinedida: richness	13.9	1.6			4			5
Actinedida: diversity	7.9	1.2			5			4
Acarina, Oribatida								
<i>Adoristes</i>	0.5	0.6	5					
<i>Achipteria</i>	10.8	13.3	8			3		
<i>Atopochthonius</i>	0.7	1.0			4			6
<i>Austrocarabodes</i>	0.3	0.4						3
<i>Autogneta</i>	1.4	2.1			5			
<i>Carabodes</i> spp.1	12.3	9.9	9					
<i>Ceratozetella</i>	0.3	0.4		3		8		
<i>Ceratozetes</i>	18.1	24.4	8					
<i>Chamobates</i>	9.1	6.9	8		3	3		
<i>Ctenobelba</i>	1.9	2.1						5
<i>Cymbaeremaeus</i>	0.7	0.4	7			5		
<i>Epidamaeus</i>	0.4	0.4	9					
<i>Eulohmannia</i> spp.2	1.6	1.4		3	6			5
<i>Eupelops</i>	0.3	0.2				5		

Appendix B (Continued)

	Density (1000 m ⁻²)	Confidence interval	Correlation (×10)				
			Spruce (axis 1+)	Herb (axis 1–)	Heath (axis 3+)	Unmanaged (axis 2+)	Exploited (axis 2–)
<i>Hoplophthiracarus</i>	0.8	0.5	7				
<i>Liacarus</i>	1.9	2.0	9				
<i>Malaconothrus</i>	26.0	33.6		3	4		6
<i>Melanozetes</i>	0.4	0.8					
<i>Nanhermannia</i>	8.8	17.0					
<i>Neomycobates</i> spp.1	1.0	1.1			4		
<i>Oppiella</i>	121.3	136.1	9				
<i>Oribatula</i> spp.2	0.4	0.5				5	
<i>Oribella</i>	0.7	1.2				6	
<i>Palaeacarus</i>	0.7	0.4		7			
<i>Phyllhermannia</i>	6.7	8.9					
<i>Platynothrus</i>	1.2	1.5		4			5
<i>Quadroppia</i>	2.0	2.0					
<i>Suctobelba</i>	11.9	6.1			5	6	
<i>Tectocepheus</i>	12.3	9.8			5	3	
<i>Zygoribatula</i>	0.3	0.5					
Larvae	331.1	250.9	7				3
Oribatida: total density	587.0	410.7	8				
Oribatida: richness	17.6	1.4			8		
Oribatida: diversity	6.1	1.4		6		7	
Acarina Acaridida							
<i>Acaridae</i> spp.1	1.0	0.9		3			
<i>Acaridae</i> spp.2	0.7	0.3					
<i>Acaridae</i> spp.3	0.6	0.5					6
Acarina Gamasida							
<i>Gamasina</i>	22.3	10.4	7			6	
Miscellaneous	5.5	1.5				8	
<i>Uropodina</i>	0.3	0.3				4	
Myriapoda							
<i>Diplopoda</i>	0.3	0.3				6	
<i>Pauropoda</i>	9.0	4.2					
<i>Symphyla</i>	2.3	2.2		4			4
Diptera (larvae)							
<i>Cecidomyiidae</i>	2.3	1.8	6				
<i>Chironomidae</i>	1.0	1.3		5			
<i>Empididae</i>	0.5	0.5	5				
<i>Sciaridae</i>	5.5	5.8	6				4
Miscellaneous	0.5	0.2				4	
Araneae	0.3	0.2	5		3	4	
Crustacea, Copepoda	3.7	4.5		3		7	
Hexapoda, Diplura	1.1	1.3	7				4
Hexapoda, Protura	32.7	19.4	7				
Olichochaeta, Enchytraeidae	103.9	46.6			8		
Olichochaeta, Lombricidae	0.5	0.5					3
Platyhelminthes, Turbellaria	0.6	0.6				4	
Tardigrada	12.0	9.2		5			
Insecta							
<i>Coleoptera</i> (larvae)	0.9	0.4	5				
<i>Homoptera</i> (aphids)	10.8	7.7	6			5	
<i>Thysanoptera</i>	0.3	0.2			5		
<i>Diptera</i> (imago)	1.0	0.6	6				
Fauna: total density	1050.3	564.8	9				
Fauna: supra-family richness	22.3	2.1					5
Fauna: supra-family diversity	5.5	1.1		6		5	

Appendix C. Humus composition of the sampled sites (% in volume), supplementary variables and correlations with MFA axes (i.e., all humus layers together). Only correlations farthest from the axis origin are shown. All data are active in MFA except *.

	U8-P	E2-PO	U10-PL	E2-PV	E2-AO	U8-Vp	E2-Vp	E2-Vr	U10-Ag	U10-AO	E2-R	Correlation ($\times 10$)					
												Spruce (axis 1+)	Herb (axis 1–)	Heath (axis 3+)	Exploited (axis 2–)	Unmanaged (axis 2+)	
Lichen	2											7					
Spruce																	
Intact needle	2	4	10		1	1	1		1	2		7					3
Bleached needle	3		7				1					7		4			
Perforated needle	2	2	8		1							7					
Fragmented needle	13	6	12	3	2	1	1		1		2	7					
Twig	3	1	2	1						1		6					
Bark	10	1	1	14	1	2	2		1	1		9					
Scale	5	1	3	2		1	1			1		8					
Root	20	8	24	11	1	8	4	2	3	5	1	9					
Moss		2	9	1	3	1	1	3	4	1		3	5			4	
Bilberry																	
Intact leaf							1							7			
Leaf nervure			1			1	5	1	2					9			
Twig						3	2	3						7		4	
Root			1			9	8	6			1			7		4	
Herb litter*			1	5		2		19	16	0		4		6			
Herb root*			2	6	3	2	7	24		4		6	4				
Fern litter*									3	14		4					
Hemiorganic feces																	
Diptera larva	28											7					
Diplopoda	2	1	2	1			6		1	1		5					3
Enchytreid	5	1	24	9		5	15		5	6		6		5			3
Organo-mineral feces																	
Enchytreid		14	2	20	5	10	21	24	7	19	5		7				
Earthworm	1	37		15	37	12	1	27	11	15	26		7				
Compact mineral material	2		2	4	19	5	6	3		7		6		5			
Stone	21		9	34	12	14	21	4	4	20		8		5			
Forest regime*																8	
																	8
													8				
												9					
Plant ecology*													7				
													7				
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