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1 **Colonization of heavy metal polluted soils by Collembola: preliminary**
2 **experiments in compartmented boxes**

3
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5
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8
9 **Abstract**

10
11 Two-week laboratory experiments were carried out in plastic boxes separated in two connected
12 compartments filled with a neutral soil (mull humus) at pH 7.7 and an acid soil (moder humus) at pH
13 4.3, containing their original faunas. Migration of Collembola from one compartment to the other was
14 allowed through a perforated wall. The mull was contaminated with three concentrations of lead (as
15 lead acetate) at 50, 6,000 and 60,000 ppm. When combined with moder in the adjacent compartment,
16 6 times more individuals and 5 times more species were observed in the mull at the highest
17 concentration applied, compared to mull combined with itself. *Parisotoma notabilis* proved to be highly
18 sensitive to lead, and shifted to the moder compartment even at the lowest concentration. Densities of
19 other mull species such as *Pseudosinella alba* were affected by medium to high concentrations of lead
20 but these species did not move to the moder soil despite their high motility. Acidophilic species living
21 in moder only, such as *Willemia anophthalma*, *Xenylla tullbergi*, *Proisotoma minima* and *Xenylla*
22 *tullbergi*, colonized contaminated mull treatments with densities increasing with lead concentrations
23 but the result of this process was erratic. *Folsomia manolachei* was present in both humus forms but
24 was much more abundant in the moder. This species colonized mull at medium to high lead
25 concentrations, where it restored totally or partly its original abundance in the uncontaminated mull.
26 These results suggested differences between mull and moder populations of *Folsomia manolachei*.

27

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1 *Keywords:* Collembola, Acidophily, Heavy metals, Migration, Sensitivity.

2

3 **1. Introduction**

4

5 The sensitivity of Collembola (Hexapoda) to heavy metals has been the subject of recent
6 investigations, pointing on the heritability of resistance in populations submitted to long-term
7 contamination of soils (Posthuma, 1990; Posthuma et al., 1993; Tranvik et al., 1994). Several studies
8 have been carried out on collembolan communities, showing that shifts in species composition
9 occurred under the influence of heavy metal contamination, together with a decrease in biodiversity
10 (Hågvar and Abrahamsen, 1990; Filser and Holscher, 1997; Bruus Pedersen et al., 1999).

11

12 The sensitivity of different species of Collembola to soil acidity has been recognized for a long
13 time (Gisin, 1943; Mertens, 1975; Hågvar and Abrahamsen, 1984; Loranger et al., 2001). Experiments
14 with artificial acid rain have shown that species living only in acid soils such as *Willemia anophthalma*,
15 *Micranurida pygmaea* and *Mesaphorura yosii* were favoured by the application of sulphuric acid. Other
16 species, present in acid soils but more abundant in neutral soils, such as *Parisotoma notabilis*, were
17 eliminated by the same experimental conditions (Bååth et al., 1980; Hågvar and Kjøndal, 1981;
18 Hågvar, 1984).

19

20 The presence of high concentrations of aluminum, iron and other metals in the soil solution
21 when soils are very acid (Bergkvist, 1987; Lundström et al., 2000), and the increased ecological
22 effects of heavy metals at low pH (Crommentuijn et al., 1997), led us to postulate that tolerance to
23 heavy metals and tolerance to acidity could be ecologically related. Specifically, animals living in acid
24 soils, either at the species or the sub-species level, could be more tolerant to heavy metals than
25 animals commonly living in neutral or weakly acidic soils. The threshold of pH 5, below which changes
26 in collembolan species composition have been recorded (Ponge, 1983; Ponge, 1993; Ponge, 2000a),
27 is also a threshold under which aluminum passes into the soil solution as a metal cation and may exert
28 severe toxicity, mostly by negatively interacting with phosphorus metabolism (Clarkson, 1969; James
29 and Riha, 1984; Berggren et al., 1990). Given a common detoxication strategy in Collembola and
30 other Hexapoda, i.e. by periodically renewing the midgut epithelium (Joosse and Buker, 1979; Hopkin,

1 1995), it can be hypothesized that species living in naturally acidic soils (and thus thought tolerant or
2 resistant to free metallic forms) are able to colonize neutral or weakly acidic soils contaminated with
3 heavy metals as a consequence of human activities such as mining, agriculture and industry.

4
5 It is intended to test this hypothesis in the long-term by inoculating acid humus profiles, with
6 their complete acido-tolerant collembolan communities, into metal-contaminated sites. Prior to
7 undertaking field experiments, a preliminary study was conducted in order to verify whether
8 *Collembola* living in acid soils are able to leave their original habitat to colonize a neutral soil polluted
9 with heavy metals.

11 2. Materials and Methods

12
13 Short-term experiments were conducted in experimental boxes where animals were free to
14 move between compartments, one filled with an acid soil (moder humus), and another filled with a
15 neutral soil (mull humus) treated with lead acetate at different concentrations. Two soils were chosen,
16 a Dysmoder, characterized by the accumulation of organic matter in the form of small enchytraeid
17 faeces, and an Eumull, characterized by a rapid mixing of organic matter to mineral matter through
18 earthworm activity (Brêthes et al., 1995; Ponge, 1999). These soils contain very different collembolan
19 communities (Ponge, 1993; Chagnon et al., 2000). Lead acetate was chosen as the metal salt in order
20 to avoid possible toxic effects of the anion. Given the rapid disappearance of acetate in a biologically
21 active soil (Verschueren, 2001), most lead becomes rapidly complexed by soil organic matter (Sarret
22 et al., 1997; Balabane et al., 1999).

23
24 Topsoil horizons, with their complete original fauna, were collected in May 2000. The Eumull
25 material (pH 7.7) was collected in a rendzina soil in the park adjacent to the laboratory (Brunoy, 20km
26 south of Paris) under oak (*Quercus robur* L.) and hornbeam (*Carpinus betulus* L.), with a ground flora
27 of ivy (*Hedera helix* L.) and dog's mercury (*Mercurialis perennis* L.). The sparse litter horizon was
28 discarded, together with aerial parts of ground vegetation, and the top 10cm of the A horizon were
29 collected over a square meter area. The Dysmoder material (pH 4.3) was collected over the same
30 area in a pine stand (*Pinus sylvestris* L.) located in the Senart forest near the laboratory. The ground

1 cover was mainly bramble (*Rubus fruticosus* L.) and bracken [*Pteridium aquilinum* (L.) Kuhn]. The
 2 superficial litter (OL horizon) was discarded, and only the OF horizon (fragmented litter) and the thick
 3 OH horizon (humified litter, 10cm thick) were collected. In both cases the soil was thoroughly crumbled
 4 by hand, most woody subterranean parts of vegetation, earthworms and stones being discarded.

5

6 Experiments were carried out in polystyrene boxes (175x115mm, 65mm deep) which were
 7 divided in two compartments by a 2mm thick millboard (Isorel®) division, pierced with 4mm diameter
 8 holes at a rate of 30 holes per wall. The division allowed passage by fauna but prevented physical
 9 contact between the two soils. Eumull was treated with lead acetate/deionized water solutions at three
 10 dilution rates, giving rise to three concentrations in the soil at 50, 6,000 and 60,000 ppm, referred to as
 11 low, medium and high concentration, respectively. These concentrations were chosen on the basis of
 12 preliminary assays. Control boxes (Eumull or Dysmoder) received deionized water only. Different
 13 combinations were established with five replicates each:

14

15	E0/E0	Eumull versus Eumull, without any addition of lead in the two compartments
16	E1/E1	Eumull versus Eumull, with lead at 50 ppm in the two compartments
17	E2/E2	Eumull versus Eumull, with lead at 6,000 ppm in the two compartments
18	E3/E3	Eumull versus Eumull, with lead at 60,000 ppm in the two compartments
19	E0/E1	Eumull versus Eumull, with lead at 50 ppm in only one compartment (E0/E1 =
20		unpolluted Eumull compartment, E1/E0 = polluted Eumull compartment)
21	E0/E2	Eumull versus Eumull, with lead at 6,000 ppm in only one compartment (E0/E2 =
22		unpolluted Eumull compartment, E2/E0 = polluted Eumull compartment)
23	E0/E3	Eumull versus Eumull, with lead at 60,000 ppm in only one compartment (E0/E3 =
24		unpolluted Eumull compartment, E3/E0 = polluted Eumull compartment)
25	E0/D	Eumull versus Dysmoder, without any addition of lead acetate in the Eumull (E0/D =
26		Eumull compartment, D/E0 = Dysmoder compartment)
27	E1/D	Eumull versus Dysmoder, with lead at 50 ppm in the Eumull (E1/D = Eumull
28		compartment, D/E1 = Dysmoder compartment)
29	E2/D	Eumull versus Dysmoder, with lead at 6,000 ppm in the Eumull (E2/D = Eumull
30		compartment, D/E2 = Dysmoder compartment)

- 1 E3/D Eumull versus Dysmoder, with lead at 60,000 ppm in the Eumull (E3/D = Eumull
2 compartment, D/E3 = Dysmoder compartment)
3 D/D Dysmoder versus Dysmoder
4

5 The experimental boxes were incubated in the laboratory at 15°C in darkness during two
6 weeks. At the end of the incubation period arthropods were extracted by the dry-funnel method. The
7 identification of Collembola was done to the species level under a light microscope at 400x
8 magnification. After extraction of the microarthropods, the water pH of the dried soil was measured
9 electrometrically in a 1:3 (w:w) soil:water slurry.
10

11 Data (pH values, abundance of species or groups of species, number of species) were
12 analysed by one-way ANOVA, using boxes as replicates. For treatments where both compartments
13 were filled with the same soil (E0/E0, E1/E1, E2/E2, E3/E3, D/D), average values between paired
14 compartments were used for comparisons with other treatments. When necessary data were log-
15 transformed in order to ensure additivity of variances. Comparisons among means following ANOVA
16 were achieved a posteriori by the SNK procedure (Glantz, 1997). When homogeneity of variances
17 could not be achieved through log-transformation of the data, non-parametric Mann-Whitney rank
18 tests were performed in place of ANOVA (Glantz, 1997).
19

20 **3. Results**

21 *3.1. Comparison between Eumull and Dysmoder populations*

22 A total of 37 collembolan species were found over the whole set of samples (Table 1). Among
23 these, 17 most frequent species were selected for further analyses (Table 2).
24

25 Total abundance of Collembola and species composition of Eumull and Dysmoder soils used
26 for the experiment differed to a great extent, as well as pH values (Table 2). At the end of the
27 experiment Collembola were twice more abundant in Dysmoder compared to Eumull (Table 2, Fig. 1,
28 compare E0/E0 to D/D), and the number of species was significantly higher (Fig. 2). Some species
29
30

1 were common to both soils, viz. *Dicyrtoma fusca*, *Folsomia manolachei*, *Friesea truncata*, *Isotomiella*
2 *minor*, *Lepidocyrtus lanuginosus*, *Megalothorax minimus*, *Paratullbergia callipygos* and *Sphaeridia*
3 *pumilis*. These species were called ubiquitous species. Nevertheless, among this group, some species
4 were much more abundant in one or other of the soils. For instance *Folsomia manolachei* was 6 times
5 more abundant in Dysmoder than in Eumull (Fig. 3), while *Isotomiella minor* was twice more abundant
6 in Eumull than in Dysmoder (Table 1). Among species living only in Eumull, called Eumull species, the
7 most frequent ones were *Heteromurus nitidus*, *Parisotoma notabilis* and *Pseudosinella alba*. The most
8 frequent species living only in Dysmoder, called Dysmoder species, were *Micranurida pygmaea*,
9 *Proisotoma minima*, *Pseudosinella mauii*, *Sminthurinus signatus*, *Willemia anophthalma* and *Xenylla*
10 *tullbergi*. It must be noticed that these features describe the two soil samples at the end of the
11 experimental period. They refer only to one square meter (the area over which the soil was sampled)
12 in each site and they include possible changes due to experimental conditions, thus they do not
13 picture the original population.

14

15 The efficiency of the perforated wall for allowing animals to pass from a compartment to
16 another can be assessed by observing that *Parisotoma notabilis*, absent from the Dysmoder soil used
17 for the experiment, was retrieved in this soil when paired to Eumull at densities equal or even higher
18 than those of Eumull (Fig. 4). Conversely, all Dysmoder species were retrieved in the Eumull
19 compartment when these soils were paired (Fig. 2).

20

21 3.2. Experiments on Eumull alone

22

23 Eumull treatments where both compartments were given the same concentration of lead
24 (E0/E0, E1/E1, E2/E2 and E3/E3) allowed us to quantify, in our experimental conditions, the short-
25 term impact of lead contamination on collembolan communities. Although soil pH increased
26 significantly at the highest treatment, the increase was small (from 7.7 to 7.8), thus no departure from
27 neutrality was observed in polluted Eumull (Table 3). The total abundance of Collembola, as well as
28 the number of species, decreased only at high concentration (Table 3, Figs. 1 and 2). The general
29 trend of decreased abundance at high concentration only was apparent for the most abundant
30 species, *Isotomiella minor*, which comprised 57% of the collembolan population in unpolluted Eumull.

1 *Lepidocyrtus lanuginosus* and *Heteromurus nitidus* exhibited also a decrease in abundance at high
2 concentration only. Nevertheless some species did not follow this general trend. *Pseudosinella alba*
3 and *Sphaeridia pumilis* decreased significantly in abundance at medium concentration and totally
4 disappeared at high concentration. *Folsomia manolachei* (Fig. 3) decreased progressively and
5 significantly in abundance at all three concentrations but never disappeared totally. It was the most
6 abundant species at the end of the experiment at high concentration. *Parisotoma notabilis* (Fig. 4)
7 decreased only at medium then nearly disappeared at high concentration. *Paratullbergia callipygos*
8 and *Friesea truncata* displayed an increase from nil to medium concentration (significant in *P.*
9 *callipygos*, not significant in *F. truncata*), then disappeared totally at high concentration.

10

11 Treatments with Eumull in both compartments but with only one of them polluted with lead
12 allowed to test the hypothesis of a possible refuge effect of unpolluted zones within a polluted site.
13 Increasing the lead concentration in the compartment adjacent to unpolluted Eumull did not affect
14 abundance and species richness of collembolan communities in the unpolluted compartment (Table 4,
15 Figs. 1 and 2). Effects observed in the polluted compartment were similar to those observed when
16 both compartments were equally polluted, i.e. a decrease in abundance of species richness at high
17 concentration only (Table 5, Figs. 1 and 2). At the species level, *Folsomia manolachei* exhibited a
18 significant decrease in unpolluted Eumull at medium and high concentrations (Table 4, Fig. 3). In the
19 adjacent (polluted) compartment, this species exhibited a strong significant decrease at high
20 concentration only, contrary to the experiment with both compartments equally polluted, where it
21 exhibited a significant decrease as soon as low concentration was applied (Table 3, Fig. 3). No
22 change in pH was observed in the different treatments (Tables 4 and 5).

23

24 3.3. Experiments on Eumull paired with Dysmoder

25

26 Treatments with Eumull combined with Dysmoder allowed us to test the hypothesis that
27 collembolan species living in acid soils were able to colonize neutral soils polluted with heavy metals.
28 The collembolan community of Eumull exhibited some significant changes when freely communicating
29 with Dysmoder (Table 6, Figs. 1 and 2). In the absence of lead, a significant decrease was observed
30 in the abundance of ubiquitous species, although no significant change occurred in the total

1 abundance nor in the total number of species (compare E0/E0 with E0/D). At the species level, only
2 *Pseudosinella alba* was affected by the presence of Dysmoder, its abundance decreasing by a factor
3 of ten (Table 1). Other species did not react significantly.

4
5 After lead application, the total population of Eumull increased significantly at low and medium
6 concentrations (compare E1/D and E2/D to E0/D). This increase, not observed when Eumull was
7 alone (Table 3, Fig. 1), was due to a strong increase in the abundance of ubiquitous species. At high
8 concentration, the total abundance of Collembola decreased, but was six times higher than when
9 Eumull was alone (Tables 3 and 6, Fig. 1). The improvement due to the presence of Dysmoder was
10 even more pronounced if we take into account the number of species. In the presence of Dysmoder,
11 no decrease in the number of species occurred at the high concentration of lead (Table 6, Fig. 2),
12 although this number was divided by six when Eumull was used alone. The decrease in the
13 abundance of *Parisotoma notabilis* observed at medium and high concentration when Eumull was
14 used alone (Table 3) was smoothed, although still significant, in the presence of Dysmoder (Table 6,
15 Fig. 4). The same phenomenon was observed, but in a more pronounced way, in *Folsomia*
16 *manolachei*, an ubiquitous species. At medium concentration the abundance of this species in Eumull
17 more than doubled under the influence of Dysmoder (Fig. 3, Tables 3 and 6). At high concentration its
18 abundance increased sixfold compared to Eumull alone. The abundance of *Isotomiella minor* nearly
19 doubled after lead application at low concentration (Table 6), then significantly decreased at high
20 concentration but its abundance was three times that observed in the absence of Dysmoder (Table 3).
21 The *Lepidocyrtus lanuginosus* population collapsed at high concentration of lead in the absence of
22 Dysmoder, and its abundance remained unchanged below this threshold (Table 3). In the presence of
23 Dysmoder *L. lanuginosus* exhibited a significant increase in abundance when lead concentration
24 increased, reaching a maximum at medium concentration, then decreased at high concentration
25 (Table 6) but remained 38 times more abundant than in the absence of Dysmoder (Table 3). A small
26 although significant increase (around a tenth unit) in soil pH was observed at high concentration only
27 (Table 6), of the same order as when Eumull was alone (Table 3), and the presence of Dysmoder in a
28 paired compartment did not influence the pH of Eumull.

29

1 In the absence of lead a few animals belonging to the Dysmoder group of species
2 (*Micranurida pygmaea*, *Pseudosinella mauli*, *Sminthurinus signatus*, *Willemia anophthalma*, *Xenylla*
3 *tullbergi*) were found in the Eumull compartment, and their number increased with lead concentration
4 (Table 6, Fig. 1). Nevertheless this trend was not significant, due to strong departures from a box to
5 another (see standard error values on Table 6).

6
7 The Dysmoder compartment was affected by the presence of the Eumull compartment. In the
8 absence of lead in the Eumull compartment, the number of ubiquitous species decreased significantly
9 in adjacent Dysmoder, as well as the density of the Dysmoder species *Willemia anophthalma*, and the
10 pH increased slightly but significantly (Table 7, Figs. 1 and 2). When lead was applied to Eumull, the
11 number and the abundance of Eumull species increased with lead concentration in the Dysmoder
12 compartment, their abundance reaching a level nearly twice that of unpolluted Eumull (Table 6). This
13 was mostly due to *Parisotoma notabilis*, the abundance of which at medium and high concentration of
14 lead reached in Dysmoder a level 2.8 and 2.5 times that of original Eumull (Fig. 4, Table 7). Other
15 species increased their abundance in Dysmoder when lead was applied to Eumull, as for instance the
16 ubiquitous *Isotomiella minor*, the abundance of which trebled when lead was at medium concentration,
17 and the ubiquitous *Lepidocyrtus lanuginosus*, the abundance of which near trebled at high
18 concentration (Table 7). The pH of Dysmoder increased with lead concentration (Table 7).

19 20 **4. Discussion**

21
22 Despite the absence of significant colonization of the polluted neutral soil by strongly
23 acidophilic species such as *Willemia anophthalma*, which was yet well-represented in the acid soil
24 used for the experiment, migration movements were clearly demonstrated between the polluted mull
25 and the moder. In the presence of lead, moder acted as a refuge for the isotomid *Parisotoma notabilis*,
26 coming from the polluted mull. This species is known to live both in acid and neutro-acidocline soils
27 (Ponge 1993), although it proved to be highly sensitive to experimental acidification with sulphuric acid
28 (Bååth et al., 1980; Hågvar and Kjøndal, 1981; Hågvar, 1984), preferred alkalinity in pH-preference
29 tests (Van Straalen and Verhoef, 1997) and was favoured by ash or lime application (Abrahamsen et
30 al., 1980; Hågvar and Abrahamsen, 1980; Vilkkamaa and Huhta, 1986). It should be noticed that

1 *P. notabilis*, also known for its sensitivity to heavy metals (Tranvik et al., 1993; Bruus Pedersen et al.,
2 1999), was strongly depressed in our experiments at medium concentration of lead (6,000 ppm).
3 Contrary to moder, unpolluted mull did not act as a refuge for animals escaping contamination by
4 heavy metals. Several reasons could explain this unexpected phenomenon, such as too many
5 predators or a lack of food resources and habitats, but our experiment was not designed to explore
6 these factors.

7
8 The colonization of the polluted mull by the isotomid *Folsomia manolachei* coming from the
9 moder was clear. This species was present in both humus forms, but it was much more abundant in
10 the moder, which acted as a source for the polluted mull. At medium lead concentration and only in
11 the presence of moder the abundance of this species increased in polluted mull compartments to a
12 level so high that it cannot be explained by another cause than a colonization by specimens coming
13 from the moder. Although the appearance of typical acidophilic species in the polluted mull was not
14 significant, their presence in lead-polluted mull compartments, even at high concentration (60,000
15 ppm), indicated that they were able to colonize soils polluted by heavy metals, but were poorly
16 attracted to them. One possible reason for the lack of a more intense colonization of the polluted mull
17 by the mycetophagous poduromorph *Willemia anophthalma* (Ponge, 1991; Ponge, 2000b) could be
18 the scarcity of fungi in the mull at neutral pH used for the experiments, and a subsequent lack of
19 attraction by fungal odour (Bengtsson et al., 1988; Sadaka-Laulan et al., 1998), while fungi were
20 abundant in the acidic moder, as ascertained by visual inspection. Another reason could be the lack of
21 motility of this species, which has particularly short legs compared to that of entomobryomorph
22 (entomobryid and isotomid) species. Isotomid species such as *Folsomia manolachei* and *Parisotoma*
23 *notabilis* have a less specialized feeding habit, their diet being mainly composed of humified organic
24 matter (Ponge, 1991; Ponge, 2000b). They are also much more motile than poduromorphs, due to
25 possessing longer legs and functional furcula (Hopkin, 1997), and these two species are indifferent to
26 soil pH (Ponge, 1993). These attributes make them better able to move to other places when
27 environmental conditions become unfavourable or when more space or food are available somewhere
28 else.

29

1 If we compare populations of *Folsomia manolachei* from the acid and neutral soils used for our
2 experiments, it appears that mull specimens were more sensitive to lead application than moder ones.
3 The existence of populations tolerant or intolerant to heavy metals in *Folsomia manolachei* could be
4 compared to the case of *Orchesella cincta* where heritability of tolerance to heavy metals has been
5 demonstrated (Posthuma, 1990; Posthuma et al., 1992; Posthuma et al., 1993). In our experiments
6 animals attracted to a soil contaminated by heavy metals did not come from a polluted site but from an
7 acidic coniferous forest soil. The importance of tolerant strains of *Folsomia manolachei* for the
8 possible reclamation of polluted sites should be stressed, given its wide occurrence in all types of soils
9 (Rusek, 1989; Mateos and Selga, 1991; Ponge, 1993). As in our experiments with lead acetate, this
10 species recolonized soil cores polluted with copper sulphate where it exhibited higher densities than in
11 the unpolluted control (Filser and Hölischer, 1997), and was attracted to copper sulphate solutions in
12 choice experiments (Filser et al., 2000). The same phenomenon was observed with soil polluted by
13 copper-containing fungicides (Filser et al., 2000). In a naturally lead-contaminated site Hågvar and
14 Abrahamsen (1990) classified *Folsomia quadrioculata* (a nearby species) as tolerant to lead, its
15 abundance being not affected at concentrations as high as 5,000 ppm.

16
17 Changes in pH cannot explain the above mentioned movements of collembolan populations
18 from a humus type to another. Although soil pH was significantly affected by the application of lead
19 acetate, the rise observed at the end of the experiment in the neutral soil was very weak (at most 0.1
20 pH unit), thus it was not high enough to force some species to escape from polluted compartments. A
21 possible attraction of acidophilic species by a decrease of pH in the mull soil can be disregarded for
22 the same reason. We cannot rule out possible toxic (or attractive) effects of the acetate moiety, but the
23 absence of acidification of the soil at the end of the experiment led us to conclude that such effects, if
24 any, were probably temporary. Nevertheless, acetate toxicity could explain at least partly, together
25 with an increase in osmotic pressure of the soil solution (Heungens and Van Daele, 1984), the
26 collapse in collembolan abundance and diversity we observed at high concentration. Lead, acetate
27 and osmotic pressure acted probably both directly and indirectly on soil collembolan communities.
28 Indirect effects could be suspected to occur through changes in predatory pressure (Grelle et al.,
29 2000) and quantity and quality of the microflora (Tranvik and Eijsackers, 1989; Hopkin, 1994) which
30 may have occurred during the two weeks of the experiment.

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1 **6. Figure captions**

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3 **Fig. 1** Abundance of Collembola (mean and standard error of five replicates) in experimental
4 compartments (1 dm³ each). E = Eumull. D = Dysmoder. E0 = Eumull without lead. E1 =
5 Eumull with 50 ppm lead. E2 = Eumull with 6,000 ppm lead. E3 = Eumull with 60,000 ppm
6 lead. Opposite bars relate to adjacent compartments

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8 **Fig. 2** Number of species of Collembola (mean and standard error of five replicates) in experimental
9 compartments (1 dm³ each). E = Eumull. D = Dysmoder. E0 = Eumull without lead. E1 =
10 Eumull with 50 ppm lead. E2 = Eumull with 6,000 ppm lead. E3 = Eumull with 60,000 ppm
11 lead. Opposite bars relate to adjacent compartments

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13 **Fig. 3** Abundance of *Folsomia manolachei* (mean and standard error of five replicates) in experimental
14 compartments (1 dm³ each). E = Eumull. D = Dysmoder. E0 = Eumull without lead. E1 =
15 Eumull with 50 ppm lead. E2 = Eumull with 6,000 ppm lead. E3 = Eumull with 60,000 ppm
16 lead. Opposite bars relate to adjacent compartments

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18 **Fig. 4** Abundance of *Parisetoma notabilis* (mean and standard error of five replicates) in experimental
19 compartments (1 dm³ each). E = Eumull. D = Dysmoder. E0 = Eumull without lead. E1 =
20 Eumull with 50 ppm lead. E2 = Eumull with 6,000 ppm lead. E3 = Eumull with 60,000 ppm
21 lead. Opposite bars relate to adjacent compartments

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Table 1. List of collembolan species found in the experiment, 0: absence, 1: presence

	Eumull	Dysmoder	Ubiquitous	Dubious
<i>Allacma fusca</i> (Linné, 1758)	1	0	0	0
<i>Arrhopalites caecus</i> (Tullberg, 1871)	1	0	0	0
<i>Arrhopalites sericus</i> Gisin, 1947	0	1	0	0
<i>Dicyrtoma fusca</i> (Lucas, 1842)	0	0	1	0
<i>Dicyrtomina minuta</i> (Fabricius, 1783)	1	0	0	0
<i>Folsomia manolachei</i> Bagnall 1939	0	0	1	0
<i>Friesea truncata</i> Cassagnau, 1958	0	0	1	0
<i>Heteromurus nitidus</i> (Templeton, 1835)	1	0	0	0
<i>Isotomiella minor</i> (Schäffer, 1896)	0	0	1	0
<i>Isotomurus palustris</i> (Müller, 1776)	1	0	0	0
<i>Kalaphorura burmeisteri</i> (Lubbock, 1873)	1	0	0	0
<i>Lepidocyrtus lanuginosus</i> (Gmelin, 1788)	0	0	1	0
<i>Megalothorax minimus</i> (Willem, 1900)	0	0	1	0
<i>Mesaphorura</i> gr <i>krausbaueri</i> (Börner, 1900)	0	0	1	0
<i>Mesaphorura</i> gr <i>sylvatica</i> (Rusek, 1971)	1	0	0	0
<i>Mesaphorura</i> gr <i>yosii</i> (Rusek, 1967)	0	0	1	0
<i>Micranurida pygmaea</i> (Börner, 1901)	0	1	0	0
<i>Monobella grassei</i> (Denis, 1923)	1	0	0	0
<i>Neanura muscorum</i> (Templeton, 1835)	1	0	0	0
<i>Onychiurus pseudogranulosus</i> Gisin, 1951	1	0	0	0
<i>Orchesella cincta</i> (Linné, 1758)	1	0	0	0
<i>Paratullbergia callipygos</i> (Börner, 1902)	0	0	1	0
<i>Parisotoma notabilis</i> (Schäffer, 1896)	1	0	0	0
<i>Proisotoma minima</i> (Absolon, 1901)	0	1	0	0
<i>Pseudachorutes parvulus</i> Böener, 1901	1	0	0	0
<i>Pseudosinella alba</i> (Packard, 1873)	1	0	0	0
<i>Pseudosinella maui</i> Stomp, 1972	0	1	0	0
<i>Sminthurinus aureus</i> (Lubbock, 1862)	1	0	0	0
<i>Sminthurinus signatus</i> (Krausbauer, 1898)	0	1	0	0
<i>Sphaeridia pumilis</i> (Krausbauer, 1898)	0	0	1	0
<i>Stenaphorurella denisi</i> (Bagnall, 1935)	1	0	0	0
<i>Tomocerus minor</i> (Lubbock, 1862)	0	0	1	0
<i>Willemia anophthalma</i> Börner, 1901	0	1	0	0
<i>Willemia buddenbrocki</i> Hüther, 1959	1	0	0	0
<i>Xenylla grisea</i> Axelson, 1900	1	0	0	0
<i>Xenylla tullbergi</i> Börner, 1903	0	1	0	0
<i>Xenyllodes armatus</i> (Axelson, 1903)	0	0	0	1

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Table 2. Mean abundance (\pm S.E.) of most frequent collembolan species and groups of species and water pH in Eumull and Dysmoder at the end of the experiment. Means followed by a common letter indicate groups which do not differ significantly. E = Eumull species, D = Dysmoder species, U = ubiquitous species

	Eumull	Dysmoder
U <i>Dicyrtoma fusca</i>	1.8 \pm 0.6	0.6 \pm 0.2
U <i>Folsomia manolachei</i>	18.5\pm1.3b	113.4\pm18.6a
U <i>Friesea truncata</i>	0.5 \pm 0.3	0.6 \pm 0.1
E <i>Heteromurus nitidus</i>	1.3\pm0.3a	0b
U <i>Isotomiella minor</i>	51.3\pm3.8a	25.7\pm3.4b
U <i>Lepidocyrtus lanuginosus</i>	1.6\pm0.3b	4.8\pm0.6a
U <i>Megalothorax minimus</i>	0.5\pm0.5b	8.9\pm0.6a
D <i>Micranurida pygmaea</i>	0b	1.9\pm0.6a
U <i>Paratullbergia callipygos</i>	0.6\pm0.3b	3.1\pm0.5a
E <i>Parisotoma notabilis</i>	8.7\pm1.3a	0b
D <i>Proisotoma minima</i>	0b	0.4\pm0.1a
E <i>Pseudosinella alba</i>	2.0\pm0.4a	0b
D <i>Pseudosinella mauii</i>	0b	0.7\pm0.3a
D <i>Sminthurinus signatus</i>	0b	1.4\pm0.3a
U <i>Sphaeridia pumilis</i>	2.1 \pm 0.7	2.9 \pm 0.5
D <i>Willemia anophthalma</i>	0b	28.6\pm3.0a
D <i>Xenylla tullbergi</i>	0b	0.3\pm0.1a
Total abundance	90.4\pm5.5b	194.6\pm17.2a
Abundance of Eumull species	13.3\pm1.6a	0b
Abundance of Dysmoder spec	0b	33.3\pm2.5a
Abundance of ubiquitous spec	77.1\pm4.4b	161.3\pm16.4a
Total number of species	8.9\pm0.4b	12.0\pm0.3a
Number of Eumull species	4.8\pm0.5a	0b
Number of Dysmoder species	0b	5.2\pm0.4a
Number of ubiquitous species	6.4\pm0.7b	9.6\pm0.5a
Water pH	7.66\pm0.03a	4.29\pm0.01b

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Table 3. Mean abundance (\pm S.E.) of most frequent collembolan species and groups of species and water pH in Eumull after application of lead acetate in the two compartments of experimental boxes, compared to control boxes without addition of lead. Means followed by a common letter indicate groups which do not differ significantly. E = Eumull species, U = ubiquitous species. E0/E0 = No Pb, E1/E1 = Pb at 50 ppm, E2/E2 = Pb at 6,000 ppm, E3/E3 = Pb at 60,000 ppm

	E0/E0	E1/E1	E2/E2	E3/E3
U <i>Dicyrtoma fusca</i>	1.8 \pm 0.6	1.2 \pm 0.3	2.0 \pm 0.7	0.5 \pm 0.2
U <i>Folsomia manolachei</i>	18.5\pm1.3a	13.3\pm1.8b	8.1\pm1.0c	0.9\pm0.7d
U <i>Friesea truncata</i>	0.5\pm0.3ab	1.5\pm0.5a	1.6\pm0.4a	0b
E <i>Heteromurus nitidus</i>	1.3\pm0.3a	0.6\pm0.2ab	1.0\pm0.2ab	0.3\pm0.2b
U <i>Isotomiella minor</i>	51.3\pm3.8a	53.7\pm10.6a	46.8\pm7.9a	0.7\pm0.7b
U <i>Lepidocyrtus lanuginosus</i>	1.6\pm0.3a	1.3\pm0.4a	1.2\pm0.3a	0.2\pm0.1b
U <i>Megalothorax minimus</i>	0.5 \pm 0.5	0.1 \pm 0.1	0	0
U <i>Paratullbergia callipygos</i>	0.6\pm0.3bc	1.0\pm0.2b	1.9\pm0.4a	0c
E <i>Parisotoma notabilis</i>	8.7\pm1.3a	5.8\pm0.3a	2.3\pm0.3b	0.2\pm0.2c
E <i>Pseudosinella alba</i>	2.0\pm0.4a	1.3\pm0.3ab	0.6\pm0.3bc	0c
U <i>Sphaeridia pumilis</i>	2.1\pm0.7a	1.3\pm0.5ab	0.3\pm0.3b	0b
Total abundance	90.4\pm5.5a	86.3\pm14.5a	68.3\pm9.6a	2.8\pm1.5b
Abundance of Eumull species	13.3\pm1.6a	12.7\pm1.3a	6.4\pm0.7b	0.5\pm0.2c
Abundance of ubiquitous spec	77.1\pm4.4a	73.6\pm13.7a	61.9\pm9.0a	2.3\pm1.3b
Total number of species	8.9\pm0.4a	10.3\pm0.9a	9.1\pm0.3a	1.5\pm0.5b
Number of Eumull species	4.8\pm0.5a	6.4\pm0.7a	5.8\pm1.0a	0.6\pm0.2b
Number of ubiquitous species	6.4\pm0.7a	6.8\pm0.7a	6.0\pm0.0a	2.0\pm0.6b
Water pH	7.66\pm0.03b	7.63\pm0.03b	7.65\pm0.01b	7.8\pm0.02a

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Table 4. Mean abundance (\pm S.E.) of most frequent collembolan species and groups of species and water pH in unpolluted Eumull after application of lead acetate in the adjacent Eumull compartment, compared to control boxes without addition of lead. Means followed by a common letter indicate groups which do not differ significantly. E = Eumull species, U = ubiquitous species. E0/E0 = No Pb, E0/E1 = Pb at 50 ppm, E0/E2 = Pb at 6,000 ppm, E0/E3 = Pb at 60,000 ppm

	E0/E0	E0/E1	E0/E2	E0/E3
U <i>Dicyrtoma fusca</i>	1.8 \pm 0.6	1.4 \pm 0.4	1.8 \pm 0.4	0.8 \pm 0.6
U <i>Folsomia manolachei</i>	18.5\pm1.3a	16.8\pm1.9ab	12.4\pm0.5bc	9.6\pm2.1c
U <i>Friesea truncata</i>	0.5 \pm 0.3	1.0 \pm 0.8	0.8 \pm 0.4	0.8 \pm 0.4
E <i>Heteromurus nitidus</i>	1.3\pm0.3a	0.4\pm0.2b	0.6\pm0.2ab	0b
U <i>Isotomiella minor</i>	51.3 \pm 3.8	59.2 \pm 10.5	51.2 \pm 10.2	33.2 \pm 7.7
U <i>Lepidocyrtus lanuginosus</i>	1.6 \pm 0.3	1.4 \pm 0.5	1.6 \pm 0.4	1.4 \pm 0.7
U <i>Megalothorax minimus</i>	0.5\pm0.5ab	1.0\pm0.3a	0b	0b
U <i>Paratullbergia callipygos</i>	0.6 \pm 0.3	0.4 \pm 0.2	1.6 \pm 0.7	1.6 \pm 0.6
E <i>Parisotoma notabilis</i>	8.7 \pm 1.3	7.8 \pm 0.7	8.8 \pm 2.7	3.8 \pm 0.9
E <i>Pseudosinella alba</i>	2.0 \pm 0.4	1.8 \pm 0.6	1.4 \pm 0.5	0.6 \pm 0.4
U <i>Sphaeridia pumilis</i>	2.1 \pm 0.7	1.4 \pm 0.5	1.6 \pm 0.9	0.8 \pm 0.2
Total abundance	90.4 \pm 5.5	94.0 \pm 13.8	84.6 \pm 8.9	55.2 \pm 8.5
Abundance of Eumull species	13.3 \pm 1.6	11.2 \pm 0.9	13.6 \pm 2.7	6.8 \pm 2.2
Abundance of ubiquitous spec	77.1 \pm 4.4	82.8 \pm 13.1	71.0 \pm 9.7	48.4 \pm 8.6
Total number of species	8.9 \pm 0.4	9.4 \pm 0.9	10.8 \pm 0.7	8.6 \pm 0.9
Number of Eumull species	4.8 \pm 0.5	3.2 \pm 0.5	4.8 \pm 0.6	3.2 \pm 0.9
Number of ubiquitous species	6.4 \pm 0.7	6.2 \pm 0.6	6.0 \pm 0.4	5.4 \pm 0.6
Water pH	7.66 \pm 0.03	7.68 \pm 0.01	7.66 \pm 0.02	7.78 \pm 0.02

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Table 5. Mean abundance (\pm S.E.) of most frequent collembolan species and groups of species and water pH in lead acetate-polluted Eumull adjacent to unpolluted Eumull, compared to control boxes without any addition of lead in both compartments. Means followed by a common letter indicate groups which do not differ significantly. E = Eumull species, U = ubiquitous species. E0/E0 = No Pb, E1/E0 = Pb at 50 ppm, E2/E0 = Pb at 6,000 ppm, E3/E0 = Pb at 60,000 ppm

	E0/E0	E1/E0	E2/E0	E3/E0
U <i>Dicyrtoma fusca</i>	1.8 \pm 0.6	1.4 \pm 0.4	1.6 \pm 0.4	0.8 \pm 0.6
U <i>Folsomia manolachei</i>	18.5\pm1.3a	14.6\pm0.7a	14.8\pm2.0a	1.2\pm0.7b
U <i>Friesea truncata</i>	0.5\pm0.3b	0.8\pm0.5b	2.0\pm0.4a	0.2\pm0.2b
E <i>Heteromurus nitidus</i>	1.3 \pm 0.3	0.6 \pm 0.4	0.6 \pm 0.2	0.2 \pm 0.2
U <i>Isotomiella minor</i>	51.3\pm3.8a	52.6\pm8.4a	50.0\pm13.6a	1.4\pm0.7b
U <i>Lepidocyrtus lanuginosus</i>	1.6 \pm 0.3	1.6 \pm 0.7	2.6 \pm 1.2	1.8 \pm 0.7
U <i>Megalothorax minimus</i>	0.5 \pm 0.5	0.8 \pm 0.5	0.4 \pm 0.4	0
U <i>Paratullbergia callipygos</i>	0.6 \pm 0.3	0.8 \pm 0.4	0.8 \pm 0.4	0
E <i>Parisotoma notabilis</i>	8.7\pm1.3a	6.0\pm0.6b	5.2\pm1.0b	0.4\pm0.4c
E <i>Pseudosinella alba</i>	2.0\pm0.4a	1.6\pm0.4ab	1.0\pm0.5ab	0.2\pm0.2b
U <i>Sphaeridia pumilis</i>	2.1 \pm 0.7	1.6 \pm 0.9	1.4 \pm 0.7	0.4 \pm 0.2
Total abundance	90.4\pm5.5a	84.0\pm9.7a	85.8\pm15.2a	7.8\pm2.0b
Abundance of Eumull species	13.3\pm1.6a	9.6\pm1.0a	12.2\pm2.6a	2.0\pm0.7b
Abundance of ubiquitous spec	77.1\pm4.4a	74.4\pm9.1a	73.6\pm14.0a	5.8\pm2.0b
Total number of species	8.9\pm0.4a	9.0\pm0.7a	10.8\pm1.0a	4.8\pm0.7b
Number of Eumull species	4.8\pm0.5a	3.4\pm0.7ab	4.6\pm0.9a	1.6\pm0.5b
Number of ubiquitous species	6.4\pm0.7a	5.8\pm0.4a	6.2\pm0.7a	3.0\pm0.8b
Water pH	7.66 \pm 0.03	7.67 \pm 0.01	7.73 \pm 0.04	7.73 \pm 0.05

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Table 6. Mean abundance (\pm S.E.) of most frequent collembolan species and groups of species and water pH in Eumull adjacent to Dysmoder, at different levels of lead application in Eumull, compared to control boxes with unpolluted Eumull in both compartments. Means followed by a common letter indicate groups which do not differ significantly. E = Eumull species, D = Dysmoder species, U = ubiquitous species. E0/E0 and E0/D = No Pb, E1/D = Pb at 50 ppm, E2/D = Pb at 6,000 ppm, E3/D = Pb at 60,000 ppm

	E0/E0	E0/D	E1/D	E2/D	E3/D
U <i>Dicyrtoma fusca</i>	1.8 \pm 0.6	1.6 \pm 0.7	1.4 \pm 0.5	1.0 \pm 0.6	0.8 \pm 0.4
U <i>Folsomia manolachei</i>	18.5\pm1.3a	12.4\pm1.5a	12.2\pm1.7a	18.8\pm3.9a	5.6\pm0.6b
U <i>Friesea truncata</i>	0.5\pm0.3ab	0.4\pm0.2ab	1.4\pm0.5ab	2.0\pm0.7a	0b
E <i>Heteromurus nitidus</i>	1.3 \pm 0.3	0.6 \pm 0.4	0.2 \pm 0.2	0.4 \pm 0.2	0.2 \pm 0.2
U <i>Isotomiella minor</i>	51.3\pm3.8ab	38.4\pm6.4b	69.0\pm10.8a	57.6\pm6.6ab	2.0\pm0.4c
U <i>Lepidocyrtus lanuginosus</i>	1.6\pm0.3b	2.2\pm0.4b	3.2\pm1.0ab	7.6\pm2.3a	3.6\pm0.4a
U <i>Megalothorax minimus</i>	0.5\pm0.5ab	0b	1.2\pm0.4a	0.4\pm0.2ab	0b
D <i>Micranurida pygmaea</i>	0	0	0	0.2 \pm 0.2	0
U <i>Paratullbergia callipygos</i>	0.6\pm0.3ab	2.4\pm1.0a	0.6\pm0.4ab	0.6\pm0.2ab	0b
E <i>Parisotoma notabilis</i>	8.7\pm1.3a	6.2\pm1.6ab	6.2\pm2.2ab	3.0\pm0.8b	1.6\pm0.7b
E <i>Pseudosinella alba</i>	2.0\pm0.4a	0.2\pm0.2b	0.4\pm0.2b	1.2\pm0.4ab	0.2\pm0.2b
D <i>Pseudosinella mauii</i>	0	0.2 \pm 0.2	0.2 \pm 0.2	0	0
D <i>Sminthurinus signatus</i>	0	0.2 \pm 0.2	0	0	0
U <i>Sphaeridia pumilis</i>	2.1 \pm 0.7	1.6 \pm 0.4	0.6 \pm 0.2	0.8 \pm 0.6	0.8 \pm 0.2
D <i>Willemia anophthalma</i>	0	0	0.2 \pm 0.2	0.6 \pm 0.6	1.6 \pm 0.7
D <i>Xenylla tullbergi</i>	0	0	0.2 \pm 0.2	1.6 \pm 1.6	0.2 \pm 0.2
Total abundance	90.4\pm5.5ab	70.0\pm6.3b	99.6\pm11.2a	97.8\pm6.1a	17.4\pm2.6c
Abundance of Eumull species	13.3\pm1.6a	10.4\pm1.1a	9.2\pm3.0a	5.8\pm0.7a	2.4\pm1.0b
Abundance of Dysmoder spec	0	0.4 \pm 0.4	0.6 \pm 0.4	2.4 \pm 1.7	2.0 \pm 0.9
Abundance of ubiquitous spec	77.1\pm4.4a	59.2\pm5.7b	89.8\pm10.8a	89.0\pm6.6a	13.0\pm1.2c
Total number of species	8.9 \pm 0.4	10.8 \pm 1.0	9.8 \pm 0.9	9.6 \pm 1.1	7.2 \pm 1.0
Number of Eumull species	4.8\pm0.5a	4.2\pm0.7a	2.8\pm0.6ab	3.2\pm0.5ab	1.6\pm0.5b
Number of Dysmoder species	0	0.4 \pm 0.4	0.6 \pm 0.4	0.6 \pm 0.4	1.0 \pm 0.5
Number of ubiquitous species	6.4 \pm 0.7	6.2 \pm 0.5	6.4 \pm 0.7	5.8 \pm 0.8	4.6 \pm 0.4
Water pH	7.66\pm0.03b	7.64\pm0.03b	7.61\pm0.01b	7.68\pm0.02b	7.78\pm0.05a

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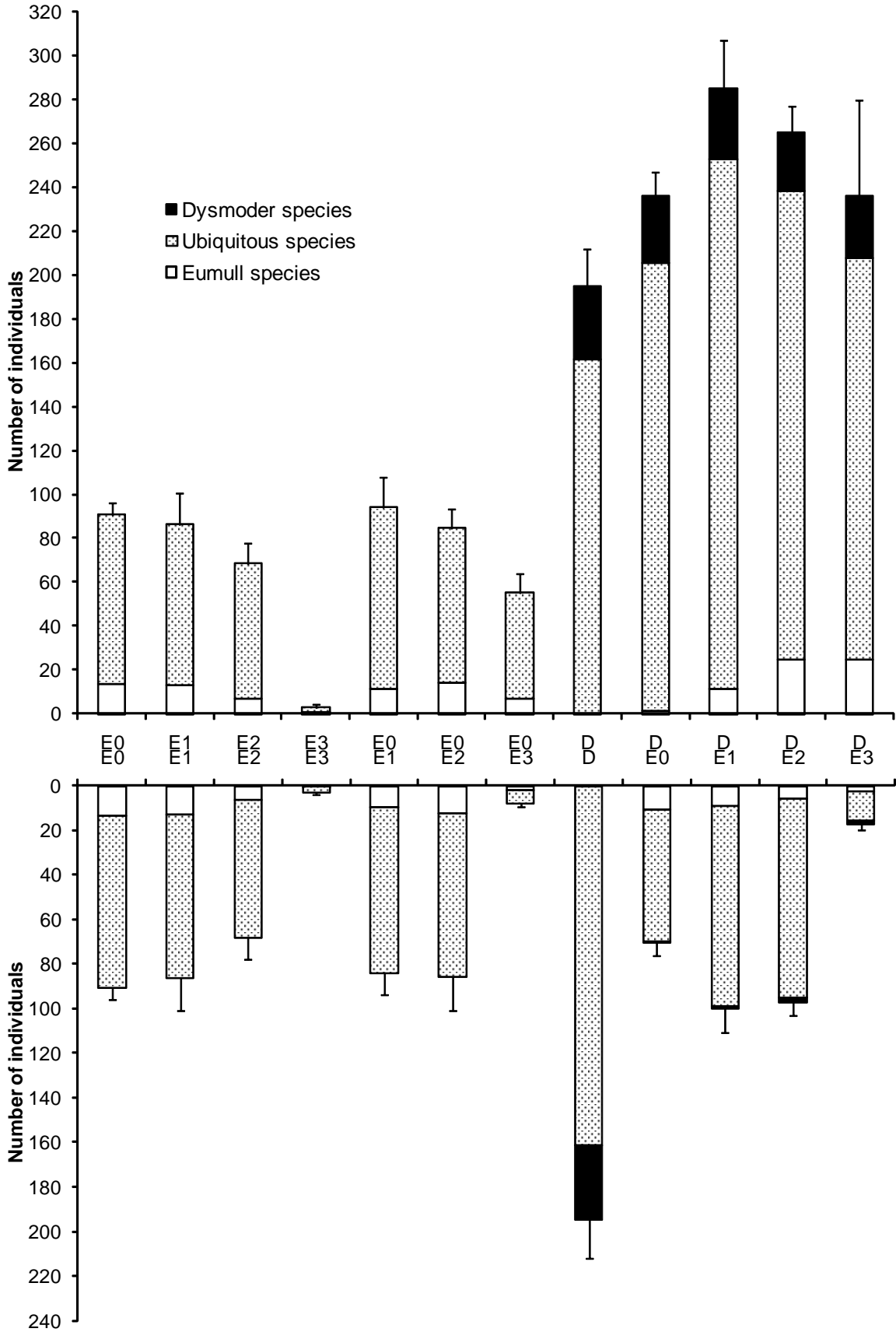
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Table 7. Mean abundance (\pm S.E.) of most frequent Collembolan species and groups of species and water pH in Dysmoder adjacent to Eumull, at different levels of lead application in Eumull, compared to control boxes with Dysmoder in both compartments. Means followed by a common letter indicate groups which do not differ significantly. E = Eumull species, D = Dysmoder species, U = ubiquitous species. E0/E0 and E0/D = No Pb, E1/D = Pb at 50 ppm, E2/D = Pb at 6,000 ppm, E3/D = Pb at 60,000 ppm

	D/D	D/E0	D/E1	D/E2	D/E3
U <i>Dicyrtoma fusca</i>	0.6 \pm 0.2	1.2 \pm 0.5	0	1.2 \pm 0.4	1.0 \pm 0.0
U <i>Folsomia manolachei</i>	113.4\pm18.6ab	152.2\pm12.0ab	182.6\pm23.6a	105.6\pm6.4b	116.6\pm23.2ab
U <i>Friesea truncata</i>	0.6 \pm 0.1	1.2 \pm 0.6	1.4 \pm 0.4	0.4 \pm 0.4	1.8 \pm 0.5
E <i>Heteromurus nitidus</i>	0	0	0	0	0.2 \pm 0.2
U <i>Isotomiella minor</i>	25.7\pm3.4b	29.4\pm3.2b	37.4\pm6.2b	84.6\pm7.7a	43.0\pm11.6b
U <i>Lepidocyrtus lanuginosus</i>	4.8\pm0.6b	5.4\pm1.3b	7.4\pm1.2b	4.4\pm0.9b	13.2\pm1.1a
U <i>Megalothorax minimus</i>	8.9\pm0.6b	8.6\pm0.8b	9.6\pm0.8b	12.4\pm1.4a	4.6\pm0.5c
D <i>Micranurida pygmaea</i>	1.9 \pm 0.6	2.2 \pm 0.5	1.4 \pm 0.7	1.2 \pm 0.8	0.6 \pm 0.4
U <i>Paratullbergia callipygos</i>	3.1\pm0.5a	2.6\pm0.9ab	0.4\pm0.2c	2.2\pm0.7ab	0.8\pm0.2bc
E <i>Parisotoma notabilis</i>	0c	1.0\pm0.4c	10.6\pm3.6b	24.4\pm4.5a	22.0\pm5.1a
D <i>Proisotoma minima</i>	0.4\pm0.1b	3.0\pm1.1ab	6.0\pm0.6a	5.0\pm1.4ab	6.4\pm1.9a
D <i>Pseudosinella maui</i>	0.7 \pm 0.3	0.8 \pm 0.4	0.8 \pm 0.5	0.4 \pm 0.2	0.4 \pm 0.2
D <i>Sminthurinus signatus</i>	1.4 \pm 0.3	1.0 \pm 0.4	1.0 \pm 0.3	0.6 \pm 0.2	1.8 \pm 0.6
U <i>Sphaeridia pumilis</i>	2.9 \pm 0.5	2.6 \pm 1.1	1.6 \pm 0.7	0.6 \pm 0.4	0.8 \pm 0.2
D <i>Willemia anophthalma</i>	28.6\pm3.0a	18.8\pm2.6bc	20.8\pm5.9abc	10.8\pm2.5c	17.4\pm0.9b
D <i>Xenylla tullbergi</i>	0.3 \pm 0.1c	4.6 \pm 2.2	1.6 \pm 1.1	8.4 \pm 5.7	1.8 \pm 1.0
Total abundance	194.6\pm17.2b	235.8\pm11.0ab	284.8\pm22.0a	264.4\pm12.2a	235.8\pm43.6ab
Abundance of Eumull species	0c	1.2\pm0.5c	11.2\pm3.7b	24.6\pm4.6a	24.6\pm6.2a
Abundance of Dysmoder spec	33.3 \pm 2.5	30.4 \pm 4.0	32.2 \pm 7.1	26.4 \pm 6.6	28.6 \pm 3.8
Abundance of ubiquitous spec	161.3 \pm 16.4	204.2 \pm 11.3	241.4 \pm 21.1	213.4 \pm 13.4	182.6 \pm 35.5
Total number of species	12.0 \pm 0.3	13.0 \pm 0.7	12.8 \pm 0.7	12.6 \pm 1.1	15.0 \pm 1.4
Number of Eumull species	0c	0.8\pm0.4bc	1.4\pm0.2b	1.2\pm0.2b	2.4\pm0.5a
Number of Dysmoder species	5.2 \pm 0.4	4.8 \pm 0.5	4.8 \pm 0.5	4.0 \pm 0.4	4.6 \pm 0.6
Number of ubiquitous species	9.6\pm0.5a	7.2\pm0.6b	6.6\pm0.5b	7.4\pm0.7b	8.0\pm0.5ab
Water pH	4.29\pm0.01d	4.33\pm0.02c	4.51\pm0.07abc	4.46\pm0.02b	4.65\pm0.03a

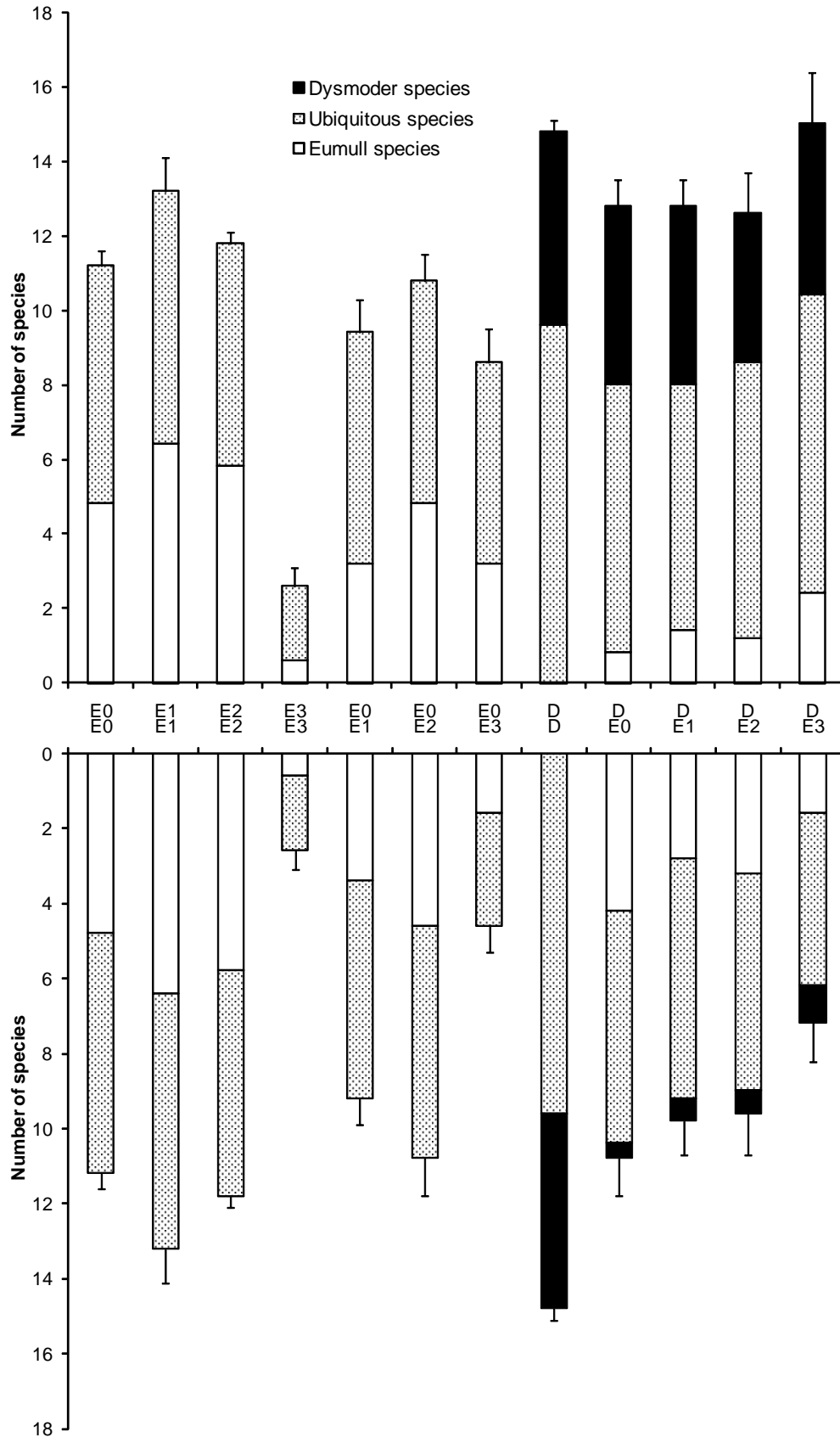
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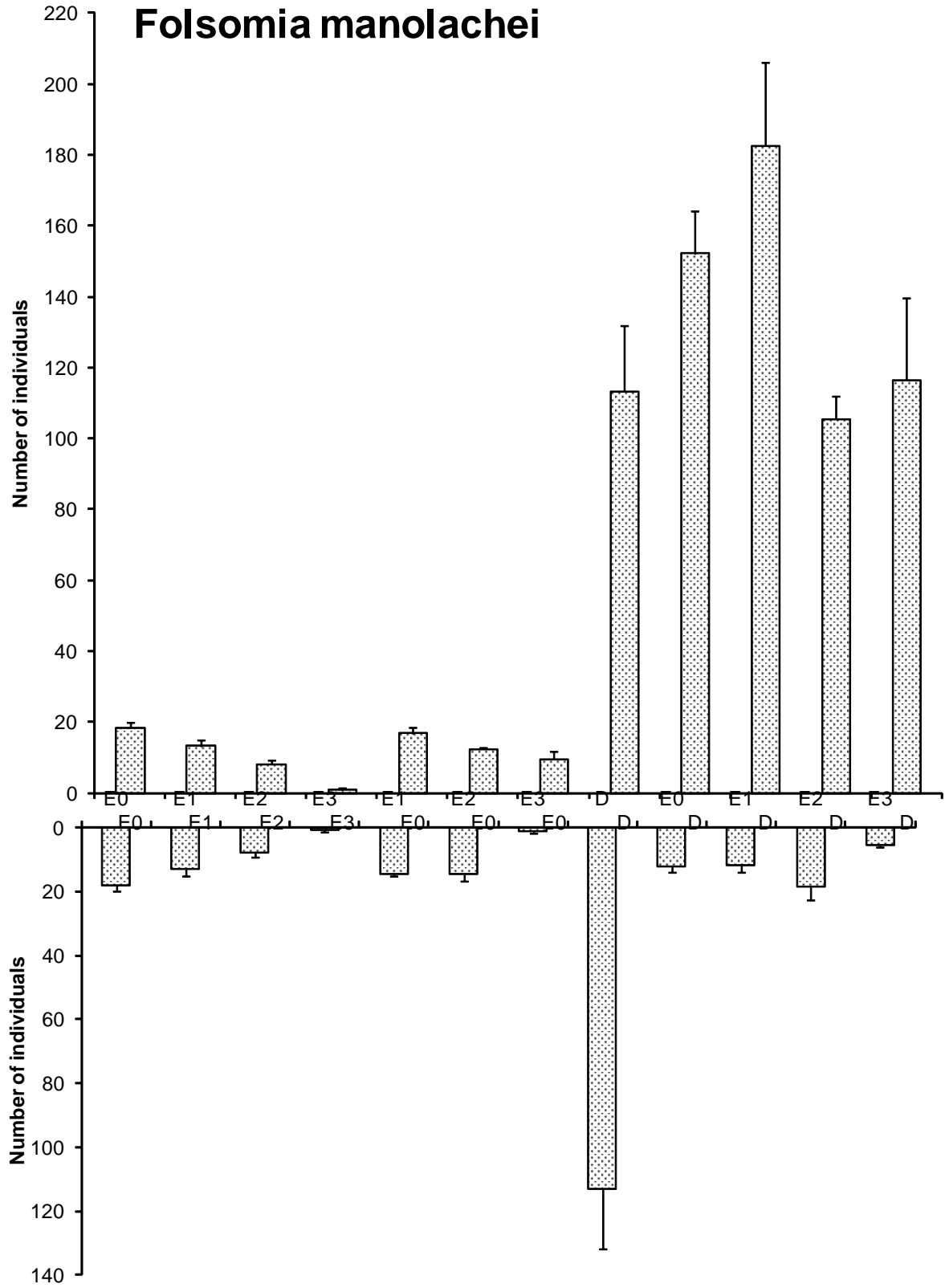
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2 Fig. 1



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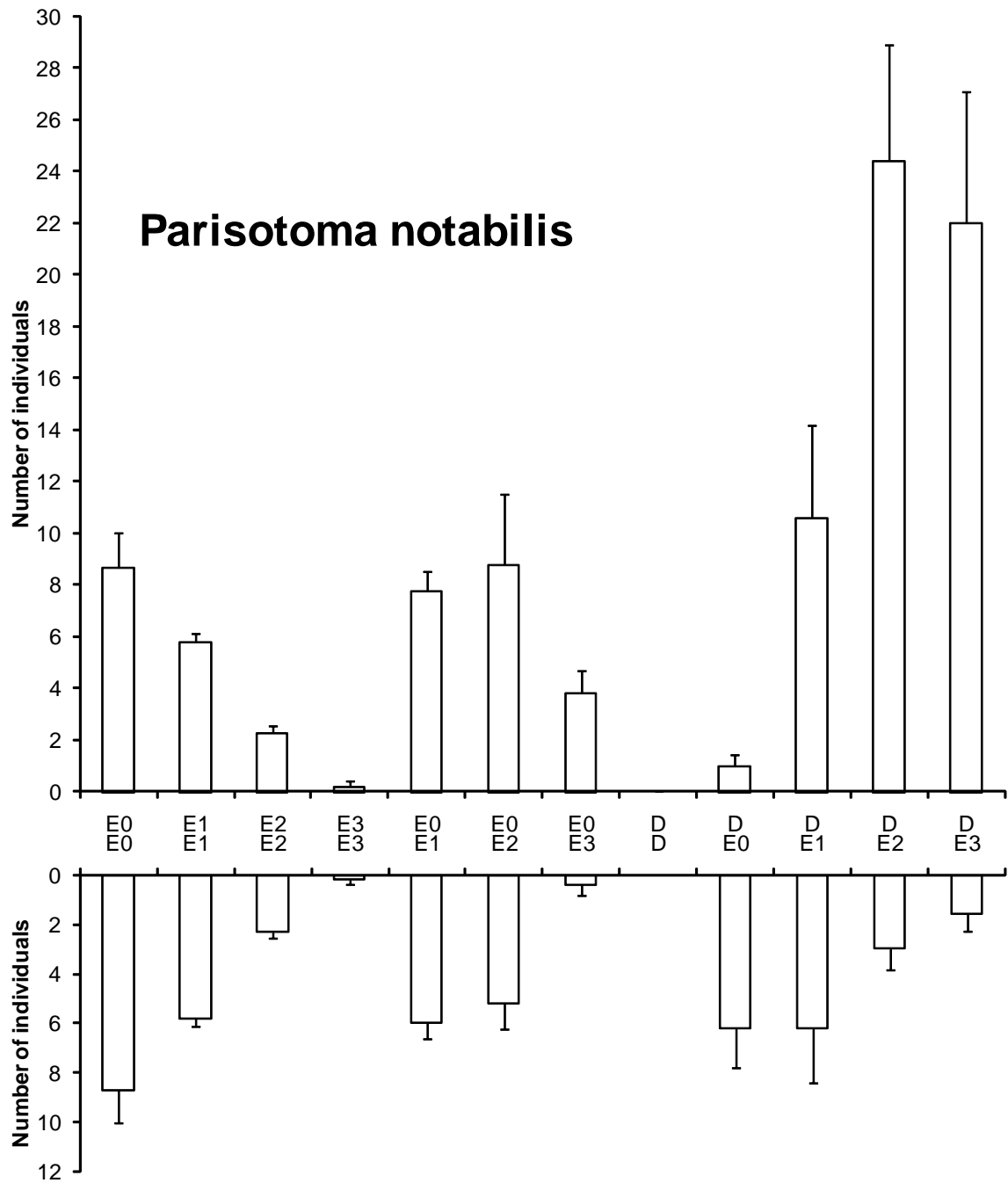
2 Fig. 2



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2 Fig. 3

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2 Fig. 4