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On the advantage of *Folsomia fimetarioides* over *Isotomiella minor* (Collembola) in a metal polluted soil

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Summary. Food preference, metal avoidance behaviour and desiccation tolerance were investigated for two collembolan species, *Folsomia fimetarioides* and *Isotomiella minor*, in order to test some hypotheses for their different distributions in relation to a heavy metal gradient. *F. fimetarioides* showed a higher preference for metal tolerant fungi than *I. minor* when they were offered fungi of different metal tolerance. When they could choose between polluted and unpolluted fungi and substrate, *F. fimetarioides* significantly avoided the polluted source while *I. minor* did not. Both species were negatively affected by drought. *I. minor* was more tolerant than *F. fimetarioides* when exposed to drought in combination with metal pollution. High supply of preferred fungal species and a better ability to avoid heavy metals favour *F. fimetarioides* and determine its dominance over *I. minor* in polluted soils.

Key words: Collembola – Distribution metals – Food preference – Avoidance

In the course of a large scale study on long term effects of heavy metals emitted by a brass mill at Gusum, SE Sweden, on forest soil, the dominant soil fauna groups were investigated. A survey of Collembola along the metal gradient revealed, that the distribution of *Folsomia fimetarioides* (Axelsson) was inversely related to that of *Isotomiella minor* (Schäffer) and that *F. fimetarioides* had become the dominant collembolan species in the most polluted sites of the gradient, whereas *I. minor* dominated in the unpolluted sites (Bengtsson and Rundgren 1988).

I. minor is a common and often dominant collembolan species in Scandinavian coniferous forest soil (Forsslund 1944, Persson et al. 1980, Hågvar 1982, Huhta et al. 1986), whereas *F. fimetarioides* occurs more irregularly, occasionally highly abundant (Forsslund 1945, Huhta et al. 1986).

Many collembolan species, including *I. minor* (Poole 1959, Bödvardsson 1970), are fungivores and tend to discriminate between fungal species (Gilmore and Raffensberger 1970, McMillan 1976, Visser and Whittaker 1977, Bengtsson et al. 1985). Though no data are available on the food preference of *F. fimetarioides* the importance of fungi as a food source for other *Folsomia* species (Singh 1969, Anderson and Healey 1972) makes it reasonable to assume that *F. fimetarioides* is also fungivorous.

As fungal biomass and species composition are affected by metal contamination (Nordgren et al. 1983, Rühling et al. 1984) fungal feeding Collembola in metal polluted soils will presumably be influenced by changes in their food source. Species that graze selectively on metal sensitive fungal species should be more disfavoured than those preferring metal tolerant fungi.

Rather than reducing the total abundance of Collembola in a metal polluted soil, the metals may enhance the abundance of certain species by changing the proportions of their preferred fungal species. This may be one possible mechanism determining the relative abundance of *F. fimetarioides* and *I. minor* in the metal gradient at Gusum. Another possible steering variable, secondarily affected by the metals, is the soil moisture content. The lowered biological activity in the polluted soils at Gusum has resulted in a reduced litter decomposition (Tyler 1984, Bengtsson et al. 1988) and as a consequence, altered physical conditions of the soil (Eijsackers and Tranvik in prep.). Lower soil moisture content and water holding capacity of the polluted soil may negatively affect soil invertebrates sensitive to desiccation.

Avoidance of metals has been observed for snails (Russel et al. 1981), earthworms (Eijsackers 1981), isopods (van Capelleveen 1987) and Collembola (Joosse and Verhoef 1983) when offered contaminated food or soil amended with metals. The heterogeneity of the soil and the variability of fungal species available may present sites and food sources of different metal concentration in an overall polluted site. This implies a selective advantage to species with a highly developed ability to detect and avoid metals, and may result in an enhanced abundance compared to other species in polluted soils.

The aim of this study was to examine if any of the factors mentioned above could be rejected as an explanation for the distribution of *F. fimetarioides* and *I. minor* in a metal polluted soil. Three hypotheses were raised: 1) the abundances of the two collembolan species are determined by the quality, distribution and occurrence of their preferred food sources; 2) the ability to avoid local metal enrichment, i.e. to select less polluted microhabitats, differs between the two species; and 3) the two species have different desiccation tolerance; the lower water holding capacity of the polluted soil determines their survival.

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Material and methods

Specimens of *F. fimetarioides* and *I. minor* were extracted from the mor of coniferous forest soils at Gusum by a high gradient extractor (modified after Macfadyen 1961), *F. fimetarioides* from a metal polluted soil and *I. minor* from a control soil (site II and V, respectively, in Bengtsson and Rundgren [1984]). They were kept in plastic dishes with a bottom of plaster of Paris and activated carbon (9:1 vol: vol) and fed mycelium of *Verticillium bulbillosum* or *Mortierella isabellina*. Both collembolan species are fragile and have to be carefully handled. Their reproductive rates were insufficient in our cultures to provide all the animals needed, and for each experiment fresh specimens were extracted from Gusum soils, and stored at 9° C in darkness. Incubation temperatures and light conditions were optimized in order to obtain best survival conditions during the experiments. The combination of 12° C and darkness was most preferable, but results obtained under other incubation regimes were also used.

The fungal species were selected from the most abundant taxa present in polluted and unpolluted soils of the Gusum area (Table 1). They were grown on 2% malt agar (MA) or on 2% MA + 50 µg/g Cu and 500 µg/g Zn (copper and zinc were added as chloride salts) in small plastic cups (5 or 9 mm ∅, 3 or 5 mm h) serving as food cups in the experiments described below (cf. also Bengtsson et al. 1983).

Metal analyses of animals and fungi were measured by atomic absorption spectrometer (AAS) according to the micromethod developed by Bengtsson and Gunnarsson (1984).

Food preference experiment. Plastic dishes (52 mm ∅, 40 mm h) were divided by ribs into four subchambers, which permitted free admission in between. Each subchamber was provided with a food cup. *V. bulbillosum* was used as an internal standard and always offered in the preference tests (the numbers of animals on this fungi were set at 1). The relative preference of a certain fungus was determined by comparing the number of springtails present on it with that on *V. bulbillosum*. Ten animals of either *F. fimetarioides* of *I. minor* were placed in the centre of each dish. The experiment was carried out in triplicate and the numbers of animals present in a subchamber were counted four times a day during one week. The experiment was performed in daylight and room temperature (18–20° C). The food cups were randomly placed and the dishes were turned 90° after each observation in order to reduce effects of phototaxis.

As we observed that the animals also ingested activated carbon from the plaster of Paris mixture, glass fiber filter (Whatman GF/C) was henceforth used to cover the bottom of the dishes.

Preference experiments with contaminated and uncontaminated fungi. Plastic dishes (see above) with a bottom of moistened, sterile glass fiber filter were used. Four preferred fungal species, viz. *V. bulbillosum*, *Geomyces pannorum*, *M. isabellina* and *Penicillium loliense*, were selected for the tests. The two former species are metal tolerant and the latter ones metal sensitive (Table 1). The fungal species were grown both on unpolluted and polluted agar and offered to the collembolans.

Ten individuals of *F. fimetarioides* or *I. minor*, starved one week prior to the experiment, were placed in the centre of each dish (in triplicate). Food selection was determined by counting the animals present in a chamber four times per day up to ten days. The experiment was performed in daylight and room temperature (18–20° C). The food cups were randomly placed and the dishes were turned 90° after each observation.

Table 1. Fungal species from the Gusum area, their Cu tolerance (µg/g), and their hyphal concentrations (µg/g) of Cu and Zn when grown on malt agar with 50 µg/g Cu and 500 µg/g Zn added. The degree of Cu-tolerance of the used species (measured as the conc. at which a 50% radial growth reduction was observed) corresponds to distribution of the fungi in the field. The most tolerant taxa are abundant in the vicinity of the brass mill, while more sensitive species are much less abundant (Nordgren et al. 1983). Figures on Cu tolerance are from Arnebrant et al. (1987)

Fungal species	Cu tolerance		Hyphal conc. (µg/g) of	
	mean	sd	Cu	Zn
Paecilomyces farinosus (Holm ex SF Gray) A.H. Brown & G. Smith	590	220	343	564
Verticillium bulbillosum (W. Gams and Malla)	170	88	379	5500
Geomyces pannorum (Link) Sigler & Carmichael I	110	17	784	2600
Mortierella isabellina (Oudem.)	58	3.8	$5.4\ 10^4$	$2.9\ 10^5$
M. ramanniana (Möller) Linnemann	65	2.8	327	855
Penicillium montanense (Christensen & Backus)	67	1.1	1916	$4.9\ 10^3$
P. loliense (Pitt)	81	9.2	4821	$9.6\ 10^3$
Penicillium sp. 1	98	15	581	$2.2\ 10^3$
Penicillium sp. 2	73	19	1073	$9.9\ 10^3$
Oidodendron tenuissimum (Peck) Hughes	93		$5.3\ 10^4$	$1.3\ 10^5$

Metal avoidance. V. bulbillosum grown on agar or on metal agar was offered the collembolans in plastic dishes (the same size as above) provided with one central food cup. The glass fibre filter was moistened either with sterile distilled water or with a sterile metal solution (1500 µg/g Cu and 2000 µg/g Zn; corresponding to the soil concentration at site II in Bengtsson and Rundgren [1984]).

By combining polluted or unpolluted food with polluted or unpolluted substrate four different experimental situations were presented each collembolan species in triplicate. Ten individuals, starved for one week, were added to each dish, which were incubated at 19° C in darkness. Positions and mortality of the animals were determined once a day for ten days or until all animals had died.

Specimens of *F. fimetarioides*, still alive at the end of the experiment were sampled for metal analysis. *I. minor* proved to be more sensitive leaving insufficient numbers for analysis.

If a collembolan species naturally avoids metal polluted microhabitats in the field, specimens reared in soil should contain lower metal concentrations than those living on dishes with polluted filter substrate and fungi where no unpolluted choice is available. We therefore conducted an additional experiment with *F. fimetarioides* in soil samples from the Gusum area. Ten grams sieved mor soil (mesh size 3,75 mm) from the polluted (II) and unpolluted (V) sites, respectively, were added to plastic dishes. The soil was repeatedly frozen and thawed with two days interval to remove the indigenous fauna. Ten *F. fimetarioides* were added to each dish in triplicate, and incubated at 12° C in darkness. Water losses were compensated for by adding sterile distilled water once a week. After four weeks the soil was flooded with water and animals floating to the surface were sampled and analysed for Cu and Zn content.

Desiccation tolerance. Mor soils from sites II and V at Gusum were sifted through a 3,75 mm sieve and repeatedly frozen and thawed. 5 g of each soil was supplied to each of sixteen plastic dishes (36 mm ∅, 30 mm h). Half of the dishes were kept moist (40%), whereas half of them were allowed to dry during the experiment. The species were tested separately and ten individuals of either *F. fimetarioides* or *I. minor* were added to a dish. Both species were thus exposed to two soil types and two moisture conditions, each in quadruplicate. The dishes were incubated at 12° C in darkness and moist ones were weighed once a week and corrected for water losses. After five weeks the animals were extracted by flooding.

Results

Food preference experiments. The three fungal species most preferred by *F. fimetarioides* were, in order of preference, *M. isabellina*, *G. pannorum* and *V. bulbillosum*, whereas *I. minor* ranked the fungi in the order *Penicillium montanense*, *M. isabellina* and *Penicillium sp.2*. Two fungal species highly ranked by *F. fimetarioides* are relatively tolerant to copper, whereas those favoured by *I. minor* are not (Table 1).

Since *P. montanense* and *Penicillium sp. 2* are Cu-sensitive and grow badly on polluted agar, *P. loliense*, that grows better, was chosen to represent the *Penicillium* species. Together with *M. isabellina* it represented the sensitive fungal species used in the experiments.

F. fimetarioides selected the two Cu-tolerant fungi *G. pannorum* and *V. bulbillosum* regardless of the substrate they grew on, whereas *I. minor* preferred *M. isabellina* and *P. loliense* when growing on unpolluted agar but switched to Cu-tolerant fungal species when these fungal species were grown on polluted agar (Fig. 1).

Metal avoidance. F. fimetarioides significantly avoided polluted fungi or substrate when offered an unpolluted alternative, whereas *I. minor* did not (Fig. 2).

If individuals of *F. fimetarioides* were given a polluted diet and substrate, their body burden of metals increased. However, when they could choose between polluted and unpolluted food or substrate, their Cu and Zn concentrations remained at about the same level as when they were reared on unpolluted substrate and food (S-/F-). The animals took up more Cu and Zn from the experimentally polluted substrate and fungi than from metal polluted soil (cf. Tables 2 and 3).

The high body burdens of Cu and Zn in *F. fimetarioides* kept on unpolluted substrate and fungi (S-/F-) (Table 2)

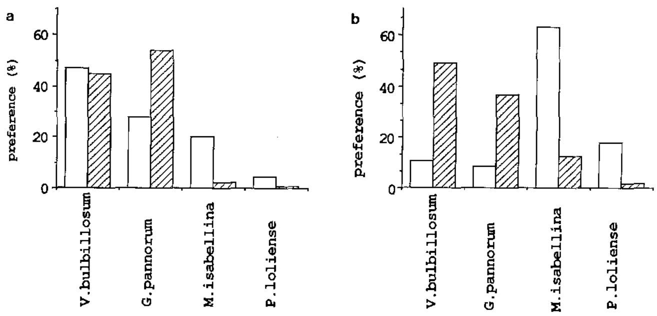

Fig. 1a, b. Food preference (% of total observed visits) of **a** *F. fimetarioides* and **b** *I. minor* for selected fungi when grown on unpolluted agar (□) (2% MA) or on polluted agar (▨) (2% MA + 50 µg/g Cu and 500 µg/g Zn). *F. fimetarioides* did not change its choice of tolerant species due to metal pollution (two-way ANOVA, $F = 18.9$, $P < 0.001$), but rather increased the preference for those species ($F = 3.8$, $P < 0.05$). The preference of *I. minor* was completely altered by addition of metals ($F = 3.2$, $P < 0.01$)

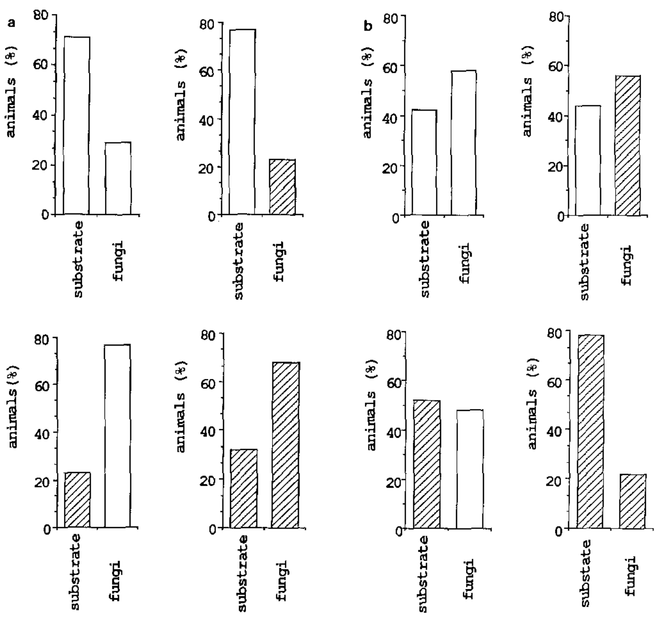

Fig. 2a, b. Distribution of **a** *F. fimetarioides* and **b** *I. minor* on unpolluted (□) or polluted (▨) fungi (F) and substrate (S). The fungi were grown on 2% MA (−) or on 2% MA + 50 µg/g Cu + 500 µg/g Zn (+). The substrate was a glass fibre filter paper moistened with sterile distilled water (−) of heavy metal solution (+) containing 1500 µg/g Cu + 2000 µg/g Zn. The distribution, tested by Students t-test, were for *F. fimetarioides*: S−/F− $P < 0.05$, S−/F+ $P < 0.05$, S+F− $P < 0.001$, S+/F+ $P < 0.05$ and for *I. minor*: S−/F− $P < 0,05$, S−/F+ n.s, S+/F− n.s, S+/F+ $P < 0.001$.

were probably a consequence of their previous exposure to metals in the soil from which they were extracted a few days before the experiment started.

Desiccation tolerance. Both species showed a significantly decreased survival under desiccating conditions (Fig. 3a, b), but *F. fimetarioides* suffered more from a dry and polluted soil than from a dry soil only.

Discussion

The distribution pattern of *F. fimetarioides* with respect to the metal gradient in the Gusum area is almost inversely

Table 2. Copper and zinc concentrations (μg/g) of *F. fimetarioides* reared on unpolluted or polluted substrate for ten days and offered unpolluted or polluted *V. bulbillosum*. The fungus was grown on 2% MA or on 2% MA + 50 μg/g Cu + 500 μg/g Zn. The substrate was a glass fibre filter, moistened with sterile distilled water or with a heavy metal solution of 1500 μg/g Cu + 2000 μg/g Zn. ($n=2$ when sd is given, otherwise $n=1$)

Unpolluted substrate				Polluted substrate			
Unpoll. fungi		poll. fungi		unpoll. fungi		poll. fungi	
mean	sd	mean	sd	mean	sd	mean	sd
Cu (μg/g)							
310	–	410	82	288	218	2770	–
Zn (μg/g)							
1760	–	1060	523	2000	–	20740	–

Table 3. Copper and zinc concentrations (μg/g) of soils (unpolluted and polluted) and of *F. fimetarioides* reared for four weeks in respective soil

Heavy metal concentration (μg/g)							
in soil ($n>2$)				in animals ($n=2$)			
Cu		Zn		Cu		Zn	
mean	sd	mean	sd	mean	sd	mean	sd
unpolluted							
10	2	45	19	60	18	929	482
polluted							
212	85	2068	384	706	621	4188	5700

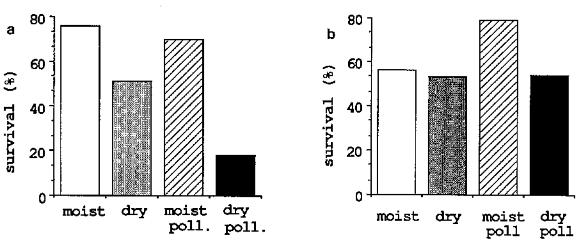

Fig. 3a, b. Survival of **a** *F. fimetarioides* and **b** *I. minor* in unpolluted and polluted soils, moist and desiccating, respectively. Desiccation significantly affected the survival of both species (two-way ANOVA *F. fimetarioides* $F=52.8$, $P<0.001$, *I. minor* $F=4.8$, $P<0.05$). Pollution enhanced the negative effect of desiccation for *F. fimetarioides* ($F=16.6$, $P<0.01$) but not for *I. minor*

related to that of *I. minor* (Bengtsson and Rundgren 1988). The response of *F. fimetarioides* and *I. minor* might illustrate two extremes of a gradual shift in performance with *F. fimetarioides* being an early colonizer, highly adaptive to extreme environments and able to utilize the polluted soil close to the brass mill, and *I. minor* a slowly adapting species, more sensitive to environmental changes induced by the metal contamination.

In our experiments we have tried to clarify if the dominance of *F. fimetarioides* and the absence of *I. minor* in the vicinity of the brass mill is a response to metal toxicity *per se*, or an indirect response through food shortage, malnutrition or changed moisture contents of the soil. Apparently, *F. fimetarioides* has an advantage in finding its favourable fungal species in excess at the polluted site, whereas *I. minor* is forced to use a lower ranked food source, since preferred fungal species become less frequent. Hence, heavy metals present in the soil not only are toxic to the animals but indirectly also deteriorate food quality and quantity which may lead to malnutrition and starvation. In a series of experiments with *Onychiurus armatus* (Tullb.) Bengtsson et al. (1985) showed that addition of food to a metal polluted soil did not suffice to compensate for the decreased growth caused by the metals, unless the food was nitrogen enriched. *G. pannorum* and *V. bulbillosum*, selected by *F. fimetarioides*, are not only more metal tolerant than *M. isabellina* and *P. loliense*, but also contain relatively high quantities of protein, 41,0% and 26,5% (dw) respectively, compared with 14,0% in *M. isabellina* (Bengtsson et al. 1985). Certain proteins are known to complex with and detoxify metals in fungi (Gadd and Griffiths 1978), and the protein content of the fungi may thus be of importance for the animals not only for its high nutritive value but also for its detoxifying effect. Moreover, the protein content of *M. isabellina* is higher when it grows on metal polluted agar than on common malt agar (Bengtsson et al. 1985). Thus, metals added to a substrate seem to stimulate production of proteins and hence metal binding in certain fungi. Metal sensitive fungal species, on the other hand, seem to accumulate metals to a greater extent than tolerant species (Table 1). The figures of Cu tolerances and contents of Cu and protein for four fungal species given in Table 4 clearly show the relation between protein content and metal tolerance.

Table 4. Copper tolerance, copper content, and protein content of four fungal species. Fungi grown on 2% MA + 50 μg/g Cu + 100 μg/g Zn were analysed for Cu concentrations, and fungi grown on 2% MA for protein content

	Copper tolerance[a] (μg/g)	Copper content[b] (μg/g)	Protein content[b] (%dw)
M. isabellina	58	54400	14
G. pannorum	110	784	41
V. bulbillosum	170	379	27
P. farinosus	590	343	62

[a] from Arnebrant et al. (1987) (see also Table 1)
[b] from Bengtsson et al. (1985)

Moulting is a major metal excretion mechanism in Collembola (Joosse and Buker 1979) and closely connected with growth. Extensive moulting in response to increased metal levels in the environment may result in a decreased growth rate (Bengtsson 1986). The collembolan *Orchesella cincta* moulted more frequently when fed Pb contaminated food (Joosse and Verhoef 1983), which was associated with an increased excretion of the metal by the animals but also with an increased survival and decreased growth rate. Given a nitrogen enriched food source the cost of the increased moulting seem to be compensated for and a sufficient growth rate can be maintained in a polluted environment (Bengtsson et al. 1985).

The capability of *F. fimetarioides* to avoid artificially polluted substrate when an unpolluted alternative is available, will be of significance in a soil that is heterogeneous and where metal concentrations vary between microhabitats. However, also *I. minor* tends to avoid polluted soil, as demonstrated in an experiment on migration in metal gradient (Sjögren 1986), but also observed when both species were given the choice between unpolluted and polluted soil (unpublished data).

Avoidance behaviour has been demonstrated for the snail *Helix aspersa* (Russel et al. 1981), the isopod *Porcellio scaber* (van Capelleveen 1987) (both decreased their food consumption when offered metal polluted food) and for substrate choice for the collembolan *Onychiurus quadriocellatus* (Eijsackers, unpublished data). The collembolan *Orchesella cincta* also avoids lead polluted algae according to Joosse and Verhoef (1983). However, van Capelleveen et al. (1986), argued that an avoidance behaviour is not needed for *O. cincta* as its tolerance to lead is mainly based on its high efficiency to excrete this metal.

The importance of the heterogeneity in the distribution of metal ions between microhabitats was demonstrated by the observation that metal content of *F. fimetarioides* inhabiting polluted soil never reached that of specimens maintained on polluted fungi or filter substrate. After four weeks in control soil *F. fimetarioides* (harvested from the polluted soil) had decreased its metal body burden to the background concentrations (Table 3). Excretion capability in combination with avoidance behaviour enables *F. fimetarioides* to decrease the toxic influence of metals and thereby to sustain in polluted soils.

Impaired soil moisture conditions at the most polluted site might affect the species differently. The low survival of *F. fimetarioides* under metal stress conditions, especially in desiccating soil, does not speak in favour of a high abundance at contaminated sites. However, at lower depths, other conditions prevail, and the moisture content is higher (Eijsackers and Tranvik unpublished work). There the metal concentration also is lower than at the soil surface (Bengtsson and Rundgren 1984). *F. fimetarioides* could overcome some of the disadvantages of pollution and desiccation in the top soil by vertical migration. Bengtsson and Rundgren (1988) found that the relative abundance of *F. fimetarioides* increased at lower depths at the most polluted site. Moreover, at the polluted sites, *F. fimetarioides* is patchily distributed and more abundant around tree trunks and in spots where a fermentation layer still exists (pers. obs.). It is reasonable to assume that the moisture content will be higher in these spots.

The low desiccation tolerance of *F. fimetarioides* may be a consequence of adaptation to metals. Regardless of its efficiency, a tolerance mechanism involves a certain cost. It can be recalled that van Capelleveen (1986) found that isopods adapted to metals had a lowered efficiency of water regulation than isopods from a non-adapted population. *I. minor* which is less sensitive to desiccation but on the other hand more sensitive to heavy metals may afford a relatively higher desiccation tolerance at the cost of metal tolerance. It should be mentioned, that for plants, it has been observed that drought tolerance often is connected to metal tolerance (Humphreys 1981, in Macnair 1987). It is likely that characteristics, unrelated to metal tolerance are selected for, which improve the adaptedness in a polluted environment. For plants this connection between metal and drought tolerance seem to be more or less general, while for animals no such relation has been found.

Access to adequate food and ability to avoid and endure heavy metals favour *F. fimetarioides* and may seem to be the most important factors determining its dominance in the polluted soil whereas the lower tolerance of *F. fimetarioides* towards desiccation seems to be less important.

Whether a genetical adaption to long-term pollution exists influencing the survival strategy of both species, remains to be proven. Another point of further research is whether direct competitive interactions between both species may have played, and may still play a role in the different distribution with respect to heavy metal pollution.

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