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**Humus profiles and successional development in a rock savanna: a  
micromorphological approach pointing to fire as a disturbance event  
(Nouragues inselberg, French Guiana)**

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Running title: Humus profiles and fire in a rock savanna

## Summary

The common development of vegetation and soil is a central question of plant succession. We asked whether places where aerial parts of woody vegetation die and accumulate on the ground (zones of destruction or ‘micro-chablis’) played a role in the successional development of vegetation patches on tropical inselbergs and whether causes could be inferred from the analysis of the organic matter accumulated along a successional gradient. The study was conducted in French Guiana (South America). Nine humus profiles (each comprised of a varying number of layers) were selected in shrub thickets (~1a each) representative of three vegetation types of the rock savanna: canopies of pure *Clusia minor* (Clusiaceae), *C. minor* in mixture with *Myrcia saxatilis* (Myrtaceae) and zones of destruction. A count point optical method for small soil volumes was used to measure under a dissecting microscope the volume ratio of each kind of humus component (107 categories) in the 62 layers thus sampled. Micromorphological data were analysed by correspondence analysis (CA). Humus profiles varied according to canopy trees and revealed traits of the past and trends for the future of the plant succession. Zones of destruction differed from other humus profiles by lack of OL and OF horizons and by the presence of charred material, which establishes the role of spatially limited fires or lightning impacts in the cyclic development of vegetation patches.

**Keywords** Tropical inselbergs; Humus profiles; Plant succession; Small-scale disturbances

## 1 Introduction

2  
3 Humus results from the biochemical transformation of residual vegetation by  
4 decomposer foodwebs (Wolters et al., 2000). The direct observation of the soil under the  
5 microscope, also called micromorphology, was developed by Kubiëna (1938) and it has been  
6 shown essential to the knowledge of biological processes in surface horizons (Bernier, 1996).  
7 Humus forms therefore deserve special attention in studies of plant succession (Emmer and  
8 Sevink, 1993; Ponge et al., 1998). Traits of the past and trends for the future at the scale of  
9 years to decades can be derived from the observation of successive horizons by quantitative  
10 optical methods (Bernier and Ponge, 1994; Gillet and Ponge, 2002) and comparisons can be  
11 made among humus profiles by means of multivariate analysis (Peltier et al., 2001).

12  
13 Tropical inselbergs are granite or sandstone outcrops which rise abruptly from the  
14 surrounding rain forest (Bremer and Sander, 2000) and support a special type of vegetation  
15 adapted to harsh and strongly varying environmental conditions. On the Nouragues inselberg  
16 (French Guiana) isolated vegetation clumps are mainly comprised of *Clusia minor*  
17 (Clusiaceae) and *Myrcia saxatilis* (Myrtaceae), two shrubs which characterize respectively  
18 successive stages of a primary plant succession in the locally called 'rock savanna' (Sarhou  
19 and Grimaldi, 1992). Places (2-5 m<sup>2</sup>) where dead stems of *C. minor* remain standing or fall on  
20 the ground ('micro-chablis') are often seen within shrub thickets (Sarhou, 1992). These zones  
21 of destruction, where intense termite activity occurs at the inside of standing dead stems and  
22 branches and numerous sporocarps of wood-destroying fungi can be observed (Kounda-Kiki,  
23 2007), testify for destructive events of unknown origin and brings up questions regarding  
24 dynamic processes generated by disturbance events such as pronounced dryness, fires, storms,  
25 and fungal diseases (Finegan, 1984). Previous studies on the Nouragues inselberg (Vaçulik et

al., 2004; Kounda-Kiki et al., 2004, 2006) showed that parallel changes occur in vegetation, humus profiles and soil animal communities throughout the plant succession, but the existence of cyclic processes and the rate at which successional transition occurs are still under question.

We described humus profiles found in zones of destruction and compared them with humus profiles previously studied beneath pure *C. minor* thickets, as an early stage, and *C. minor* thickets enriched with *M. saxatilis* and several other Myrtaceae, as a late stage of plant succession (Kounda-Kiki et al., 2006). Based on visual inspection of the rock savanna our hypothesis is that zones of destruction appear within pure, closed *C. minor* thickets, allowing more, new plant species to establish, in particular longer-lived Myrtaceae. If this hypothesis is true, then the composition of humus profiles in zones of destruction should be in an intermediate position between those under pure *Clusia* canopies and those under mixed *Clusia-Myrcia* canopies. We also aim at discovering which factors prevail in the destruction of shrub thickets, which could be reflected in the composition of humus profiles as showed by Bernier and Ponge (1994) and Gillet and Ponge (2002) in temperate environments.

## Materials and methods

### Study site

The field work was carried out at the Nouragues inselberg (411 m above sea level), which is located in the Nouragues natural reservation (4°5'N and 52°42'W). The inselberg is composed of a tabular outcrop of Caribbean granite, of pinkish monzonitic-type, containing 27% potassium-feldspar (orthoclase) and 37% plagioclase, along with 33% quartz as coarse-

grained crystals and 2% accessory minerals such as pyroxene, corundum, and apatite (Grimaldi and Riéra, 2001). The chemical composition of the whole-rock (Sarhou and Grimaldi 1992) shows that the granite is highly siliceous (76.4% SiO<sub>2</sub>) and rich in alkalis (4.6% K<sub>2</sub>O, 4.2% Na<sub>2</sub>O). The climate is tropical humid, and is characterized by a dry season from July to November and a wet season from December to June interrupted by a very short dry season in March. Mean annual precipitation reaches 3000-3250 mm. The daily temperature ranges between 18-55°C and the daily air humidity between 20-100% (Sarhou and Grimaldi, 1992). The temperature of the bare rock surface may reach 75°C in the dry season. Most of the surface of the granitic outcrop is covered by cyanobacteria (Sarhou et al., 1995). Different dynamic stages can be observed in the development of shrub thickets (Sarhou, 2001). The bromeliad *Pitcairnia geyskesii* is the most typical plant of the inselberg. *C. minor* (Clusiaceae) represents the shrub vegetation unit of the rock savanna, forming dense thickets, 2-8 m tall (Sarhou, 2001; Sarhou et al., 2003). *M. saxatilis* (Myrtaceae) is the second most important shrub species, further established within *C. minor* thickets together with some minor other Myrtaceae. Zones of destruction are places from which living woody vegetation has disappeared, only decaying stems of *C. minor* being observed still standing or fallen on the ground, with many signs of fungal attacks and strong activity of termite colonies within dead stems.

## Sampling procedure

Nine humus profiles (three in each) were sampled in zones of destruction and in two dynamic stages of the *Clusia* community (pure *Clusia* and *Clusia-Myrcia*), which were subdivided into several layers directly on the field. Different vegetation clumps were selected, thus avoiding pseudo-replication. At the centre of a canopy or a zone of destruction, a block

of surface soil 25 cm<sup>2</sup> in area and 10 cm depth was cut with a sharp knife, with as little disturbance as possible, and the litter and the soil surrounding it were gently excavated. Each humus block was separated in the field by eye into its obvious layers, without reference to any preconceived classification of horizons (Ponge, 1999; Peltier et al., 2001). The different layers were isolated and fixed immediately in 95% ethanol then transported to the laboratory. The layers were classified into OL (entire leaves), OF (fragmented leaves) and OH (humified litter) horizons (Brêthes et al., 1995), other horizons being not present in these shallow Histosols. Only OH horizons were observed in zones of destruction. Several layers could be sampled in the same horizon on the basis of visible differences. Nineteen layers in total were sampled in zones of destruction (coded Zd for zones of destruction), 21 under *Clusia* (coded Clu), and 22 under *Clusia-Myrcia* (coded Clu-Myr).

All 62 layers were analysed at the laboratory by the small volume micromorphological method developed by Bernier and Ponge (1994). We spread each layer gently with our fingers in a petri dish, taking care not to break the aggregates. The petri dish was then filled with 95% ethanol. The different components were identified under a dissecting microscope at 50 X magnification with a cross reticule in the eyepiece and quantified by the count point method (Jongerius, 1963; Bal, 1970; Bernier and Ponge, 1994). Under the dissecting microscope, a transparent film with a 429-point grid was positioned over the material. At each grid point, using the reticule as an aid for fixing the position, we identified and counted the material beneath it. The results were expressed as the relative volume percentage of given component, corresponding to the ratio of the number of points identified for each category of humus component to the total number of points inspected above the petri dish.

The various kinds of plant debris were identified visually by comparison with a collection of main plant species growing in the vicinity of the sampled humus profiles. Litter leaves were classified according to plant species and decomposition stages on the basis of morphological features. Dead and living roots were separated by colour and turgescence state, helped when possible by the observation of root sections. Animal faeces were classified by the size, the shape, the degree of mixing of mineral matter with organic matter and the colour according to animal groups when possible (Ponge, 1991a, 1991b; Topoliantz et al., 2000, 2006). When necessary, the identification of humus components was checked at higher magnification. For that purpose, a small piece of a given humus component was collected with scissors then mounted in a drop of chloral-lactophenol for examination under a phase contrast microscope at 400 X magnification.

## Data analysis

Percentages of occurrence of humus components in the 62 layers investigated were subjected to Correspondence Analysis or CA (Greenacre, 1984). The different classes of humus components were the active (main) variables, coded by their percent volume. Passive variables (OL, OF, OH horizons, vegetation types, depth levels) were added in order to make easier the interpretation of factorial charts (Sadaka and Ponge, 2003).

All variables were transformed into  $X=(x-m)/s+20$ , where  $x$  is the original value,  $m$  is the mean of a given variable, and  $s$  is its standard deviation. The addition to each standardized variable of a constant factor of 20 allows all values to be positive, CA dealing only with positive numbers. Following this transformation, factorial coordinates of variables can be interpreted directly in terms of their contribution to factorial axes (Sadaka and Ponge, 2003).



## Results

### Humus components

A total of 107 humus components were identified. They were pooled into 12 gross categories on the basis of affinities in their composition, which were used for drawing graphs and comparing the three vegetation types (Clu, Myr, Zd). Leaf material (RM) was comprised of leaves of *P. geyskesii* (Bromeliaceae), *Scleria cyperina* (Cyperaceae), *C. minor* (Clusiaceae) and *M. saxatilis* (Myrtaceae). Root material (RM) consisted of dead and living roots and roots attacked by fungi. Miscellaneous plant material (MPM) was mainly made of flower and fruit parts. Decayed plant material (DPM) included plant organs humified and degraded by soil organisms but still recognizable to the naked eye. Fungal material (FM) was mostly made of fructifying organs and rhizomorphs, fungal hyphae being not perceptible under the dissecting microscope. Humified organic matter (HOM) included plant organic material, strongly transformed and not identifiable as plant organs but not included into animal faeces. Holorganic faeces (HF) were made of organic matter ingested then defecated by animals. Organo-mineral faeces (OMF) were a mixture of organic matter and mineral particles ingested then defecated by animals. Charred material (CM) included leaves, roots, bark, wood and charcoal. Notice that these gross categories were not mutually exclusive. For instance, all components comprising pieces of fungi were included in the gross category 'Fungal mycelium', while some of them, such as 'Leaf of *Scleria* covered with fungi' (Appendix) were also included in the gross category 'Leaf material'.

### Humus profiles

The data thus obtained allowed the construction of charts representing the distribution of gross categories of humus components according to depth (Fig. 1). They showed a great homogeneity among humus profiles except for Zd3, which exhibited a dominance of humified organic matter (up to 81% of the total volume of solid matter) beneath 2 cm. Charred material was present in the three samples taken in zones of destruction (Zd1, Zd2 and Zd3) (up to 3% in Zd1, up to 12% in Zd2, up to 21% in Zd3). Leaf material was poorly represented in Zd but largely dominant in the four top cm in Clu and Clu-Myr. It decreased with depth with a corresponding increase of the root system, which was largely dominant beneath 4 cm, except in Zd3 where it was replaced by humified organic matter. Fungal material (in enough amount to be counted under a dissecting microscope) was present in zones of destruction (Zd1 and Zd3 in the top 4 cm, Zd1 and Zd2 beneath). A large increase in humified organic matter was observed beneath 4 cm, especially in Clu-Myr and Zd. In all humus profiles, the examination of faecal material showed that holorganic faeces (millipedes, earthworms, enchytraeids and mites) began to accumulate in the first centimetre and increased with depth (up to 44% at the bottom of Clu-Myr3). They were much less abundant in Zd. Organo-mineral animal faeces (millipedes and earthworms) were only present in Clu. Mineral particles were always in a small amount in the studied profiles, but they were more abundant in Zd3 (up to 8%) and Zd2 (up to 4%).

## Multivariate analysis

The projection of active and passive variables in the plane of the first two factorial axes of CA (7.8 and 7.1% of the total variance, respectively) showed a marked heterogeneity among horizons (Fig. 2). In general values of Axis 1 and Axis 2 decreased when depth

increased (OL, then OF then OH). However, surface layers of Zd (identified as OH horizons) were projected on the positive side of Axis 2, like OL and OF layers of Clu and Clu-Myr, but differed in their Axis 1 values, which were negative, like all other OH horizons. There was a gradient in the composition of horizons in Clu and Myr e.g. decayed plant material followed by miscellaneous plant material followed by humified organic matter, holorganic faeces, organo-mineral faeces then root material. Zd differed by the presence of charred material and by the scarcity of leaf litter, which isolated it from the other two vegetation types.

The projection of depth level indicators (additional or passive variables) in the plane of Axes 1 and 2 of CA clarified vertical changes in the composition of humus profiles (Fig. 2). Linking successive depth levels by straight lines displayed trajectories that help to show changes in humus composition along topsoil profiles under the three vegetation types. Zones of destruction did not exhibit any pronounced change in organic matter composition according to depth (short trajectories), in contrast to *Clusia* and *Clusia-Myrcia*. They were characterized by negative values of Axis 1 (only OH horizons were present) and positive values of Axis 2 in the first two cm, which corresponds to the presence of charred material (categories 5, 17, 23, 30, 37, 61) but also of *S. cyperina* litter (categories 1 to 4). *Clusia* and *Clusia-Myrcia* were both characterized by positive values of Axes 1 and 2 in surface layers and negative values of the same axes in deeper layers. However, there was a better differentiation of OH horizons under *Clusia* than under *Clusia-Myrcia* and the passage from OL to OH horizons was more abrupt under *Clusia* than under *Clusia-Myrcia*. It should be also noted that, although surface layers may differ between *Clusia* and *Clusia-Myrcia* on one part, and zones of destruction on the other part, deeper layers of the three vegetation types tended to reach a similar composition.

## 1 Discussion

2  
3 On the basis of their horizons, all humus profiles under *Clusia* and *Clusia-Myrcia* and  
4 one humus profile (Zd1) under zones of destruction, seemed rather similar (Fig. 1). However,  
5 all three zones of destruction (Zd1, Zd2 and Zd3) exhibited an accumulation of charred  
6 material and mineral particles, which points to small-scale disturbances, other than biological,  
7 which occurred in zones of destruction. Fire has been reported to occur on the Nouragues  
8 inselberg, and charcoal has been found in the summital forest (Tardy et al., 2000), however  
9 this is the first report of the existence of spatially-limited fires, probably of lightning strike  
10 origin, which locally destroy the vegetation during pronounced dry seasons (El Niño years).  
11 Wardle et al. (1997) showed that the frequency of lightning strikes on small-sized Sweden  
12 lake islands explained why the plant succession could not reach a late stage of development  
13 and was renewed at more frequent intervals. In our study site, small size (10-50 m<sup>2</sup>) and  
14 isolation of shrub thickets prevent fire to be propagated at longer distance and to destroy the  
15 whole rock savanna.

16  
17 Charred material could remain in the soil for centuries, constituting an important sink  
18 of carbon and a source of persistent soil organic matter (Seiler and Crutzen, 1980; Glaser et  
19 al., 2001; Ponge et al., 2006). Charcoal is also an efficient adsorbent of soluble organic and  
20 mineral compounds leached from litter and can support microbial communities, due to its  
21 high internal surface area made of interconnected micropores (Pietikäinen et al. 2000). In  
22 boreal forests it has been demonstrated that charcoal played a fundamental role in forest  
23 regeneration (Zackrisson et al., 1996; Wardle et al., 1998). These features are typical of  
24 disturbed areas, favouring the establishment of new species within a community or the  
25 renewal of the same community (Grubb, 1977). Combined to charcoal, the absence of leaf

material in the zones of destruction (Table 1) probably also favours the early establishment by seed of plant species by decreasing the level of chemical and physical interference (Facelli and Pickett, 1991; Wardle et al., 1998). The presence of charcoal, the absence of OL and OF horizons, combined with the presence of plant species typical of open environments, such as *S. cyperina* (Sarhou and Villiers, 1998), is an argument for the role of zones of destruction in the passage from a plant community characterized by the early establishment and vegetative spread of the epilithic *C. minor* to a more species-rich community, including *M. saxatilis* and a variety of other woody and liana species.

Roots could be considered as an important component of humus profiles on the Nouragues inselberg (Fig. 1, Table 1), except in Zd3 where this important source of soil organic matter had been near totally transformed in humified organic matter without being renewed. The development of root systems is an important cause for the distribution of organic matter in mountain (Frak and Ponge, 2002) and boreal soils (Tedrow, 1977) but its role seems even more important in tropical soils on hard, unweatherable parent rocks (Loranger et al., 2003).

Fungal material was found in higher amounts in the surface layers of zones of destruction (Table 1) which can be compared with our observation of the local attack of woody vegetation by wood-destroying basidiomycetes and the increased termite and xylosidase activity in zones of destruction (Kounda-Kiki, 2007). We also recorded a particular abundance of soil invertebrates in zones of destruction, twice that of *Clusia* canopies (Kounda-Kiki, 2007). Due to the intense activity of fungi and invertebrates, wood and bark are rapidly converted into humus (humified organic matter and animal faeces), thus they do not accumulate in the humus profiles.

It is probable that the vegetation dynamics on the Nouragues inselberg is more complex than previously thought and that biological factors such as fungal and invertebrate activity, following the local action of fires, prevail in the regeneration niche of a variety of non-epilithic rock savanna plants, thereby ensuring renewal and species enrichment of vegetation clumps. However, main limits of our investigations lie in the absence of temporal scales for the observed processes, which should be assessed by long-term monitoring.

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**Table 1.** Mean volume (%  $\pm$  SE) of the gross categories of humus components at the three stages Clusia, Clusia-Myrcia and micro-chablis (three replicates each) at two different 4 depth levels. Significant differences between pairs of sites according to Mann-Whitney tests are indicated by different letters and in bold type

| Gross category               | Code | Clusia                             | Clusia-Myrcia                      | Micro-chablis                    | Clusia                            | Clusia-Myrcia                      | Micro-chablis                    |
|------------------------------|------|------------------------------------|------------------------------------|----------------------------------|-----------------------------------|------------------------------------|----------------------------------|
| Depth (cm)                   |      | 0-4 cm                             |                                    |                                  | 4-10 cm                           |                                    |                                  |
| Leaf material                | LM   | <b>51.93<math>\pm</math>17.27a</b> | <b>40.66<math>\pm</math>15.54a</b> | <b>7.26<math>\pm</math>2.9b</b>  | 2.54 $\pm$ 1.5                    | 1.31 $\pm$ 0.82                    | 0.28 $\pm$ 0.28                  |
| Root material                | RM   | 29.9 $\pm$ 12.59                   | 30.03 $\pm$ 9.91                   | 37.17 $\pm$ 16.11                | 61.44 $\pm$ 7.91                  | 44.97 $\pm$ 5.58                   | 53.7 $\pm$ 16.74                 |
| Miscellaneous plant material | MPM  | <b>0.98<math>\pm</math>0.46b</b>   | <b>1.9<math>\pm</math>0.35ab</b>   | <b>4<math>\pm</math>1.07a</b>    | 1.21 $\pm$ 0.14                   | 0.67 $\pm$ 0.37                    | 3 $\pm$ 1.23                     |
| Decayed plant material       | DPM  | 3.85 $\pm$ 1.09                    | 8.07 $\pm$ 2.33                    | 2.79 $\pm$ 1.18                  | 1.69 $\pm$ 0.78                   | 2.89 $\pm$ 2.4                     | 1.43 $\pm$ 1.43                  |
| Cyanobacteria                | C    | 0 $\pm$ 0                          | 0 $\pm$ 0                          | 0.69 $\pm$ 0.5                   | 0 $\pm$ 0                         | 0 $\pm$ 0                          | 0.07 $\pm$ 0.07                  |
| Fungal material              | FM   | 0 $\pm$ 0                          | 0 $\pm$ 0                          | 0.39 $\pm$ 0.21                  | 0 $\pm$ 0                         | 0 $\pm$ 0                          | 1.16 $\pm$ 0.76                  |
| Humified organic matter      | HOM  | 4.38 $\pm$ 3.49                    | 9.45 $\pm$ 5.44                    | 22.42 $\pm$ 10.4                 | 10.48 $\pm$ 5.38                  | 35.11 $\pm$ 8.52                   | 34.88 $\pm$ 19.54                |
| Holorganic faeces            | HF   | 8.13 $\pm$ 3.19                    | 9.14 $\pm$ 2.87                    | 16.14 $\pm$ 7.09                 | <b>17.65<math>\pm</math>2.68a</b> | <b>13.82<math>\pm</math>5.92ab</b> | <b>3.28<math>\pm</math>2.34b</b> |
| Organo-mineral faeces        | OMF  | 0.08 $\pm$ 0.08                    | 0.04 $\pm$ 0.04                    | 0.43 $\pm$ 0.27                  | <b>2.18<math>\pm</math>1.77a</b>  | <b>0<math>\pm</math>0b</b>         | <b>0<math>\pm</math>0b</b>       |
| Mineral particles            | MP   | 0.3 $\pm$ 0.3                      | 0.3 $\pm$ 0.3                      | 2.28 $\pm$ 1.48                  | 2.35 $\pm$ 1.23                   | 0.4 $\pm$ 0.18                     | 1.75 $\pm$ 1.63                  |
| Charred material             | CM   | <b>0<math>\pm</math>0b</b>         | <b>0<math>\pm</math>0b</b>         | <b>5.87<math>\pm</math>2.56a</b> | 0 $\pm$ 0                         | 0 $\pm$ 0                          | 0.46 $\pm$ 0.46                  |
| Soil fauna                   | SF   | 0.43 $\pm$ 0.09                    | 0.4 $\pm$ 0.19                     | 0.56 $\pm$ 0.52                  | 0.45 $\pm$ 0.29                   | 0.83 $\pm$ 0.7                     | 0 $\pm$ 0                        |

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## Figure legends

**Figure 1.** Diagrammatic representation of the distribution according to depth of twelve gross categories (leaf material, root material, miscellaneous plant material, decayed plant material, cyanobacteria, fungal material, humified organic matter, holorganic faeces, organo-mineral faeces, mineral particles, charred material and soil fauna) in the nine studied humus profiles (Zd = zones of destruction; Clu = *Clusia*; Clu-Myr = *Clusia-Myrcia*).

**Figure 2.** Correspondence analysis of 62 humus layers. Projection of passive variables (gross categories, horizon names, depth indicators and vegetation types) in the plane of the first two axes. Codes of gross categories as in Table 1

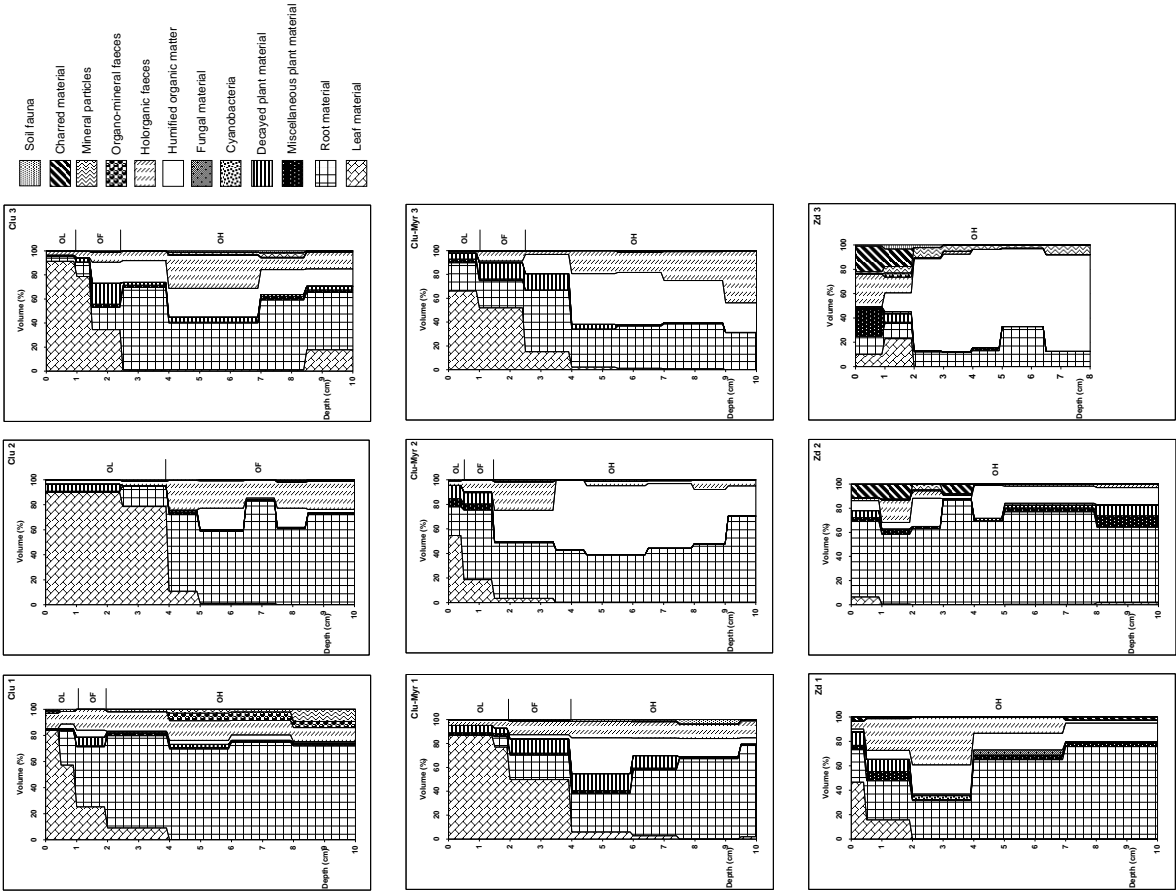
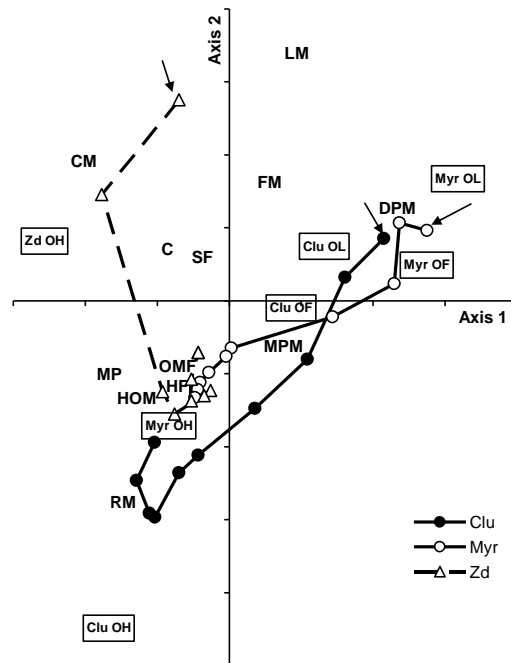


Fig. 1



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2 Fig. 2