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Gladys Loranger, Ipsa Bandyopadhyaya, Barbara Razaka, Jean-François Ponge

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9 Title: **DOES SOIL ACIDITY EXPLAIN ALTITUDINAL SEQUENCES IN COLLEMBOLAN**
10 **COMMUNITIES?**

11

12 Names of authors: Gladys Loranger*, Ipsa Bandyopadhyaya**, Barbara Razaka*** and Jean-François
13 Ponge

14

15 Address: *Museum National d'Histoire Naturelle, Laboratoire d'Écologie Générale, 4 avenue du Petit-*
16 *Château, 91800 Brunoy, France*

17

18 * Present address: Université de Paris Sud, Laboratoire de Biologie Végétale, Bat. 362, 91405 Orsay
19 Cedex, France

20

21 ** Present address: Simantapalli, Santiniketan, Birbhum, West Bengal PIN-731235, India

22

23 *** Present address: 11 rue Guichard, 94230 Cachan, France

24

25

26

27 **Corresponding author:** Jean-François Ponge, Tel. +33 1 60479213, Fax +33 1 60465009, E-mail:

28 jean-francois.ponge@wanadoo.fr

29

1 **Abstract**

2

3 Altitudinal changes in collembolan communities were studied by sampling soil microarthropods along
4 a gradient from 950 to 2150m a.s.l., under a wide range of forest vegetation types. A multivariate
5 method showed that most changes in species composition followed changes in soil chemistry, humus
6 forms and vegetation. A transition from mull to mor humus, with concomitant soil acidification, was
7 observed with increasing elevation. It was observed that at a given elevation changes in soil acidity
8 occurring in the course of forest dynamics exerted the same effects than altitude, thus soil acidity
9 explained better the composition of collembolan communities. Densities and local diversity of
10 Collembola were observed to increase with soil acidity, which can be explained by i) physiological
11 adaptations to acid soils inherited from palaeozoic times and ii) more habitat and food resources when
12 organic matter accumulates at the top of the soil profile.

13

14

15 **Keywords:** Collembola, Altitude, Acidity, Humus form, Vegetation

16

17

18 **1. Introduction**

19

20 Biocenoses of Collembola (Hexapoda) have been studied at scales varying from that of a regional
21 landscape (Gisin, 1943; Haybach, 1959; Cassagnau, 1961; Nosek, 1967; Ponge, 1980; Hågvar, 1982;
22 Pozo, 1986; Deharveng and Bedos, 1993; Ponge, 1993; Lauga-Reyrel and Lauga, 1995) to that of the
23 plant cushion or of the boulder (Bonnet et al., 1970; Booth and Usher, 1984, 1985). Scientists
24 endeavouring to find out factors which could explain the observed variations in species composition
25 are faced with a puzzling problem. If the scale is too large, discrepancies in the occupation of space
26 by species may arise quite independent of ecological factors, due to time-related processes such as
27 fragmentation of habitats or extinction-colonization processes (Christiansen and Bullion, 1978). If the
28 scale is too small, then interactions between species may overwhelm the selective action of ecological
29 factors (Usher, 1985; Usher and Booth, 1986). Thus the choice of an appropriate scale is a
30 prerequisite to any community study. The second more important aspect is the heterogeneity of the

1 sampled site or region, which could be due both to abiotic factors, such as lithology, climate and
2 aspect (Ponge, 1980; Ponge and Delhay, 1995; Theurillat et al., 1998), and to biotic factors such as
3 vegetation dynamics (Bernier, 1996; Miles 1979).

4

5 In a previous study on the Macot forest (Savoy, France) the heterogeneity of humus forms has been
6 shown to reflect that of the forest patchwork, varying according to altitude, phases of the forest cycle
7 and competition between the spruce forest and the bilberry heath (Bernier and Ponge, 1994; Bernier,
8 1996). Since ecological factors affecting humus forms, and humus forms themselves, were known to
9 affect collembolan communities (Ponge, 1980, 1983; Hågvar and Abrahamsen, 1984; Ponge 1993), it
10 has been decided to sample these animals at the scale of the eco-unit (Oldeman, 1990). As defined
11 by Oldeman (1990), eco-units are unit components of the forest patchwork. They are made of trees
12 and other organisms which have undergone a common history following a disturbance event, the so-
13 called zero-event, that created locally the eco-unit. In mountain coniferous forests of the French
14 northern Alps, most frequent disturbances are storms and cutting operations. At the montane level in
15 the Macot forest the forest renewal resulted from an improvement in humus form which occurred
16 before trees actually died and the canopy was opened. Improved humus allowed the rapid
17 establishment of a new cohort of Norway spruce (*Picea abies*) regardless of any long-lasting
18 successional processes (Bernier and Ponge, 1994; Bernier, 1996; Ponge et al., 1998). At the
19 subalpine level, the regeneration niche of spruce and other conifers was mostly decaying wood but the
20 subalpine heath competed strongly with the forest, thus decreasing the size of forest eco-units
21 (Bernier 1996, 1997).

22

23 The present study tested whether the scale of the eco-unit accounted for major variations in species
24 composition observed over an altitudinal gradient ranging from 950 to 2150m a.s.l., and explained
25 these variations. For that purpose collembolan communities and humus profiles were sampled near
26 each other at the approximate centre of the different kinds of eco-units which formed the forest
27 patchwork, care being taken to exclude micro-scale factors such as dead wood, stones, moss
28 cushions and proximity of tree trunk bases, all of which are known to influence collembolan
29 communities (Cassagnau, 1961; Bonnet et al., 1970; Ponge, 1980; Wolters, 1983; Arpin et al., 1984;
30 Kopeszki, 1992a, 1992b, 1993; Setälä and Marshall, 1994; Kopeszki, 1997),

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2. Methods

2.1 Study sites and sampling design

Five sites were selected along an altitudinal range from 950 to 2150 m, i.e. the altitudinal range of the communal forest of Macot La Plagne (Savoy, France), which nearly covers a north facing slope along the river Tarentaise. Each site was characterized by a variety of vegetational types, according to phases of sylvigenesis (Oldeman, 1990) and competition between heath and forest (Bernier, 1997). Different kinds of forest and heath eco-units with similar aspect and soil type were identified by vegetational features on as small scale as possible (at most 0.5 ha). Sites have been described in detail in previously published papers, together with results concerning humus profiles and earthworm communities (Bernier and Ponge, 1994; Bernier, 1996, 1997). A total of 37 eco-units were used for sampling humus profiles and soil fauna. Soil microarthropods were sampled by forcing a 15cm diameter x 10cm height aluminum cylinder into the topsoil, flush to the ground surface, at the approximate centre of each eco-unit. The place chosen for sampling humus and fauna was devoid of fallen wood and moss cushions and further than 0.5m from a tree base or stump. Sites were sampled in a week during June 1991, after snowmelt and before summer drought. Soil samples were immediately placed into sealed plastic bags then transported to the laboratory for extracting microarthropods.

2.2 Collection and identification of fauna

Animals were extracted within a week by the dry funnel method (Macfadyen, 1957) into 96% ethyl alcohol. Collembola were sorted, mounted in chloral-lactophenol (lactic acid, chloral hydrate, phenol 25:50:25 v/w/v), and they were identified at the species level under a light microscope with phase contrast at x400 magnification. A list of the 65 identified species is given in Table 1. Morphological characters fitted well with published descriptions of these species except that i) the fourth mucronated hair did not exist on the third pair of legs of *Hypogastrura cf. affinis*, ii) the sensilla s was not flame-like

1 on the third thoracic segment of *Mesaphorura cf. italica*, iii) the a2 hair was lacking on the fifth
2 abdominal tergite of *Xenylla cf. brevicauda*, iv) there was only a single hair on the mucrodens of
3 *Xenylla cf. xavieri*.

4 5 2.3 Multivariate statistics

6
7 Data (densities of animals per unit surface) were treated by correspondence analysis, a multivariate
8 method using the chi-square distance (Benzécri, 1969, 1973; Hill, 1974; Greenacre, 1984). This
9 method has been already used successfully to analyse changes in the species composition of
10 collembolan communities, with or without a priori hypotheses concerning the possible influence of
11 external factors (Bonnet et al., 1970, 1976, 1979; Ponge, 1980; Ponge and Prat, 1982; Poursin and
12 Ponge, 1982; Ponge, 1983; Gers and Izarra, 1983; Arpin et al., 1984; Poursin and Ponge, 1984; Pozo,
13 1986; Ponge, 1993; Lauga-Reyrel and Lauga, 1995; Loranger et al., 1998; Salmon and Ponge, 1999).
14 Variations in species composition are analysed without resorting to the suspected influence of external
15 factors, but rather factors are extracted from multiple measurements in order to explain the trends
16 depicted by main inertia axes (eigen vectors) of a between-species chi-square distance matrix.
17 Variables (species) and samples are simultaneously projected on a space formed by the first factorial
18 axes, i.e. those explaining better the global variation. Variables and samples are indicated by points,
19 the bulk sample being thus represented by a cloud of points. Each species is projected in the vicinity
20 of samples to the species composition of which it contributes the best. The proximity of species and
21 samples and the contribution of the different species to the factorial axes allow detection of gradients
22 or discontinuities in the species composition, following one or several of the first factorial axes, which
23 are linearly independent. Each factorial axis represents a dimension of the sub-space into which the
24 cloud of data has been projected. The introduction of additional (passive) variables helps interpretation
25 of factorial axes in ecological terms when these variables prove to be well-correlated with factorial
26 axes. Additional variables are projected as if they had been used in the analysis but they do not
27 influence to any extent the formation of the factorial axes. Their projection is a point in the vicinity of
28 the samples (and species) which it characterizes best. For example if pH has been measured, this
29 parameter will be represented by a unique point falling near the samples exhibiting the highest pH.

1 In order to give the same weight to all parameters, all variables (discrete as well as continuous) were
2 transformed into $X = (x-m)/s + 20$, where x is the original value, m is the mean of a given variable, and
3 s is its standard deviation. The addition to each standardized variable of a constant factor of 20 allows
4 all values to be positive, correspondence analysis dealing only with positive numbers (normally
5 counts). Following this transformation, factorial coordinates of variables can be interpreted directly in
6 term of their contribution to the factorial axes: the farther a variable is projected from the origin of the
7 axes (barycentre) along a given direction (along a factorial axis) the more it contributes to this axis.
8 Variables were doubled in order to allow for the dual nature of most parameters (the absence of a
9 given species is as important as its presence, low pH values are as important as high pH values). To
10 each variable X was thus associated a twin X' varying in an opposite sense ($X' = 40 - X$). Such a
11 doubling proved useful when dealing with ecological gradients (Ponge et al., 1997) or when it was
12 judged interesting to classify samples according to their bulk abundance, besides changes in species
13 composition (Loranger et al., 1998). Originally, correspondence analysis was performed to deal only
14 with count numbers. Later it has been extended to other types of variables (Greenacre, 1984). The
15 transformations used here give to correspondence analysis most properties of the well-known
16 principal components analysis (Hotelling, 1933), while keeping the advantage of the simultaneous
17 projection of rows (variables) and columns (samples) onto the same factorial axes and the robustness
18 due to the principle of distributional equivalence.

19

20 *2.4 Soil chemical analyses*

21

22 Once the extraction of microarthropods was completed, dried samples from the top first 10cm were
23 used for chemical analyses. Samples were sieved to 2mm, homogenized, then chemical analyses
24 were performed on several sub-samples. Water pH and potassium chloride pH were measured on a
25 5g sub-sample diluted with deionized water (soil:water 1:1 w/w). A 50g sub-sample was crushed with
26 pestle and mortar, then sieved at 200 μm for further analyses. Cation exchange capacity was
27 measured on a 10g sub-sample by percolating the soil with 1N calcium chloride until saturation of
28 exchange sites then displacing calcium with 1N potassium nitrate. Determination of calcium and
29 chloride content was performed in the filtrate by flame nitrous oxide-acetylene atomic absorption
30 photometry, and complexometry with a Technicon® autoanalyser, respectively. Exchangeable cations

1 (Ca, Mg, K, Na) were determined on a 10g sub-sample after displacement of sorbed cations with
2 ammonium nitrate. Potassium and sodium were determined on the filtrate by flame emission
3 photometry, calcium and magnesium by flame atomic absorption photometry. Total carbon and
4 nitrogen were determined with a CHN Carlo Erba® analyser on a 5mg sub-sample. Total bases (Ca,
5 Mg, K, Na), iron and manganese were determined on 1g sub-sample after boiling with concentrated
6 hydrochloric acid. Potassium and sodium were determined by flame air-acetylene emission
7 photometry, magnesium, iron and manganese by flame air-acetylene atomic absorption photometry,
8 and calcium by flame nitrous oxide-acetylene atomic absorption photometry. Total phosphorus was
9 determined on a 1g sub-sample with a Techicon® autoanalyser after treatment with concentrated
10 hydrogen peroxide followed by boiling with perchloric acid.

11

12 *2.5 Other data*

13

14 Other data were used as additional variables in the multivariate analysis of Collembola communities.
15 Particle size distribution was calculated on the same samples as for chemical analyses, i.e. on the top
16 first 10cm of soil (litter comprised) after extraction of fauna and sieving at 2mm the dried material.
17 Humus form was determined during sampling of humus profiles, part of which have been thoroughly
18 described in Bernier and Ponge (1994) and Bernier (1996). The study of humus profiles helped to
19 notice the presence of main moss, herb, shrub and tree species in the litter. Species richness and total
20 abundance of Collembola were added, too.

21

22 Some other analyses were done using the age of trees forming the eco-units into which Collembola
23 were sampled. The age was calculated either by recording successive whorls on the stem of young fir
24 or spruce trees or by counting annual increments on a probe taken as near as possible from the
25 ground (correction was made by adding the age of saplings of similar height growing in the same site).

26

27

28 **3. Results**

29

30 *3.1 Influence of altitude and soil chemistry*

1

2 The first factorial axis extracted 14.4% of the total variance. Despite this low value, this axis was the
 3 only one clearly interpretable on the basis of the data collected in the present study. Thus further order
 4 axes were considered as background noise and they were ignored in the following. Projection of
 5 samples and main and additional variables was thus only done on axis 1. At first sight the significance
 6 of this axis can be found in the altitudinal gradient. Figure 1 and Table 1 show that axis 1 was strongly
 7 correlated with altitude, the correlation being even better when based on logarithms of factorial
 8 coordinates. If we consider axis 1 of correspondence analysis as a compound index of species
 9 composition, this means that the species composition of collembolan communities varied according
 10 with altitude, but that the observed variation decreased when higher elevation was reached. For
 11 instance more variation in species composition occurred from 1000 to 1500m than from 1500 to
 12 2000m.

13

14 Figure 2 shows the projection of collembolan species and some additional variables such as humus
 15 form, altitude, and vegetation. The species composition at 2150m (the upper limit of the forest) did not
 16 differ greatly from that at 1850m (the subalpine forest), even though the difference in elevation was
 17 300m (Fig. 1). Most changes occurred at the montane level from 950m (the lower montane level) to
 18 1550m (the upper montane level). Species typical of upper slope forest were *Archaphorura absoloni*
 19 (AAB), *Isotoma nivalis* (INI), *Mesaphorura tenuisensillata* (MTE), *Ceratophysella denticulata* (CDE),
 20 *Folsomia sensibilis* (FSE), *Pogonognathellus flavescens* (PFL), *Hypogastrura cf. affinis* (HAF), *Friesea*
 21 *claviseta* (FCL), *Lepidocyrtus lignorum* (LLI). Species typical of lower slope forest were *Protaphorura*
 22 *armata* (PAR), *Mesaphorura hylophila* (MHY), *Pseudosinella edax* (PED), *Willemia intermedia* (WIN),
 23 *Lepidocyrtus lanuginosus* (LLA), *Lipothrix lubbocki* (LLU), *Pseudosinella alba* (PAL), *Folsomia*
 24 *penicula* (FPE), *Parisotoma notabilis* (PNO), *Arrhopalites gisini* (AGI), *Allacma sp.* (ASP), *Bourletiella*
 25 *sp.* (BSP), *Xenylla cf. brevicauda* (XBR), *Sminthurinus aureus* (SAU), *Tomocerus minor* (TMI).

26

27 Humus forms varied from mull (macrofaunal activity dominant) to moder (mesofaunal activity
 28 dominant) then to mor (poor faunal activity) according to axis 1, but it should be highlighted that the
 29 position of moder and mor was quite similar. These two humus forms were thus inhabited by the same
 30 community although mor was characterized by scarcity of animal faeces. The projection of plant

1 species along axis 1 reflected their preferential position along the altitudinal gradient, with silver fir
2 (*Abies alba*) and hazel (*Corylus avellana*) as typical lower slope species, and Alpen rose
3 (*Rhododendron ferrugineum*) as typical upper slope species. Most other common plant species were
4 centered around the origin, thus indicating their wide distribution over the studied altitudinal gradient.

5

6 Particle size distribution did not seem to vary along the studied altitudinal gradient, lower and higher
7 values of all categories being centered around the origin (Fig. 3). On the contrary, variables describing
8 chemical properties of soils were stretched along axis 1, indicating strong chemical variations with
9 altitude (Fig. 4). The topsoil of the upper slope forest was characterized by higher acidity, expressed
10 by i) lower pH (water as well as potassium chloride pH), ii) lower content in total bases (chiefly calcium
11 and magnesium), iii) higher exchangeable acidity (D pH), iv) accumulation of organic matter (more C
12 and N), and by a lower iron content. The C/N ratio did not vary at all according to axis 1, and some
13 other chemical features such as cation exchangeable capacity (and exchangeable bases), total
14 phosphorus, potassium, sodium and manganese were roughly centered around the origin, thus
15 indicating that they did not contribute greatly to axis 1.

16

17 Local species richness and abundance of Collembola increased along Axis 1 (Fig. 4). Both were
18 significantly correlated between themselves and with Axis 1 (Table 2). Local species richness was
19 negatively correlated with water pH, but neither abundance nor local species richness were correlated
20 significantly with elevation.

21

22 *3.2 Influence of vegetation*

23

24 We may wonder whether vegetation influenced directly or indirectly collembolan communities
25 independently of altitude. The fact that vegetation factors were not represented by lower-order axes of
26 correspondence analysis might indicate either that vegetation did not influence collembolan
27 communities or that this influence was superimposed on that of altitude and soil chemistry. Two
28 arguments favour the second hypothesis, i) the existence of cycling processes embracing both soil
29 properties and development of the forest ecosystem at the montane level (Bernier and Ponge, 1994;
30 Bernier 1996), ii) demonstration that the influence of altitude was superimposed on that of soil acidity,

1 the latter being known to vary according to the forest cycle (Ponge and Bernier, 1995; Bernier, 1996).
2 In order to verify this hypothesis at the montane level (lower and upper), coordinates of the eco-units
3 along axis 1 and pH (water) values were simultaneously crossed with the mean age of the trees (Fig.
4 5). At 950m, where pH values vary from 5 to 7 it appears that these variations closely follow that of
5 axis 1 coordinates in a chronosequence. At 1550m, where pH values vary from 3.5 to 5, coordinates
6 along axis 1 did not vary to the same extent, especially during the time of most active growth of trees
7 (55 to 60 years), but they follow the same trend as pH values. This means that at the montane level
8 the species composition of collembolan communities (depicted by axis 1) varies during the forest cycle
9 as does soil acidity.

10

11

12 **4. Discussion**

13

14 *4.1. Altitude, vegetation and soils*

15

16 These results suggest that the effects of altitude, vegetation and soils on collembolan communities are
17 superimposed, and are probably reinforced by a number of positive feed-back loops involving climate,
18 nutrient availability, plant secondary metabolism and soil foodwebs (Perry et al., 1989; Ponge et al.,
19 1997, 1998; Northup et al., 1998; Ponge, 1999; Ponge et al., 1999). Since it has been demonstrated
20 that soil acidity varies cyclically under the development of vegetation (Ponge and Bernier, 1995;
21 Bernier, 1996), it follows that the effect of vegetation on soil collembolan communities is probably
22 through acidification and deacidification of the soil beneath. Such reversible effects in the course of
23 vegetation dynamics have been already observed on earthworm communities, and on the humus
24 forms they build (Miles, 1985; Bernier and Ponge, 1994; Ponge and Delhaye, 1995). Collembolan
25 communities are sensitive to soil acidity (Ponge, 1980, 1983; Hågvar and Abrahamsen, 1984; Pozo,
26 1986; Ponge, 1993; Van Straalen and Verhoef, 1997), although pH itself is not responsible for the
27 observed changes in species composition (Hågvar, 1990; Salmon and Ponge, 1999). The joint effect
28 of vegetation and altitude upon collembolan communities is best measured by a combination of pH,
29 exchange acidity, redox potential, nutrient availability, free forms of aluminum and other toxic metals,
30 accumulation of poorly humified organic matter, remanence of plant secondary metabolites, toxicity of

1 the soil atmosphere (Lafond, 1950; Wilde, 1954; Ovington, 1954; Verdier, 1975; Ritchie and Posner,
 2 1982; James and Riha, 1984; Ulrich, 1986; Muller et al., 1987; Sexstone and Mains, 1990; Kuiters,
 3 1990; White, 1994; Northup et al., 1995). When altitude increases, i) erosion impoverishes upper
 4 slope soil to the benefit of lower slope soils, ii) mineralization is slowed by low temperature, and thus
 5 organic matter tends to accumulate, iii) plants produce more secondary metabolites, in particular
 6 phenolic compounds, which inhibit proteins and make nitrogen, sulphur and phosphorus unavailable,
 7 iii) humification is slowed, and thus small organic molecules may act as ligands which leach metals
 8 and bases down the soil profile (podzolization). When trees grow actively, i.e. when forest eco-units
 9 are in the aggradation phase (Oldeman, 1990), the uptake of nutrients by roots exceeds their release
 10 through decomposition of litter and weathering of mineral particles, thus temporarily impoverishing the
 11 soil locally. Thus from the point of view of soil acidification altitude and vegetation dynamics may have
 12 similar side effects on soil collembolan communities.

13

14 4.2 Acidification effects

15

16 Now, let us examine whether the present data explain the acidification hypothesis. If we compare the
 17 distribution of species along axis 1 (Figs. 2, 3, 4) with the classification of acidophilic and acido-
 18 intolerant temperate lowland species by Ponge (1980, 1983, 1993), we can notice that three acido-
 19 intolerant species, namely *Mesaphorura hylophila* (MHY), *Pseudosinella alba* (PAL) and *Folsomia*
 20 *penicula* (FPE), appear on the negative side of axis 1, and none on the positive (acid) side. On the
 21 contrary acidophilic species such as *Mesaphorura macrochaeta* (MMA), *Micranurida pygmaea* (MPY),
 22 *Protaphorura lata* (PLA, = *P. subuliginata*), *Willemia anophthalma* (WAN), *Friesea claviseta* (FCL),
 23 *Friesea mirabilis* (FMI), appear on the positive (acid) side of axis 1. An exception is the position of
 24 *Willemia intermedia* (WIN), an acidophilic species according to Ponge (1993), which is here on the
 25 negative side of axis 1.

26

27 Some species found to live here at higher elevation have been frequently recorded in northern
 28 coniferous forests (Bödvarsson, 1973; Bååth et al., 1980; Hågvar, 1982; Hågvar and Abrahamsen,
 29 1984; Huhta et al., 1986; Fjellberg, 1998), such as *Archaphorura absoloni* (AAB), *Mesaphorura*
 30 *tenuisensillata* (MTE), *Hymenaphorura sibirica* (HSI, = *H. polonica*), *Willemia denisi* (WDE = *W.*

1 *aspinata*), *Xenylla boernerii* (XBO), *Anurida granulata* (AGR), *Pogonognathellus flavescens* (PFL),
 2 *Lepidocyrtus lignorum* (LLI), *Pseudanurophorus binoculatus* (PBI), *Anurophorus laricis* (ALA). All
 3 these species, except *Anurophorus laricis* (ALA), have been commonly found by Ponge (2000a) under
 4 beech in a range of acidic soils of the Belgian Ardennes. Thus most of them do not seem to be
 5 restricted to northern coniferous forests, but rather to strongly acidic conditions.

6

7 4.2 Adaptations

8

9 An alternative hypothesis to the influence of soil acidification is the adaptation of collembolan
 10 communities to climate conditions prevailing at higher elevation, i.e. more sun and snow and colder
 11 mean temperatures. Special adaptations to these conditions have been registered in alpine as well as
 12 circumpolar collembolan populations, such as dark pigmentation (Rapoport 1969), cold hardness
 13 strategies and cryoprotectants (Zettel et al., 1989; Block, 1983; Vannier, 1994), efficiency of low
 14 temperature metabolism (Block and Tilbrook, 1975; Burn, 1984), behavioural response to changes in
 15 barometric pressure (Zettel, 1984), long distance migration strategies (Hågvar, 1995). Some typical
 16 alpine species are present at high elevation only in our samples, such as *Deutonura conjuncta* (DCO),
 17 *Hypogastrura meridionalis* (HME), *Xenylla obscura* (XOB), *Folsomia sensibilis* (FSE), *Folsomia*
 18 *inoculata* (FIN), *Isotoma nivalis* (INI), *Vertagopus montanus* (VMO). The presence of *Hypogastrura*
 19 *meridionalis* (HME) and *Xenylla obscura* (XOB) is remarkable, since these two species were only
 20 known from the Pyrenees and the Himalayas, respectively. For all these species we cannot find any
 21 proof of their strong acidophily in the literature, thus they rather seem to be adapted to cold climate
 22 conditions which are to be found at the upper subalpine level.

23

24 Species which are well-known from lowland sites for their acidophily are *Willemia anophthalma*
 25 (WAN), *Friesea mirabilis* (FMI), *Micranurida pygmaea* (MPY) and *Protaphorura lata* (PLA). They could
 26 be thought not to live at the same sites than the mountain species *Deutonura conjuncta* (DCO),
 27 *Hypogastrura meridionalis* (HME), *Xenylla obscura* (XOB), *Folsomia sensibilis* (FSE), *Folsomia*
 28 *inoculata* (FIN), *Isotoma nivalis* (INI) and *Vertagopus montanus* (VMO). In fact densities of these two
 29 groups were highly correlated, as verified by their Spearman rank correlation coefficient (Sokal and
 30 Rohlf, 1995). Thus it can be predicted that species tolerant of acidity will be tolerant of altitude. Soil

1 acidification, which is known to have been favoured by atmospheric pollution during the last three
2 decades in Scandinavia and Central Europe (Wittig, 1986; Falkengren-Grerup, 1987), may cause less
3 dramatic changes in mountain biocenoses of Collembola than in lowland biocenoses, and perhaps
4 even mountain biocenoses may be favoured by atmospheric pollution. This prediction is in partial
5 agreement with results of the survey done from 1968 to 1990 by Rusek (1993) in the Tatra mountains.
6 The increase in numbers of the formerly rare boreo-alpine *Pseudanurophorus binoculatus* recorded by
7 this author can be attributed to acid deposition, but the disappearance of *Folsomia alpina*, a typical
8 inhabitant of alpine pioneer ecosystems on dolomite and limestone (Nosek, 1967), does not follow the
9 above prediction. It should be noted that our results hold only for siliceous bedrocks and that at the
10 alpine level a decrease in species richness and total abundance of Collembola has been observed
11 (Lauga-Reyrel and Lauga, 1995). The subalpine level seems to be most favourable to Collembola, but
12 not the alpine level and even less the nival level.

13

14 We observed an increase in local species richness and abundance according to axis 1 of
15 correspondence analysis (Fig. 4), which could be better explained by an increase in soil acidity than
16 by an increase in elevation (Table 2). Since soil acidification implies a decrease in litter decomposition
17 rates (Ulrich, 1986) and is reinforced by slow humification of organic matter (Stevenson, 1994) we
18 may expect a correlation between acidification and accumulation of soil organic matter, at least on
19 siliceous bedrocks. This has been demonstrated in previous studies on the same sites (Bernier and
20 Ponge, 1994; Bernier, 1996) and can be explained at first sight by an increase in available habitat and
21 food. Since most collembolan species are known to ingest humus (Gilmore and Raffensperger, 1970;
22 Wolters, 1987; Saur and Ponge, 1988; Ponge, 1991) it can be postulated that the more humus will
23 accumulate the more food and habitat will be available to Collembola. A similar increase in local
24 species richness and abundance of Collembola has been observed from the montane to the subalpine
25 level by Deharveng and Bedos, (1993), which could be seemingly explained by the observed increase
26 in soil acidity.

27

28 These results indicate a physiological adaptation of the whole group to acid soils, that corroborates
29 with the primitive nature of Collembola, which appeared as soon as the Silurian age, and then radiated
30 during the Devonian age (Rolfe, 1985; Dunger, 1987). At this time topsoils were probably strongly

1 acid, due to chemical properties of primitive plants (lichens, bryophytes, pteridophytes, later on
2 gymnosperms), scarcity of base-rich substrates, and to acid rains (Elmi and Babin, 1996; Lethiers,
3 1998). Thus it may be thought that acidophilic species appeared sooner in the evolution than acid-
4 intolerant species, which lost some important physiological adaptations, this idea being reinforced by
5 the examination of phylogenetic trees (Ponge 2000b). Contrary to more recently evolved invertebrate
6 groups such as terrestrial oligochaetes which increase in species richness in richer soils
7 (Abrahamsen, 1972a, 1972b), soil acidity does not decrease the species richness of Collembola, at
8 least in mountain and boreal sites where acid environments played the role of refuges for primitive
9 adaptations.

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1 **Figure captions**

2

3 **Fig. 1.** Correlation between the first factorial axis of correspondence analysis and altitude. Bars are
4 standard errors of the mean factorial coordinates at each altitude. ** = significant at the 0.01
5 threshold (d.f. = 35).

6

7 **Fig. 2.** Correspondence analysis. Projection of collembolan species and some additional variables on
8 the first factorial axis. Collembolan species (higher values only) are indicated by a three-letter
9 code in bold type. Origin of the axis (barycentre) is indicated by an arrow. For the sake of
10 clarity codes or names of variables have been displaced horizontally, their projection on axis
11 1 being indicated only by their vertical position.

12

13 **Fig. 3.** Correspondence analysis. Projection of collembolan species and particle size classes on the
14 first factorial axis. Collembolan species (higher values only) are indicated by a three-letter
15 code in bold type. Higher values of particle size percentages are indicated in bold type, while
16 lower values are in italic. Otherwise as for Fig. 2.

17

18 **Fig. 4.** Correspondence analysis. Projection of collembolan species, soil chemical variables and
19 population estimates on the first factorial axis. Collembolan species (higher values only) are
20 indicated by a three-letter code in bold type. Higher values of soil chemical variables and
21 population estimates are indicated in bold type, while lower values are in italic. S = sum of
22 exchangeable bases. D pH is the difference between water pH and KCl pH. Soil chemical
23 variables and population estimates significantly correlated with axis 1 (Spearman rank
24 correlation) were placed into boxes. Otherwise as for Fig. 2.

25

26 **Fig. 5.** Changes in the course of time of pH and axis 1 coordinates at the montane level.

27

PONGE

Table 1. Mean abundance of Collembolan species (ind m⁻²) in the five investigated sites

codes		950m	1550m	1750m	1850m	2150m
AAB	<i>Archaphorura absoloni</i>	0	1330	1698	1787	2252
AGI	<i>Arrhopalites gisini</i>	7	0	0	0	0
AGR	<i>Anurida granulata</i>	0	96	81	24	136
ALA	<i>Anurophorus laricis</i>	0	334	9281	2417	1120
ASE	<i>Arrhopalites sericus</i>	35	34	32	0	57
ASP	<i>Allacma sp.</i>	7	0	0	0	0
BSP	<i>Bourletiella sp.</i>	14	0	0	259	0
CDE	<i>Ceratophysella denticulata</i>	0	124	0	3929	215
CTH	<i>Cryptopygus thermophilus</i>	0	0	0	0	11
DCO	<i>Deutonura conjuncta</i>	0	28	8	0	23
DSY	<i>Deutonura sylvatica</i>	0	0	0	40	23
EMA	<i>Entomobrya marginata</i>	0	0	267	251	464
ENI	<i>Entomobrya nivalis</i>	0	136	477	170	0
FCL	<i>Friesea claviseta</i>	0	447	226	1205	0
FIN	<i>Folsomia inoculata</i>	0	0	1140	0	0
FLA	<i>Folsomia lawrencei</i>	2695	2965	89	1180	0
FMA	<i>Folsomia manolachei</i>	0	0	0	1948	68
FMI	<i>Friesea mirabilis</i>	0	323	412	0	0
FPE	<i>Folsomia penicula</i>	4449	4544	4737	0	0
FQU	<i>Folsomia quadrioculata</i>	0	6	0	0	0
FSE	<i>Folsomia sensibilis</i>	0	175	105	73	1562
HAF	<i>Hypogastrura affinis</i>	0	6	40	129	68
HME	<i>Hypogastrura meridionalis</i>	0	0	243	13921	0
HSI	<i>Hymenaphorura sibirica</i>	0	0	186	0	0
IMI	<i>Isotomiella minor</i>	1118	2960	1997	1536	12133
INI	<i>Isotoma nivalis</i>	0	1086	1277	1835	6146
ITI	<i>Isotoma tigrina</i>	0	0	8	0	0
LLA	<i>Lepidocyrtus lanuginosus</i>	2165	741	6629	1334	0
LLI	<i>Lepidocyrtus lignorum</i>	0	0	404	356	249
LLU	<i>Lipothrix lubbocki</i>	120	6	24	8	0
LVI	<i>Lepidocyrtus violaceus</i>	0	175	849	978	0
MCR	<i>Mesaphorura critica</i>	7	68	0	49	0
MHY	<i>Mesaphorura hylophila</i>	835	475	0	0	0
MIT	<i>Mesaphorura italica</i>	149	232	89	0	0
MMA	<i>Mesaphorura macrochaeta</i>	311	3712	574	178	170
MMI	<i>Megalothorax minimus</i>	99	51	0	0	238
MPY	<i>Micranurida pygmaea</i>	57	628	816	49	192
MSY	<i>Mesaphorura sylvatica</i>	0	11	0	89	407
MTE	<i>Mesaphorura tenuisensillata</i>	0	351	558	113	1879
NMU	<i>Neanura muscorum</i>	0	85	113	137	11
OBI	<i>Orchesella bifasciata</i>	0	141	113	0	0
OCR	<i>Oncopodura crassicornis</i>	0	23	0	0	0
OEM	<i>Odontella empodialis</i>	0	0	194	493	68
PAL	<i>Pseudosinella alba</i>	672	368	0	0	0
PAR	<i>Protaphorura armata</i>	3027	0	0	0	0
PAS	<i>Pseudachorutella asigillata</i>	0	28	49	719	192
PBI	<i>Pseudanurophorus binoculatus</i>	0	198	40	8	113
PCA	<i>Paratullbergia callipygos</i>	64	0	8	0	215
PED	<i>Pseudosinella edax</i>	424	0	0	0	0
PFL	<i>Pogonognathellus flavescens</i>	0	113	388	8	0
PLA	<i>Protaphorura lata</i>	0	0	1568	1043	1098
PNO	<i>Parisotoma notabilis</i>	11282	2563	574	275	2456
PPA	<i>Pseudachorutes parvulus</i>	594	102	32	65	11
PSE	<i>Pseudisotoma sensibilis</i>	0	340	49	0	0
SAU	<i>Sminthurinus aureus</i>	21	0	0	0	0
SIN	<i>Schoettella inermis</i>	0	0	0	8	0
TMI	<i>Tomocerus minor</i>	7	0	8	0	0
VCI	<i>Vertagopus cinereus</i>	0	0	16	65	0
VMO	<i>Vertagopus montanus</i>	0	28	16	16	0
WAN	<i>Willemia anopthalma</i>	177	3027	234	73	939
WDE	<i>Willemia denisi</i>	42	1358	0	24	668
WIN	<i>Willemia intermedia</i>	28	0	0	0	0
XBO	<i>Xenylla boemeri</i>	0	0	453	0	11
XBR	<i>Xenylla brevicauda</i>	3516	74	14373	0	0
XOB	<i>Xenylla obscura</i>	0	1777	8	711	26359
XXA	<i>Xenylla xavieri</i>	0	6	32	73	0
Total		31923	31276	50517	37575	59554
Mean species richness		13.3	17.1	17.9	14.4	19.6
Bulk species richness		27	43	46	40	32
Number of samples		8	10	5	7	7

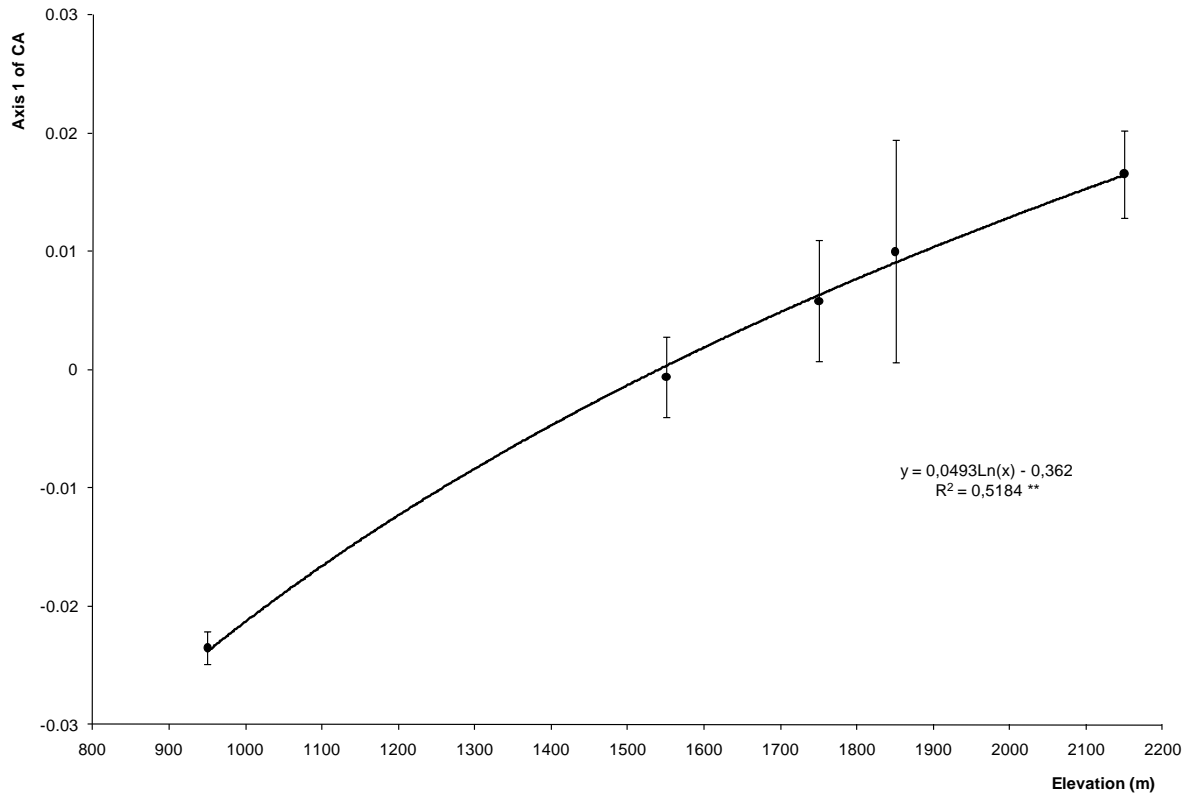
1

Table 2. Spearman rank correlation coefficients between some ecological factors and axis 1 of correspondence analysis ($n = 37$). Significant values at $P = 0.05$ are in bold type, others in italic

	Abundance	Species richness	Water pH	Elevation
Abundance				
Species richness	0.65			
Water pH	<i>-0.22</i>	-0.48		
Elevation	<i>0.19</i>	<i>0.31</i>	-0.60	
1 Axis 1	0.51	0.72	-0.70	0.73

2

PONGE

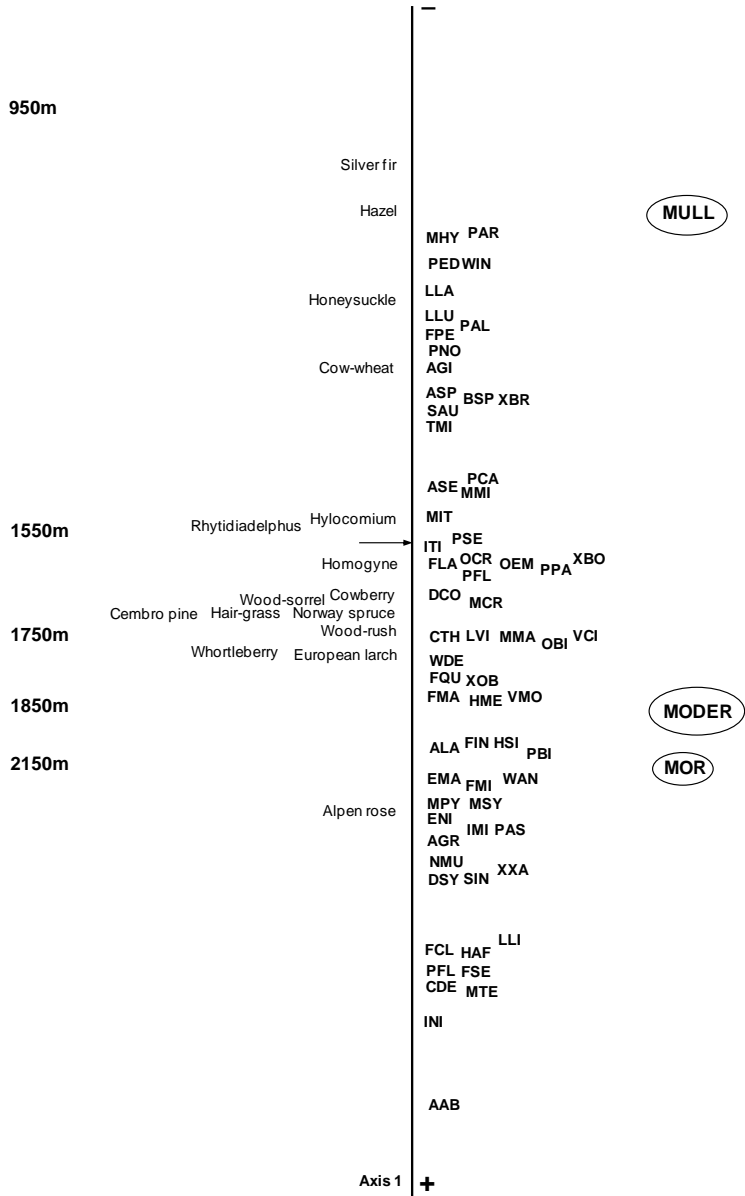


1

2 Fig. 1

3

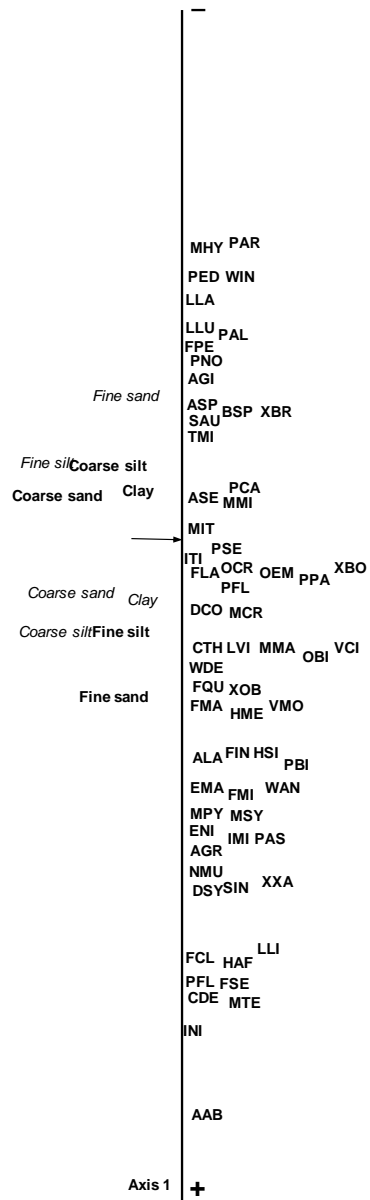
PONGE



1

2 Fig. 2

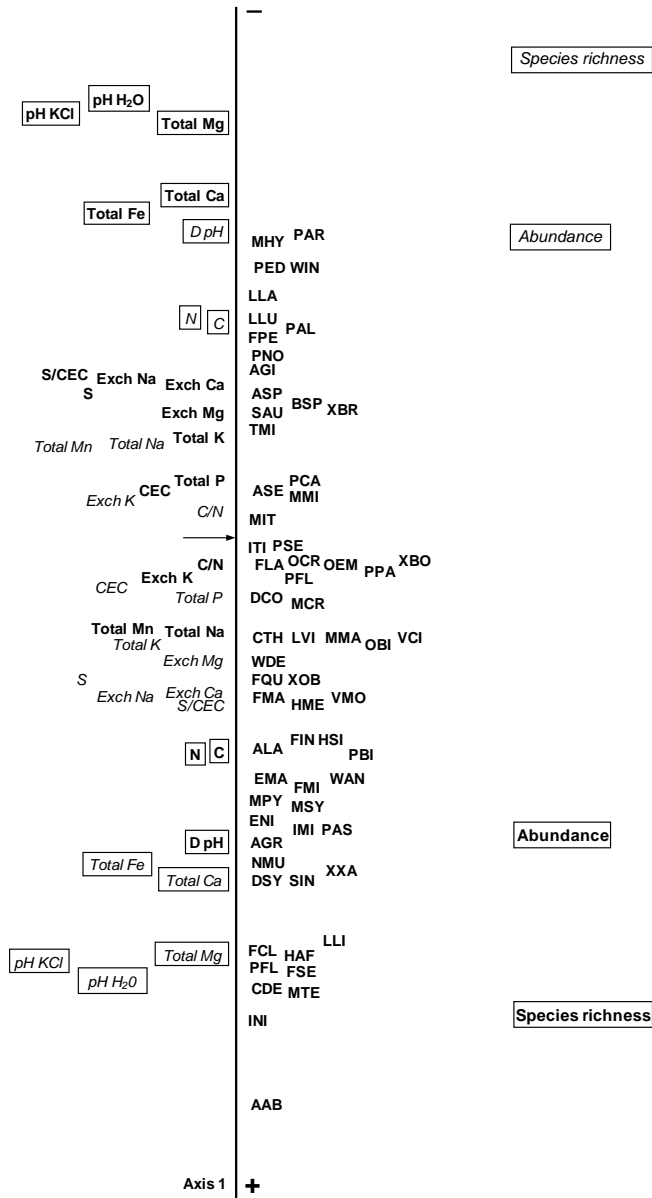
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1

2 Fig. 3

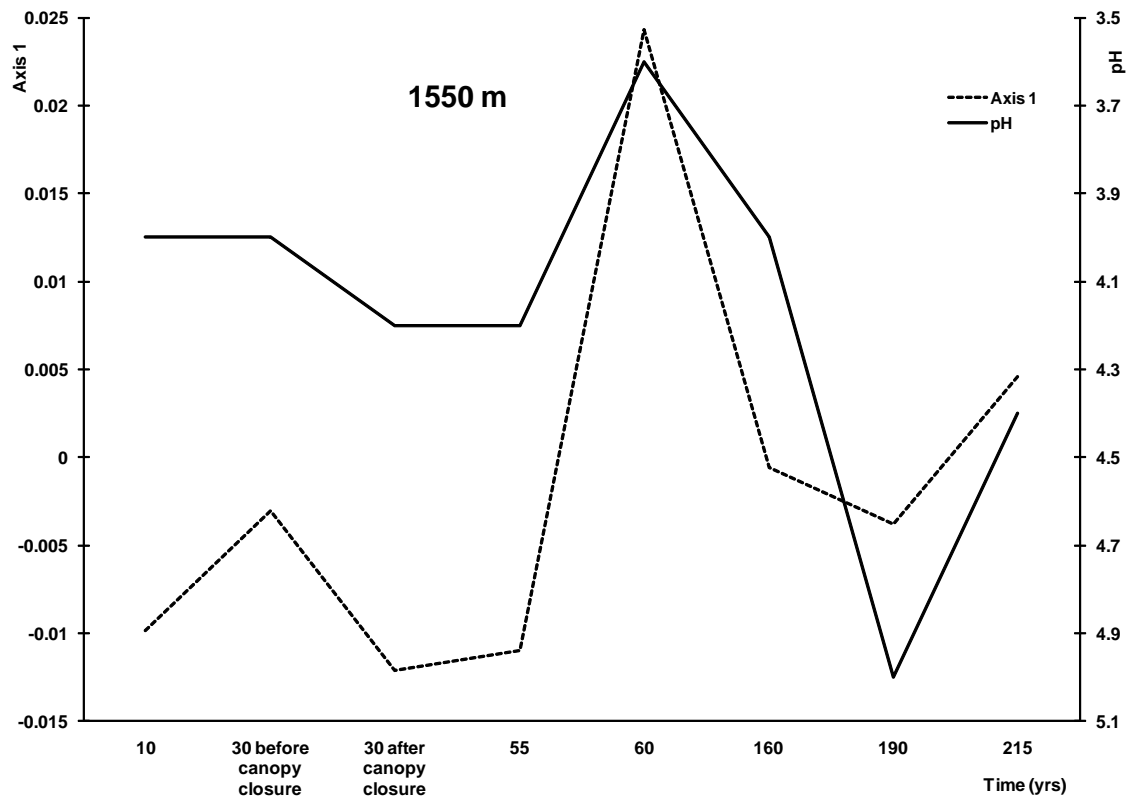
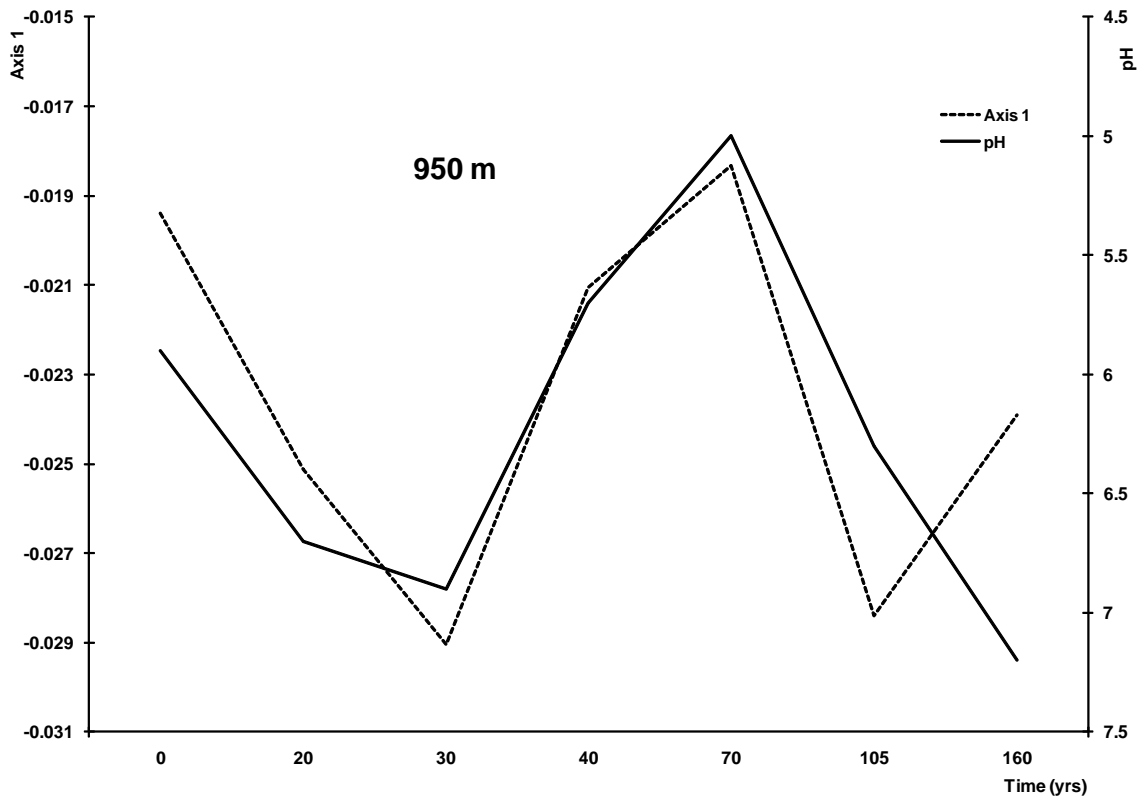
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2 Fig. 4

3



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2 Fig. 5