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11 **Title:** ACID-TOLERANT COLLEMBOLA CANNOT COLONIZE METAL-POLLUTED
12 SOILS AT NEUTRAL PH

13

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1 **Acid-tolerant Collembola cannot colonize metal-polluted soils at neutral pH**

2

3

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4

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8 **Abstract**

9

10

A microcosm experiment was performed to test the hypothesis that Collembola

11

living in an acid soil (pH 4) were able to colonize a heavy metal-polluted soil of pH 7.

12

After 6-month incubation, the added fauna were not recovered, except for a few

13

individuals, while the original fauna were still as abundant as at the beginning of the

14

experiment. It was concluded that, despite similarities between the chemical

15

environment of acid soils and that of metal-polluted soils, differences in biotic and

16

abiotic factors prevent acid-tolerant populations to survive and reproduce in a polluted

17

site.

18

19

Keywords: Heavy metals, Collembola, Acid-tolerance, Inoculation

20

21

1. Introduction

22

23

The use of acid-tolerant organisms for the bioremediation of polluted soils has

24

been proposed, on the basis of affinities between the chemical environment of acid and

25

polluted soils, in particular those polluted with heavy metals (Chauvat and Ponge,

26

2002; Gillet and Ponge, submitted). The lack of metal specificity in detoxication

27

mechanisms of soil invertebrates (Vandenbulcke et al., 1998; Köhler, 2002), and the

28

presence of free (ionic) forms of aluminum, iron, manganese and other metals at low

1 pH (Tan, 1982), suggested that tolerance to acidity could allow tolerance to a broad
2 range of heavy metals, too. However, neutral pH, excess of calcium and dramatic
3 changes in food resources and habitat could affect survival and reproductive rate upon
4 inoculation to metal-polluted sites (Kreutzer, 1995; Gillet and Ponge, 2002, 2003). The
5 objective of this study was to initiate a self-reinforcing process by adding more, better
6 adapted fauna, in order to i) stimulate humification (Bernier, 1998; Ponge, 1999;
7 Davidson et al., 2002), ii) increase the number of micro-sites able to fix heavy metals
8 (Senesi et al., 1987; Dupuy and Douay, 2001), thus preventing metals from circulating
9 through the ecosystem.

10

11 Several experiments were performed to check whether acid-tolerant Collembola
12 were able to colonize heavy-metal polluted soils. Short-term microcosm experiments
13 using compartmented boxes showed that some species dispersed from an acid source
14 (a dysmoder humus of pH 4) to a neutral soil heavily polluted with metals such as lead,
15 zinc, or cadmium (Chauvat and Ponge, 2002; Gillet and Ponge, submitted). However,
16 these dispersal experiments were of a too short duration for allowing reproduction and
17 survival success to be assessed. A field site polluted with zinc, cadmium and lead was
18 inoculated with microarthropods but resampling of the site after 7 and 14 months failed
19 to reveal any significant dispersal from the inoculum, which kept its original population
20 even after 14 months (Gillet, unpublished data). We suspected that the animals did not
21 disperse to a great extent because they were not forced to leave their original habitat
22 under environmental pressure (Tranvik and Eijsackers, 1989). As a consequence, it
23 was decided to perform laboratory experiments, into which a known amount of acid-
24 tolerant fauna could be introduced and monitored over six months, thus allowing the
25 assessment of survival and reproduction of the introduced population. This time lapse
26 was within a range between one generation time (1 to 2 months) and maximum
27 longevity (1 to 2 years) for most Collembola (Siepel, 1994).

28

1 2. Materials and methods

2

3 The acid soil used for inoculating acid-tolerant fauna was a dysmoder humus
4 (Brêthes et al., 1995) of pH H₂O 4.4 and pH KCl 3.3, originating from a beech forest at
5 Willerzie, Belgium (Ponge et al., 1997; Gillet and Ponge, submitted). The metal-
6 polluted soil was obtained from a field downwind a zinc smelter at Auby, France. It
7 corresponded to the most polluted plot P1, as described in Gillet and Ponge (2002,
8 2003). The top 10 cm of the soil, which was a mor humus (Ponge et al., 2000) of pH
9 H₂O 6.9 and pH KCl 6.5, contained 35,000 mg/kg of Zn (Gillet and Ponge, 2003), half of
10 which was in a bioavailable form (Gillet and Ponge, submitted). The two soils were
11 collected on the same day (2002.09.22). They included only ectorganic horizons, which
12 were homogenized by hand in a large plastic sheet after discarding fresh litter and
13 ground vegetation. After homogenization, samples were directly put in microcosms
14 before transport to the laboratory.

15

16 Experimental microcosms were 11 x 8 x 4 cm (L x l x h) polystyrene boxes with
17 lids, which were filled with soil, leaving enough overhead space for free movement of
18 surface-active invertebrates. Lids were pierced at their centre with a 2 cm diameter
19 hole, covered with nylon gauze, to allow gas exchange with the surrounding
20 atmosphere. Ten replicates with the polluted soil (300 cm³) were kept closed without
21 any further treatment. Ten other replicates were placed under Berlese funnels used for
22 the extraction of microarthropods (Edwards and Fletcher, 1971) and were inoculated
23 with fauna from 300 cm³ dysmoder humus. In parallel, microarthropods from 300 cm³
24 of both substrates were extracted using the same method. During the extraction, which
25 took 10 days, uninoculated boxes were also incubated in the extractor. Once the
26 inoculation was completed, all microcosms (10 inoculated, 10 uninoculated) were
27 incubated in an air-forced chamber at constant temperature (15°C), in darkness.

1 Incubation lasted for 6 months, after which time microarthropods were extracted in the
2 same way.

3

4 The microcosms were kept at field moisture, their weight being kept constant by
5 adding deionized water each fortnight.

6

7 Extracted animals were collected and preserved in 95% ethyl alcohol. They
8 were sorted under a dissecting microscope and mounted in chloral-lactophenol for
9 examination in phase contrast microscopy. Several keys were used for the
10 identification of Collembolan species. In particular the (still experimental) key by Hopkin
11 (in prep.) was judged very handy. It was completed by more detailed monographs by
12 Gisin (1960), Zimdars & Dunger (1994), Jordana et al. (1997), Fjellberg (1998), Bretfeld
13 (1999) and Potapov (2001).

14

15 A special attention was apid to the tullbergiid species *Mesaphorura*
16 *macrochaeta* Rusek. The sex ratio of adult specimens was determined after pooling all
17 animals from the same treatment (Dysmoder, Original Mor, Incubated Mor, Inoculated-
18 incubated Mor). We have noted before that this parthenogenetic species shifted to
19 sexual reproduction under environmental stress, including pollution by heavy metals
20 (Niklasson et al., 2000; Gillet and Ponge, 2003). The gut contents of all specimens of
21 *M. macrochaeta* were examined under phase contrast and classified into 6 categories
22 (Empty guts, Holorganic humus, Hemorganic humus, Fungi, Bacteria, Exuviae), since it
23 has been shown that the same species changed its food diet when submitted to a
24 higher dose of heavy metals (Gillet and Ponge, 2003). Gut contents were characterized
25 for each individual. Most intestines were void or displayed only one food category. In
26 cases where several categories were present in the same gut, each category was
27 scored to the nearest 0.1, the sum of the scores being fixed to 1 for each individual.

28

1 Densities of the different species, as well as total abundance of Collembola and
2 number of species per sample were compared between treatments using Mann-
3 Whitney procedure at .05 significance threshold (Glantz, 1997).

4

5 **3. Results**

6

7 The species composition of the dysmoder humus largely differed from that of
8 the polluted soil (Table 1, Fig. 1). The dysmoder humus exhibited more than ten times
9 the total abundance of the mor (polluted) humus, and more than three times its number
10 of species. Some species were present in the acid soil but were totally lacking in the
11 neutral (polluted) soil, the most abundant ones being *Protaphorura eichhorni* (Gisin),
12 *Folsomia quadrioculata* (Tullberg), *Friesea truncata* Cassagnau, *Isotomiella minor*
13 (Schäffer), *Mesaphorura tenuisensillata* Rusek and *Ceratophysella denticulata*
14 (Bagnall). They were classified as dysmoder species. Some others were present in the
15 neutral soil, but were totally lacking in the acid soil, the most abundant ones being
16 *Protaphorura armata* (Tullberg) and *Lepidocyrtus cyaneus* Tullberg. They were
17 classified as mor species. Finally, some species were present in both substrates, such
18 as *M. macrochaeta*, *Parisotoma notabilis* (Schäffer) and *Sphaeridia pumilis*
19 (Krausbauer). They were classified as common species.

20

21 No males were recorded in *M. macrochaeta* from the acid soil (337 ind.), while a
22 quarter of the adults were males in the population from the neutral soil (189 ind.).
23 Prominent differences were observed between dysmoder and mor in the distribution of
24 gut contents (Fig. 2). Holorganic humus was dominant in *M. macrochaeta* from the
25 beech forest, while empty guts, followed by hemorganic humus, were dominant in the
26 polluted soil before incubation. Fungi were also notable in acid soil guts. On the
27 contrary fungi, together with bacteria and exuviae, were scarcely observed in the
28 neutral, polluted soil.

1

2 After incubation, no decrease was observed in the number of individuals living
3 in the polluted soil (Table 1), but the number of species decreased to a large extent
4 (Table 1, Fig. 1). The collapse in species richness was due to the disappearance of
5 epigeic species such as *Isotoma viridis* Bourlet, *L. cyaneus*, *Sminthurinus elegans*
6 (Fitch), *S. pumilis* and *Willowsia nigromaculata* (Lubbock). However, two hemiedaphic
7 species were also observed to disappear at the end of the incubation period, namely *P.*
8 *notabilis* and *Micranurida pygmaea* Boerner. The dominant species *M. macrochaeta*
9 and *P. armata*, which comprised 80% of the total population, were not affected at all by
10 incubation conditions (Table 1).

11

12 Food habits of *M. macrochaeta* were not affected to a great extent by
13 incubation, apart from a small increase in the proportion of empty guts (Fig. 2). After 6
14 months, hemorganic humus was still dominant in the food bolus, although mineral
15 matter was practically absent in the holorganic humus used for the experiment, as
16 ascertained by the composition of humus profiles (Gillet and Ponge, 2002). The sex
17 ratio of *M. macrochaeta* changed little during the experiment, the proportion of males
18 passing from a quarter to a third of the adult population (Table 1).

19

20 Inoculation with dysmoder fauna doubled the number of species of mor humus
21 when compared with the incubated, uninoculated substrate (Table 1, Fig. 1), but it did
22 not increase the number of individuals (Table 1). Thus, most introduced animals were
23 not recovered at the end of the experiment. Only four dysmoder species were found
24 after incubation, namely *F. truncata*, *P. eichhorni*, *Pseudosinella alba* (Packard) and
25 *Pseudosinella mauli* Stomp, but only in very low densities (less than one specimen per
26 microcosm in average). The abundance of *M. macrochaeta*, which was dominant in
27 mor humus but was also present in dysmoder, was not affected by the inoculation
28 procedure (Table 1), thus it can be concluded at first sight that most introduced

1 specimens of *M. macrochaeta* died during incubation. On the contrary, the other
2 dominant species in the polluted soil, *P. armata*, decreased in abundance when acid-
3 tolerant fauna was inoculated, while it did not in the absence of inoculation (Table 1).

4

5 The examination of gut contents of *M. macrochaeta* at the end of the incubation
6 period (Fig. 2) showed that inoculation of dysmoder fauna caused a small increase in
7 empty guts, a strong decrease in the fraction of hemorganic humus and a strong
8 increase in holorganic humus and fungi. The sex ratio of *M. macrochaeta* was not
9 affected by inoculation (Table 1), suggesting that the population recovered at the end
10 of the experiment was the original population of the mor humus.

11

12 **Discussion**

13

14 From our experimental results, it can be concluded that most inoculated
15 specimens died within 6 months, despite an increase in species richness due to a trace
16 population and thus that most acid-tolerant microarthropods were unable to colonize
17 heavily polluted soil used for the experiment. Interestingly, introduced species like *M.*
18 *macrochaeta*, which were abundant in the mor (polluted, neutral) humus, but were also
19 abundant in the dysmoder (unpolluted, acidic) humus, died too. Only the original
20 population of the polluted site can be considered tolerant to the environmental
21 conditions (chemical, biotic) prevailing in mor humus. We ruled out the possibility of a
22 mixing of *M. macrochaeta* specimens from the two sites in inoculated microcosms at
23 the end of the experiment. Even though the examination of gut contents (more fungi,
24 more holorganic humus, compared to uninoculated microcosms) could lead us to this
25 conclusion, the absence of any change in the sex ratio clearly indicated that no
26 parthenogenetic females from the dysmoder were added to the original population of
27 the mor humus. The constant density of *M. macrochaeta* following inoculation indicated
28 that no juveniles were added, too. The observed changes in gut contents could be

1 caused by i) the fall of some debris which accompanied the escape by animals of the
2 drying substrate in Berlese funnels (although most of them were retrieved and sorted
3 out by hand after inoculation), ii) the use of cadavers of introduced specimens by the
4 original fauna of mor humus. The second cause is hardly probable, since arthropod
5 exoskeletons were absent from *M. macrochaeta* intestines in inoculated microcosms,
6 although some were observed in the absence of inoculation (Fig. 2).

7
8 The duration of the experiment was enough to allow reproduction to occur,
9 given the generation time (from egg to egg) of most Collembola (Siepel, 1994). In the
10 presence of predators, the absence of any significant change in the collembolan
11 population (apart from the disappearance of rare species, which is expected in
12 microcosms) was indicative of an equilibrium condition. The disappearance of most
13 introduced specimens could be due to saturation of the original population (Longstaff,
14 1976; Bernier and Ponge, 1998; Winkler and Kampichler, 2000) or to unfavourable
15 food and environmental conditions. The first cause can be ruled out, given the
16 abundance of food (decaying roots, fungi, humus) present in the sampled holorganic
17 profiles, as ascertained from direct observation and from quantitative analyses (Gillet
18 and Ponge, 2002). However, poor food quality could be suspected, since the food
19 habits of introduced specimens of *M. macrochaeta* clearly differed from that of
20 conspecific specimens living in the polluted soil. It is remarkable that mineral matter,
21 which was nearly absent in the sampled profiles (Gillet and Ponge, 2002), was
22 retrieved in high amount in the gut contents of *M. macrochaeta*, even after 6 months.
23 This species was thus able to search for fine mineral particles (supposed to have
24 detoxifying properties) in an environment in which these were nearly absent. It can be
25 hypothesized that the population from the beech forest, where holorganic humus was
26 the main food source but could be consumed without any danger, was unable to mix it
27 with mineral matter in the polluted mor humus. The litter of the polluted mor was partly
28 made of plant debris from hyper-accumulating plants such as *Arabidopsis halleri* (L.)

1 O'Kane & Al-Shehbaz, which accumulates zinc in its above-ground parts (Sarret et al.,
2 2002). The inadaptation of added specimens of *M. macrochaeta* to toxic food or soil
3 solution is a possible cause for the observed phenomenon. Ecotoxicological tests on
4 the isotomid springtail *Folsomia candida* have shown that reproduction and growth of
5 Collembola were affected by heavy metals, in particular Cd and Zn, at doses far under
6 those found in our polluted soil (Sandifer and Hopkin, 1996; Smit et al., 1997; Crouau
7 et al., 1999), thus toxic effects were not unexpected. However, it has been
8 demonstrated that tolerance to heavy metals varies between populations of the same
9 species and that contamination by trace elements may select better-adapted
10 genotypes (Posthuma, 1990; Chenon et al., 2000). In the case of the two populations
11 we compared, that of Auby, living in a soil with 35,000 mg/kg Zn, 190 mg/kg Cd and
12 6000 mg/kg Pb (Gillet and Ponge, 2003) can be considered strongly adapted to heavy
13 metals, either by a better selection of its food (Fountain and Hopkin, 2001; Tranvik and
14 Eijsackers, 1989; present results) or by physiological adaptation such as increased metal
15 excretion rate or shortening of the juvenile period (Posthuma et al., 1992, 1993) or by
16 shifting from parthenogenesis to sexual reproduction (Niklasson et al., 2000; Gillet and
17 Ponge, 2003; present results). At last, a shock effect caused by a sharp increase in pH
18 when animals living at pH 4 were introduced into a soil of pH 7 can be another possible
19 cause for the failure of colonization (Crouau et al., 1999), even for species know to live
20 over a wide range of pH conditions such as *M. macrochaeta* (Ponge, 1993).

21

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23

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Figure captions

1

2

3 **Fig. 1.** Distribution of dysmoder, mor and common species in the four treatments.

4 DYSMODER = original acid (unpolluted) soil. MOR = original neutral (polluted)

5 soil. MOR+6 = polluted soil after 6-month incubation in microcosms.

6 MOR+DYSMODER = polluted soil after inoculation with dysmoder arthropods

7 and 6-month incubation in microcosms. Letters indicate significant differences

8 between total numbers of species per sample (n = 10) according to the four

9 treatments (Mann-Whitney U test). Bars are means and whiskers are standard

10 errors of the means.

11

12 **Fig. 2.** Distribution of gut contents of *Mesaphorura macrochaeta* according to the four

13 treatments (codes of treatments according to Figure 1)

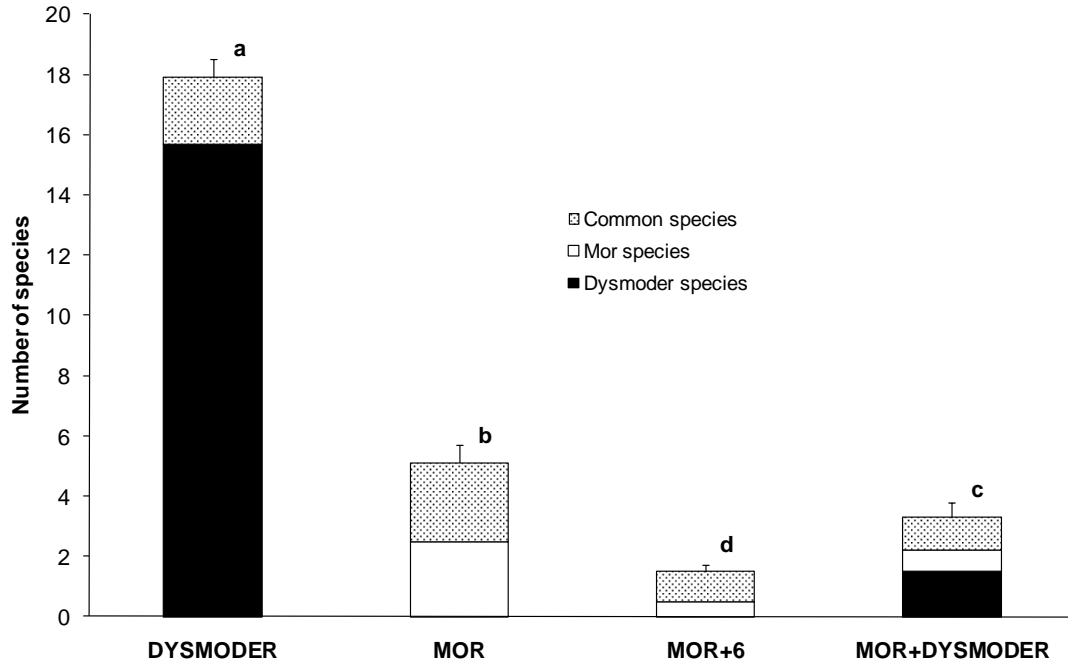
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Table 1 Population parameters of Collembola in the original substrates (dysmoder, mor) and after 6-month incubation in microcosms (means of 10 replicates followed by standard errors). Dysmoder species which were retrieved at the end of the experiment in mor humus are indicated in bold type. Letters in indices indicate significant differences between treatments (Mann-Whitney U test)

	Dysmoder	Mor (original)	Mor (incubated)	Mor (incubated, and inoculated with fauna from dysmoder)
<i>Allacma fusca</i>	0.1±0.1	0	0	0
<i>Arrhopalites spinosus</i>	0.5±0.2 _a	0 _b	0 _b	0 _b
<i>Ceratophysella denticulata</i>	11±0.8 _a	0 _b	0 _b	0 _b
<i>Entomobrya nivalis</i>	0.6±0.5	0	0	0
<i>Folsomia quadrioculata</i>	67.4±6.8 _a	0 _b	0 _b	0 _b
<i>Friesea truncata</i>	51.1±4.4_a	0_c	0_c	0.8±0.3_b
<i>Heteromurus major</i>	0.1±0.1	0.1±0.1	0.1±0.1	0
<i>Isotoma viridis</i>	0	0.1±0.1	0	0
<i>Isotomiella minor</i>	42.8±3.5 _a	0 _b	0 _b	0 _b
<i>Lepidocyrtus cyaneus</i>	0 _b	1.3±0.5 _a	0 _b	0 _b
<i>Lepidocyrtus lignorum</i>	0.2±0.2	0	0	0
<i>Lipothrix lubbocki</i>	6.6±1 _a	0 _b	0 _b	0 _b
<i>Megalothorax minimus</i>	5.4±0.8 _a	0 _b	0 _b	0 _b
<i>Mesaphorura leitzaensis</i>	0.1±0.1	0	0	0
<i>Mesaphorura macrochaeta</i>	33.7±3 _a	18.8±6.5 _b	20.1±7.1 _b	20.6±7.2 _b
(sex ratio M/F)	0	0.26	0.32	0.34
<i>Mesaphorura jevanica</i>	7.7±1.2 _a	0 _b	0 _b	0 _b
<i>Mesaphorura tenuisensillata</i>	19.3±3.9 _a	0 _b	0 _b	0 _b
<i>Mesaphorura yosii</i>	6.4±1.4 _a	0 _b	0 _b	0 _b
<i>Micranurida pygmaea</i>	0 _b	0.4±0.2 _a	0 _b	0 _b
<i>Paratullbergia callipygos</i>	0.3±0.2	0	0	0
<i>Parisotoma notabilis</i>	11.1±1.6 _a	1.8±0.4 _b	0 _c	0 _c
<i>Proisotoma minima</i>	0.4±0.4	0	0	0
<i>Protaphorura armata</i>	0 _c	7.5±1.1 _a	8±4.3 _{ab}	3.6±1.2 _b
<i>Protaphorura eichhorni</i>	128.9±13.9_a	0_b	0_b	0.5±0.3_b
<i>Pseudanurophorus binoculatus</i>	0.7±0.4	0	0	0
<i>Pseudisotoma sensibilis</i>	2.1±0.8 _a	0 _b	0 _b	0 _b
<i>Pseudosinella alba</i>	0.4±0.2	0	0	0.2±0.1
<i>Pseudosinella maui</i>	2.2±0.4_a	0_c	0_c	0.5±0.2_b
<i>Schaefferia emucronata</i>	0.3±0.2 _a	0 _b	0 _b	0 _b
<i>Sminthurinus elegans</i>	0 _b	0.5±0.2 _a	0 _b	0 _b
<i>Sminthurinus signatus</i>	0.2±0.1	0	0	0
<i>Sphaeridia pumilis</i>	0.2±0.2 _b	1.7±0.6 _a	0 _b	0.3±0.3 _b
<i>Willemia anophthalma</i>	4.9±1.2 _a	0 _b	0 _b	0 _b
<i>Willemia denisi</i>	1.1±0.4 _a	0 _b	0 _b	0 _b
<i>Willowsia nigromaculata</i>	0	0.1±0.1	0	0
Total Collembola	405.8±32.3 _a	32.3±7.6 _b	28.2±7.5 _b	26.5±7.3 _b
Number of species	17.9±0.6 _a	5.1±0.6 _b	1.5±0.2 _d	3.3±0.5 _c

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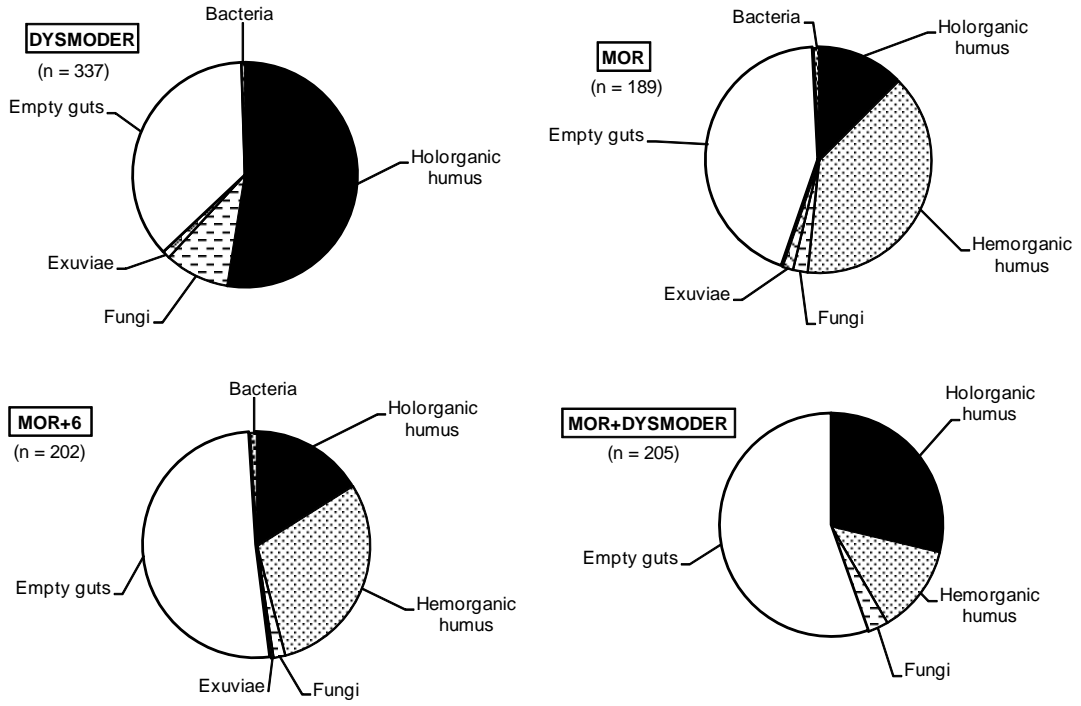
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2 Fig. 1

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2 Fig. 2