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Soil animal communities in holm oak forests: influence of horizon, altitude and year

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Running title: Soil animals in holm oak forests

Abstract

Soil animals (macro- and microarthropods, annelids, nematodes) were sampled along an altitudinal gradient and over two years in holm oak (*Quercus rotundifolia*) forests of the Moroccan Atlas. We studied the influence of elevation and year on the vertical distribution of soil fauna. Whatever the elevation (1500, 1700 and 1900 m), the humus form was a Dysmull, with a thick litter horizon and a fine crumb A horizon. Thirty-six categories of fauna were found and classified at the group level. The influence of horizon, altitude and year was analysed by ANOVA (on seven broad zoological groups and on total fauna) and correspondence analysis (on thirty-six zoological groups). There was a decrease in the population size of most zoological groups from organic (OL, OF) to mineral horizons (A, S), but OL and OF horizons varied as the most populated horizon according to years and animal groups. More animals and more animal groups were present at higher elevation, following an increase in food and habitat availability.

Keywords: Soil fauna/Vertical distribution/Holm oak

1. Introduction

The vertical distribution of soil animal communities has been poorly studied because of the lack of appropriate methods for recovering all animals living in organic as well as mineral horizons of the topsoil. Soil sections without soil-drying [3, 19, 35] and rhizotrons [18, 28] prove efficient in the observation of soil animals at the true place where they are living, but the small observable volume implies that many repeated counts are made before quantitative data can be obtained. Microstratification is used to separate the different layers of a soil profile before extracting fauna [14], but extraction methods are in general more efficient for some groups than for others [48].

Thus, there are few studies on the vertical distribution of soil animals embracing a wide range of animal groups, from microfauna to macrofauna [4, 59]. Direct counts obtained by dissecting soil horizons with forceps prove more efficient than extraction procedures for some mesofauna groups which play a major role in plant litter decomposition and building of the soil structure, such as enchytraeids, insect larvae and phthiracarid oribatid mites [48].

Changes in the vertical distribution of soil animals occur through variation in the distribution of soil organic matter, in particular in the thickness of organic compared to mineral horizons [4, 15, 44]. Seasonal changes, in particular litter fall, winter frost and summer drought, are responsible for cyclic variations of soil animal vertical distribution [1, 11, 64]. In addition, year-to-year changes in the amount of litterfall, rain and temperature will exert similar effects through their influence on decomposition processes [68]. Similarly, altitude, and climate and nutrient effects mediated by this factor, may influence the vertical distribution of soil animals through changes in the thickness of organic horizons, which increases or decreases according to vegetation types [8, 13].

The present study focused on holm oak forests, an important component of mediterranean woody landscapes [21]. Edible holm oak (*Quercus rotundifolia* Lam.) is an evergreen Mediterranean oak being common in western Mediterranean countries (Morocco, Algeria, Tunisia, Central Spain), mostly in the mountains where it tolerates a dry and cold climate [2, 5]. This tree is characterized by a persistent, spiny, stiff foliage. Litter fall is scattered over the year but there is a maximum input of dead leaves to the ground from April to June. In holm oak stands the thickness of litter layers is determined by seasonal litter fall, decomposition rate, and biennial cycles of high and low litter input [38, 52, 54].

In a previous study on humus forms of holm oak forests (Sadaka and Ponge submitted) we observed that the thickness of O (organic) and A (hemorganic) horizons was modifed by altitude and varied from year to year. Thus we may expect that the same factors which act on the distribution of topsoil horizons will act on the distribution of soil animals, and that both animal communities and humus forms are linked by feed-back processes [25, 43, 44]. The purpose of the present study was to determine to what extent the distribution of topsoil horizons, and its altitudinal and annual variation, may explain the vertical distribution of soil animals.

2. Materials and methods

2.1. Study sites

The study was conducted in February 1999 and February 2002 in an holm oak forest (*Q. rotundifolia*) at Toufliht (northern slope of the High Atlas, Morocco). The climate is subhumid to semiarid mediterranean, with most precipitation from October to February followed by a long warm dry period from May to September (mean annual rainfall 840 mm; maximum summer temperature *ca.* 30.5°C and minimum winter temperature *ca.* 1°C). The parent rock consists of triassic molasses made of an alternance of red clay, sandstone and conglomerate [6].

Three sites (SI, SII and SIII), where *Q. rotundifolia* is the dominant tree species (3-7 m height, 85-95 % cover), were chosen according to an altitudinal gradient from 1500 to 1900 m above sea level. At site SI (1500 m, N-NE aspect), the shrub layer consists of *Juniperus oxycedrus* L. and *Cistus monspeliensis* L. At SII (1700 m, N-NE aspect), the shrub layer consists of *J. oxycedrus*, *C. monspeliensis*, *Cistus salvifolius* L. and *Nerium oleander* L. At SIII (1900 m, E-SE aspect), the evergreen oak is associated with *J. oxycedrus*, *Pinus halepensis* L., *Cistus laurifolius* L. and *Chamaerops humilis* L.

Despite variations in litter thickness the humus form is always a Dysmull [10], with a thick (more than 1 cm) OF horizon and an A horizon (2 to 4 cm thick) with a microcrumb structure [56]. The $pH_{(water)}$ of the A horizon is 5.5 to 5.8. The A horizon overlays a S horizon, made of weathered parent rock.

2.2. Sampling procedure

In 1999 and 2002, at each site, and at more than 1 m from tree trunks, an unique humus block 5 x 5 cm in surface and 8.5 to 11.5cm depth was carefully excavated, according to the method devised by Ponge [39]. It was cut with a sharp knife, with as little disturbance as possible, and the litter and soil surrounding it were gently excavated. Layers, about 0.5 to 2.5cm thickness, were separated directly in the field from the top to the bottom of the profile on the basis of morphological differences which were visible to the nake eye, and immediately preserved in 95% ethyl alcohol (Table 1). Their thickness was noted before collection. Samples were classified into OL (entire leaves), OF (fragmented leaves with faecal pellets), A (hemorganic horizon) and S (mineral horizon), taking as a basis the classification of forest humus horizons by Brêthes et al. [10]. When several layers were sampled in the same horizon (on the basis of visible differences) they were numbered according to their order from the top to the bottom of this horizon, for example OL1, OL2, OF1, OF2... Thus A2 (Table 1) was not an A_2 horizon (eluvial horizon in past European classifications) but it was just the second layer sampled in the A horizon (the A_1 horizon in the old classification).

Each layer was carefully transferred to a Petri dish filled with ethyl alcohol, then a quantitative analysis of humus components was done by a point-count method [13, 36, 56]. Afterwards, the material was thoroughly dissected with forceps under a dissecting microscope and each animal found was assigned to a group level (Table 2).

2.3. Data analysis

The population size of each group in each unit sample was subjected to correspondence analysis, a multivariate method using the chi-square distance [17]. The different zoological groups were the active variables. The nature of the corresponding horizon (OL, OF, A, S), the year (1999, 2002), the site (SI, SII, SIII) and the depth at which the sample was taken were put as passive variables, i.e. they were projected on the factorial axes as if they had been involved in the analysis, without contributing to the factorial axes. They were coded as 1 or 0. All the variables (active and passive) were transformed according to the method of Ponge and Delhaye [51], in order to give them the same weight and variance. The formula used was as follow: $X = (x–m)/s + 20$, where X is the standardized value, x the original value, m the mean of the variable and s its standard deviation. The addition to each standardized variable of a constant factor of 20 allows all values to be positive, because correspondence analysis deals only with positive numbers. Thus, factorial coordinates of variables can be interpreted directly in terms of their contribution to factorial axes. The farther a variable was projected from the origin of the axes (barycentre) along a factorial axis, the more it contributed to this axis. In order to depict gradients of bulk faunal abundance, every active variable (zoological group) was split into two symmetrical variables, the one being the original value (standardized and refocused as abovementioned), the other being created by complementing the original value to 40. The second variable had thus the same mean (20) and the same standard deviation (1) as the first variable but varied in an inverse sense. Higher values of the former (original) variable corresponded to lower values of the latter (complementary) variable, and the reverse. Each zoological group was thus represented by two points, the one for higher values (the original variable), the other for lower values (the complement), and

by this way the analysis was able to discern between rich (with abundant fauna) and poor samples, and to depict gradients of population size [26].

Analyses of variance (3-way ANOVAs without replication, followed by SNK procedure [16]) were performed on broad zoological groups encompassing one or several of the groups listed in Table 2, as well as on total population size and zoological richness. Zoological richness was expressed by the number of zoological groups, sensu Ponge [45]. Horizon (OL, OF, A, S), altitude (1500 m, 1700 m, 1900 m) and year (1999, 2002) were used as main factors. Data (counts) were log-transformed before analysis in order to ensure additivity of variances.

3. Results

3.1. Analysis of variance

Figure 1 is a graphical presentation of the population size of the main broad zoological groups. A strong variation exists between horizons, altitude and year and the effects of these three factors vary according to invertebrate categories. Results of variance analysis (main effects) and a posteriori comparisons among means are summarized in Table 3. Horizon, altitude and year can be classified in a decreasing order of influence on the population size of broad zoological groups, judging from the number of groups exhibiting significant variation: six groups among seven were significantly influenced by horizon, four by altitude and only two by year.

Springtail densities were influenced by altitude ($P = 0.03$) and year ($P = 0.004$), but not by horizon ($P = 0.35$), without any significant interaction effect. Among the seven broad groups they were unique in having an even vertical distribution. Collembola were the most abundant animal group in A and S horizons. Their

population size increased with altitude, SIII (1900 m) harbouring four times more springtails than SI (1500 m) and SII (1700 m). Four times more animals were found in 2002 compared to 1999.

Mites were influenced by horizon (P = 0.0008) and year (P = 0.003), not by altitude (P = 0.18), without any significant interaction effect. There was a decrease in the population size from surface to deeper horizons, A and S (mineral horizons) harbouring less animals than OL and OF (organic horizons). Mites were the most abundant animal group in the OL horizon. Three times more animals were found in 2002 compared to 1999.

Nematodes were influenced by horizon (P = 0.01) and altitude (P = 0.03), not by year (P = 0.53), without any significant interaction effect. Like for mites, there was a decrease of the population size in the mineral soil (A and S), but the A horizon was intermediate between OF and S horizons. A strong increase in the abundance of nematodes was observed with altitude, SIII harbouring more animals than SI (x8) and SII (x3). Nematodes were the second most abundant animal group in OL and OF horizons.

Enchytraeids were influenced only by horizon (P = 0.03), without any significant interaction effect. They were more abundant in the OF horizon than in A (x7) and S (x12) horizons, the OL horizon being intermediate. Lumbricids, like enchytraeids, were influenced only by horizon (P= 0.01), without any significant interaction effect. They were more abundant in the OF horizon than in OL (x5), A (x4) and S (x9) horizons.

Insect larvae were influenced by horizon (P = 0.003) and altitude (P = 0.02), not by year (P = 0.20), without any significant interaction effect. They were more abundant in the OF horizon compared to OL (x2), A (x4) and S (x28) horizons and the S horizon

harboured less animals than OL and A. Thus there was a vertical gradient of increasing (from OL to OF) then decreasing abundance (from OF to deeper horizons). Insect larvae were the most abundant invertebrate group in the OF horizon.

Miscellaneous animals (adult insects, Symphyla, spiders and pseuscorpions) were influenced by horizon ($P = 0.01$) and altitude ($P = 0.02$), but interactions between all couples of factors were significant ($P < 0.05$), suggesting that the effects of horizon and altitude were not additive, and depended on the year. This was not unexpected, since the miscellaneous group was strongly heterogeneous in its composition.

The size of the total invertebrate population (the total faunal abundance) was influenced by horizon ($P = 0.008$), altitude ($P = 0.03$) and year ($P = 0.01$), without any interaction effect. There were more animals in OL and OF horizons than in the S horizon (x4 and x5, respectively) and the A horizon was intermediate. There were more animals in SIII compared to SI (x1.6) and SII (x1.3). There were approximately 1.6 times more animals in 2002 than in 1999.

The zoological richness (number of zoological groups as classified in Table 2) was influenced by horizon ($P = 0.0005$) and altitude ($P = 0.02$), not by year ($P = 0.2$), but there was a significant interaction between horizon and year ($P = 0.02$). The number of animal groups decreased in the A horizon compared to OL (x0.7) and OF (x0.6) horizons and still decreased in the S horizon (0.6 times the number of groups found in the A horizon). The interaction between horizon and year was due to the fact that there were more animal groups in OF compared to OL in 1999, while the reverse was observed in 2002, but this did not obscure the overall decrease observed just beneath the organic horizons. The zoological richness increased with altitude, more animal groups being present at SIII than at SI (x1.6) and SII (x1.3).

3.2. Correspondence analysis

A correspondence analysis was perfomed on a data matrix crossing 40 samples with 36 zoological groups (main variables) and 23 descriptors (additional variables). The first two factorial axes extracted 17% and 13% of the total variance, respectively, thus 30% of the total variance was extracted by the plane formed by Axes 1 and 2. Only these two axes could be interpreted in light of the additional variables (horizon, altitude, year). The projection of zoological groups in the plane of Axes 1 and 2 (Fig. 2) showed an overall trend of decreasing faunal abundance from organic (OL and OF) to mineral (A and S) horizons. Axis 1 displayed the most important information about the vertical distribution of soil invertebrates. Higher values of all but three zoological groups were projected on the positive side of Axis 1 (corresponding to OL and OF horizons) while most lower values were projected symetrically on the negative side (corresponding to A and S horizons). The three groups which did not follow the global trend of decreasing density with depth were Symphyla (18), Heteroptera (35) and Hymenoptera (32). All other groups were more abundant in organic than in mineral horizons, those being in the most superficial position (more attracted to litter) being nymph and adult oribatid mites (8), nematodes (15) and entomobryid springtails (3). The vertical distribution of the different invertebrate categories can be quantified by their coordinates along Axis 1 (Table 2). Axis 1 coordinates can be considered as an index of epigeicity, varying from –0.009 (Symphyla) to 0.041 (adult and nymphal Cryptostigmata). Sites SI, SII and SIII were not projected at the same place along Axis 1, indicating that changes in the vertical distribution of Collembola occurred along the altitudinal gradient. SIII was projected on the positive side, while SI and SII were projected on the negative side. This indicated that litter-dwelling animal groups (those projected far from the origin on the positive side of Axis 1) were more abundant at higher altitude.

Axis 2 was strongly related with year, since 1999 and 2002 were projected far from the origin along this axis, the positive side corresponding to 1999 and the negative side to 2002. As ascertained from the projection of animal groups and horizon names it can be said that litter-dwelling fauna occupied mainly the OF horizon in 1999 and mainly the OL horizon in 2002 (see also Fig. 1) and that different faunal groups were involved. For instance animal groups far from the origin on the positive side of both Axis 1 and Axis 2, such as chironomid larvae (20), sciarid larvae (19), empidid larvae (23), spiders (13) and enchytraeids (16), were typically found in the OF horizon in 1999 (see Fig. 1 for enchytraeids). Conversely, animal groups far from the origin on the positive side of Axis 1 and on the negative side of Axis 2, such as neanurid springtails (4), astigmatid mites (7, 11) and larvae of mesostigmatid and oribatid mites (9, 12), were typically found in the OL horizon in 2002. Coordinates along Axis 2 could be taken as a measure of their affinity with one or the other of the two years 1999 and 2002 (Table 2), positive values indicating a higher abundance in 1999, negative values a higher abundance in 2002.

Correspondence analysis can be used also to discern changes in faunal communities according to depth levels rather than to horizons. Putting as additional variables the different depth levels (from 0-1 cm to 11-12 cm), these can be projected in the plane of the first two factorial axes and linked by running segments (Fig. 3). The faunal composition typical of the OL horizon encompasses the first three centimetres, with positive values along Axis 1 (indicating an epigeic fauna) and negative values along Axis 2 (indicating that fauna of this horizon is mostly represented in 2002). The faunal composition typical of the OF horizon is observed between 3 and 5 cm depth, and is mostly represented in 1999. Beneath 5 cm the faunal composition does not change to a great extent. These trends are mean trends which do not account for site (altitude) and year effects. Such effects can be displayed by coding separately the different depth levels according to the three sites or the two years.

The influence of altitude on the vertical distribution of soil animals is shown by Figure 4. Site III, at the highest elevation (1900 m) shows profound changes in faunal abundance and composition according to depth, while these changes are smoother in SII and even less pronounced in SI. While animal communities do not differ to a great extent in the first top cm, most differentiation between the three sites occurs in the two centimetres beneath. Between 1 and 3 cm depth the fauna remains typically that of an OL horizon at SIII, while it rather turns to that of an OF horizon at SII and to that of an A horizon at SI.

The influence of the year is shown by Figure 5. Differences according to year exist both in organic horizons (OL and OF are clearly separated along Axis 2), but also in the mineral soil, even though year differences in faunal abundance and composition are less so pronounced in A and S horizons than in OL and OF horizons. In 1999 (positive side of Axis 2) the fauna of the first top cm is poorly differentiated (the 0-1 cm of 1999 is projected not far from the origin), while strong differentiation occurs from 1 to 5 cm, with a faunal community more abundant and typical of an OF horizon. At 5 cm depth the community passes abruptly to that of the mineral soil. In 2002 (negative side of Axis 2), the fauna of the first top cm (as well as that of the first three cm) is typical of an OL horizon, then shifts to one typical of the mineral soil under 5 cm, the faunal composition being intermediate between 3 and 5 cm depth.

4. Discussion

In the three sites investigated the humus form was a Dysmull [56]. It was characterized by a thick litter layer (OL and OF horizons) overlying an organo-mineral A horizon with a crumb structure [10]. Two compartments were thus present in the topsoil: a multi-layered organic compartment, made of plant debris at different stages of

decomposition and intervened by organic- and mineral-dominant animal faeces, and a mineral compartment, made of mineral-dominant faeces and weathering mineral particles, permeated by living and dead roots (rhizosphere). This constituted habitat and food resources of the animal communities we studied. Faeces of dominant animal groups were retrieved during micromorphological investigations, in particular those of enchytraeids, earthworms (small epigeic species) and insect larvae [56]. Faeces of springtails and mites were probably ingested by other animal groups, such as enchytraeids and earthworms [40, 43], since they were not retrieved in noticeable amounts, although springtails and mites were abundant.

The present study showed that, although most faeces were found in OF and A horizons (Sadaka and Ponge submitted), most animals were living in OL and OF horizons (depending on year), at least at the time of sampling (February) and if we except springtails which exhibited an even distribution at the group level. Thus it may be hypothesized that OL and OF horizons was the zone of most saprophagous activity (litter decomposition and mixing of organic matter with mineral matter), while underlying horizons resulted from the accumulation of end-products of faunal activity [42]. The root system in A and S horizons is a source of nutrients, both direct through growth and death of plant tissues and indirect through its action on soil microflora [34, 40, 53]. In particular, we noted that most of the microbial biomass was produced by the black mycorrhizal ascomycete *Cenococcum geophilum* Fr. [56]. Surprisingly, these subterranean resources, which were abundant at the time of sampling, seemed to be neglected, most animals being found rather in the litter compartment. Several reasons could be invoked to explain this phenomenon. First, the mycelium of *C. geophilum* is mechanically and chemically resistant, hard to digest and is hardly consumed by soil animals [28, 32, 40]. The stiff fungal sheath surrounding the roots colonized by *C. geophilum* protects them against desiccation [31] and pathogenic infection [30] and also against consumption by soil fauna [62]. Second, saprophagous animals could be

attracted by fungi living in the litter layer. For instance, it has been demonstrated that the onychiurid springtail *Onychiurus folsomi* Schäffer (syn. *O. sinensis* Stach), was attracted to the white-rot basidiomycete *Marasmius quercophilus* Pouzar and to several other fungal strains isolated from decaying holm oak leaves [55, 57]. These fungi were highly palatable to *O. folsomi* and ensured optimum growth and reproduction. Third, soil animals may move between several food sources [58, 66] or between a place for feeding and another place for reproduction, moulting or protection from adverse events [23], and faeces can be deposited in the meantime [42]. The third reason can be invoked to explain the deposition of organo-mineral faeces in OF and even OL horizons of the humus profiles [56].

As an exception among the soil populations we studied, Collembola exhibited a regular vertical distribution and were by far the most abundant animal group in the S horizon, especially during the year 2002. The same phenomenon has been observed in mull [29] and is particularly pronounced under Mediterranean climate [37]. This can be explained by the abundance of roots and their mycorrhizal symbionts, a food source for soil-dwelling springtails [18, 46, 58], in mineral horizons of Mediterranean mull profiles [36]. Note that dead roots were particularly abundant in 2002, i.e. when the density of Collembola was at its highest in the S horizon [56].

The main effect of altitude was probably to increase the thickness of horizons where most animals were living, more especially an increase in the thickness of the OL horizon was observed at 1900 m altitude, compared to the two lower sites, and an increase in the thickness of the OF horizon was observed from 1500 to 1700 m [56]. More habitat, more food and a better protection against harmful climate events (drought and frost) were thus provided to fauna, the abundance of which increased from 1500 to 1700 m and even more from 1700 to 1900 m. This reinforces the view that the litter compartment, both as a food source and as a habitat, governs the

abundance of most forest soil fauna [12, 24]. Reasons for the increased abundance of organic matter at higher elevation [8, 21, 61] can be found in a decreased rate of microbial decomposition due lower temperature [22, 65, 67]. This influences the balance between microbial and animal contribution to plant litter decomposition [60]. In a previous paper it had been postulated that the observed increase in litter thickness was probably due to a decrease in the activity of litter-feeding animals [56]. This hypothesis can be refuted to the light of the present results.

At increasing altitude the thickness of the A horizon did not decrease while more litter accumulated on the ground. This horizon was made of enchytraeid and earthworm organo-mineral faeces, the abundance of these animals remaining nearly unchanged. Thus we may think that along the studied altitudinal gradient the threshold of tolerance of mull animal communities was not reached [7, 8, 44] and that, despite an increase in litter thickness, no shift towards less active humus forms such as moder and mor was prone to occur, contrary to what was observed under colder and moister climates [8, 47, 50]. We can now reconstruct the chain of processes which may explain the observed patterns. Since no corresponding increase was observed in animal groups able to mix plant debris with mineral matter (here not only earthworms but also enchytraeids), the slower decay of litter at higher elevation was not compensated by a more rapid incorporation to the mineral soil. A similar phenomenon has been observed in a litter-doubling experiment with sessile oak litter, where an increase in litter thickness had been observed, without any corresponding increase in soil animal populations [12, 49]. This can be attributed to the existence of two superposed but relatively independent functional domains, litter and rhizosphere [25], which is particularly well-represented in nutrient-poor (acid) mull profiles with thick litter [33].

Changes from year to year, in particular the strong increase in springtail and mite densities from 1999 to 2002, cannot be explained by a corresponding increase in

litter thickness [63], since less litter was present in 2002 at the top of soil profiles [56]. This increase in faunal abundance was accompanied by a shift of litter-dwelling animals from OF to OL horizons. The most probable reason was that the OL horizon was moistened by a recent rain. This was the case in 2002, since 17 mm rain fell during the week previous to sampling. The attraction of litter-dwelling animals to the more superficial litter and even to tree trunks has been observed after a rainfall [9, 20]. This phenomenon could be due to a sudden increase in food resources, more especially for microbial feeders such as cryptostigmatid (oribatid) mites and springtails [27, 41].

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Figure captions

Fig. 1. Number of individuals of the broad zoological groups in each horizon of the six humus profiles investigated (three altitudes, two years)

Fig. 2. Correspondence analysis. Projection of the zoological groups as main (active) variables in the plane of the first two factorial axes (significance of coding according to Table 2). Horizons (OL, OF, A, S), altitudes (SI, SII, SIII) and years (1999, 2002) have been projected as additional (passive) variables

Fig. 3. Correspondence analysis. Projection of bulk depth indicators (depth values in cm) as passive variables in the plane of the first two factorial axes, together with sites and horizons

Fig. 4. Correspondence analysis. Projection of depth indicators separated by sites (depth values in cm) as passive variables in the plane of the first two factorial axes, together with horizons

Fig. 5. Correspondence analysis. Projection of depth indicators separated by years (depth values in cm) as passive variables in the plane of the first two factorial axes, together with horizons

Table 1. List of layers (with their thickness in cm) sampled in the three study sites

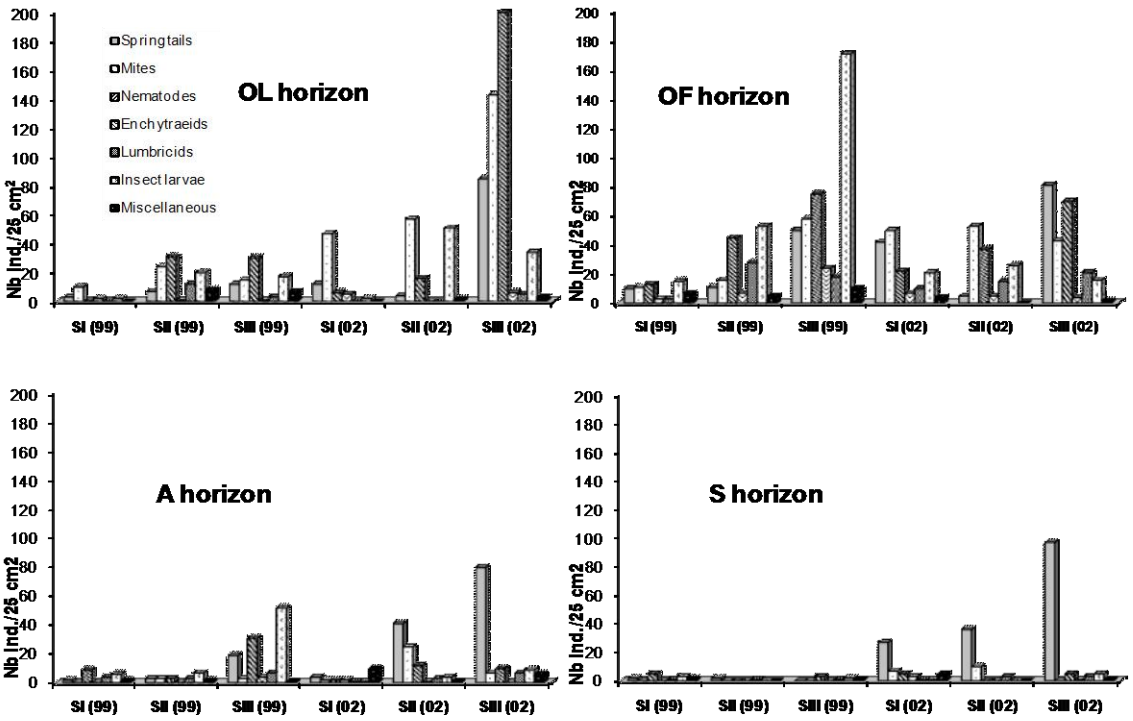
	SI (1999)	SII (1999)	SIII (1999)	SI (2002)	SII (2002)	SIII (2002)
OL1	0.5	0.5	1	0.5	1	1
OL2	-	0.5	1.5	-	-	1.5
OF1	1.5	2.5	0.5	1	1.5	2
OF2	-	1.5	2	1.5	1.5	-
A1	2	1	1.5	2.5	2	1.5
A2	-	1.5	1	-	2	1.5
S1	2	2.5	2	2	1.5	1.5
S2	2.5	-	1.5	2.5	2	2
Total thickness	**8.5**	**10**	**11**	**10**	**11.5**	**11**

Table 2. Zoological groups found in the whole set of samples and coordinates along the first two axes of correspondence analysis

Zoological group	Code	Axis 1	Axis 2	Number of specimens
Collembola Onychiuridae	**1**	0.011	-0.014	391
Collembola Isotomidae	**2**	0.016	-0.018	160
Collembola Entomobryidae	**3**	0.039	0.013	43
Collembola Neanuridae	**4**	0.030	-0.028	41
Acarina Mesostigmata (nymphs+adult	**5**	0.030	0.012	90
Acarina Prostigmata (nymphs+adults)	**6**	0.019	-0.019	14
Acarina Astigmata (nymphs+adults)	**7**	0.034	-0.023	17
Acarina Cryptostigmata (nymphs+adu	**8**	0.041	-0.008	175
Acarina Mesostigmata (larvae)	**9**	0.031	-0.026	197
Acarina Prostigmata (larvae)	**10**	0.018	-0.011	15
Acarina Astigmata (larvae)	**11**	0.031	-0.030	11
Acarina Cryptostigmata (larvae)	**12**	0.032	-0.027	65
Araneida	**13**	0.027	0.029	15
Pseudoscorpionida	**14**	0.004	0.004	4
Nematoda	**15**	0.040	-0.011	630
Oligochaeta Enchytraeidae	**16**	0.033	0.028	76
Oligochaeta Lumbricidae	**17**	0.028	0.015	150
Symphyla	**18**	-0.009	-0.003	30
Diptera Sciaridae (larvae)	**19**	0.030	0.035	104
Diptera Chironomidae (larvae)	**20**	0.029	0.037	161
Diptera Cecidomyidae (larvae)	**21**	0.020	-0.007	163
Diptera Dolichopodidae (larvae)	**22**	0.029	0.016	36
Diptera Empididae (larvae)	**23**	0.018	0.033	7
Diptera Tipulidae (larvae)	**24**	0.035	0.014	8
Diptera Asilidae (larvae)	**25**	0.036	-0.010	7
Coleoptera Staphylinidae (larvae)	**26**	0.013	0.006	8
Coleoptera Scarabeidae (larvae)	**27**	0.002	0.009	2
Coleoptera Elateridae (larvae)	**28**	0.014	-0.007	6
Coleoptera incertae sedis (larvae)	**29**	0.009	0.011	1
Insecta incertae sedis (larvae)	**30**	0.020	-0.022	15
Coleoptera Lathridiidae (adults)	**31**	0.009	0.020	9
Hymenoptera (adults)	**32**	-0.005	-0.001	2
Diptera Tipulidae (adults)	**33**	0.000	0.002	4
Diptera Nematocera (adults)	**34**	0.003	0.004	2
Heteroptera (adults)	**35**	-0.006	-0.001	1
Incertae sedis	**36**	0.021	-0.004	12

Table 3. Mean densities (number of individuals per 25 cm2) of the main zoological groups and zoological richness according to horizon, altitude and year. Subscript letters refer to homogeneous groups (3-way ANOVA followed by SNK procedure)

	Horizon				Altitude (m)			Year	
	OL	**OF**	**A**	**S**	**1500**	**1700**	**1900**	**1999**	**2002**
Springtails	20.5	33.2	24.8	27.3	12.8_{b}	13.6_{b}	53.0_{a}	10.1_{b}	42.8_{a}
Mites	49.3_{a}	38.5_{a}	6.7_{b}	2.8_{b}	15.9	23.5	33.6	11.7_{b}	37.0_{a}
Nematodes	47.2_{a}	43.7_{a}	$11.2_{a,b}$	3.0_{b}	7.8_{b}	18.0_{b}	53.0_{a}	20.4	32.1
Enchytraeids	$2.5_{a,b}$	8.3_{a}	1.2_{b}	0.7_{b}	2.8	1.8	5.0	3.5	2.8
Lumbricids	3.3_{b}	15.8_{a}	4.2_{b}	1.7_{b}	2.5	8.1	8.1	6.8	5.8
Insect larvae	21.0_{b}	50.3_{a}	13.2_{b}	1.8_{c}	6.4_{b}	$20.1_{a,b}$	38.2_{a}	29.0	14.2
Miscellaneous	3.3_{a}	4.7_{a}	3.7_{a}	1.5_{b}	3.8_{a}	2.3_{b}	3.9_{a}	3.8	2.8
Total	**$147.2_{a,b}$**	**194.5_{a}**	**$64.8_{b,c}$**	**38.8_{c}**	**51.8_{b}**	**$87.4_{a,b}$**	**194.9_{a}**	**85.2_{b}**	**137.5_{a}**
Zoological richness	**15.7_{a}**	**18.3_{a}**	**10.3_{b}**	**6.2_{c}**	**10.1_{b}**	**12.0_{b}**	**15.8_{a}**	**12.7**	**12.6**


Springtails
Mites
Nematodes
Enchytraeids
Lumbricids
Insect larvae
Miscellaneous
OL horizon
OF horizon
A horizon
S horizon
Nb Ind./25 cm2
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20
40
60
80
100
120
140
160
180
200
SI (99)
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SIII (99)
SI (02)
SII (02)
SIII (02)

Fig. 1

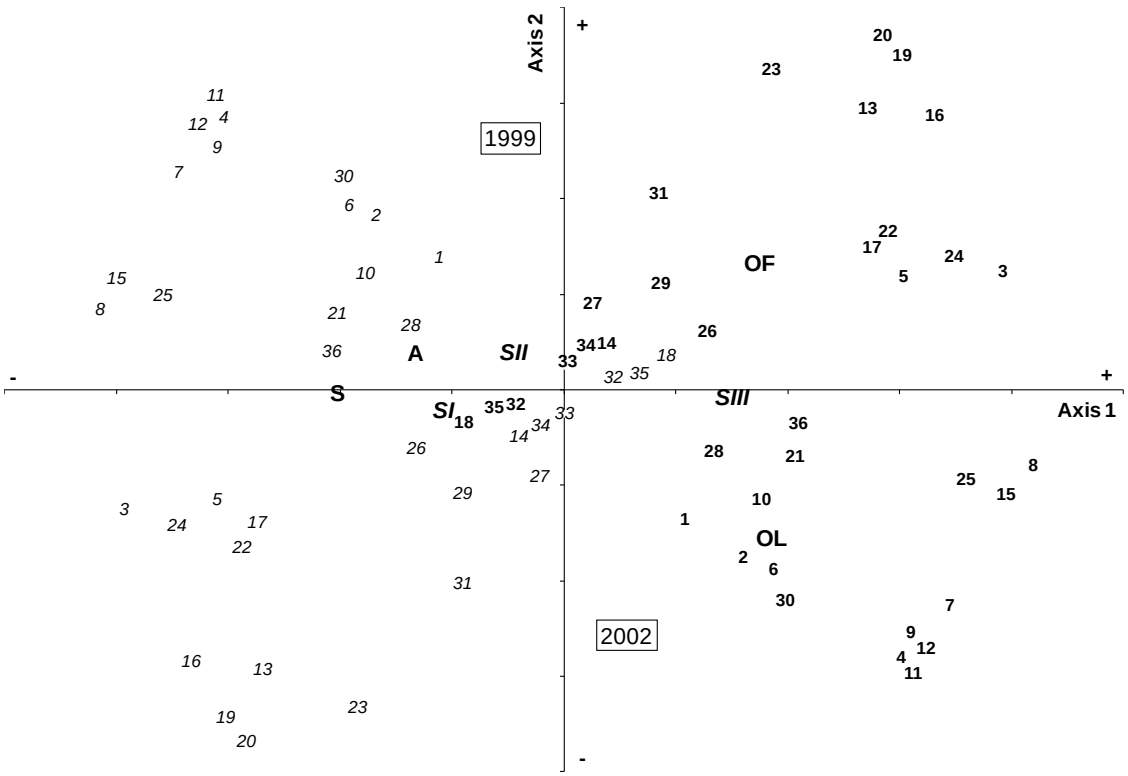

Fig. 2

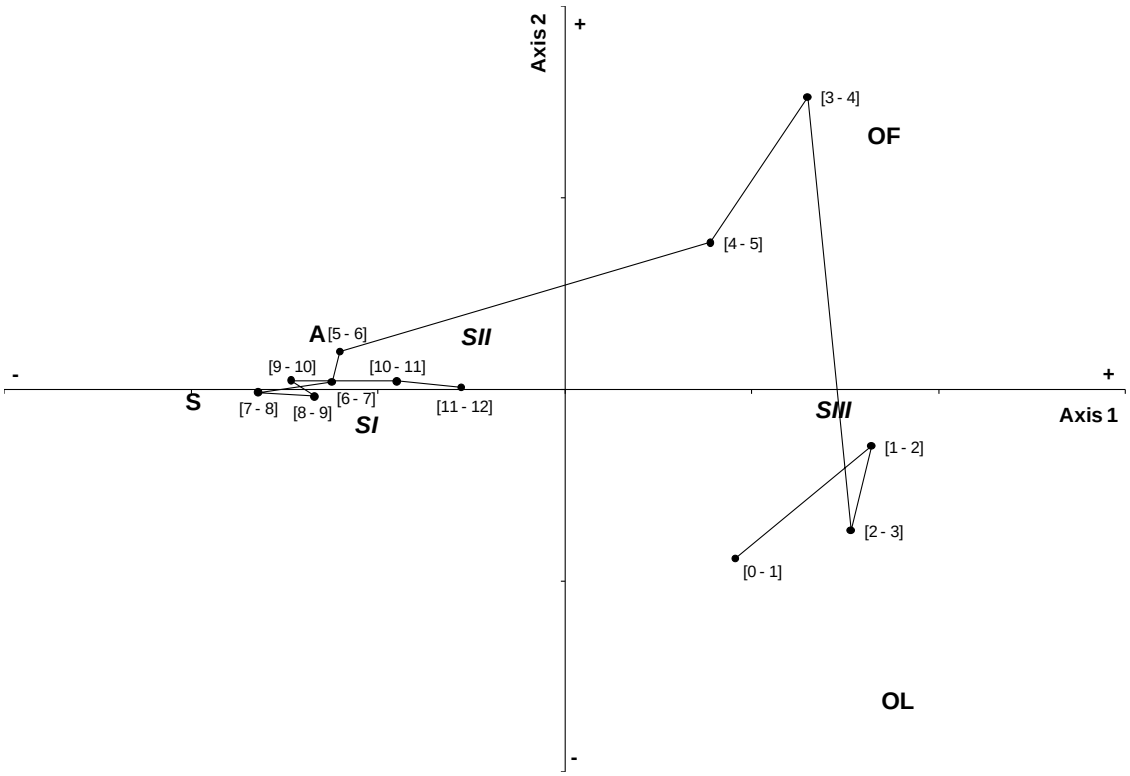
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Fig. 3

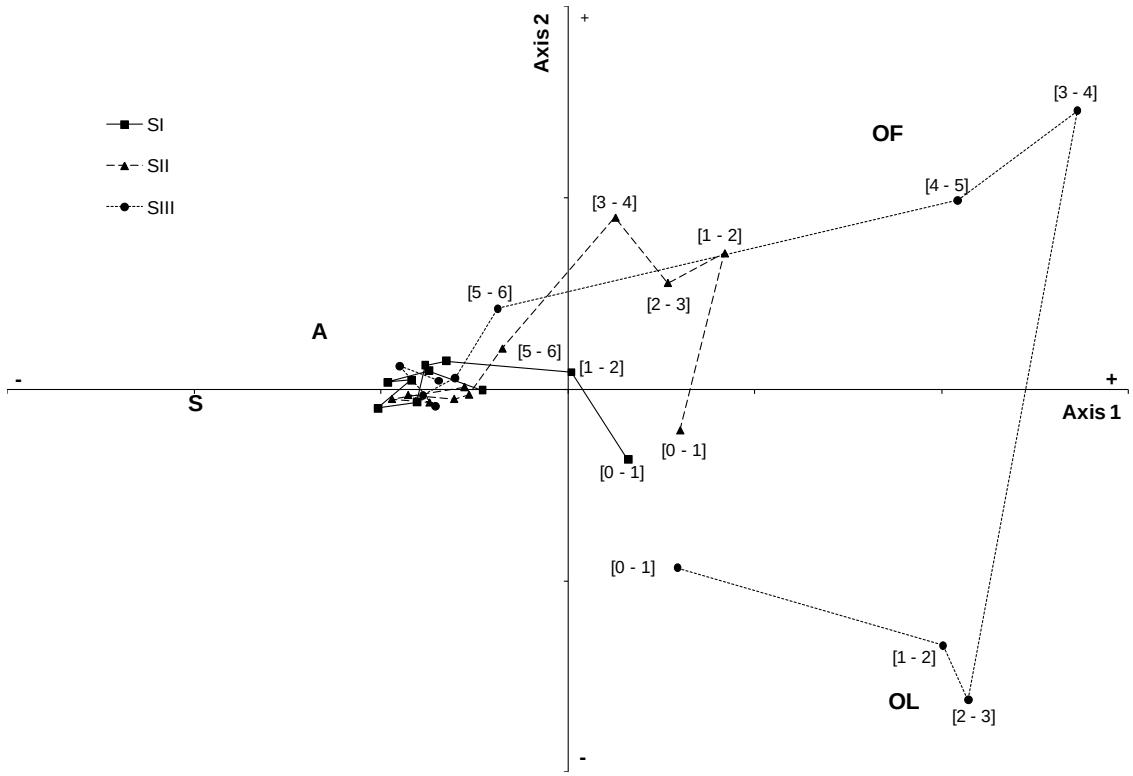
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Fig. 4

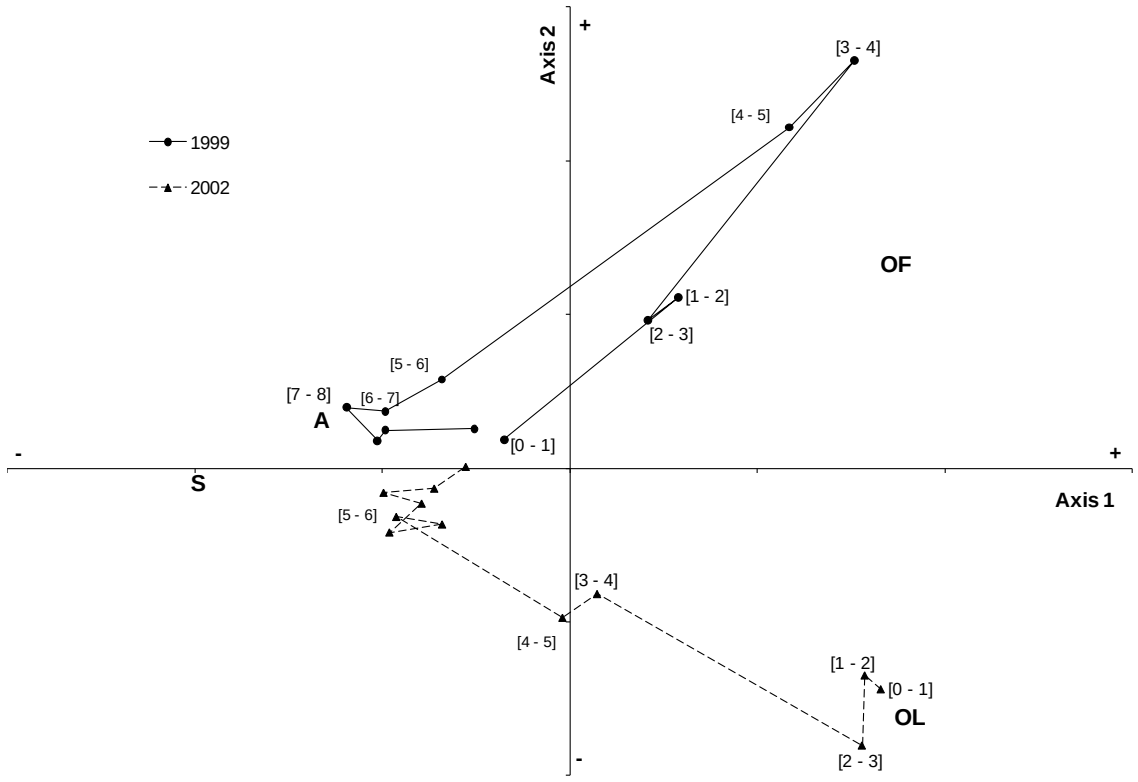
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Fig. 5