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► **To cite this version:**

Paola Galvan, Jean-François Ponge, Silvia Chersich, Augusto Zanella. Humus components and soil biogenic structures in Norway spruce ecosystems. *Soil Science Society of America Journal*, 2008, 72 (2), pp.548-557. 10.2136/sssaj2006.0317 . hal-00495339v1

HAL Id: hal-00495339

<https://hal.science/hal-00495339v1>

Submitted on 25 Jun 2010 (v1), last revised 3 Aug 2010 (v2)

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1 **Humus components and soil biogenic structures in Norway**
2 **spruce [*Picea abies* (L.) Karst.] ecosystems**

3

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5

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15

16 **Acknowledgements**

17

18 The authors are greatly indebted to the staff of the Centro Studi per l'Ambiente Alpino
19 (Università di Padova), to Franco Previtali (Università degli Studi di Milano-Bicocca,
20 Dipartimento di Scienze dell'Ambiente e del Territorio), to the staff of the Centro di Ecologia
21 Alpina for commodities, technical help and free access to the sites, to Roberto Zampedri who
22 gathered information about ecological features of the study sites, and to the Province of
23 Trento for financial support (DINAMUS Project, decision N° 437/2002) and grant given to
24 the junior author.

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3

4

ABSTRACT

5

6 Whether the structure of Oa and A horizons varies according to animal activity is still
7 a matter of conjecture, especially in amphi, a humus form with mixed features of mull and
8 moder, which has been described in environments with strong seasonal contrasts. The Oa and
9 A horizons of spruce [*Picea abies* (L.) Karst.] coniferous forests of the Province of Trento
10 (Italy) were sampled in six sites with a total of 134 humus profiles along transect lines,
11 embracing the variety of parent rocks, climate and vegetation conditions which prevail at the
12 upper montane level in this region. The distribution of humus components (plant debris, roots,
13 animal faeces, minerals) was assessed by an optical method and analysed with
14 correspondence analysis (CA). Moder humus forms were characterized by enchytraeid
15 activity, with concomitant deposition of organic and mineral-organic faeces in Oa and A
16 horizons, respectively. Conversely, amphis were characterized by the concomitant deposition
17 of organic and mineral-organic earthworm faeces in Oa and A horizons, respectively. We
18 conclude that Oa and A horizons of moders and amphis differed only quantitatively in the
19 content of mineral matter in animal faeces. The fine-grained mineral-organic structure which
20 is mostly found in the A horizon of amphis results from the alimentary activity of small
21 epigeic earthworms which mix organic matter with mineral matter, like anecic earthworms do
22 in mulls.

23

1 **Abbreviations:** AN, Acid North; AS, Acid South; BN, Basic North; BS, Basic South; CA,
2 correspondence analysis; IN, Intermediate North; IS, Intermediate South

3
4 Coniferous forests, in particular Norway spruce [*Picea abies* (L.) Karst.] stands, are
5 known for the accumulation of organic matter in thick litter horizons (Ovington, 1954;
6 Nihlgård, 1971). Space-for-time substitution (Pickett, 1989) studies on indigenous multi-
7 layered forest stands showed that this accumulation occurs during the pole stage of tree
8 development and is reversible under mature trees (Bernier and Ponge, 1994; Bernier, 1996;
9 Sagot et al., 1999), whereas studies dealing with even-aged plantations show a continuous
10 increase until mature trees are cut (Chauvat et al., 2006). The influence of stand development
11 on soil nutrient pools and decomposer communities (Nilsson et al., 1982; Miller, 1984;
12 Ulrich, 1994) and the patchy structure of coniferous forests (Bernier and Ponge, 1998; Ponge
13 et al., 1998; Ponge, 1999a) are thought to be responsible for the observed patterns.

14
15 Moders, mulls and mors are the dominant humus forms in the topsoil of forest
16 ecosystems (Ponge, 2003). They differ by the distribution of organic and mineral-organic
17 horizons, called Oi (organic, slightly decomposed), Oe (organic, moderately decomposed), Oa
18 (organic, highly decomposed) and A (mineral mixed with humus, decomposed) in the most
19 complete case (Schaetzl and Anderson, 2005). Mulls are characterized by a crumby structure
20 (mostly created by earthworms) in the mineral-organic A horizon. Moders are characterized
21 by the accumulation of organic invertebrate faeces in the overlying Oa horizon. Amphimulls
22 (Brêthes et al., 1995; Ponge et al., 2002; Galvan et al., 2005), now called amphis (Jabiol et al.,
23 2004; Graefe and Beylich, 2006), exhibit mixed features of moders and mulls, and are widely
24 represented in Mediterranean as well as mountain and tropical forest ecosystems (Loranger et
25 al., 2003; Jabiol et al., 2004). They are characterized by a crumby structure in the mineral-

1 organic A horizon, like in mulls, and by the concomitant accumulation of organic invertebrate
2 faeces in the overlying Oa horizon, like in moders. The objective of the current study was to
3 investigate whether the two horizons should be considered as two largely independent
4 compartments of the topsoil, or whether the same kind of animal activity could explain their
5 common occurrence. In other words, when lumbricids (typical of mulls) are present, are they
6 able to process the organic matter accumulated in Oa horizons? When earthworms are
7 replaced by animals of a smaller size, such as enchytraeids (typical of moders), does the latter
8 animal group create the structures observed in the A horizon? Is there any influence of the age
9 of trees on these patterns? Answering these questions may improve our knowledge of the
10 biological processes by which organic matter may accumulate or not in mountain and boreal
11 coniferous forests, known worldwide as active carbon sinks (Vetter et al., 2005).

12

13

MATERIALS AND METHODS

14

15

Study sites

16

17 Six Norway spruce sites were chosen in the northern Italian Alps, Province of Trento,
18 embracing the wide range of environmental conditions (substrate, elevation, aspect, rainfall)
19 which prevail in the western European part of its present-day natural distribution area (Scotti
20 et al., 2000).

21

22 Three geological substrates (referred to as Acid, Intermediate and Basic), each with
23 two aspects (North, South), were selected at an altitude ranging from 1650 to 1870 m, i.e. at
24 the upper montane level (Odasso, 2002) (Fig. 1). Table 1 summarizes climatic and geological
25 features of the six sites. All study sites were managed with natural regeneration (selection

1 system) as the prevailing system for successive croppings. At each site the selected transect
2 crossed a mosaic of trees or clumps of trees of different ages.

3

4

Sampling

5

6 A transect line was drawn in six spruce stands, representing a wide variety of
7 environmental conditions site. At each site the transect crossed the widest possible variation
8 in vegetation, in particular the four main stand developmental phases: 'gap', 'regeneration',
9 'intermediate' and 'mature'. Oa and A horizons were sampled every three meters, thus
10 totalling 134 samples (19 in AN, 27 in AS, 18 in IN, 25 in IS, 22 in BN, 23 in BS). They were
11 analysed microscopically according to the 'small volume' method (Sadaka and Ponge, 2003).
12 The sampling method for humus profiles was described in detail by Bernier et al. (1993) and
13 Bernier and Ponge (1994). A block, 25 cm² in area and with such a depth as to reach the B
14 horizon, was prepared directly in the field with a sharp knife. Each Oa and A horizon was
15 isolated and fixed immediately in 95% ethyl alcohol in a 400 ml hermetic seal polypropylene
16 box, with as little disturbance as possible, then transported to the laboratory until analysis.
17 Several layers may be sampled separately within the same Oa or A horizon, providing they
18 exhibit clear differences (to the naked eye) in their apparent composition.

19

20

Laboratory analyses

21

22 In the laboratory, each sampled horizon was studied under a dissecting microscope,
23 after spreading it out as gently as possible in a 15 cm diameter Petri dish, filled with 95%
24 ethyl alcohol. The different components were quantified by the point-count method first
25 described by Jongerius (1963) for the study of soil sections. Under the dissecting microscope,

1 humus components under each point of a transparent film with a 157-points grid were
2 recorded, resulting in a table showing the distribution (percent volume) of 84 categories of
3 humus (Table 2) among the 375 layers investigated. In a given layer the relative volume of
4 each component of the soil matrix was estimated by the number of times it has been recorded
5 divided by the total number of points of the grid.

6
7 Chemical analyses were performed on a selection of soil samples taken along each
8 transect line. Only data for the top 1 cm of the A horizon were shown (Table 3). Organic
9 carbon (organic C) and total nitrogen (total N) were measured in 10-20 mg of dried soil. Air-
10 dried soil samples were sieved to 200 μm and homogenized, then C and N were dosed in a
11 CHN atomic analyzer (Perkin-Elmer CHNS/O Analyzer 2400 Series II). Ca-carbonates were
12 removed with HCl prior to analysis. Soil pH-H₂O and pH-KCl were measured with a glass-
13 electrode in a 1:2.5 w:v suspension of soil in deionised water or KCl solution, mixed for 2
14 hours, pH being measured on the supernatant. The cation-exchange capacity (CEC) was
15 measured in BaCl₂ (pH 8.2). A successive addition of MgSO₄ allowed the complete exchange
16 between Ba and Mg, followed by analysis of supernatant for Mg by complexometry (West,
17 1969). Exchangeable Ca⁺⁺, Mg⁺⁺ and K⁺ were determined by atomic absorption
18 spectrophotometry (Perkin-Elmer Analyst 200). Base saturation was calculated as the ratio
19 $\Sigma(\text{exchangeable Ca}^+, \text{Mg}^{++}, \text{K}^+)/\text{CEC} \times 100$. Total acidity was determined by titrating with HCl
20 the solution obtained by treating the soil sample with BaCl₂, buffered at pH 8.2. To obtain
21 exchangeable acidity, KCl was added to the soil sample and the solution was titrated with
22 NaOH. By adding NaF (10 mL) to this solution and titrating with HCl we obtained
23 exchangeable Al⁺⁺⁺. H⁺ was calculated by subtracting exchangeable Al from exchangeable
24 acidity.

25

Statistical treatment

Correspondence analysis or CA (Greenacre, 1984) was used to see whether clusters with similar distributions of humus components could be distinguished within the whole set of layers. Raw data (percent volumes of categories) were considered as active (main) variables and were not transformed before analysis. The six sites (AN, AS, IN, IS, BN, BS) and the Oa and A horizons were included as passive (additional) variables, in order to show whether there was a correspondence between the horizons, the sites and the animal groups.

The product-moment correlation coefficient (Sokal and Rohlf, 1995) was used to test the correlation between either the same humus component sampled in different horizons, or between different humus components sampled in the same horizons. When several successive layers of the same horizon (Oa or A) had been sampled, they were averaged by weighting them according to thickness.

Multivariate statistics and other statistical treatment of the data were performed using the StatboxPro® software package (Grimmersoft).

RESULTS

Were there different kinds of Oa and A horizons?

The 84 categories of humus components identified under the dissecting microscope are listed in Table 2, together with their numerical codes in the CA. They were comprised mainly of plant debris (mostly spruce needles and roots but other plant parts were identified,

1 too) at varying stages of transformation by microbes, and animal faeces. Faeces were
2 attributed to animal groups (epigeic and anecic earthworms, millipedes, enchytraeids, mites,
3 insects) according to their sizes, shapes and colors (Galvan et al., 2005). Only one category
4 (69) was left unidentified. Mineral particles and assemblages, as well as animals (bodies,
5 moults) were also included in the analysis. Miscellaneous humus components were plant
6 debris not attributable to any plant parts (category 41) or too transformed and without any
7 recognizable plant or animal origin (category 52).

8

9 The first four axes explained 11.4, 10.2, 7.9 and 7.0% of the total variance,
10 respectively (eigen values 0.49, 0.44, 0.34, 0.3). Although they explained only 36% of the
11 total variance, the first four factorial axes allowed to discern clearly interpretable clusters in
12 both Oa and A horizons, which was the criterion used for the detection of significant trends
13 according to Benzécri (1969). The projection of categories of humus components in the plane
14 of the first two axes (Fig. 2) displayed three branches, one corresponding to Oa horizons, the
15 others to two different kinds of A horizons. Axis 1 reflected the opposition between Oa
16 (positive side) to A (negative side) horizons. As expected, Oa horizons were characterized by
17 organic faeces (categories 62, 65, 66, 68 and 70), bodies of epigeic animals (categories 76 and
18 77) and numerous plant debris (categories 1 to 41, with a few exceptions), while A horizons
19 were characterized by mineral-organic faeces (categories 63, 64 and 67), roots (categories 42
20 to 51) and mineral particles (categories 71 to 75). Axis 2 showed the contrast between two
21 kinds of A horizons, the one (positive side) with mineral-organic epigeic earthworm faeces
22 (category 63), the other (negative side) with anecic (all mineral-organic) earthworm faeces
23 (category 64) and mineral-organic enchytraeid faeces (category 67). The projection of layers
24 on the same two axes (Fig. 3) showed that the distinction between Oa and A horizons, as done
25 by naked eye in the field as organic or mineral-organic, respectively, was fairly good, except

1 in BN where most layers exhibited intermediary features (corresponding points were
2 projected not far from the origin, indicating the paucity of characteristic features). A few A
3 horizons had been misidentified as Oa horizons, in particular in AS. Conversely, a few Oa
4 horizons had been misidentified as A horizons, in particular in AN. The two kinds of A
5 horizons (with either anecic/enchytraeid or epigeic worm faeces) were not equally distributed
6 in the 6 sites. While A horizons with epigeic worm faeces were absent from Intermediate
7 North (IN), Intermediate South (IS) and near absent from Basic North (BN) and Basic South
8 (BS), they were dominant in Acid North (AN) and present (although as a minor part of the
9 samples) in Acid South (AS).

10

11 The projection of the categories in the plane of Axes 1 and 3 (Fig. 4) showed the same
12 clustering of Oa horizons on the positive side of Axis 1 (same as in Fig. 2), but now two
13 categories of A horizons were separated along Axis 3, the one with mineral-organic
14 enchytraeid faeces (category 67), on the positive side, the other with anecic earthworm faeces
15 (category 64) on the other side. These two categories belonged to the same branch in the
16 plane of Axes 1 and 2 (Fig. 2). The projection of layers in this plane of Axes 1 and 3 (Fig. 5)
17 shows that A horizons with mineral-organic enchytraeid faeces were mostly present in AS,
18 but some horizons of this kind were also present, although less frequently, in AN and IS, and
19 practically not in IN, BN and BS. If we combine results from the first three axes, taking into
20 account only the three main groups of mineral-organic faeces (epigeic and anecic earthworms,
21 enchytraeids), it appears that the A horizon of AN was mostly characterized by epigeic
22 earthworm activity, whereas AS was mostly characterized by enchytraeid activity and the
23 other sites by anecic earthworm activity, IS being in an intermediate position between AS and
24 BN/BS.

25

1 While Axes 2 and 3 did not distinguish clusters within the Oa horizon, Axis 4 (Fig. 6)
2 opposed Oa horizons with organic earthworm faeces (projected on the positive side of this
3 axis) to another cluster, characterized by organic enchytraeid and mite faeces (projected on
4 the negative side). The projection of layers (Fig. 7) showed that both clusters of Oa horizons
5 were present in AN and AS, only the cluster with enchytraeid and mite activity was present in
6 IN and IS, and poor differentiation (but rather on the earthworm side) occurred in BN and BS.

7

8

Biotic relationships between Oa and A horizons

9

10 We further investigated whether earthworm and enchytraeid activity occurred both in
11 Oa and A horizons, or whether different animal groups were living in these horizons. The
12 percent volume of organic enchytraeid faeces in the Oa horizon was positively correlated with
13 that of mineral-organic faeces of the same animal group in the corresponding A horizon ($r =$
14 0.50 , $P < 0.0001$). The correlation of organic enchytraeid faeces in the Oa horizon with
15 organic faeces of the same animal group in the A horizon was insignificant ($r = 0.11$, $P =$
16 0.26). The correlation of organic enchytraeid faeces in the Oa horizon with mineral-organic
17 epigeic earthworm faeces in the A horizon was negative ($r = -0.36$, $P < 0.001$). Thus, Oa
18 horizons with high enchytraeid activity (in the form of organic deposits) were associated with
19 high enchytraeid activity (in the form of mineral-organic deposits) in the underlying A
20 horizon. Similarly, organic epigeic earthworm faeces in the Oa horizon were positively
21 correlated with mineral-organic epigeic earthworm faeces in the A horizon ($r = 0.50$, $P <$
22 0.0001). Thus, the two kinds of Oa horizons which had been depicted by CA, the one
23 dominated by enchytraeid activity and the other by earthworm activity, were associated with
24 A horizons showing dominance of the same animal groups.

25

1 Although poorly represented in the studied layers (at most 2% of the matrix against
2 57% for organic enchytraeid faeces), mite faeces were positively correlated with organic
3 enchytraeid faeces ($r = 0.20$, $P < 0.001$), indicating the coincidence of these two animal
4 groups, with mites largely subordinate to the other animal group.

5

6 Anecic earthworm faeces in the A horizon were positively correlated with the same
7 category of faeces in the overlying Oa horizon ($r = 0.41$, $P < 0.0001$) and were negatively
8 correlated with organic epigeic earthworm faeces in the Oa horizon ($r = -0.22$, $P < 0.05$).
9 Thus, anecic earthworm activity was concomitant in Oa and A horizons, but these animals
10 deposit mineral-organic faeces in both horizons, contrary to enchytraeids and epigeic
11 earthworms, the faeces of which were in agreement with the organic or mineral-organic
12 nature of the horizon.

13

14 We further investigated whether the depth of the Oa horizon was related to biogenic
15 structures. Organic enchytraeid faeces exhibited by far the highest (and positive) correlation
16 with depth of the Oa horizon ($r = 0.42$, $P < 0.0001$). Thus, the thicker the Oa horizon, the
17 more enchytraeid faeces it contained.

18

19 **Influence of the age of trees on the composition of Oa and A horizons**

20

21 Mineral-organic enchytraeid faeces in the A horizon exhibited a positive significant
22 correlation with age of trees ($r = 0.41$, $P < 0.0001$). Conversely, anecic earthworm faeces in A
23 horizons exhibited a negative significant correlation with age of trees ($r = -0.21$, $P < 0.05$).
24 This points to a change in the balance between enchytraeid and anecic earthworm activity

1 during stand development. The correlation between age of trees and depth of the Oa horizon
2 was insignificant ($r = 0.06$, $P = 0.51$).

3

4

DISCUSSION

5

6

Enchytraeid activity and the formation of moder

7

8 Correspondence analysis and correlation studies showed that a few distinct
9 assemblages of Oa and A horizons were present in our study sites, and that each of them
10 could be characterized by a particular kind of animal activity. Awaiting for experimental
11 studies, it can be considered that the common occurrence of the same category of faeces in
12 both Oa and A horizons is an indirect evidence that the same organisms are involved in the
13 building of their structures, according to the view stressed by Faber (1991) that the same
14 species may exert different roles in different horizons. It can also be considered that the
15 distribution of faecal categories reflected the activity of different animal groups. Oa horizons
16 with high enchytraeid activity were associated with A horizons with high enchytraeid activity,
17 too, although these animals deposited organic faeces in the Oa horizons and mineral-organic
18 faeces in the underlying A horizons. Different species could be involved in this process but,
19 as an animal group, these tiny annelid worms seem to characterize a dysmoder sensu Brêthes
20 et al. (1995) or mormoder sensu Green et al. (1993), i.e. a moder with a thick Oa horizon (> 1
21 cm). Among our study sites, this humus form was absent on dolomitic substrates (BN, BS),
22 but it was present from place to place on the more acidic substrates (Figures 4-7). In the latter
23 case, this points to a possible influence of overlying vegetation, if we consider the positive
24 correlation between the amount of enchytraeid faeces in the A horizon and the age of the trees
25 at the sampling point. In their study of 13 beech forest stands growing under various

1 environmental conditions, Ponge et al. (1997) showed that, among mesofaunal and
2 macrofaunal invertebrates, enchytraeid worms were the dominant animal group in dysmoder.
3 Other studies showed that enchytraeid worms create a micro-granular structure (at the scale of
4 20-100 μm , not visible to the naked eye) in agricultural fields with poor earthworm activity
5 (Didden, 1990; Van Vliet et al., 1993; Chan and Heenan, 1995) as well as in the A horizon of
6 moder (Babel, 1968; Pawluk, 1987; Ponge, 1999b). Thus, these small annelids, known to
7 ingest humified organic matter, pure or mixed with mineral matter (Ponge, 1991; Dawod and
8 FitzPatrick, 1993), and to perform vertical movements over several centimeters (Springett et
9 al., 1970), could be considered as mainly responsible for the continuous passage from an Oa
10 to an A horizon, without any abrupt transition, which has been considered as a prominent
11 feature of moder (Green et al., 1993; Ponge, 1999b). This contradicts the contention that the
12 A horizon of moders, contrary to that of mulls, would be made of a side-by-side assemblage
13 of organic and mineral matter, resulting from leachates of dissolved substances and suspended
14 faunal droppings (Bal, 1970; Babel, 1975; Brêthes et al., 1995). This might hold for sandy or
15 gravelly soils, where the size of mineral grains exceeds the silt size (2-50 μm) required for
16 their passage through an enchytraeid gut, as shown in soil sections by Zachariae (1965), but
17 not for finer-grained soils where these animals are able to mix organic matter with mineral
18 matter (Didden, 1990; Topoliantz et al., 2000).

19

20 Regarding the increased role played by enchytraeid worms in Oa horizons of
21 increasing thickness, some authors argued that enchytraeids did not play a significant part in
22 the degradation of organic matter, and that their abundance could not contribute to the
23 decomposition of litter nor to the mixing of organic matter with mineral matter (Zachariae,
24 1964; Toutain et al., 1982). The observations made by Ponge (1984, 1985, 1988) on *Pinus*
25 *sylvestris* L. litter showed that these animals, in particular the acidophilic *Cognettia*

1 *sphagnetorum* Vejd., ingested well-decayed coniferous needles but digested only the fungi
2 they hosted, and that they consumed (and degraded in their guts) a great amount of
3 mycorrhizal fungal hyphae. It has also been shown that enchytraeids increased the
4 mineralization of O horizons by stimulating the microflora, if not overgrazed (Standen, 1978;
5 Wolters, 1988; Briones et al., 1998). We suggest that these animals may find more food, and a
6 moister environment in the organic matter accumulated in coniferous forests, especially when
7 a rich fungus flora is present, which is the case in particular in moder humus forms (Ponge,
8 2003). This may also explain their dominance (as ascertained by fecal deposits) under older
9 trees. In the course of time, the ectomycorrhizal root system of coniferous trees is known to
10 densify (Persson, 1980), thus increasing the resource available for enchytraeids through the
11 development of mycorrhizal flora. However, we showed that the amount of enchytraeid
12 faeces in the A horizon increased with the age of trees, to the detriment of anecic earthworm
13 faeces (a feature indicating a change from mull to moder), but without any relationship with
14 the depth of the Oa horizon. This points to the existence of two kinds of Oa horizons, one
15 associated with moders (and enchytraeid activity), the other with amphis (and earthworm
16 activity).

17

18 The fact that mite faeces seemed to be largely subordinate to enchytraeid faeces
19 should not be considered to reflect the respective population sizes of these animal groups.
20 Oribatid mites are abundant in thick O horizons where they reach population sizes (but not
21 biomasses) higher than those of enchytraeids (Petersen and Luxton, 1982; Hartmann et al.,
22 1989; Ponge et al., 1997). However, Ponge (1991, 1999a) observed that enchytraeids ingested
23 oribatid mite faeces, where the reverse phenomenon was not recorded. We infer that in the
24 course of time, and with increasing depth in the soil, mite faeces are progressively replaced by
25 enchytraeid faeces even where both animal groups are present at similar densities.

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Earthworm activity and the formation of amphi

If we disregard a few samples of mull, near all humus profiles sampled in the study transects belonged either to moder or to amphi humus forms. In the latter case, earthworm activity was prominent in both Oa and A horizons. However, the two ecological categories of earthworms we identified (anecic and epigeic earthworms) were not distributed equally among the sites, judging from the part played by their excrements in the composition of A horizons (Table 4). Epigeic earthworm activity was dominant in AN (Fig. 3), while anecic earthworm activity was dominant in BN and BS (Fig. 5), and enchytraeids and anecic earthworms were present in IN and IS (Figures 3 and 5). It seems that two distinct forms of amphi were present in the study region, according to the presence or the absence of anecic earthworms (Table 4). A fine-grained structure in the A horizon (size of aggregates <5 mm in diameter) is typical of epigeic earthworm activity, forming the form 1 which is present in AN and AS, while anecic activity (even when epigeic earthworms are present) results in bigger aggregates (Galvan et al., 2005), forming the form 2 which is present in BN, BS, IN, IS.

We may wonder whether epigeic earthworms, known to live in litter, are able to mix organic matter with mineral matter in the same way as anecic earthworms do. *Dendrobaena octaedra* (Savigny) was the dominant epigeic species in our study sites (Guella, 2006, personal communication) and was near the only earthworm species living in AN, where all amphis were of the epigeic form. This small, slender acidophilic species (10-60 mm, width 1 mm) is known to feed not only on litter components, such as coniferous needles, but also on humified mineral matter, and to burrow in the mineral soil (Ponge, 1988). However, vertical distribution data differ according to authors. Abrahamsen (1972) never found it below 5 cm in

1 Norwegian coniferous forest soils while Martinucci and Sala (1979), working not too far from
2 our study sites (in the Venetian Alps) considered this species to be a weak burrower, which
3 was also found in the mineral soil, especially in the fall.

4

5 **Moder versus amphi and the balance of annelid communities**

6

7 The difference between moders and amphis was depicted by a strong negative
8 correlation between enchytraeid and epigeic earthworm faeces. This could be ascribed to the
9 competitive interactions which have been observed, first by co-occurrence data, second by
10 laboratory experiments, between the lumbricid *D. octaedra* and the enchytraeid *C.*
11 *sphagnetorum* (Huhta and Viberg, 1999), showing suppression of the enchytraeid population
12 by earthworms. The growth of spruce may influence this balance in favor of the less nutrient-
13 consuming animal group (enchytraeids) through an increase in the net nutrient uptake of trees,
14 which impoverishes the soil (Miller, 1984). A reversal of this phenomenon in favor of the
15 earthworm population has been observed under old trees (~200 years) in the French northern
16 Alps (Bernier and Ponge, 1994; Ponge et al., 1998).

17

18 Our observations in different upper montane spruce forests of the Trentino revealed
19 the gradual passage from moder to amphi humus forms, the former more typical for acid, the
20 latter for basic domains (Table 4). Despite our lack of knowledge on the conditions favoring
21 amphi, the role played by soil fauna in the building of this humus form can be established by
22 the quantitative analysis of animal faeces. Our results point to the need to reconsider and to
23 precise the juxtaposition of mineral matter and organic matter in the A horizon as a diagnostic
24 feature of moders (as opposed to mulls). We showed that the structure created by enchytraeid
25 activity in the A horizon of moders was similar to that of earthworm mulls and amphis (i.e. a

1 mixing of mineral and organic matter), but it was much finer. The widely reported assemblage
2 of coarse mineral grains, covered or mixed with organic deposits, in moders, results more
3 from the coarse texture of sandy soils (more prone to the formation of moders because of their
4 poor nutrient availability) than from the absence of burrowing activity in the A horizon.
5 Amphis differ from moders by the coarser grain of the structure in the A horizon (earthworm
6 faeces instead of enchytraeid faeces) but also in the Oa horizon, which is comprised of
7 earthworm faeces. In that sense, the Oa horizon of amphis does not differ from that of
8 eumoders (Brêthes et al., 1995), which is thin (≤ 1 cm) and comprised of faecal pellets visible
9 to the naked eye ($> 100 \mu\text{m}$).

10

11 Awaiting further observations and laboratory experiments, it can be hypothesized that
12 the main difference between moders and amphis lies in the important part played by epigeic
13 earthworms (compared to other macro-invertebrates) in the saprophagous community of the
14 latter, combined with seasonal influences on their vertical distribution: earthworms are known
15 to live deeper in the ground than most other litter-dwelling macro-invertebrates when the cold
16 (or dry) season becomes unfavorable to epigeic activity (Schaefer, 1991).

17

18 Concerning the independence of Oa and A horizons, it can be concluded that they are
19 inhabited by the same animal groups: when enchytraeid or earthworm activity is dominant in
20 the A horizon, it also dominates in the Oa horizon. The same animal group (maybe the same
21 species, not proved in the present study) ingests organic matter in Oa or a mixture of mineral
22 and organic matter in A. This had been already shown to occur in moders in beech forests of
23 Belgium (Ponge, 1999b). Reasons for the incomplete incorporation of organic matter (Oa
24 horizon) within the A horizon of amphi is still a matter of conjecture, even though climatic

1 reasons are highly probable, given its geographical location in European Alpine and
2 Mediterranean régions.

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REFERENCES

5

6 Abrahamsen, G. 1972. Ecological study of Lumbricidae (Oligochaeta) in Norwegian
7 coniferous forest soils. *Pedobiologia* 12: 267-281.

8

9 Ammer, S., and F. Makeschin. 1994. Auswirkungen experimenteller saurer Beregnung und
10 kalkung auf die Regenwurmfauna (Lumbricidae, Oligochaeta) und die Humus formen
11 in einem Fichtenaltbestand (Höglwaldexperiment). (In German) *Forstw. Cbl.* 113: 70-
12 85.

13

14 Babel, U. 1968. Enchytraeen-Lösungsgefüge in Löss. *Geoderma* 2: 57-63.

15

16 Babel, U. 1975. Micromorphology of soil organic matter. p. 369-473. *In* J.E. Gieseking (ed.)
17 *Soil components. I. Organic components.* Springer, Berlin, Germany.

18

19 Bal, L. 1970. Morphological investigation in two moder-humus profiles and the role of the
20 soil fauna in their genesis. *Geoderma* 4: 5-36.

21

22 Benzécri, J.P. 1969. Statistical analysis as a tool to make patterns emerge from the data. p. 35-
23 74. *In* S. Watanabe (ed.) *Methodologies of pattern recognition.* Academic Press, New
24 York, NY.

25

- 1 Bernier, N. 1996. Altitudinal changes in humus form dynamics in a spruce forest at the
2 montane level. *Plant Soil* 178: 1-28.
3
- 4 Bernier, N., and J.F. Ponge. 1994. Humus form dynamics during the sylvogenetic cycle in a
5 mountain spruce forest. *Soil Biol. Biochem.* 26: 183-220.
6
- 7 Bernier, N., and J.F. Ponge. 1998. *Lumbricus terrestris* L. distribution within an experimental
8 humus mosaic in a mountain spruce forest. *Biol. Fertil. Soils* 28: 81-86.
9
- 10 Bernier, N., Ponge, J.F., and J. André. 1993. Comparative study of soil organic layers in two
11 bilberry-spruce forest stands (*Vaccinio-Piceetea*). Relation to forest dynamics.
12 *Geoderma* 59: 89-108.
13
- 14 Brêthes, A., Brun, J.J., Jabiol, B., Ponge, J.F., and F. Toutain. 1995. Classification of forest
15 humus forms: a French proposal. *Ann. Sci. For.* 52: 535-546.
16
- 17 Bridges, E.M., Batjes, N.H., and F.O. Nachtergaele. 1998. World Reference Base for soil
18 resources. ISRIC, FAO, ISSS, Leuven, Belgium.
19
- 20 Briones, M.J.I., Carreira, J., and P. Ineson. 1998. *Cognettia sphagnetorum* (Enchytraeidae)
21 and nutrient cycling in organic soils: a microcosm experiment. *Appl. Soil Ecol.* 9: 289-
22 294.
23
- 24 Chan, K.Y., and D.P. Heenan. 1995. Occurrence of enchytraeid worms and some properties
25 of their casts in an Australian soil under cropping. *Austr. J. Soil Res.* 33: 651-657.

- 1
- 2 Chauvat, M., Ponge, J.F., and V. Wolters. 2007. Humus structure during a spruce forest
3 rotation: quantitative changes and relationship to soil biota. *Eur. J. Soil Sci.* (in press).
4
- 5 Dawod, V., and E.A. FitzPatrick. 1993. Some population sizes and effects of the
6 Enchytraeidae (Oligochaeta) on soil structure in a selection of Scottish soils.
7 *Geoderma* 56: 173-178.
8
- 9 Didden, W.A.M. 1990. Involvement of Enchytraeidae (Oligochaeta) in soil structure
10 evolution in agricultural fields. *Biol. Fertil. Soils* 9: 152-158.
11
- 12 Faber, J.H. 1991. Functional classification of soil fauna: a new approach. *Oikos* 62: 110-117.
13
- 14 Galvan, P., Scattolin, L., Ponge, J.F., Viola, F., and A. Zanella. 2005. Le forme di humus e la
15 pedofauna. Interpretazione delle interrelazioni e chiavi di riconoscimento. (In Italian)
16 *Sherwood* 112: 33-39.
17
- 18 Graefe, U., and A. Beylich. 2006. Humus forms as tool for upscaling soil biodiversity data to
19 landscape level? *Mitteilgn. Dtsch. Bodenkundl. Gesellsch.* 108: 6-7.
20
- 21 Green, R.N., Trowbridge, R.L., and K. Klinka. 1993. Towards a taxonomic classification of
22 humus forms. *For. Sci. Monogr.* 29: 1-49.
23
- 24 Greenacre, M.J. 1984. *Theory and applications of correspondence analysis.* Academic Press,
25 London, UK.

- 1
- 2 Hartmann, P., Scheitler, M., and R. Fischer. 1989. Soil fauna comparisons in healthy and
3 declining Norway spruce stands. p. 137-150. *In* E.D. Schulze, O.L. Lange and R. Oren
4 (eds.) Forest decline and air pollution. Springer, Berlin, Germany.
- 5
- 6 Huhta, V., and K. Viberg. 1999. Competitive interactions between the earthworm
7 *Dendrobaena octaedra* and the enchytraeid *Cognettia sphagnetorum*. *Pedobiologia*
8 43: 886-890.
- 9
- 10 Jabiol, B., Zanella, A., Englisch, M., Hager, H., Katzensteiner, K., and R.W.de Waal. 2004.
11 Towards an European classification of terrestrial humus forms. Eurosoil Congress,
12 Freiburg, September 2004.
- 13
- 14 Jongerius, A. 1963. Optic-volumetric measurements on some humus forms. p. 137-148. *In* J.
15 Doeksen and J. Van der Drift (eds.) Soil Organisms. North-Holland Publishing
16 Company, Amsterdam, The Netherlands.
- 17
- 18 Loranger, G., Ponge, J.F., and P. Lavelle. 2003. Humus forms in two secondary semi-
19 evergreen tropical forests. *Eur. J. Soil Sci.* 54: 17-24.
- 20
- 21 Martinucci, G., and G. Sala. 1979. Lumbricids and soil types in prealpine and alpine woods.
22 *Boll Zool.* 46: 279-297.
- 23

- 1 Miller, H.G. 1984. Dynamics of nutrient cycling in plantation ecosystems. p. 53-78. *In* G.D.
2 Bowen and E.K.S. Nambiar (eds.) Nutrition of forest trees in plantations. Academic
3 Press, London, UK.
4
- 5 Nihlgård, B. 1971. Pedological influence of spruce planted on former beech forest soils in
6 Scania, South Sweden. *Oikos* 22: 302-314.
7
- 8 Nilsson, S.I., Miller, H.G., and J.D. Miller. 1982. Forest growth as a possible cause of soil and
9 water acidification: an examination of the concepts. *Oikos* 39: 40-49.
10
- 11 Odasso, M. 2002. I tipi forestali del Trentino. Catalogo, guida al riconoscimento,
12 localizzazione e caratteristiche ecologico-vegetazionali. (In Italian) Rep. Centr. Ecol.
13 Alp. 25: 1-192.
14
- 15 Ovington, J.D. 1954. Studies of the development of woodland conditions under different
16 trees. II. The forest floor. *J. Ecol.* 42: 71-80.
17
- 18 Pawluk, S. 1987. Faunal micromorphological features in moder humus of some Western
19 Canadian soils. *Geoderma* 40: 3-16.
20
- 21 Persson, H., 1980. Death and replacement of fine roots in a mature Scots pine stand. *Ecol.*
22 *Bull.* 32: 251-260.
23
- 24 Petersen, H., and M. Luxton, 1982. A comparative analysis of soil fauna populations and their
25 role in decomposition processes. *Oikos* 39: 287-388.

- 1
- 2 Pickett, S.T.A. 1989. Space-for-time substitution as an alternative to long term studies. p.
- 3 110-135 *In* G.E. Likens (ed.) Long term studies in ecology. Springer, New York, NY.
- 4
- 5 Ponge, J.F. 1984. Étude écologique d'un humus forestier par l'observation d'un petit volume,
- 6 premiers résultats. I. La couche L₁ d'un moder sous pin sylvestre. (In French) Rev.
- 7 Ecol. Biol. Sol 21: 161-187.
- 8
- 9 Ponge, J.F. 1985. Étude écologique d'un humus forestier par l'observation d'un petit volume.
- 10 II. La couche L₂ d'un moder sous *Pinus sylvestris*. (In French) Pedobiologia 28: 73-
- 11 114.
- 12
- 13 Ponge, J.F. 1988. Étude écologique d'un humus forestier par l'observation d'un petit volume.
- 14 III. La couche F₁ d'un moder sous *Pinus sylvestris*. (In French) Pedobiologia 31: 1-64.
- 15
- 16 Ponge, J.F. 1991. Food resources and diets of soil animals in a small area of Scots pine litter.
- 17 Geoderma 49: 33-62.
- 18
- 19 Ponge, J.F. 1999a. Heterogeneity in soil animal communities and the development of humus
- 20 forms. p. 33-44. *In* N. Rastin and J. Bauhus (eds.) Going underground. Ecological
- 21 studies in forest soils. Research Signpost, Trivendrum, India.
- 22
- 23 Ponge, J.F. 1999b. Horizons and humus forms in beech forests of the Belgian Ardennes. Soil
- 24 Sci. Soc. Am. J. 63: 1888-1901.
- 25

- 1 Ponge, J.F. 2003. Humus forms in terrestrial ecosystems: a framework to biodiversity. Soil
2 Biol. Biochem. 35: 935-945.
3
- 4 Ponge, J.F., André, J., Zackrisson, O., Bernier, N., Nilsson, M.C., and C. Gallet. 1998. The
5 forest regeneration puzzle: biological mechanisms in humus layer and forest vegetation
6 dynamics. BioScience 48: 523-530.
7
- 8 Ponge, J.F., Arpin, P., Sondag, F., and F. Delecour. 1997. Soil fauna and site assessment in
9 beech stands of the Belgian Ardennes. Can. J. For. Res. 27: 2053-2064.
10
- 11 Ponge, J.F., Chevalier, R., and P. Loussot. 2002. Humus Index: an integrated tool for the
12 assessment of forest floor and topsoil properties. Soil Sci. Soc. Am. J. 66: 1996-2001.
13
- 14 Sadaka, N., and J.F. Ponge. 2003. Climatic effects on soil trophic networks and the resulting
15 humus profiles in holm oak (*Quercus rotundifolia*) forests in the High Atlas of
16 Morocco as revealed by correspondence analysis. Eur. J. Soil Sci. 54: 767-777.
17
- 18 Sagot, C., Brun, J.J., Grossi, J.L., Chauchat, J.H., and G. Boudin. 1999. Earthworm
19 distribution and humus forms in the development of a semi-natural alpine spruce
20 forest. Eur. J. Soil Biol. 35: 163-169.
21
- 22 Schaefer, M. 1991. The animal community: diversity and resources. p. 51-120. In E. Röhrig
23 and B. Ulrich (eds.) Ecosystems of the World. VII. Temperate deciduous forests.
24 Elsevier, Amsterdam, The Netherlands.
25

- 1 Schaetzl, R.J., and S. Anderson. 2005. Soils, genesis and geomorphology. Cambridge
2 University Press, Cambridge, UK.
3
- 4 Scotti, I., Vendramin, G.G., Matteotti, L.S., Scarponi, C., Sari-Gorla, M., and G. Binelli.
5 2000. Postglacial recolonization routes for *Picea abies* K. in Italy as suggested by the
6 analysis of sequence-characterized amplified region (SCAR) markers. Mol. Ecol. 9:
7 699-708.
8
- 9 Sokal, R.R., and F.J. Rohlf. 1995. Biometry, 3rd ed. Freeman, New York, NY.
10
- 11 Springett, J.A., Brittain, J.E., and B.P. Springett. 1970. Vertical movement of Enchytraeidae
12 (Oligochaeta) in moorland soils. Oikos 21: 16-21.
13
- 14 Standen, V. 1978. The influence of soil fauna on decomposition by micro-organisms in
15 blanket bog litter. J. Anim. Ecol. 47: 25-38.
16
- 17 Topoliantz, S., Ponge, J.F., and P. Viaux. 2000. Earthworm and enchytraeid activity under
18 different arable farming systems, as exemplified by biogenic structures. Plant Soil
19 225: 39-51.
20
- 21 Toutain, F., Villemin, G., Albrecht, A., and O. Reisinger. 1982. Étude ultrastructurale des
22 processus de biodégradation. II. Modèle enchytréides-litière de feuillus. Pedobiologia
23 23: 145-156.
24

- 1 Ulrich, B. 1994. Process hierarchy in forest ecosystems: an integrative ecosystem theory. p.
2 353-397. *In* A. Hutterman and D. Godbold (eds.) Effects of acid rain on forest
3 processes. Wiley-Liss, New York, NY.
- 4
- 5 Van Vliet, P.C.J., West, L.T., Hendrix, P.F., and D.C. Coleman. 1993. The influence of
6 Enchytraeidae (Oligochaeta) on the soil porosity of small microcosms. *Geoderma* 56:
7 287-299.
- 8
- 9 Vetter, M., Wirth, C., Böttcher, H., Churkina, G., Schulze, E.D., Wutzler, T., and G. Weber.
10 2005. Partitioning direct and indirect human-induced effects on carbon sequestration
11 of managed coniferous forests using model simulations and forest inventories. *Global*
12 *Change Biol.* 11: 810-827.
- 13
- 14 West, T.S. 1969. Complexometry with EDTA and related reagents, 3rd ed. BDH Chemicals
15 Ltd., Poole, Dorset, UK.
- 16
- 17 Wolters, V. 1988. Effects of *Mesenchytraeus glandulosus* (Oligochaeta, Enchytraeidae) on
18 decomposition processes. *Pedobiologia* 32: 387-398.
- 19
- 20 Zachariae, G. 1964. Welche Bedeutung haben Enchytraeen im Waldböden? p. 57-68. *In* A.
21 Jongerius (ed.) Soil micromorphology. Elsevier, Amsterdam, The Netherlands.
- 22
- 23 Zachariae, G., 1965. Spuren tierischer Tätigkeit im Boden des Buchenwaldes. *Forstw. Forsch.*
24 20: 1-68.
- 25

FIGURE CAPTIONS

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Figure 1. Geographical position of the six study sites Acid North (AN), Acid South (AS), Intermediate North (IN), Intermediate South (IS), Basic North (BN) and Basic South (BS) in the Province of Trento.

Figure 2. Projection of the categories of humus components (main variables) in the plane of the first two axes of correspondence analysis, together with additional variables (horizons, sites). Most prominent animal faeces in A horizons were arrowed

Figure 3. Projection of the samples in the plane of the first two axes of correspondence analysis. (black dots = Oa horizons, empty dots = A horizons)

Figure 4. Projection of the categories of humus components (main variables) in the plane of Axes 1 and 3 of correspondence analysis., together with additional variables (horizons, sites). Most prominent animal faeces in A horizons were arrowed

Figure 5. Projection of the samples in the plane of Axes 1 and 3 of correspondence analysis. (black dots = Oa horizons, empty dots = A horizons)

Figure 6. Projection of the categories of humus components (main variables) in the plane of Axes 1 and 4 of correspondence analysis., together with additional variables (horizons, sites). Most prominent animal faeces in Oa horizons were arrowed

1 **Figure 7.** Projection of the samples in the plane of Axes 1 and 4 of correspondence analysis.

2 (black dots = Oa horizons, empty dots = A horizons)

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Table 1. Main features of the six study sites. Soil types according to World Reference Base (Bridges et al., 1998). Humus forms according to Brêthes et al. (1995).

Site code	AN	AS	IN	IS	BN	BS
Site name	Pellizzano	Madonna di Campiglio	Paneveggio	Paneveggio	Gardeccia	Fondo
Soil types	Podzols, Histosols, Umbrisols	Umbrisols, Cambisols, Podzols	Cambisols, Podzols, Leptosols	Cambisols, Podzols, Regosols	Cambisols, Regosols	Cambisols, Leptosols, Regosols
Humus forms	Mor, dysmoder, dysmull, amphimull	Mor, dysmoder, eumoder, oligomull, amphimull	Mor, dysmoder, dysmull, amphimull	Mor, dysmoder, dysmull, oligomull, amphimull	Eumoder, dysmull, oligomull, amphimull	Eumoder, dysmull, mesomull, amphimull
Parent material	Acid boulder clay overlying granitic stones	Plutonic granite often covered by late-Wurm silica- rich deposits	Permian rhyolite	Mixed volcanic/dolomit ic moraine	Dolomitic moraine with granitic erratic boulders	Dolomitic moraine with granitic erratic boulders
Exposure	North	South	North	South	North	South
Elevation	1650-1870 m	1720-1865 m	1660-1780 m	1620-1818 m	1620-1820 m	1640-1690 m
Mean slope	27%	32%	16%	15%	18%	15%
Mean annual temperature	4.2°C	4.0°C	9.2°C	4.4°C	4.3°C	5.3°C
Mean annual rainfall	962 mm	1303 mm	782 mm	1103 mm	1049 mm	863 mm

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Table 2. List of categories used to describe the composition of Oa and A horizons.

1	Brown entire spruce needle
2	Grey entire spruce needle
3	Entire spruce needle with Lophodermium
4	Browsed entire spruce needle with Lophodermium
5	Red entire collapsed larch needle
6	Brown browsed entire spruce needle
7	Brown fragmented spruce needle
8	Dark fragmented spruce needle
9	Brown fragmented spruce needle with Lophodermium
10	Red fragmented collapsed larch needle
11	Brown browsed fragmented spruce needle
12	Grey fragmented spruce needle
13	White fragmented spruce needle
14	White collapsed entire spruce needle
15	White collapsed fragmented spruce needle
16	Brown collapsed entire spruce needle
17	Brown collapsed fragmented spruce needle
18	White collapsed browsed spruce needle
19	Brown empty fragmented spruce needle
20	White empty fragmented spruce needle with Lophodermium
21	Entire leaf

- 22 Fragmented leaf
- 23 Intact leaf base of grass
- 24 Fragmented leaf base of grass
- 25 Intact grass leaf
- 26 Fragmented grass leaf
- 27 Fragmented grass stem
- 28 Fragmented forb leaf
- 29 Twig
- 30 Intact moss
- 31 Fragmented moss
- 32 Bark
- 33 Intact flower scale
- 34 Fragmented flower scale
- 35 Wood
- 36 Intact seed
- 37 Fragmented seed
- 38 Cone scale
- 39 Spruce cone
- 40 Pollen
- 41 Unidentifiable plant fragment
- 42 Brown intact fine root
- 43 Brown fragmented fine root
- 44 Brown intact mycorrhiza
- 45 Brown fragmented mycorrhiza

- 46 Brown collapsed fine root with white mycelium
- 47 White intact fine root
- 48 White fragmented fine root
- 49 Brown intact large root
- 50 Brown fragmented large root
- 51 White large root
- 52 Fine organic matter
- 53 Charcoal
- 54 White mycelium
- 55 Dark mycelium
- 56 Yellow mycelium
- 57 Rhizomorphs
- 58 Cenococcum mycorrhiza
- 59 Cenococcum sclerotium
- 60 Cenococcum mycelium
- 61 Fragmented fungal carpophore
- 62 Organic epigeic earthworm faeces
- 63 Mineral-organic epigeic earthworm faeces
- 64 Mineral-organic anecic earthworm faeces
- 65 Millipede faeces
- 66 Organic enchytraeid faeces
- 67 Mineral-organic enchytraeid faeces
- 68 Mite faeces
- 69 Red unidentified faeces

- 70 Insect faeces
 - 71 Gravel
 - 72 Stone
 - 73 Mineral mass
 - 74 Mica
 - 75 Quartz sand
 - 76 Epigeic earthworm
 - 77 Snail
 - 78 Insect larva
 - 79 Mite
 - 80 Springtail
 - 81 Enchytraeid
 - 82 Dead scissiparity enchytraeid parts
 - 83 Insect moult
 - 84 Mite moult
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Table 3. Main physico-chemical features of selected samples of A horizons in the six study sites (mean \pm SE).

Site code	AN	AS	IN	IS	BN	BS
Chemical analyses	8 samples	15 samples	11 samples	15 samples	17 samples	18 samples
Organic C (g.kg ⁻¹)	186 \pm 36	200 \pm 16	126 \pm 21	124 \pm 19	97 \pm 9	135 \pm 20
Total N (g.kg ⁻¹)	10.2 \pm 2.1	9.9 \pm 0.7	7.5 \pm 1.4	6.0 \pm 0.8	6.0 \pm 0.4	8.0 \pm 0.9
C/N	18.6 \pm 0.9	20.3 \pm 0.5	17.2 \pm 0.9	20.2 \pm 0.8	16.2 \pm 0.8	16.5 \pm 0.8
Carbonates (g.kg ⁻¹)	-	-	3.6 \pm 0.1	-	23.0 \pm 4.3	24.4 \pm 4.1
pH KCl	3.4 \pm 0.1	3.6 \pm 0.1	4.3 \pm 0.1	4.2 \pm 0.3	5.8 \pm 0.2	5.5 \pm 0.4
pH H ₂ O	4.2 \pm 0.1	4.3 \pm 0.1	4.2 \pm 0.1	5.1 \pm 0.2	6.3 \pm 0.2	6.2 \pm 0.3
CEC pH soil (cmol.kg ⁻¹)	98 \pm 13	92 \pm 4	63 \pm 5	86 \pm 8	85 \pm 4	90 \pm 9
CEC pH 7 (cmol.kg ⁻¹)	68 \pm 6	51 \pm 6	44 \pm 4	57 \pm 7	57 \pm 3	64 \pm 6
Exchangeable Ca (cmol.kg ⁻¹)	3.7 \pm 1.6	10.4 \pm 1.4	5.2 \pm 1.2	28.6 \pm 8.5	46.0 \pm 3.4	41.6 \pm 7.2
Exchangeable Mg (cmol.kg ⁻¹)	1.9 \pm 1.3	1.6 \pm 0.2	0.8 \pm 0.1	5.8 \pm 1.9	13.4 \pm 1.3	13.5 \pm 2.1
Exchangeable K (cmol.kg ⁻¹)	0.5 \pm 0.2	1.0 \pm 0.1	0.7 \pm 0.1	0.7 \pm 0.1	0.6 \pm 0.1	0.7 \pm 0.1
Base saturation (%)	5.2 \pm 1.5	13.8 \pm 2.1	10.1 \pm 1.7	38.4 \pm 8.5	70.6 \pm 4.2	62.2 \pm 9.6
Exchangeable acidity (cmol.kg ⁻¹)	11.2 \pm 0.6	7.3 \pm 0.9	7.0 \pm 1.8	3.6 \pm 1.2	0.3 \pm 0.02	4.2 \pm 0.7
Exchangeable Al ⁺⁺⁺ (cmol.kg ⁻¹)	8.9 \pm 0.7	4.7 \pm 0.7	5.3 \pm 1.5	2.8 \pm 0.9	0.2 \pm 0.02	2.8 \pm 0.5
Exchangeable H ⁺ (cmol.kg ⁻¹)	2.3 \pm 0.2	2.5 \pm 0.3	1.6 \pm 0.4	0.8 \pm 0.2	0.1 \pm 0.01	1.4 \pm 0.4
Total acidity (cmol.kg ⁻¹)	121 \pm 8	99 \pm 7	54 \pm 7	34 \pm 6	25 \pm 3	54 \pm 11
Particle size distribution	5 samples	8 samples	8 samples	8 samples	8 samples	8 samples
Coarse sand (g.kg ⁻¹)	175 \pm 33	307 \pm 35	330 \pm 53	190 \pm 41	35 \pm 4	61 \pm 13
Fine sand (g.kg ⁻¹)	169 \pm 12	233 \pm 20	162 \pm 29	148 \pm 15	132 \pm 8	145 \pm 13
Coarse silt (g.kg ⁻¹)	156 \pm 15	136 \pm 11	102 \pm 14	146 \pm 21	230 \pm 20	140 \pm 11
Fine silt (g.kg ⁻¹)	262 \pm 19	201 \pm 13	232 \pm 29	252 \pm 11	391 \pm 19	334 \pm 17
Clay (g.kg ⁻¹)	238 \pm 32	123 \pm 13	174 \pm 15	264 \pm 43	211 \pm 12	321 \pm 9

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Table 4. Dominant humus forms and biogenic structures in the six study sites.

Site codes	AN	AS	IN	IS	BN	BS
Dominant humus forms	moder, amphi 1	moder, amphi 1	amphi 2, moder	amphi 2, moder	amphi 2	amphi 2
Faecal deposits in Oa horizon						
epigeic earthworms	**	**	nil	nil	***	***
enchytraeids and mites	**	**	***	***	*	*
Faecal deposits in A horizon						
anecic earthworms	nil	*	***	***	***	***
epigeic earthworms	***	**	nil	nil	*	*
enchytraeids	**	***	*	**	*	*

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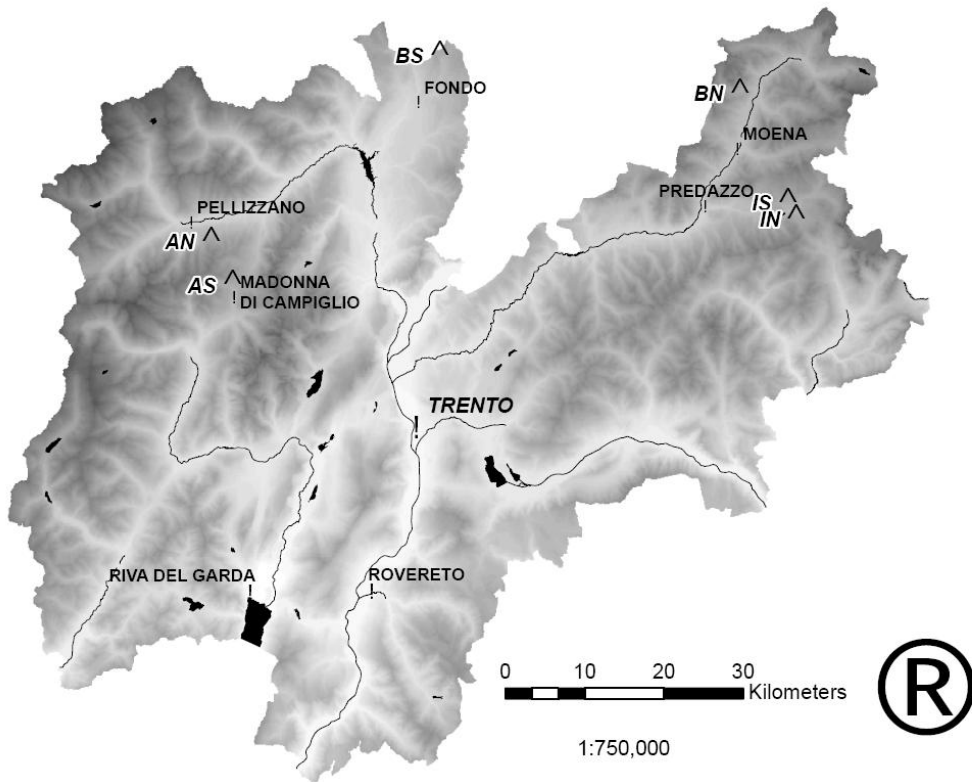
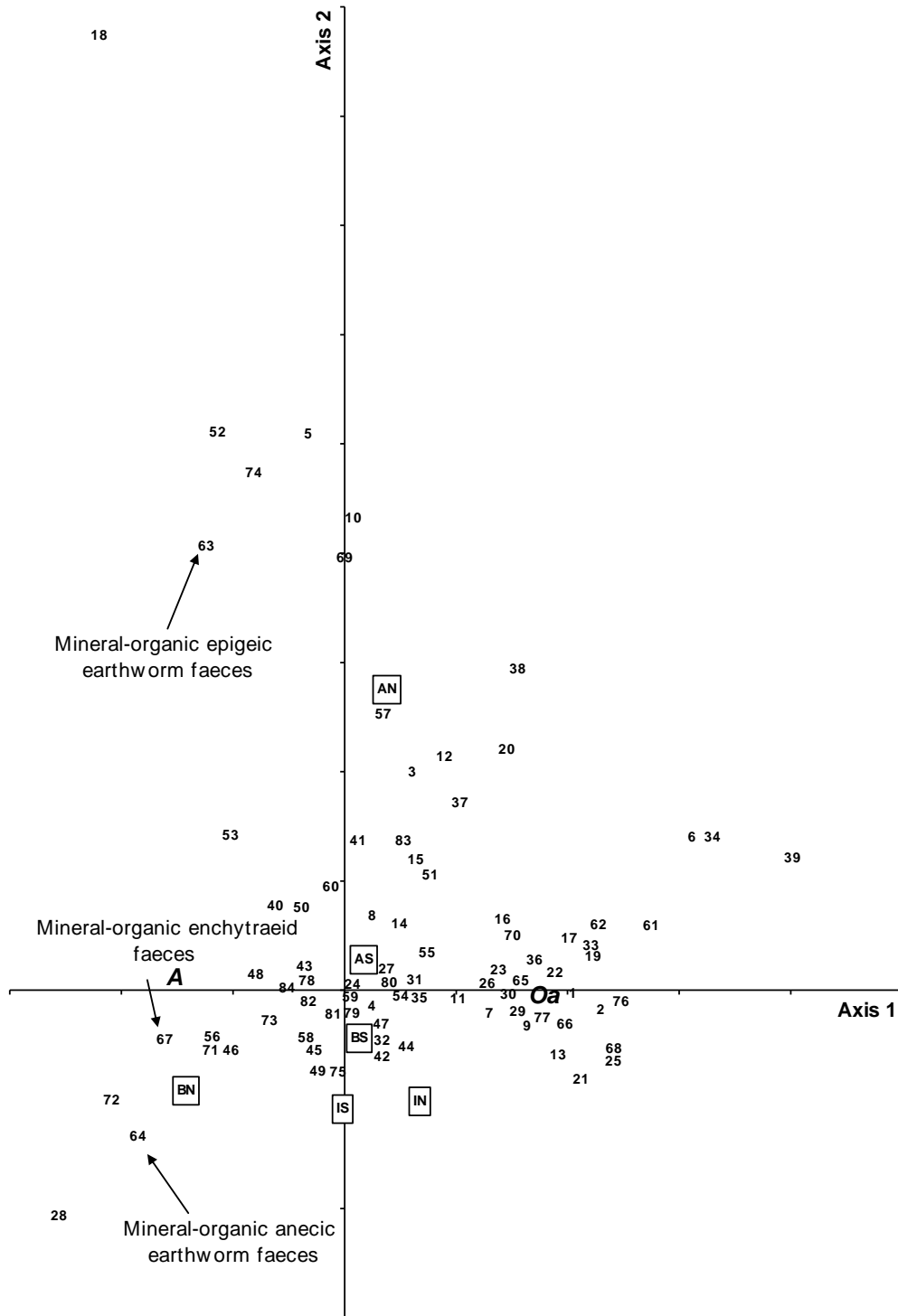
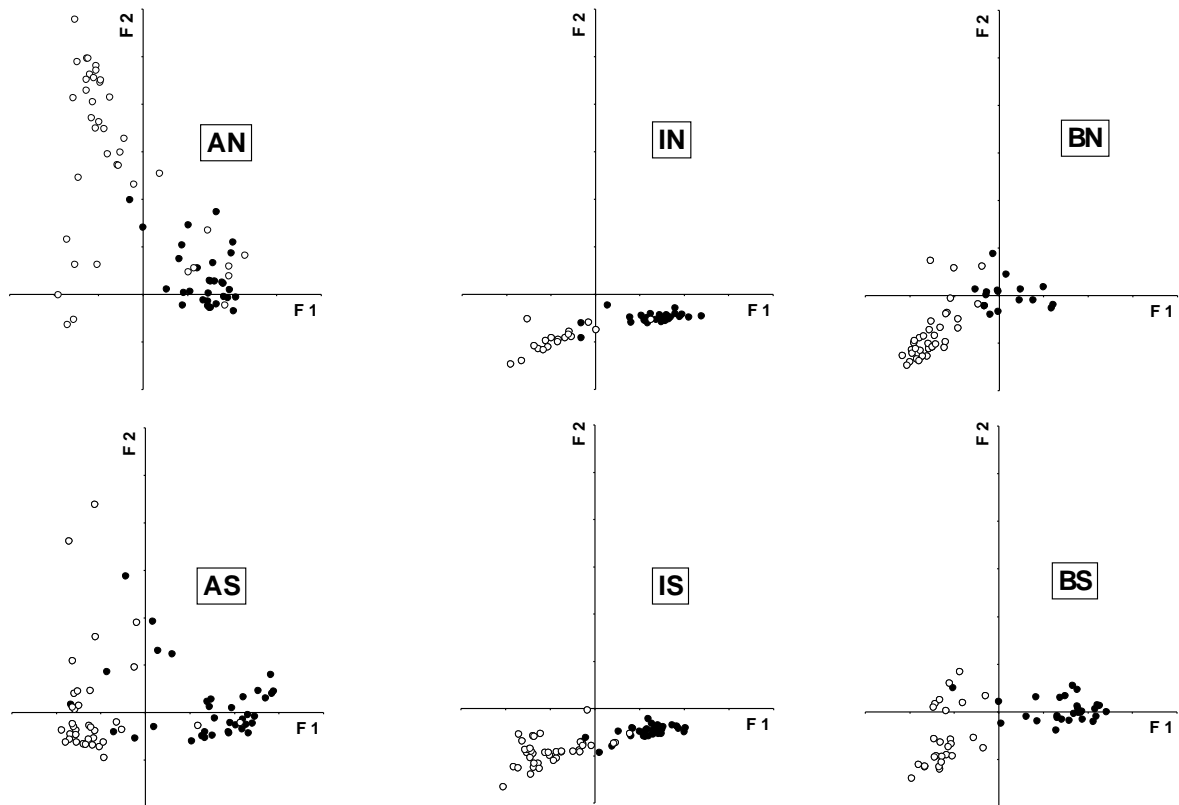


Figure 1. Geographical position of the six study sites Acid North (AN), Acid South (AS), Intermediate North (IN), Intermediate South (IS), Basic North (BN) and Basic South (BS) in the Province of Trento.



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2 **Figure 2.** Projection of the categories of humus components (main variables) in the plane of
 3 the first two axes of correspondence analysis, together with additional variables
 4 (horizons, sites). Most prominent animal faeces in A horizons were arrowed. Numbers
 5 (1 to 84) refer to humus components listed in Table 2. AN, AS, BN, BS, IN and IS
 6 code for the six sites mapped on Fig. 1.



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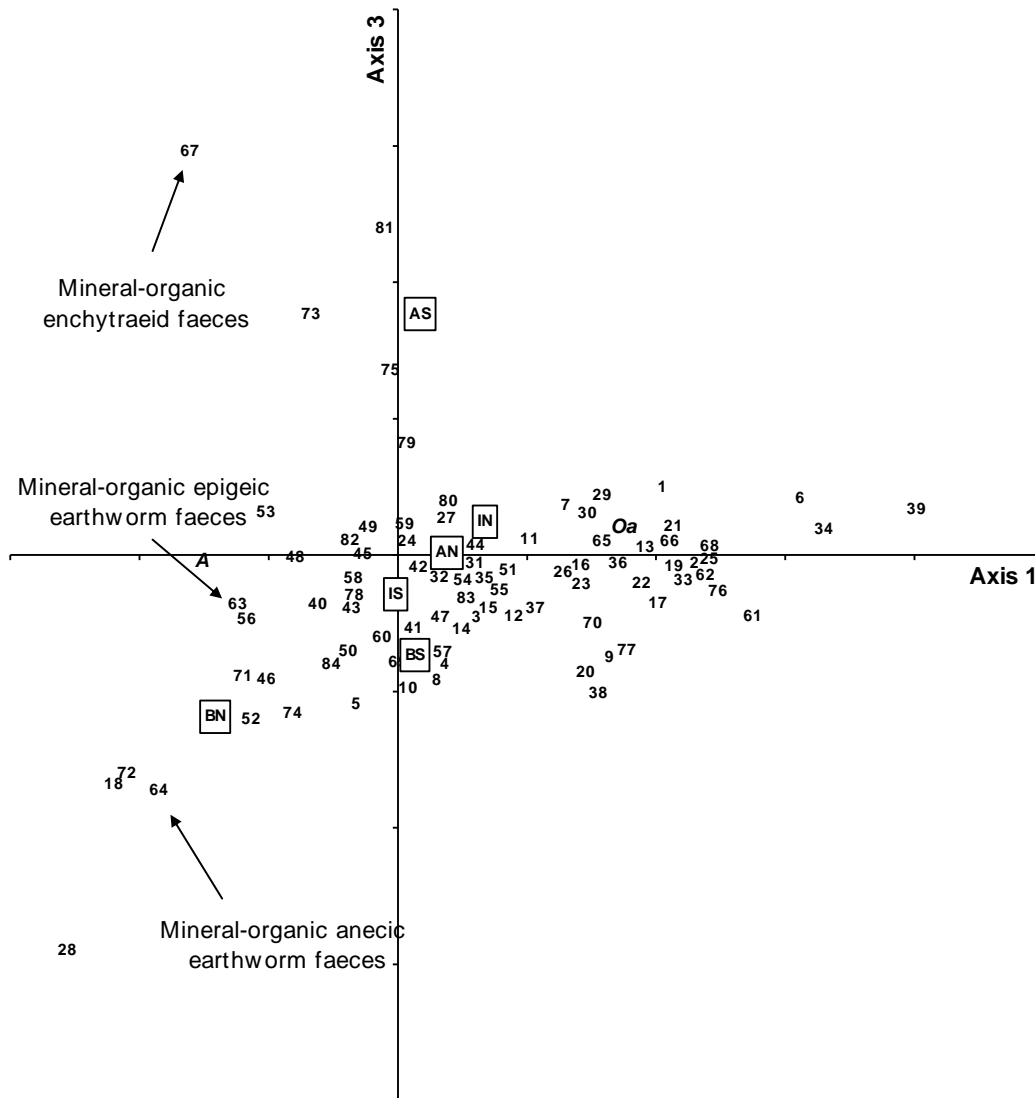
3 **Figure 3.** Projection of the samples in the plane of the first two axes of correspondence

4 analysis. Black dots = Oa horizons, empty dots = A horizons. AN = Acid North, AS =

5 Acid South, BN = Basic North, BS = Basic South, IN = Intermediate North, IS =

6 Intermediate South.

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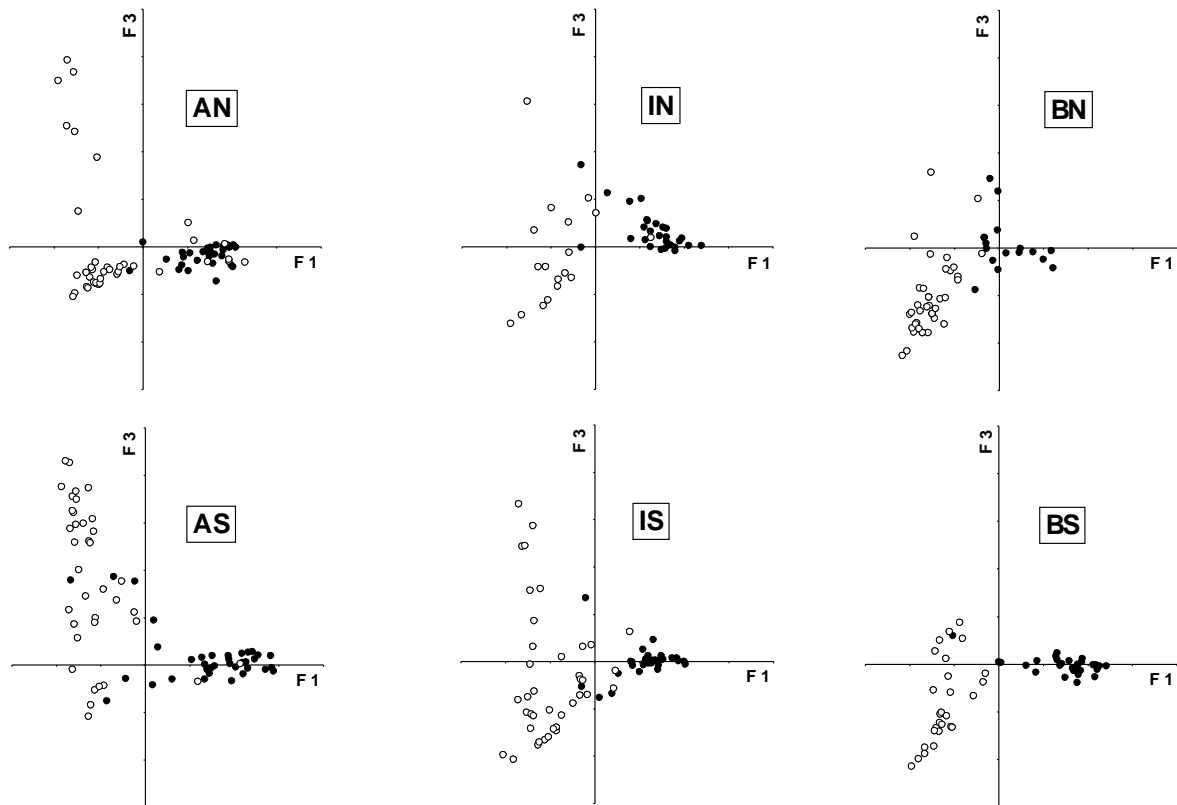
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2 **Figure 4.** Projection of the categories of humus components (main variables) in the plane of

3 Axes 1 and 3 of correspondence analysis, together with additional variables (horizons,

4 sites). Most prominent animal faeces in A horizons were arrowed. Otherwise as for

5 Fig. 2.



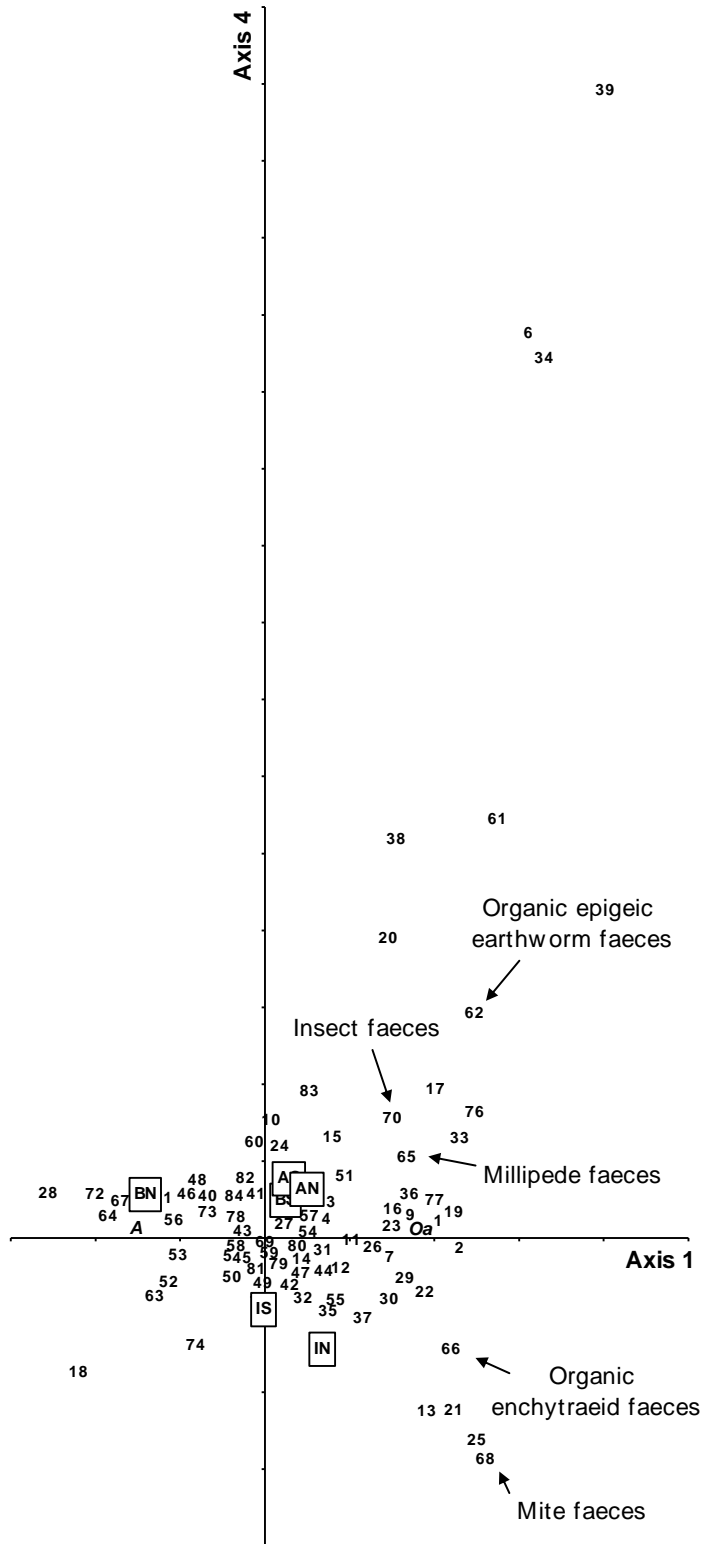
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3 **Figure 5.** Projection of the samples in the plane of Axes 1 and 3 of correspondence analysis

4 (black dots = Oa horizons, empty dots = A horizons). Otherwise as for Fig. 3.

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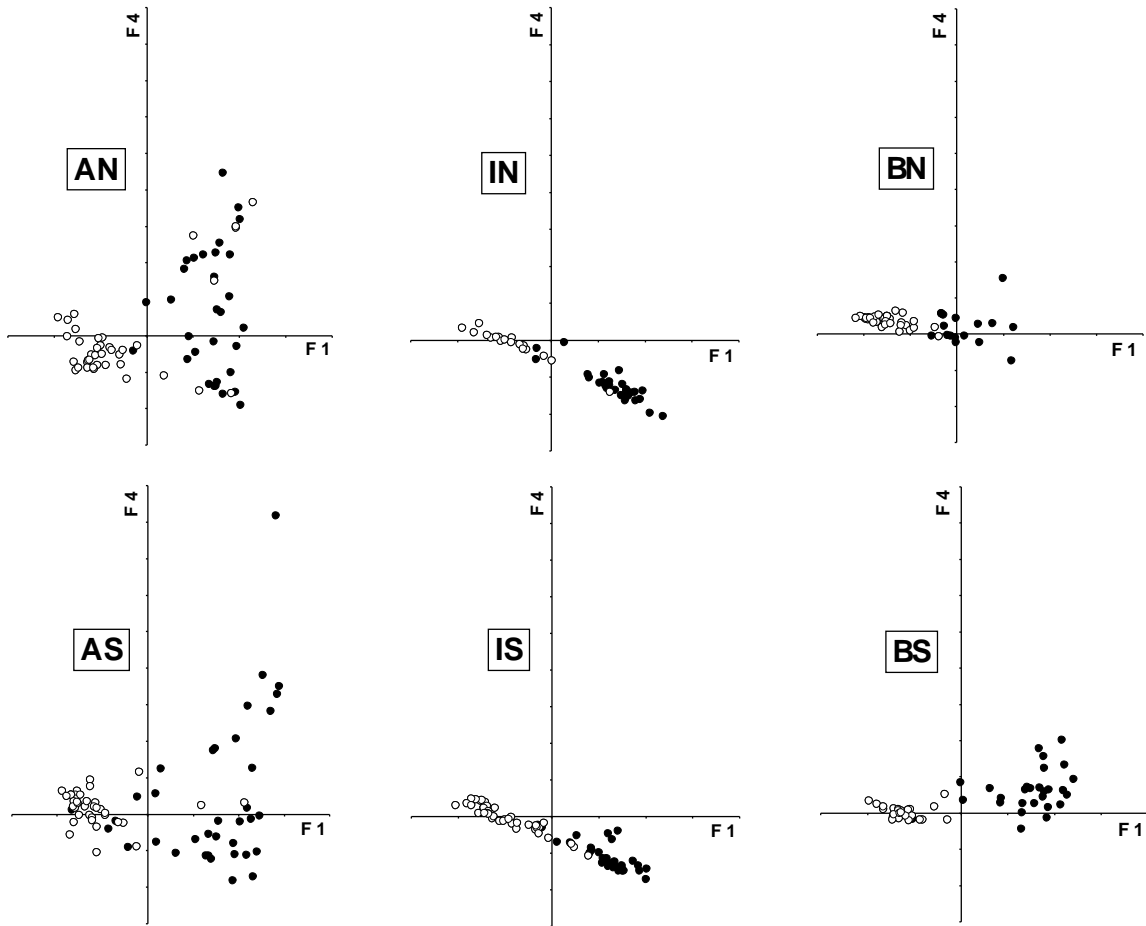
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2 **Figure 6.** Projection of the categories of humus components (main variables) in the plane of

3 Axes 1 and 4 of correspondence analysis, together with additional variables (horizons,

4 sites). Most prominent animal faeces in Oa horizons were arrowed. Otherwise as for

5 Fig. 2.



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3 **Figure 7.** Projection of the samples in the plane of Axes 1 and 4 of correspondence analysis

4 (black dots = Oa horizons, empty dots = A horizons). Otherwise as for Fig. 3.