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1 **Horizons and humus forms in beech forests of the Belgian Ardennes**

2
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17

Horizons and humus forms in beech forests of the Belgian Ardennes

ABSTRACT

Forest soil organic horizons are named on the basis of visual observations made directly in the field, thus this is often subjective. Humus form horizons were compared in thirteen beech stands (*Fagus sylvatica* Ehrh.) of the Belgian Ardennes (western Europe) embracing a wide range of ecological conditions, in order to find more objective bases for their classification. We used a semi-quantitative micromorphological method for the description of horizons, and a multivariate method for data analysis. These methods helped to discern objective discontinuities between Oi, Oe and Oa horizons, adding new criteria for their characterization, such as the root system of trees. Within these horizons, transitions between sub-horizons are gradual, thus do not lie on clear-cut criteria. The transition between Oa and A horizons was also gradual. The composition of Oa and A horizons varies according to humus form. The vertical distribution of soil organisms and their vertical movements were considered the origin of discontinuous and continuous processes taking part in the transition from one horizon to another. The observation of horizons under a dissecting microscope may help to find more reliable bases for their nomenclature, even without the use of costly soil sections.

INTRODUCTION

1
2
3 Since the pioneering work of Müller (1889), who described two basic humus forms, mull and torf,
4 beneath Danish beech forests, on the basis of microscopic observations, there have been many attempts
5 to classify humus profiles in forest soils. Different horizons or sub-horizons are generally recognized
6 within the O Horizon (Brady, 1984) or Ao (Duchaufour, 1997) horizon. Although discrepancies concerning
7 the terminology of these strata exist, three main strata are recognized, Oi (entire leaves), Oe (fragmented
8 leaves), and Oa (holorganic faecal pellets). Differences in the development of these horizons, together
9 with structure and chemical properties of the underlying A horizon, allow recognition of three main humus
10 forms, now called mull, moder, and mor (Klinka et al., 1981; Delecour, 1983; Green et al., 1993; Brêthes
11 et al., 1995; Jabiol et al., 1994, 1995). The mor humus form, together with dysmoder (moder with a thick
12 H stratum), has been also called raw humus (Kubiëna, 1953; Delecour, 1980). The recognition of
13 biological processes taking place in the development of humus profiles (Hartmann, 1965; Zachariae,
14 1965; Bal, 1982) suggested that some features, such as compaction of the soil matrix, deposition of
15 faecal pellets, skeletonization of leaves or tunnelling of needles, are the direct result of soil faunal activity.
16 Thus, as for most biological processes, the transition from one horizon to another should be considered
17 discontinuous, due to tolerance limits and food and habitat preferences of soil organisms.

18
19 Characterization of organic horizons and humus forms on the basis of morphological features is
20 common; however, the existence of clear-cut changes between one horizon and another has been poorly
21 demonstrated through quantitative or semi-quantitative morphological data. Federer (1982) pointed out
22 that simple remeasurements of thickness of forest soil horizons may lead to false conclusions if done by
23 two individuals. Discrepancies between field and laboratory observable features of horizons have been
24 reported (Bernier et al., 1993). This may indicate that some morphological criteria used for the definition
25 of organic horizons are inadequate or difficult to employ with accuracy in the field. This is particularly true
26 for the transition from Oa to A horizons and for subdivisions which have been recognized within Oi and
27 Oe horizons (Babel, 1971).

1
2 In the present study, our purpose was to determine whether the transition from one organic
3 horizon to another is a continuous or, rather, a step-by-step process, with sharp delineations in horizon
4 properties. In doing so, we addressed the question as to whether horizons exhibit true emergent
5 properties and have not been created by soil scientists for only classification purposes.
6

8 MATERIAL AND METHODS

10 Nomenclature

11
12 Comparable organic horizons have several different names depending on the taxonomic system
13 in use. The commonly used nomenclature of Brêthes et al. (1995) corresponds to USDA nomenclature as
14 follows: OL equals Oi, OF equals Oe, and OH equals Oa. These horizons correspond to L, F and H
15 horizons, respectively, recognized by Hesselmann (1926) and later refined by Babel (1971).
16

17 The classification of humus forms by Brêthes et al. (1995) was used in this study. It is not based
18 on a strong relationship between the features O and A horizon, as this is the case in other classifications.
19 For instance, a crumbly A horizon (typical of mull) may coexist with a thick O horizon (typical of moder).
20 Some humus forms, such as hemimoder and amphimull, were described by other authors as mull-moder
21 (Duchaufour, 1997) or mull-like moder (Kubiěna, 1953; Delecour, 1980, 1983). A hemimoder means a
22 moder humus form (A horizon with organic matter juxtaposed to mineral matter) without any Oa horizon.
23 An amphimull means a mull humus form (A horizon with organo-mineral assemblages) with a distinct Oa
24 horizon.
25

26 The nomenclature of soil types used in this study followed the FAO-UNESCO classification
27 (Driessen and Dudal, 1991). Cambisols and podzols correspond to Inceptisols and Spodosols,

1 respectively, in USDA Soil Taxonomy (Brady, 1984). Nomenclature of plant species followed Rameau et
2 al. (1989).

3 4 **Study sites**

5
6 Thirteen mature beech stands were selected in the Belgian Ardennes, covering a wide range of
7 humus forms (Table 1). Beech (*Fagus sylvatica*) forests were chosen because of their wide distribution
8 and the need for a wide range of environmental conditions, in particular soil and climate, without strong
9 variation in the composition of litter. All studied sites were located on nutrient-poor geological substrates
10 (schists, graywackes, quartzites) ranging from Cambrian to Devonian age. Altitude and related regional
11 factors (climate, mineral richness of parent rock) were found to be the main source of variation of soil
12 animal communities, humus forms and site quality over the studied range (Ponge et al., 1997). Results of
13 litter and soil chemical analyses were also reported in the aforementioned paper.

14 15 **Categories of the soil matrix in humus horizons**

16
17 At each site, two humus profiles were sampled for micromorphological description of horizons.
18 These profiles were chosen to represent the range of observed within-site variation of humus forms.
19 Sampling was completed in June 1989. Preparation of the samples (5 x 5 cm section monoliths) was
20 carried out according to the method of Bernier and Ponge (1994), except that only the top 1 cm of the A
21 horizon was sampled. Horizons were separated in the field on the basis of variation visible to the naked
22 eye, without reference to any *a priori* classification. Afterwards, they were classified into Oi, Oe, and Oa
23 horizons according to the abovementioned field criteria, and numbered according to their order from the
24 top to the bottom of a given horizon, i.e. Oi1, Oi2, Oi3, Oe1, Oe2, etc... All 172 horizons were immediately
25 immersed in ethyl alcohol then transported to the laboratory. The composition of each horizon was
26 analyzed by observing the soil matrix in alcohol under a dissecting microscope. No attempt was made to
27 quantify the volume or mass of each category. Rather, we used the following visual semi-quantitative

1 coding of the abundance of a given category in a given horizon:

2

3 absent 0

4 present but scarce 1

5 present and common 2

6 present and dominant 3

7

8 A total of 185 categories were recognized. Most of them were plant litter, in varying degrees of
9 decomposition or comminution by fauna. Animal faeces were classified according to the corresponding
10 animal group, their degree of comminution by other animals, and their degree of connection with uneaten
11 plant categories. Animals were counted and classified into broad groups.

12

13 **Multivariate analysis**

14

15 Correspondence analysis (Greenacre, 1984) was used to give an overall picture of affinities and
16 differences between horizons and/or categories. This method, using the chi-square distance, allows
17 horizons and categories to be simultaneously projected on factorial axes, thus groups of samples could
18 be directly associated with groups of categories. As was theoretically developed by Benzécri (1973), this
19 method has been refined for particular purposes such as community gradient analysis [detrended
20 correspondence analysis (Hill and Gauch, 1980)] or the study of community-environment relationships
21 [canonical correspondence analysis (Ter Braak, 1987)]. Here, our purpose was to analyze the structure of
22 a data matrix (the composition of horizons) without any a priori hypotheses concerning their relationships
23 with environmental factors and with more than one single factor suspected to result from the analysis.
24 Additional (passive) variables were used to help interpretation of the factorial axes and not to quantify
25 causal relationships. Thus, we used the approach of original correspondence analysis, that was devised
26 to evaluate global patterns underlying complex data matrices, and not that of the aforementioned derived
27 methods.

1

2 Matrices were analyzed so that horizons were observations (rows) and categories were active
3 variables (columns). Animal groups, horizon names, humus form names, phytosociological types, and
4 altitude were added as passive variables. They had no influence on the results, but they were projected
5 on factorial axes as the active variables.

6

7 Categories were coded and counted as indicated above. Animal groups were recorded as total
8 counts. Horizons, humus forms and phytosociological types were coded as 1 when a given horizon (row)
9 belonged to a given category (column), 0 when not. Altitude was recorded in meters. All variables (active
10 and passive) were standardized with unit variance and a mean of 20. This allowed contributions to
11 factorial axes to be proportional to factorial coordinates and data of a different nature, such as counts,
12 semi-quantitative coding and measurements, to be included in the same analysis (Ponge and Delhayé
13 1995). In the case of altitude, high elevation and low elevation were distinguished. Standardized altitude
14 values (high elevation) were complemented to 40 in order to create a new variable, varying in an opposite
15 sense (low elevation). The new variable had similar mean (20) and standard deviation (1). Following this
16 procedure, already used by Ponge and Delhayé (1995), the range of elevation values was described by
17 two symmetrical points.

18

19

20

RESULTS

21

22

Composition of the humus profile

23

24 We analyzed first the total 172 horizons and 185 categories. Only axes 1 and 3 were considered
25 for the global description of humus horizons. Axis 2 was neglected, because it isolated only one horizon
26 (Oe1 in the second profile studied in site 16), which was characterized by the development of the root
27 system of hair-grass (*Deschampsia flexuosa*) at the inside of decaying plant fragments. This development

1 was not apparent in other humus profiles, due to scarcity of ground vegetation, and we preferred to
2 discard the corresponding axis rather than to discard this horizon from the analysis.

3

4 The projection of horizons in the plane of axes 1 and 3 (Fig. 1) indicated that they could be
5 classified into three groups, corresponding to Oi, Oe, and Oa+A horizons, respectively. All horizons
6 sampled did not fall exactly in each of the three branches depicted by the plane of axes 1 and 3. This
7 does not indicate that Oi, Oe, and Oa+A horizons were poorly differentiated on the basis of their
8 composition. Rather, this phenomenon indicates that a few horizons had been badly classified in the field;
9 correspondence analysis revealed that they had more points in common with another group than with
10 their own group. Differences between Oa and A horizons were negligible when compared with differences
11 between Oi and Oe horizons. Oa and A horizons did not exhibit distinct branches. In addition, differences
12 within each of the Oi, Oe or Oa horizons were negligible compared to differences between these
13 horizons.

14

15 The projection of categories in the plane of axes 1 and 3 (Appendix 1) allowed us to characterize
16 each horizon or group of horizons by its composition (Table 2). The Oi horizon was characterized by
17 entire leaves of beech at varying stages of fungal conditioning and small recently fallen tree categories
18 such as bud scales, male flowers, and twigs. Smears of faecal material, holorganic or organo-mineral,
19 were observed at the surface of some beech leaves. A laminated mixing of leaf fragments and faeces of
20 litter-consuming enchytraeids, which we called "sandwich material", together with plant categories such
21 as male flowers of beech, grass stems, twigs, at some stage of decomposition, was characteristic of the
22 Oe horizon. The presence of beech petioles and nerves, mycelial strands and living bases of wood-rush
23 (*Luzula forsteri*) was also noticeable. Both Oa and A horizons were characterized by dead or senescent
24 fine roots, living and dead woody roots, old (compacted) holorganic enchytraeid faeces, and fragments of
25 parent rock (both intact or weathered). Charcoal was also present in this group of horizons. Sclerotia of
26 the mycorrhizal ascomycete *Cenococcum geophilum* also occurred.

27

1 Living fine roots of beech and faeces of litter-consuming enchytraeids were placed in an
2 intermediate position between the Oe horizon and the Oa+A horizons. This indicated that they were
3 present in all of these horizons and, thus, they did not help in differentiating among horizons. Maple (*Acer*
4 *pseudoplatanus*) and ash (*Fraxinus excelsior*) plant materials were different. These categories only
5 occurred at one site (100) which was characterized by an intense earthworm activity, with abundant cast
6 deposition within the Oi horizon (Fig. 1). The projection of corresponding samples was influenced by the
7 presence of organo-mineral material (typical of the A horizon of mull humus) together with categories
8 typical of the Oi horizon, which influenced in turn the position of the abovementioned ash and maple
9 categories.

10

11 Oa and A horizons, which were considered as diagnostic horizons for the separation of mull
12 versus moder humus forms (Delecour, 1983; Brêthes et al., 1995), were not clearly separable on the
13 basis of composition as revealed by the use of a dissecting microscope. In order to reveal possible
14 variation in the composition of these horizons, we analyzed separately Oa and A horizons (partial
15 analysis). The projection of horizons in the plane of axes 1 and 2 (Fig. 2) separated Oa and A (classified
16 by field observation), but with a high degree of overlapping. This indicated that the distinction between Oa
17 and A horizons that had been made in the field (Oa = holorganic, A = organo-mineral) did not reflect true
18 composition. The projection of some passive variables such as humus form, altitude and
19 phytosociological type (Fig. 3) helped to establish a link between Axis 2 of partial analysis and ecological
20 conditions prevailing in the studied sites. Mull humus forms were on the negative side of Axis 2; moder
21 humus forms were placed on the positive side of Axis 2.

22

23 The composition of Oa and A horizons, as indicated by the projection of categories in the plane of
24 axes 1 and 2 of partial analysis (Appendix 2), depended on the humus form. The Oa horizon of moder
25 humus forms (eumoder, hemimoder and dysmoder) was mostly characterized by compacted holorganic
26 faeces of enchytraeids, different plant organs hard to decay, bundles of skeletonized beech leaf
27 fragments, living woody roots of beech, and dead black mycorrhizae of beech produced by *Cenococcum*

1 *geophilum*. The upper part of the A horizon of mull humus forms (oligomull, amphimull, dysmull) was
2 mostly characterized by organo-mineral earthworm faeces, milliped faeces, intact stones, beech leaves
3 skeletonized by macrofauna or mesofauna and categories belonging to ground vegetation such as the
4 root system of grass species or bleached leaves of wood-sorrel (*Oxalis acetosella*). The Oa horizon of
5 amphimull shared many features with the A horizon of the mull group (indicated by its position on the
6 negative side of Axis 2). The A horizon of the moder group was placed in an intermediary position (not far
7 from the origin, on both sides of Axis 2), thus without characteristic features distinguishing both the
8 horizon and the humus form.

9 10 **Distribution of soil animals**

11
12 Animal groups found during the dissection of humus horizons (Table 3) were projected as passive
13 variables in the plane of axes 1 and 3 of total analysis (Fig. 4). Comparison with the position of horizons
14 (Fig. 1) revealed that the Oi horizon was very poor in fauna at the time of sampling (June), no animal
15 group being placed far from the origin in the direction of the Oi horizon (see also Table 3). The Oe
16 horizon was characterized by mites other than *Platynothrus peltifer* (MIT, ORI, PHT) and springtails
17 (SPR), the latter being present at a greater depth than the former as ascertained by the respective
18 position of corresponding points along Axis 1. The only group that characterized the Oa+A horizons was
19 enchytraeids (ENC). Enchytraeids mainly characterized the Oa horizon, as it appeared from the
20 comparison of Oa and A horizons (Fig. 5, Table 3). Most fauna (here mostly mesofauna) were
21 concentrated in the Oe and Oa horizons, the most abundant group being enchytraeids, followed at a far
22 lower level of abundance by mites and springtails, with an increasing preference for deeper horizons at
23 the time of sampling in the order mites < springtails < enchytraeids.

24 25 26 **DISCUSSION AND CONCLUSION**

27

1 The existence of a transitional horizon between typical Oa and A horizons, due to a progressive
2 enrichment in mineral particles of the Oa horizon, has been suggested by Delecour (1980, 1983). He
3 even considered it as a characteristic feature of the humus forms belonging to the moder group, rather
4 than the accumulation of holorganic faeces in Oe and Oa horizons which is commonly used to define
5 moder humus (Klinka et al., 1981; Green et al., 1993, Duchaufour, 1997). This feature is also used in the
6 classification of forest humus forms by Brêthes et al. (1995) where the A horizon of moder humus forms is
7 considered to be made of holorganic faeces juxtaposed to mineral particles, without true incorporation of
8 organic matter to mineral matter. This composition can be achieved by the vertical movements of small
9 animals carrying mineral particles onto their tegument and depositing them, together with faeces, in the
10 course of their wandering between food sources (Oe horizon) and refuges (Oa and A horizons). In moder
11 humus forms, where no other agent mixes organic matter with mineral matter, this behaviour is typical of
12 animals with a sticky tegument such as enchytraeid worms (Ponge, 1991), whose daily vertical
13 movements of several centimeters are well-known (Springett et al., 1970). In this case the gradual
14 passage from the Oa to the A horizon can be interpreted as an active (biological) diffusion process, the
15 source of organic matter being decaying litter, which is actively consumed by these animals and humified
16 (Ponge, 1991), and the source of mineral matter being underlying mineral horizons. As has been
17 observed in other studies (Zachariae, 1965; Ponge, 1991) enchytraeids also consume faeces of other
18 animals such as oribatid mites. As they live deeper (on average) than other litter-dwelling animals (Table
19 3) they progressively incorporate faeces of litter-consuming animals into their own faecal material. This
20 may explain why the Oa horizon of moder humus forms appears mainly made of compacted enchytraeid
21 faeces and unconsumed material rather than remains of the activity of all litter-feeding animals. They also
22 ingest silt particles (unpublished data), and carry them onto their tegument (Ponge, 1988). This pattern
23 may lead to the observed soft transition from Oa to A horizons.

24

25 The presence of clear discontinuities between Oi and Oe horizons and between Oe and Oa+A
26 horizon, and the absence of clearcut subdivisions within them, may be explained by threshold levels in
27 the vertical distribution of soil animals and other organisms. We cannot speculate from our data about the

1 depth levels at which animals consume litter and defecate at any time of the year, and about all the
2 factors which govern these patterns. Nevertheless, it can be inferred from existing literature that the
3 vertical distribution of soil fauna is determined, among others, by i) genetically fixed behavioural features
4 (Stevenson and Dindal, 1982; Kretzschmar, 1984), ii) ecophysiological requirements of animals (Atalla
5 and Hobart, 1964; Haukka, 1987), iii) the stage of decomposition of litter (Hayes, 1963; Soma and Saitô,
6 1983; David, 1986). For instance, if we take into account only leaf litter as a food, the depth level at which
7 animals will consume it can be interpreted as a compromise between the need for food of a high
8 nutritional value such as freshly fallen litter (Soma and Saitô, 1983), the toxicity or repellence of some
9 compounds present in undecayed litter (Satchell and Lowe, 1967), and the search for better micro-climate
10 conditions (Joosse, 1971). If we examine diagnostic features of Oi and Oe horizons as ascertained in our
11 analysis (Table 2) it appears that the passage from Oi to Oe horizon is characterized by the deposition of
12 faeces of small litter-consuming animals, such as oribatid mites and enchytraeids, these categories being
13 near absent in the Oi horizon.

14

15 The passage from the Oe to the Oa+A horizon is marked by the appearance of the root system of
16 beech (Table 2). This creates a new discontinuity along the humus profile. According to the humus form,
17 the feeder root system of beech will develop throughout accumulated organo-mineral earthworm faeces
18 (A horizon of mull humus) or holorganic enchytraeid faeces (Oa horizon of moder humus). This common
19 feature is probably the main reason for the absence of a clear distinction between Oa and A horizons in
20 the global analysis (Fig. 1). From existing literature, it can be concluded that the vertical distribution of
21 root tips is strongly influenced by humus form horizons and the humus form itself (Meyer and Götsche,
22 1971; Persson, 1983; Harvey et al., 1986; Ponge, 1988; Bernier and Ponge, 1994). These results point
23 out that the upper part of the Oa horizon together with the bottom of the Oe horizon is the main micro-site
24 for mycorrhizal root development in moder humus forms, mull humus forms being characterized by a
25 lower number of root tips which are widely distributed throughout the A horizon. Unfortunately
26 mechanisms which could explain these patterns are poorly understood, although the need for available
27 water and nutrients has been advocated as a reason for the preferential development of feeder roots in

1 carbon-rich substrates (Persson, 1983).

2

3 As this is now well-admitted the genesis of humus form horizons, and thus of humus forms, is
4 placed under the influence of microflora, fauna, and plant subterranean parts, whose activity is
5 determined by climate, parent rock and quantity and quality of vegetation (Kubiëna, 1955; Bal, 1982;
6 Toutain, 1987; Green et al., 1993; Brêthes et al., 1995). The existence of horizons, not for the purpose of
7 classification, but as a discernable entity, with clear emergent properties, can be understood if we take
8 into account the accumulation through time of key categories with a high longevity. This is the case for
9 dead leaves, enchytraeid faeces, earthworm faeces, or fine roots of trees. If a category present in a given
10 horizon has a low longevity, i.e. if it is rapidly transformed into another category or if it disappears from
11 the soil matrix through mineralization or leaching, then it cannot directly participate in the building of this
12 horizon. Rather, it may, i) participate in the building of underlying horizons (for instance colloidal organic
13 compounds precipitating in B horizons), ii) be taken-up by organisms, iii) diffuse in the atmosphere or in
14 the water flow. This is the case, among others, of oribatid faeces which rapidly disappears from the
15 moder profile when consumed by enchytraeids (Ponge, 1991). This is also the case for enchytraeid
16 faeces when ingested in turn by earthworms living in mull humus (Bal, 1982). The passage from one
17 horizon to another should thus be considered as a check in a continuous process (the slow maturation of
18 individual categories in the absence of disturbances), and a start for another continuous process of
19 maturation. The fact that at a given depth level the bulk of categories of a given type are transformed into
20 categories of another type (due to the activity of vertically distributed organisms) will create discontinuities
21 visible to the naked eye and thus will help us to distinguish horizons and humus forms on the field. In the
22 absence of these discontinuities (as between Oa and A horizons of moder humus forms) this distinction
23 may be more difficult and field observation may lead to false conclusions, as has been always suggested
24 by Bernier et al. (1993). In this case the identification of horizon components under a dissecting
25 microscope and the use of counting methods (Bernier et al., 1993; Bernier and Ponge, 1994) may help a
26 better characterization of these horizons.

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LEGENDS OF FIGURES

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Fig. 1. Results from total correspondence analysis of organic horizons with faunal characteristics in beech forests of the Belgian Ardennes. Projection of horizons (rows) in the plane of axes 1 and 3. Indicated names of horizons were based on field observation and were not included as main variables.

Fig. 2. Partial correspondence analysis on Oa and A horizons. Projection of horizons (rows) in the plane of axes 1 and 2. Otherwise as for Fig. 1.

Fig. 3. Partial correspondence analysis on Oa and A horizons. Projection of passive variables in the plane of axes 1 and 2. (*festuc* = *Luzulo-Fagetum festucetosum*; *melic* = *Melico-Fagetum festucetosum*; *typic* = *Luzulo-Fagetum typicum*; *vaccin* = *Luzulo-Fagetum vaccinietosum*).

Fig. 4. Total correspondence analysis. Projection of animal groups (passive variables) in the plane of axes 1 and 3. Coding of animal groups as in Table 3.

Fig. 5. Partial correspondence analysis on Oa and A horizons. Projection of animal groups (passive variables) in the plane of axes 1 and 2. Otherwise as for Fig. 4.

Table 1. Main features of the 13 studied sites. Phytosociological types according to Thill et al. (1988). Soil types according to FAO-UNESCO classification (Driessen and Dudal 1991). Humus forms according to Brêthes et al. (1995).

| Site | Altitude | Phytosociological type | Soil type | Humus form |
|-------------|-----------------|--------------------------------|------------------|----------------------|
| 1 | 370 m | Luzulo-Fagetum festucetosum | Dystric cambisol | Dysmull |
| 3 | 465 m | Luzulo-Fagetum festucetosum | Dystric cambisol | Eumoder |
| 4 | 500 m | Luzulo-Fagetum typicum | Dystric cambisol | Dysmoder |
| 5 | 505 m | Luzulo-Fagetum vaccinietesosum | Dystric cambisol | Eumoder to dysmoder |
| 16 | 445 m | Luzulo-Fagetum vaccinietesosum | Dystric cambisol | Eumoder |
| 17 | 430 m | Luzulo-Fagetum typicum | Dystric cambisol | Hemimoder to eumoder |
| 22 | 400 m | Luzulo-Fagetum typicum | Gleyic cambisol | Eumoder to dysmoder |
| 24 | 390 m | Luzulo-Fagetum festucetosum | Dystric cambisol | Dysmull to dysmoder |
| 26 | 430 m | Luzulo-Fagetum vaccinietesosum | Leptic podzol | Dysmoder |
| 28 | 375 m | Luzulo-Fagetum festucetosum | Dystric cambisol | Amphimull to eumoder |
| 40 | 385 m | Luzulo-Fagetum vaccinietesosum | Ferric podzol | Dysmoder |
| 100 | 350 m | Melico-Fagetum festucetosum | Dystric cambisol | Oligomull to dysmull |
| 307 | 380 m | Luzulo-Fagetum vaccinietesosum | Leptic podzol | Amphimull |

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2

Table 2. Most typical categories in the three main groups of horizons depicted by correspondence analysis

Oi

Entire brown leaves of beech
 Entire bleached leaves of beech
 Intact bud scales of beech
 Intact male inflorescences of beech
 Entire variegated leaves of beech
 Intact twigs
 Holorganic faecal material smearing beech leaves
 Organo-mineral material smearing beech leaves

Oe

Sandwich material made of beech leaf fragments and holorganic enchytraeid faeces
 Brown decaying male inflorescences of beech
 Fragments of grass stems browsed by fauna
 Pollen
 Woodlice shells
 Petioles and nerves of beech filled with faeces of phthiracarid oribatid mites
 Bud scales of beech, entire but brown and soft
 Intact unidentified fragments of seed wings
 Intact seed coats of beech
 Twigs filled with enchytraeid holorganic faeces
 Twigs filled with oribatid holorganic faeces
 Living leaf bases of *Luzula albida*
 White rhizomorphs

Oa+A

Dead pale yellow creamy mycorrhizae of beech
 Sclerotia of *Cenocccum geophilum*
 Intact dead fine long roots of beech
 Compacted holorganic enchytraeid faeces
 Intact living woody roots of beech
 Strongly decayed bud scales of beech
 Well-decayed bark fragments
 Intact stones
 Decaying woody roots of beech
 Weathering stones
 Charcoal
 Dead fine long roots of beech tunnelled by fauna
 Decaying grass roots
 Dead black mycorrhizae of beech
 Compacted organo-mineral material

Table 3. Mean number of animals which were found during the dissection of humus horizons (L x l x h = 5 x 5 x 1 cm)

| | | Oi (n=24) | Oe (n=59) | Oa (n=44) | A (n=24) |
|------------|---------------------------------------|----------------------------|----------------------------|----------------------------|---------------------------|
| ADB | Adult beetles | 0.02 | 0 | 0.02 | 0 |
| ADF | Adult flies | 0.01 | 0.02 | 0 | 0 |
| ANT | Ants | 0.01 | 0 | 0 | 0 |
| BEE | Beetle larvae (miscellaneous) | 0.14 | 0.3 | 0.09 | 0.04 |
| BOO | Booklice | 0.01 | 0.02 | 0 | 0 |
| CEC | Cecidomyid fly larvae | 0.27 | 0.32 | 0.22 | 0.17 |
| CEN | Centipedes | 0 | 0.06 | 0.09 | 0 |
| CER | Ceratopogonid fly larvae | 0.05 | 0.02 | 0 | 0 |
| CHI | Chironomid fly larvae | 0.25 | 0.3 | 0.64 | 0.25 |
| CLI | Click-beetle larvae | 0.06 | 0.03 | 0.19 | 0.04 |
| COC | Cochineals | 0.01 | 0.11 | 0 | 0 |
| COP | Copepods | 0.04 | 0.01 | 0 | 0 |
| DIP | Diplura | 0.14 | 0.21 | 0.15 | 0.08 |
| DOL | Dolichopodid-empidid fly larvae | 0.02 | 0.21 | 0.28 | 0.33 |
| EAR | Earthworms | 0.07 | 0.01 | 0.19 | 0 |
| ENC | Enchytraeids | 12 | 113 | 231 | 50 |
| FLY | Fly larvae (miscellaneous) | 0.02 | 0.11 | 0.06 | 0.04 |
| MIL | Millipeds | 0 | 0 | 0 | 0.04 |
| MIT | Mites (miscellaneous) | 10 | 19 | 10 | 2 |
| ORI | Oribatid mites (miscellaneous) | 10 | 20 | 14 | 2 |
| PAU | Pauropods | 0.37 | 0.48 | 0.64 | 0.08 |
| PHT | Phthiracarid oribatid mites | 2 | 24 | 8 | 1 |
| PLA | Platynothrus peltifer (oribatid mite) | 6.9 | 4.9 | 3.5 | 0.5 |
| PRO | Protura | 0 | 0.01 | 0.2 | 0.17 |
| PSE | Pseudoscorpions | 0.06 | 0 | 0 | 0.04 |
| SCI | Sciarid fly larvae | 1.5 | 4.8 | 4.4 | 0.5 |
| SLU | Slugs | 0.07 | 0 | 0 | 0 |
| SPI | Spiders | 0.17 | 0.25 | 0.06 | 0 |
| SPR | Springtails | 14 | 64 | 52 | 17 |
| SYM | Symphiles | 0.1 | 0.17 | 0.34 | 0.13 |
| THR | Thrips | 0.02 | 0.02 | 0 | 0 |
| TIP | Tipulid fly larvae | 0.02 | 0.02 | 0 | 0 |
| WOO | Woodlice | 0.05 | 0.01 | 0 | 0 |

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Appendix 1. Categories used for the description of humus horizons. Coordinates on factorial axes 1 and 3 of total correspondence analysis

| Categories | Axis 1 | Axis 3 |
|--|---------|---------|
| Entire brown leaves of beech | -0.0280 | -0.0142 |
| Bundles of entire brown leaves of beech | -0.0114 | -0.0058 |
| Brown leaves of beech skeletonized by macrofauna | -0.0140 | 0.0020 |
| Bundles of brown leaves of beech skeletonized by macrofauna | -0.0124 | 0.0011 |
| Brown leaves of beech skeletonized by mesofauna | -0.0085 | -0.0056 |
| Bundles of brown leaves of beech skeletonized by mesofauna | -0.0065 | -0.0035 |
| Entire variegated leaves of beech | -0.0219 | -0.0146 |
| Bundles of entire variegated leaves of beech | -0.0146 | -0.0078 |
| Entire variegated leaves of beech skeletonized by macrofauna | -0.0050 | -0.0013 |
| Entire variegated leaves of beech skeletonized by mesofauna | -0.0077 | 0.0018 |
| Bundles of variegated leaves of beech skeletonized by macrofauna | -0.0045 | 0.0030 |
| Entire bleached leaves of beech | -0.0265 | -0.0108 |
| Bundles of entire bleached leaves of beech | -0.0143 | -0.0066 |
| Bleached leaves of beech skeletonized by macrofauna | -0.0160 | 0.0090 |
| Bundles of bleached leaves of beech skeletonized by macrofauna | -0.0131 | 0.0048 |
| Bleached leaves of beech skeletonized by mesofauna | -0.0149 | 0.0028 |
| Bundles of bleached leaves of beech skeletonized by mesofauna | -0.0106 | -0.0083 |
| Pits done by caterpillars in beech leaves | -0.0115 | -0.0017 |
| Nests done by foliage-consuming insects | -0.0085 | -0.0073 |
| Organo-mineral material smearing beech leaves | -0.0184 | -0.0128 |
| Hologanic faecal material smearing beech leaves | -0.0216 | -0.0035 |
| Intact petioles and nerves of beech | -0.0022 | 0.0027 |
| Petioles and nerves of beech tunnelled by fauna | 0.0001 | 0.0092 |
| Petioles and nerves of beech filled with enchytraeid faeces | -0.0084 | 0.0045 |
| Petioles and nerves of beech filled with faeces of Adoristes ovatus (oribatid mite) | -0.0045 | 0.0030 |
| Petioles and nerves of beech filled with faeces of phthiracarid oribatid mites | -0.0025 | 0.0188 |
| Petioles and nerves of beech filled with faeces of sciarid dipteran larvae | -0.0014 | 0.0091 |
| Petioles and nerves of beech filled with grass roots | -0.0045 | 0.0030 |
| Petioles and nerves of beech brown and tough | -0.0112 | -0.0027 |
| Petioles and nerves of beech bleached | -0.0018 | 0.0009 |
| Sandwich material made of beech leaf fragments and hologanic enchytraeid faeces | 0.0039 | 0.0250 |
| Sandwich material made of beech leaf fragments and hologanic earthworm faeces | -0.0045 | 0.0034 |
| Sandwich material made of beech leaf fragments and hologanic oribatid faeces | 0.0033 | 0.0106 |
| Sandwich material made of beech leaf fragments and organo-mineral earthworm faeces | -0.0003 | 0.0024 |
| Sandwich material made of beech leaf fragments and organo-mineral enchytraeid faeces | 0.0037 | -0.0025 |
| Sandwich material made of beech leaf fragments and hologanic sciarid faeces | 0.0001 | -0.0007 |
| Skeletonized beech leaf fragments | 0.0098 | -0.0046 |
| Bundles of skeletonized beech leaf fragments | 0.0055 | 0.0060 |
| Brown beech leaf fragments untouched by fauna | 0.0141 | -0.0019 |
| Intact bud scales of beech | -0.0299 | -0.0037 |
| Bud scales of beech, entire but brown and soft | 0.0008 | 0.0191 |
| Strongly decayed bud scales of beech | 0.0217 | -0.0043 |
| Intact male inflorescences of beech | -0.0232 | -0.0120 |
| Brown decaying male inflorescences of beech | -0.0057 | 0.0236 |
| Pollen mass | -0.0022 | 0.0204 |
| Intact seed coats of beech | 0.0038 | 0.0175 |
| Seed coats of beech tunnelled by phthiracarid mites | 0.0006 | 0.0077 |
| Seed coats of beech tunnelled by enchytraeids | 0.0051 | 0.0037 |
| Seed coats of beech tunnelled by sciarid larvae | -0.0009 | 0.0025 |
| Seed coats of beech penetrated by roots | 0.0028 | 0.0004 |
| Intact fragments of beech burr | -0.0098 | 0.0019 |
| Soft fragments of beech burr | 0.0099 | 0.0028 |
| Soft fragments of beech burr tunnelled by oribatid mites | 0.0025 | 0.0108 |
| Soft fragments of beech burr tunnelled by enchytraeids | 0.0068 | 0.0069 |
| Soft fragments of beech burr tunnelled by sciarid larvae | 0.0029 | 0.0069 |
| Soft fragments of beech burr tunnelled by springtails | 0.0012 | 0.0043 |
| Soft fragments of beech burr penetrated by grass roots | 0.0033 | -0.0048 |
| Beech cupules tunnelled by fauna | 0.0006 | -0.0024 |
| Intact beech gallnuts | 0.0051 | 0.0010 |
| Intact twigs | -0.0225 | -0.0033 |
| Twigs decayed by white-rot | -0.0087 | -0.0031 |
| Twig fragments tunnelled by fauna | -0.0074 | 0.0106 |
| Bark remnants of twigs | 0.0079 | 0.0072 |
| Twigs filled with enchytraeid hologanic faeces | 0.0115 | 0.0205 |
| Twigs filled with enchytraeid organo-mineral faeces | 0.0102 | -0.0024 |
| Twigs filled with sciarid hologanic faeces | 0.0015 | 0.0101 |
| Twigs filled with oribatid hologanic faeces | 0.0085 | 0.0138 |
| Twigs penetrated by beech roots | 0.0129 | 0.0009 |

Continued.

Appendix 1. Continued

| Categories | Axis 1 | Axis 3 |
|--|---------|---------|
| Intact wood fragments | -0.0048 | -0.0029 |
| Decayed wood fragments | 0.0016 | -0.0093 |
| Wood fragments tunnelled by fauna | 0.0096 | 0.0036 |
| Wood fragments penetrated by grass roots | -0.0045 | 0.0030 |
| Wood fragments penetrated by beech fine roots | 0.0025 | -0.0063 |
| Intact bark fragments | 0.0072 | -0.0060 |
| Well-decayed bark fragments | 0.0179 | -0.0147 |
| Bark fragments tunnelled by enchytraeids | -0.0018 | 0.0094 |
| Bark fragments tunnelled by phthiracarid mites | 0.0001 | 0.0075 |
| Bark fragments tunnelled by sciarid larvae | -0.0022 | 0.0046 |
| Bark fragments penetrated by grass roots | -0.0045 | 0.0030 |
| Intact living fine long roots of beech | 0.0231 | 0.0184 |
| Living fine long roots of beech brow sed by fauna | 0.0123 | -0.0061 |
| Intact dead fine long roots of beech | 0.0238 | -0.0178 |
| Dead fine long roots of beech tunnelled by fauna | 0.0145 | -0.0119 |
| Dead fine long roots of beech penetrated by grass roots | 0.0031 | -0.0069 |
| Dead fine long roots of beech, voided | 0.0046 | -0.0075 |
| Living woody roots of beech | 0.0237 | -0.0031 |
| Living woody roots of beech brow sed by fauna | 0.0069 | -0.0058 |
| Decaying woody roots of beech | 0.0160 | -0.0133 |
| Living pale yellow creamy mycorrhizae of beech | 0.0221 | 0.0136 |
| Pale yellow creamy mycorrhizae of beech brow sed by fauna | 0.0181 | 0.0003 |
| Dead pale yellow creamy mycorrhizae of beech | 0.0260 | -0.0139 |
| Living orange brown mycorrhizae of beech with woolly mycelium | 0.0106 | 0.0078 |
| Orange brown mycorrhizae of beech with woolly mycelium brow sed by fauna | 0.0016 | 0.0018 |
| Dead orange brown mycorrhizae of beech with woolly mycelium | 0.0128 | -0.0068 |
| Living black mycorrhizae of beech (produced by Cenococcum geophilum) | 0.0181 | 0.0104 |
| Living black mycorrhizae of beech brow sed by fauna | 0.0019 | 0.0043 |
| Dead black mycorrhizae of beech | 0.0141 | -0.0087 |
| Living yellow mycorrhizae of beech with woolly mycelium | 0.0028 | 0.0074 |
| Living shoots of Polytrichum formosum | -0.0067 | 0.0087 |
| Fragments of stems of Polytrichum formosum, red and tough | 0.0032 | 0.0044 |
| Fragments of stems of Polytrichum formosum, voided | 0.0051 | 0.0095 |
| Dead stem bases of Polytrichum formosum | 0.0024 | -0.0001 |
| Decaying stem bases of Polytrichum formosum | 0.0047 | -0.0024 |
| Living shoots of Scleropodium purum | -0.0073 | 0.0111 |
| Dead shoots of Scleropodium purum | 0.0042 | 0.0043 |
| Living shoots of Leucobryum glaucum | -0.0064 | -0.0054 |
| Dead shoots of Leucobryum glaucum | 0.0003 | -0.0012 |
| Dead moss, undetermined | -0.0057 | -0.0035 |
| Intact leaves of Luzula forsteri | -0.0060 | -0.0057 |
| Bleached leaves of Luzula forsteri | -0.0034 | -0.0070 |
| Living leaf bases of Luzula forsteri | 0.0000 | 0.0136 |
| Decaying leaf bases of Luzula forsteri | 0.0047 | -0.0024 |
| Intact leaves of Deschampsia flexuosa | -0.0074 | -0.0030 |
| Decaying leaves of Deschampsia flexuosa | -0.0135 | 0.0017 |
| Living leaf bases of Deschampsia flexuosa | -0.0037 | -0.0003 |
| Decaying leaf bases of Deschampsia flexuosa | 0.0120 | -0.0012 |
| Intact inflorescences of Deschampsia flexuosa | -0.0058 | -0.0045 |
| Decaying inflorescences of Deschampsia flexuosa | -0.0098 | -0.0003 |
| Living grass roots | 0.0090 | -0.0022 |
| Decaying grass roots | 0.0144 | -0.0083 |
| Intact grass stems | 0.0008 | -0.0136 |
| Fragments of grass stems brow sed by fauna | -0.0022 | 0.0204 |
| Fragments of decaying grass roots | -0.0062 | -0.0026 |
| Intact leaves of Vaccinium myrtillus | -0.0075 | -0.0063 |
| Skeletonized leaves of Vaccinium myrtillus | -0.0101 | -0.0034 |
| Roots of Vaccinium myrtillus | 0.0053 | 0.0013 |
| Living rhizomes of Vaccinium myrtillus | 0.0016 | 0.0018 |
| Decaying rhizomes of Vaccinium myrtillus | 0.0072 | -0.0001 |
| Bleached leaves of Oxalis acetosella | 0.0013 | -0.0039 |
| Brown entire leaves of Acer pseudoplatanus | -0.0051 | -0.0198 |
| Brown leaves of Acer pseudoplatanus skeletonized by macrofauna | -0.0051 | -0.0198 |
| Bleached leaves of Acer pseudoplatanus | -0.0053 | -0.0192 |
| Bleached leaves of Acer pseudoplatanus skeletonized by macrofauna | -0.0051 | -0.0198 |
| Leaves of Acer pseudoplatanus skeletonized by mesofauna | -0.0018 | -0.0002 |

Continued.

Appendix 1. Continued

| Categories | Axis 1 | Axis 3 |
|--|---------|---------|
| Winged seed of <i>Acer pseudoplatanus</i> with intact wing | 0.0001 | -0.0007 |
| Winged seed of <i>Acer pseudoplatanus</i> with skeletonized wing | -0.0062 | 0.0030 |
| Wingless seed of <i>Acer pseudoplatanus</i> | -0.0012 | 0.0051 |
| Winged seed of <i>Fraxinus excelsior</i> with intact wing | -0.0053 | -0.0192 |
| Brown entire leaves of <i>Quercus petraea</i> | -0.0076 | -0.0067 |
| Leaves of <i>Quercus petraea</i> skeletonized by mesofauna | -0.0049 | -0.0013 |
| Intact unidentified fragments of seed wings | -0.0050 | 0.0176 |
| Skeletonized unidentified fragments of seed wings | -0.0027 | 0.0036 |
| Brown entire needles of <i>Picea abies</i> | -0.0010 | -0.0002 |
| Bleached entire needles of <i>Picea abies</i> | -0.0108 | -0.0034 |
| Needles of <i>Picea abies</i> browsed by fauna | -0.0002 | 0.0086 |
| Seed wings of <i>Picea abies</i> | -0.0053 | -0.0032 |
| Brown rhizomorphs | -0.0047 | 0.0075 |
| White rhizomorphs | -0.0023 | 0.0130 |
| Yellow rhizomorphs | 0.0028 | 0.0074 |
| Dead rhizomorphs of <i>Armillaria</i> | 0.0100 | -0.0074 |
| Dead rhizomorphs of <i>Armillaria</i> tunnelled by fauna | 0.0100 | -0.0074 |
| Sclerotia of <i>Cenococcum geophilum</i> | 0.0245 | -0.0136 |
| Lichens | -0.0090 | -0.0053 |
| Intact caterpillar faeces | -0.0137 | 0.0099 |
| Caterpillar faeces tunnelled by phthiracarid mites | 0.0056 | 0.0078 |
| Intact slug faeces | -0.0142 | -0.0045 |
| Slug faeces tunnelled by enchytraeids | -0.0089 | -0.0049 |
| Slug faeces tunnelled by sciarid larvae | -0.0089 | -0.0049 |
| Intact holorganic earthworm faeces | -0.0124 | 0.0118 |
| Holorganic earthworm faeces tunnelled by enchytraeids | 0.0007 | 0.0057 |
| Unidentified holorganic faeces | -0.0056 | -0.0037 |
| Intact organo-mineral earthworm faeces | -0.0025 | 0.0036 |
| Compacted organo-mineral earthworm faeces | 0.0088 | -0.0016 |
| Organo-mineral earthworm faeces tunnelled by enchytraeids | 0.0042 | 0.0034 |
| Holorganic woodlice faeces | -0.0120 | 0.0033 |
| Holorganic milliped faeces | 0.0048 | 0.0049 |
| Holorganic milliped faeces tunnelled by enchytraeids | 0.0036 | 0.0010 |
| Holorganic milliped faeces tunnelled by phthiracarid mites | 0.0036 | 0.0010 |
| Holorganic crane-fly faeces | 0.0004 | 0.0048 |
| Intact holorganic sciarid faeces | -0.0044 | -0.0007 |
| Compacted holorganic sciarid faeces | 0.0074 | -0.0069 |
| Intact holorganic enchytraeid faeces | 0.0141 | 0.0081 |
| Compacted holorganic enchytraeid faeces | 0.0219 | -0.0120 |
| Organo-mineral enchytraeid faeces | 0.0078 | -0.0044 |
| Compacted organo-mineral enchytraeid faeces | 0.0070 | -0.0117 |
| Compacted organic-dominant organo-mineral material | 0.0066 | -0.0064 |
| Compacted organo-mineral material | 0.0114 | -0.0120 |
| Compacted mineral-dominant organo-mineral material | 0.0040 | -0.0085 |
| Unidentified mineral assemblages | -0.0016 | -0.0011 |
| Charcoal | 0.0132 | -0.0153 |
| Snail shells | -0.0028 | 0.0098 |
| Woodlice shells | -0.0022 | 0.0204 |
| Intact stones | 0.0161 | -0.0103 |
| Weathering stones | 0.0147 | -0.0128 |
| Weathering stones impregnated with organic matter | 0.0048 | -0.0096 |

Appendix 2. Categories used for the description of humus horizons. Coordinates on factorial axes 1 and 2 of partial correspondence analysis (OH and A).

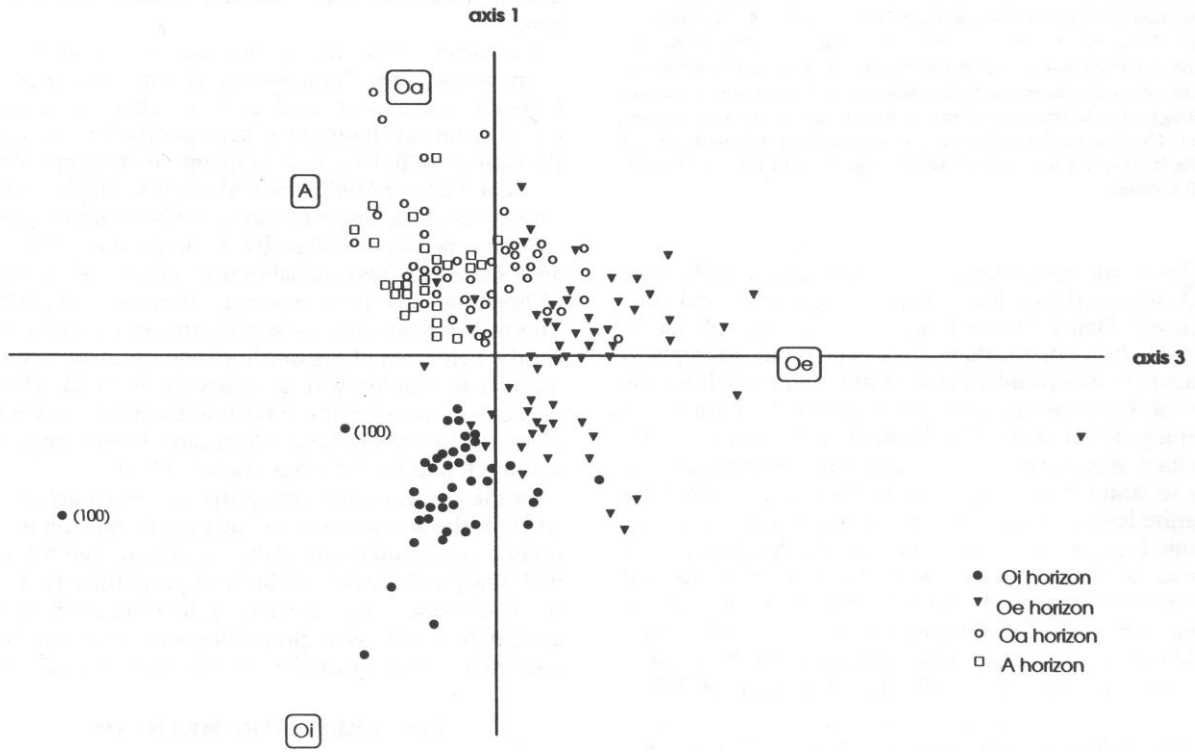
| Categories | Axis 1 | Axis 2 |
|--|---------|---------|
| Brown leaves of beech skeletonized by macrofauna | -0.0002 | -0.0319 |
| Bleached leaves of beech skeletonized by macrofauna | -0.0002 | -0.0319 |
| Bleached leaves of beech skeletonized by mesofauna | -0.0002 | -0.0319 |
| Intact petioles and nerves of beech | -0.0130 | -0.0013 |
| Petioles and nerves of beech tunnelled by fauna | -0.0100 | 0.0135 |
| Petioles and nerves of beech filled with enchytraeid faeces | -0.0051 | 0.0069 |
| Petioles and nerves of beech filled with faeces of phthiracarid oribatid mites | -0.0094 | -0.0090 |
| Sandwich material made of beech leaf fragments and holorganic enchytraeid faeces | -0.0343 | 0.0089 |
| Sandwich material made of beech leaf fragments and holorganic earthworm faeces | -0.0054 | -0.0001 |
| Sandwich material made of beech leaf fragments and holorganic oribatid faeces | -0.0383 | -0.0025 |
| Sandwich material made of beech leaf fragments and organo-mineral earthworm faeces | -0.0031 | -0.0038 |
| Sandwich material made of beech leaf fragments and organo-mineral enchytraeid faeces | -0.0002 | -0.0008 |
| Skeletonized beech leaf fragments | 0.0047 | 0.0114 |
| Bundles of skeletonized beech leaf fragments | 0.0002 | 0.0201 |
| Brown beech leaf fragments untouched by fauna | -0.0051 | -0.0081 |
| Intact bud scales of beech | -0.0214 | -0.0201 |
| Bud scales of beech, entire but brown and soft | -0.0292 | -0.0056 |
| Strongly decayed bud scales of beech | 0.0016 | 0.0205 |
| Brown decaying male inflorescences of beech | -0.0246 | 0.0038 |
| Intact seed coats of beech | -0.0105 | 0.0065 |
| Seed coats of beech tunnelled by phthiracarid mites | 0.0020 | 0.0054 |
| Seed coats of beech tunnelled by enchytraeids | -0.0015 | 0.0051 |
| Intact fragments of beech burr | -0.0152 | -0.0048 |
| Soft fragments of beech burr | 0.0041 | 0.0022 |
| Soft fragments of beech burr tunnelled by oribatid mites | -0.0106 | 0.0136 |
| Soft fragments of beech burr tunnelled by enchytraeids | 0.0012 | 0.0197 |
| Beech cupules tunnelled by fauna | 0.0051 | 0.0050 |
| Twigs decayed by white-rot | 0.0000 | -0.0066 |
| Twig fragments tunnelled by fauna | -0.0013 | 0.0229 |
| Bark remnants of twigs | 0.0008 | -0.0122 |
| Twigs filled with enchytraeid holorganic faeces | -0.0119 | 0.0159 |
| Twigs filled with enchytraeid organo-mineral faeces | -0.0289 | -0.0002 |
| Twigs filled with sciarid holorganic faeces | 0.0002 | 0.0068 |
| Twigs filled with oribatid holorganic faeces | -0.0287 | 0.0078 |
| Twigs penetrated by beech roots | -0.0294 | 0.0045 |
| Decayed wood fragments | 0.0010 | -0.0055 |
| Wood fragments tunnelled by fauna | -0.0168 | -0.0104 |
| Wood fragments penetrated by beech fine roots | 0.0024 | -0.0066 |
| Intact bark fragments | -0.0140 | 0.0038 |
| Well-decayed bark fragments | 0.0091 | 0.0086 |
| Bark fragments tunnelled by enchytraeids | -0.0090 | 0.0079 |
| Bark fragments tunnelled by phthiracarid mites | -0.0022 | -0.0101 |
| Intact living fine long roots of beech | -0.0212 | -0.0033 |
| Living fine long roots of beech browsed by fauna | -0.0021 | 0.0103 |
| Intact dead fine long roots of beech | 0.0061 | -0.0014 |
| Dead fine long roots of beech tunnelled by fauna | 0.0045 | 0.0073 |
| Dead fine long roots of beech penetrated by grass roots | 0.0049 | -0.0025 |
| Dead fine long roots of beech, voided | 0.0047 | -0.0033 |
| Living woody roots of beech | 0.0028 | 0.0182 |
| Living woody roots of beech browsed by fauna | 0.0040 | 0.0103 |
| Decaying woody roots of beech | 0.0113 | 0.0113 |
| Living pale yellow creamy mycorrhizae of beech | -0.0172 | -0.0035 |
| Pale yellow creamy mycorrhizae of beech browsed by fauna | -0.0016 | 0.0125 |
| Dead pale yellow creamy mycorrhizae of beech | 0.0040 | 0.0047 |
| Living orange brown mycorrhizae of beech with woolly mycelium | -0.0052 | 0.0069 |
| Dead orange brown mycorrhizae of beech with woolly mycelium | 0.0058 | 0.0065 |
| Living black mycorrhizae of beech (produced by Cenococcum geophilum) | -0.0079 | 0.0027 |
| Dead black mycorrhizae of beech | 0.0057 | 0.0152 |
| Living shoots of Polytrichum formosum | -0.0054 | -0.0088 |
| Fragments of stems of Polytrichum formosum, voided | 0.0010 | -0.0105 |
| Dead stem bases of Polytrichum formosum | 0.0037 | -0.0076 |
| Dead shoots of Leucobryum glaucum | -0.0012 | -0.0043 |
| Bleached leaves of Luzula forsteri | -0.0012 | -0.0063 |
| Living leaf bases of Luzula forsteri | 0.0045 | -0.0002 |

Appendix 2. Continued

| Categories | Axis 1 | Axis 2 |
|---|---------|---------|
| Decaying leaf bases of <i>Luzula forsteri</i> | 0.0037 | -0.0076 |
| Decaying leaves of <i>Deschampsia flexuosa</i> | -0.0268 | 0.0051 |
| Living leaf bases of <i>Deschampsia flexuosa</i> | 0.0045 | -0.0002 |
| Decaying leaf bases of <i>Deschampsia flexuosa</i> | 0.0066 | 0.0079 |
| Living grass roots | 0.0065 | -0.0133 |
| Decaying grass roots | 0.0085 | -0.0002 |
| Intact grass stems | 0.0026 | -0.0070 |
| Roots of <i>Vaccinium myrtillus</i> | -0.0053 | 0.0095 |
| Decaying rhizomes of <i>Vaccinium myrtillus</i> | -0.0014 | 0.0092 |
| Bleached leaves of <i>Oxalis acetosella</i> | -0.0002 | -0.0319 |
| Brown entire needles of <i>Picea abies</i> | -0.0145 | 0.0016 |
| Brown rhizomorphs | 0.0010 | -0.0071 |
| White rhizomorphs | -0.0140 | 0.0071 |
| Dead rhizomorphs of <i>Armillaria</i> | -0.0012 | 0.0015 |
| Dead rhizomorphs of <i>Armillaria</i> tunnelled by fauna | -0.0012 | 0.0015 |
| Sclerotia of <i>Cenococcum geophilum</i> | 0.0012 | 0.0035 |
| Intact caterpillar faeces | -0.0006 | 0.0123 |
| Intact holorganic earthworm faeces | 0.0018 | -0.0039 |
| Holorganic earthworm faeces tunnelled by enchytraeids | -0.0383 | -0.0025 |
| Intact organo-mineral earthworm faeces | 0.0031 | -0.0265 |
| Compacted organo-mineral earthworm faeces | -0.0040 | -0.0140 |
| Organo-mineral earthworm faeces tunnelled by enchytraeids | 0.0009 | -0.0076 |
| Holorganic milliped faeces | -0.0017 | -0.0222 |
| Holorganic milliped faeces tunnelled by enchytraeids | -0.0383 | -0.0025 |
| Holorganic milliped faeces tunnelled by pthiracarid mites | -0.0383 | -0.0025 |
| Holorganic crane-fly faeces | -0.0020 | -0.0009 |
| Compacted holorganic sciarid faeces | 0.0059 | 0.0109 |
| Intact holorganic enchytraeid faeces | -0.0083 | 0.0060 |
| Compacted holorganic enchytraeid faeces | 0.0109 | 0.0235 |
| Organo-mineral enchytraeid faeces | -0.0068 | 0.0034 |
| Compacted organo-mineral enchytraeid faeces | 0.0103 | -0.0041 |
| Compacted organic-dominant organo-mineral material | 0.0034 | -0.0035 |
| Compacted organo-mineral material | 0.0070 | -0.0078 |
| Compacted mineral-dominant organo-mineral material | 0.0048 | -0.0048 |
| Unidentified mineral assemblages | 0.0051 | 0.0050 |
| Charcoal | 0.0063 | -0.0200 |
| Intact stones | 0.0036 | -0.0269 |
| Weathering stones | 0.0092 | -0.0065 |
| Weathering stones impregnated with organic matter | 0.0077 | -0.0002 |

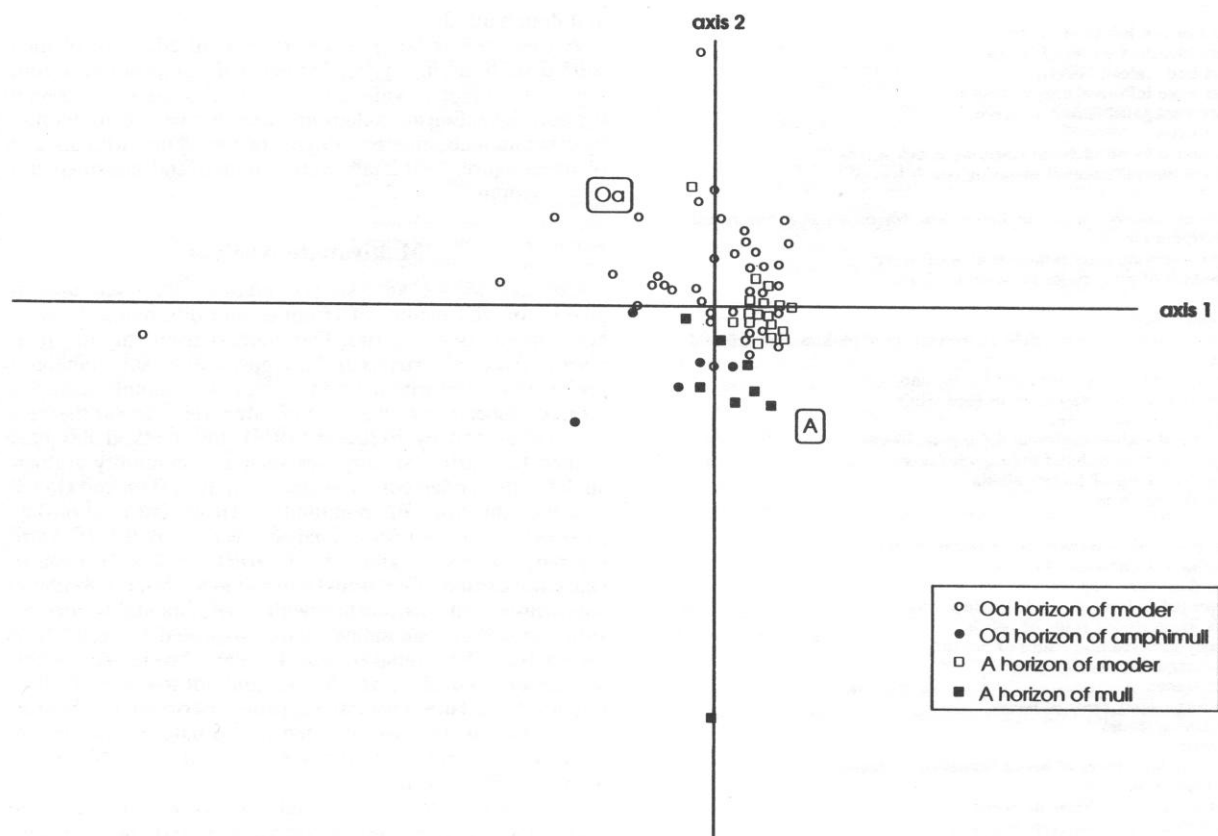
1

2



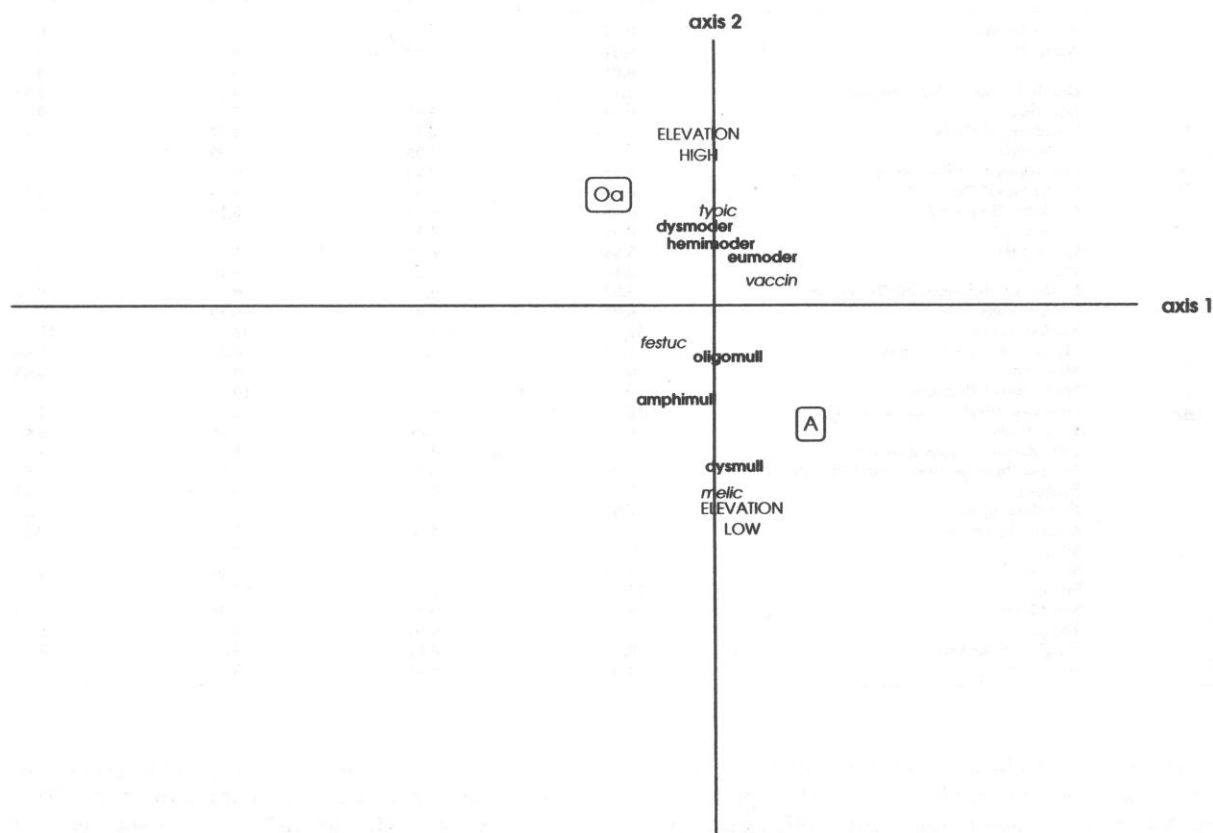
1
2
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4

Fig. 1



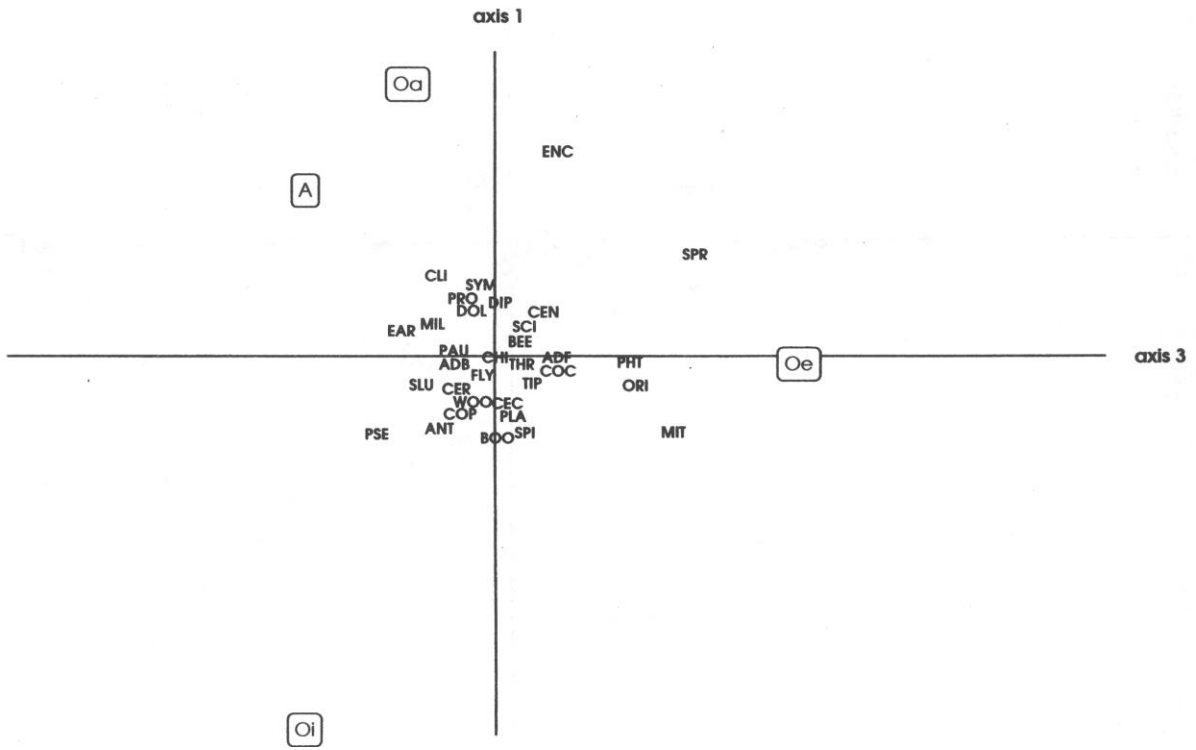
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Fig. 2



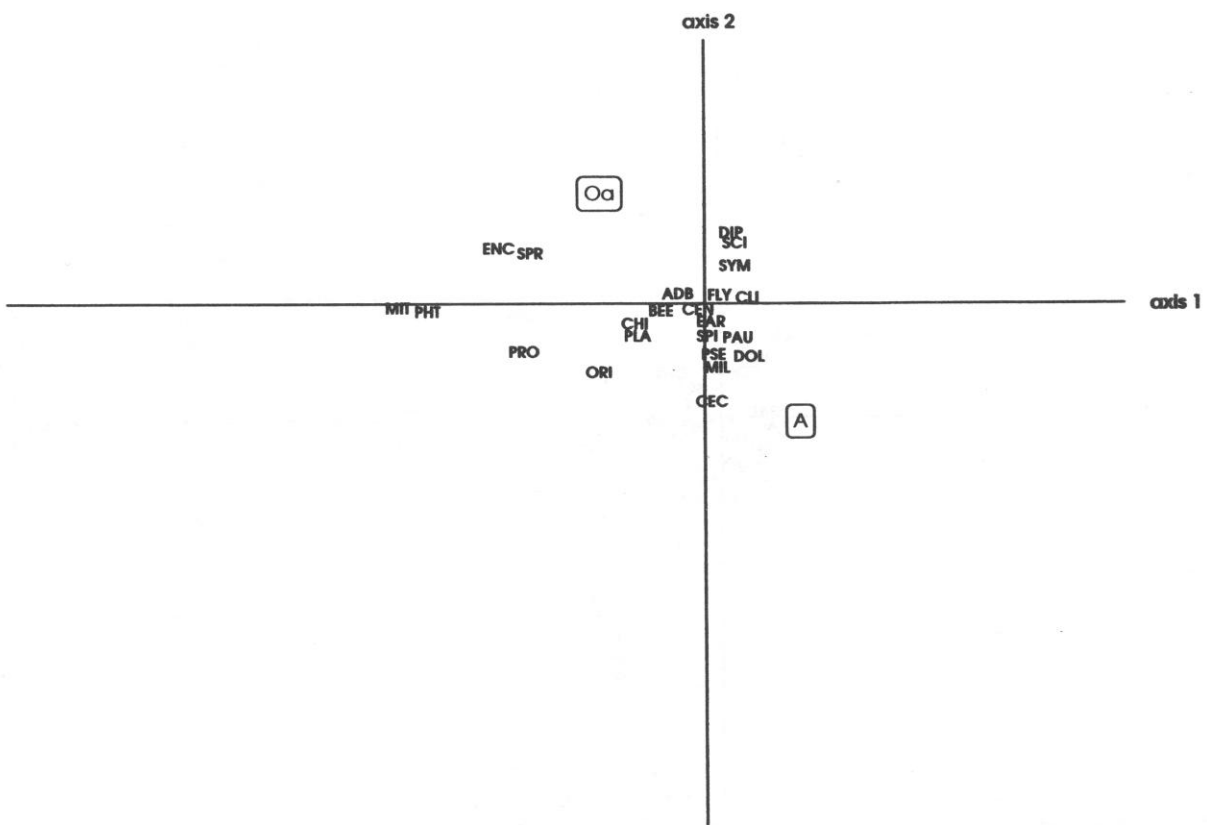
- 1
- 2
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Fig. 3



- 1
- 2
- 3
- 4

Fig. 4



1

2

3 Fig. 5