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Source: *Oikos* , Oct., 1994, Vol. 71, No. 1 (Oct., 1994), pp. 13-23

Published by: Wiley on behalf of Nordic Society Oikos

Stable URL: https://www.jstor.org/stable/3546167

Modelling dispersal distances in a soil gradient: the influence of metal resistance, competition, and experience

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Bengtsson, G., Rundgren, S. and Sjögren, M. 1994. Modelling dispersal distances in a soil gradient: the influence of metal resistance, competition, and experience. – Oikos 71: 13–23.

A discrete probability model was developed to describe the distributions of dispersal distances of two soil-living collembolan species, *Folsomia fimetarioides* and *Isotomiella minor*, in an experimental gradient with metal polluted soil. The model assumes that animals move stepwise between adjacent habitats with a probability that is influenced by soil metal concentration, metal induced mortality and resistance, interspecific competition and the capability of individuals to perceive concentration differences. Theoretical and observed distributions were compared to determine the contribution of each factor to the dispersal pattern. Mor soils from a contaminated area were used to construct gradients consisting of three connected 20-cm³ PVC rings filled with soil of different zinc and copper concentrations. Adult collembolans were added to each ring, and survivors and newly hatched juveniles were counted after 2 and 10 weeks of incubation.
The probability that individuals remained in the soil where they were released was generally < 0.5. They responded to increasing metal concentrations by an exponentially decreasing probability to settle. The model suggested that dispersal distances of *F. fimetarioides* were largely affected by resistance to metals, which was supported by independent observations of enhanced reproduction by individuals collected in the polluted field soil compared with individuals from an unpolluted soil in the same area. Both species preferred to settle in the unpolluted part of the gradient, but *F. fimetarioides* was slower due to a poorer dispersal ability or a slower response to high metal concentrations. Significantly more *F. fimetarioides* remained in the most polluted soil during the first 2 weeks of incubation when *I. minor* was also present in the gradient, but the contribution of competition to the model description of dispersal distances was weak. The closest fit to the experimental data was attained when individuals were assumed to perceive differences in metal concentrations as they moved from one soil to another.

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Toxic chemical gradients may invoke bell-shaped distributions of diversity, species numbers, and density (Bengtsson and Rundgren 1984), reflecting the cumulated frequencies of individual tolerance curves. Most often, however, the distributions decline, linearly or exponentially, towards the most contaminated section of the gradient, as illustrated by the distribution of soil fauna in the vicinity of a brass mill (Bengtsson and Rundgren 1982, 1988, Bengtsson at al. 1983). This pattern is consistent with the distribution of species-specific dose-response curves and reflects differences among species in susceptibility to a target compound.

However, there are species with an exceptional density distribution along a gradient. Among collembolan species

found in the gradient near the brass mill mentioned, *Folsomia fimetarioides* (Axelsson) was highly abundant and dominated in areas with high soil metal concentrations whereas *Isotomiella minor* (Schäffer) was common in unpolluted soil (Bengtsson and Rundgren 1988). *I. minor,* a common and often dominant species in Nordic coniferous forest soils (Forsslund 1944, Persson et al. 1980, Hågvar 1982, Huhta et al. 1986), has a short generation time and a parthenogenetic mode of reproduction, which may be advantageous when environmental conditions such as soil moisture are relatively stable, as in thick mor layers. The sexually reproducing *F. fimetarioides* occurs more sparsely and patchily but may be highly abundant where it occurs (Forsslund 1944, Huhta et al. 1986).

Several factors may be responsible for the reversed distribution curves exhibited by the two species around the brass mill. Both are fungivorous with some dietary overlap, but *F. fimetarioides* selects metal tolerant fungal species (Tranvik and Eijsackers 1989), which predominate in polluted soils close to the mill (Nordgren et al. 1983), whereas *I. minor* has a preference for susceptible species which are frequent in soils with low metal concentrations. It is possible that the rareness of metal tolerant fungal species in combination with competition from the more abundant *I. minor* for fungi utilized by both species maintains a low density of *F. fimetarioides* in areas unaffected by metal pollution. Competition, however, has rarely been described for soil animals (Strong 1983). In a few cases reduction or extinction of one of two species has been demonstrated in laboratory studies and ascribed to competition (Christiansen 1967, Culver 1974, Longstaff 1976), as has a shift of microhabitats (Anderson 1978) and a change in the intrinsic rate of population growth (LeBlanc 1985).

Polluted sites close to the brass mill are characterized by an accumulated, thick litter layer and an extremely thin mor layer. The waterholding capacity of the soil is reduced resulting in dry and unpredictable soil moisture conditions. Under these circumstances the genetic variability generated by sexual recombination might favour the establishment of a population of *F. fimetarioides* adapted through intense selection pressure from high metal concentrations, notwithstanding the 50% hazard per generation suffered relative to the asexual alternative (Fisher 1958, Williams 1975). Metal resistance, expressed as increased metal excretion efficiency, growth rate or reproductive rate, is known from some species of Collembola (Posthuma 1990, Posthuma et al. 1992, Tranvik et al. 1993, 1994), and it is possible that the high abundance of *F. fimetarioides* at the polluted sites is a result of metal adaptation.

Persistence of a population in a field gradient may also be influenced by its dispersal rate. Dispersal, defined as the scatter of individuals away from their site of origin, results in a dynamic system including export and import of more or less adapted genotypes. In soil collembolans dispersal can be controlled by population density, and

adverse habitat conditions such as limited food availability will increase the probability to move (Bengtsson et al. 1994). It is anticipated that high concentrations of toxic chemicals will lower food quality and thus have the same effect on dispersal rate as low food density. It requires that individuals can perceive concentration differences along a gradient and that adapted ones are less responsive to high concentrations adjusting their dispersal rate accordingly. Differences in abundances between *F. fimetarioides* and *I. minor* in a metal gradient may then be attributed to differences in dispersal responsiveness to metals, metal resistance and competitive ability. The contribution of each variable to abundance can be tested experimentally and addressed in models simulating the distribution of individuals along a concentration gradient.

The purpose of this study was to determine the distributions of *F. fimetarioides* and *I. minor* as a result of dispersal, persistence, and reproduction in response to copper and zinc concentrations in soil gradients. Discrete probability models were developed to account for the distribution of dispersal distances under the influence of metal concentration, mortality, interspecific competition, resistance to metals, and behavioural response to experienced gradient differences. Observed and theoretical distributions were compared to establish which, if any, of the addressed factors influenced the dispersal pattern.

Materials and methods
Distribution, persistence, and reproduction

Specimens of *F. fimetarioides* were extracted from a highly polluted mor soil and *I. minor* from an unpolluted soil (sites II and V in Bengtsson and Rundgren 1984) by a slightly modified high gradient extractor (Macfadyen 1961). Mor soils for the gradient studies were collected at three mature coniferous forest sites (II, III and V in Bengtsson and Rundgren (1984)), where copper and zinc are the major pollutants emitted by the brass mill at Gusum, SE Sweden. The combined concentrations of these metals in the upper 4 cm (mor + uppermost mineral soil) are 1312 mg/kg dry wt at the most polluted site, 268 mg/kg dry wt at the intermediately polluted site and 42 mg/kg dry wt at the unpolluted reference site (Bengtsson and Rundgren 1988). The soil samples were frozen (−18°C) and thawed three times to reduce the abundance of indigenous invertebrate fauna; a treatment that has minor effects on bacterial and fungal abundances (< 2%) (Bengtsson et al. 1988). Each sample was sieved through a screen (3.75 mm mesh) to obtain a similar structure and remove coarse roots. Three 20-cm³ PVC rings (∅ 35 mm, height 20 mm) were half-filled with soil, one for each metal concentration. Ten adult specimens were placed in the centre of each ring after which the rings were gently filled up and joined using adhesive tape. The gradient was then sealed with 60 μm mesh nets at both ends. It thus contained unpolluted soil in one end (henceforth

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denoted habitat 1) and the most polluted soil in the other (habitat 3).

Ten replicates of the following combinations were tested: 1) 30 *F. fimetarioides*/gradient, 2) 30 *I. minor*/gradient, and 3) 15 of each species/gradient. The density equalled 14 000 individuals m^{-2}, a common density of collembolans in soils close to the mill (Bengtsson and Rundgren 1988).

The gradients were incubated in darkness at 12°C placed horizontally on a tray and weighed once a week. Distilled water was added to compensate for water losses. The gradients were destructively sampled after 2 and 10 wk by separating the rings and determining the number of adults and juveniles present in each habitat by stirring the soils in water and counting the individuals floating to the surface.

Metal resistance

F. fimetarioides was extracted as above from mor soils, sampled at a highly polluted site and an unpolluted one (site II and VI in Bengtsson and Rundgren 1984). 10 ml mor, prepared as previously described, and 10 adult *F. fimetarioides* were placed in a 20-ml plastic vial and incubated in darkness at 12°C. The vials were weighed once a week and distilled water was added to maintain a constant soil moisture. Four combinations (n = 3) of mor (40 and 1312 mg Cu + Zn/kg dry wt soil) and collembolans from the two soils were tested. The collembolans were extracted after 9 wk of incubation by flooding the soil with tap water. Individuals floating to the surface were counted and separated in adults and juveniles.

Theoretical considerations

Dispersal distances in a soil gradient are assumed to be influenced by the probability to stop in a certain habitat as a function of metal concentration, interspecific competition, species-specific metal resistance, or combinations of these. Dispersal is physically constrained within three simulated habitats, and individuals are modelled as making stepwise moves between adjacent habitats in either direction. Each habitat (x) is regarded as a discrete unit, characterized by its metal concentration, C, which increases from C_1 to C_3. The probability to stop in a habitat x is a function of its metal concentration, $p(C_x)$. Animals released in C_1 can move a maximum of two steps; C_{11} denotes release and recovery in C_1, C_{12} denotes the move from C_1 to C_2, and C_{13} the move from C_1 to C_3. The probabilities of individuals to stop in the habitats where they were released, $p(0)$, are $p(C_{11})$, $p(C_{22})$, and $p(C_{33})$. By definition, $p(C_{13}) = p(C_{31}) = 1.0$, as a one directional movement is assumed and individuals can move no further. $p(0)$ can take any value between 0.0 and 1.0.

We first assume that the probability to stop in a habitat is directly proportional to the metal concentration:

$$p(C_x) = p(0) \times (1 - C_x/C_{max}) \text{ or}$$
$$p(C_x) = p(0) \times (1 - \ln(C_x)/\ln(C_{max})),$$

where C_{max} is defined as C_3. As metal concentration is expressed in relation to the maximum concentration in the gradient, $p(C_3)$ will always be 0.0.

The probability to stop may vary, for example linearly with distance moved, in response to differences in habitat quality (Miller and Carroll 1989). We let the probability to stop decrease linearly in response to increased metal concentration, $p(C_x) = p(0) + k \times (C_x/C_{max})$, so that the slope becomes $k = 1 - p(0)$ when the animals are released in C_1. When the animals move in the opposite direction, from C_3 to C_1, k will become $-(1 - p(0))$; $p(C_{33})$ is always 0.0. The probability that those released in C_2 also will be recovered there is described by: $p(C_{22}) = p(0) \times (1 - C_2/C_{max})$. The probability to stop in the final habitat in the dispersal direction will always be 1.0 as a one-directional movement is assumed, so that $p(C_{13}) = p(C_{31}) = p(C_{21}) = p(C_{23}) = 1.0$.

If a fraction, $p(C_x)$, of the individuals released in a given habitat stop where they were released, the fraction $(1 - p(C_x))$, will leave. Individuals released in C_2 will move to C_1 and C_3 with the same probability, $(1 - p(C_2))/2$, if they are unable to foresee habitat quality. The move can only take one direction from C_1 and C_3, that is all individuals leaving these habitats will first head for C_2.

Tranvik and Eijsackers (1989) suggested that the inversely related densities of *I. minor* and *F. fimetarioides* in the Gusum area may be a consequence of *F. fimetarioides* being competitively inferior at unpolluted sites. This possibility was tested here by introducing a competition coefficient, $0.0 \leq \alpha \leq 1.0$, that affects the distribution of *F. fimetarioides* in proportion to the relative density of *I. minor* in a given habitat. The probability that an individual of *F. fimetarioides* stops in a habitat in response to soil metal concentration and competition from *I. minor* can be described as:

$$p(C_x) = p(0) \times (1 - C_x/C_{max}) \times (1 - \alpha \times N_{x(i)}/N_{\Sigma x(i)}),$$

where $N_{x(i)}$ is the number of individuals of *I. minor* in habitat x, and $N_{\Sigma x(i)}$ is the total number of *I. minor* in the gradient.

The density function, $f(C_{xy})$, that describes the fraction of the population reaching C_y from C_x and stopping there can now be expressed for individuals that disperse in response to relative metal concentrations and competition:

$$f(C_{xy}) = p(C_{xy}) \times [(1 - p(0)) \times \ldots \times (1 - p(C_{x-1}))]$$
$$\text{for } C_{11}, C_{12}, C_{13}, C_{33}, C_{32} \text{ and } C_{31};$$

$$f(C_{22}) = p(C_{22});$$

$$f(C_{21}) = p(C_{21}) \times (1 - p(C_{22}))/2;$$

$$f(C_{23}) = p(C_{23}) \times (1 - p(C_{22}))/2;$$
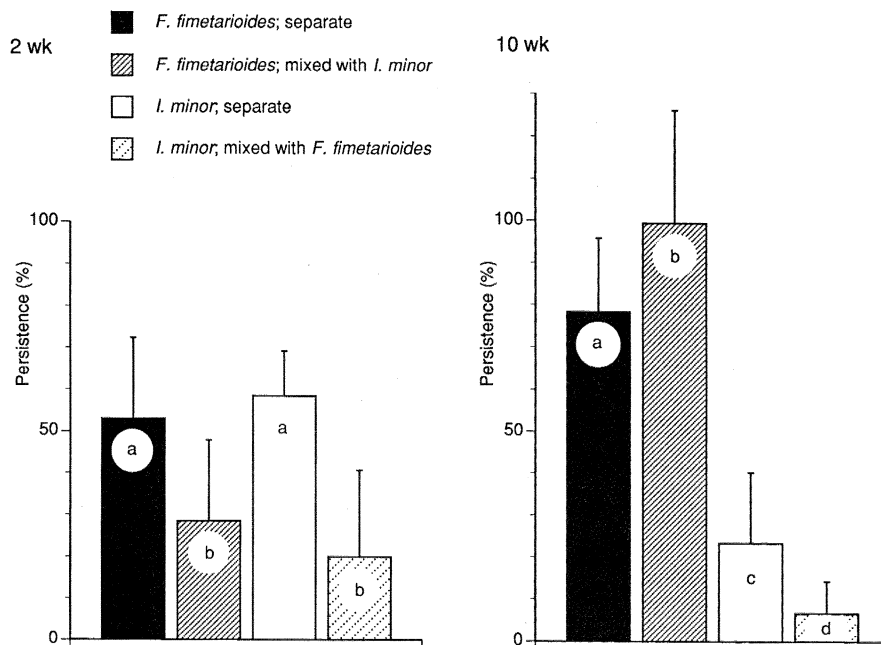
$$\Sigma f(C_{xy}) = 1.0.$$

Fig. 1. Persistence (% of numbers released) in metal gradients (n = 10) after 2 wk and 10 wk of incubation. *F. fimetarioides* and *I. minor* were kept either separately or mixed. Bars represent mean and SD (n = 10). Different letters indicate significant difference (ANOVA F = 26.4 p = 0.0001 (2 wk) and F = 54.0 p = 0.0001 (10 wk)).

2 wk

■ *F. fimetarioides*; separate

▨ *F. fimetarioides*; mixed with *I. minor*

□ *I. minor*, separate

▨ *I. minor*, mixed with *F. fimetarioides*

10 wk

So far, the distribution of individuals among habitats has been described by assuming a constant population density. The effect of enhanced mortality rates caused by toxic metal concentrations on the density distribution is considered by defining the survival, S, of a non-resistant population in the gradient during a certain time interval (9 wk) in the simplest possible way, as a linear function of the metal concentration, $S(C_y) = a + b \times C_y$. Both a and b are constants that can be estimated from independent observations of the survival of *F. fimetarioides* collected from unpolluted soil. Mortality is modelled to happen in the habitat to which the individuals have moved, C_y, since their first reaction to high metal concentrations should be to escape and settle in another habitat. The resulting density function, $f^s(C_{xy})$, describes the fraction of the population that has reached C_y from C_x, stopped there and survived its soil metal concentration during a certain time interval:

$$f^s(C_{xy}) = f(C_{xy}) \times S(C_y).$$

Increased metal excretion efficiency found in collembolans under metal stress indicates that populations may be subject to selection for metal resistance (Van Straalen et al. 1987). The possibility that such a resistance would affect the distribution of *F. fimetarioides* in the experimental gradient is considered by assuming that resistance increased survival essentially by decreasing the slope of the linear relation between survival and metal concentration. Survival of the resistant population in a polluted soil, $S_R(C_y)$, is then expressed as a function of survival of the same population, had it not been resistant, and the

contribution that resistence makes to enhance survival in the given soil: $S_R(C_y) = S(C_y) + C_y \times (b_R - b)$. b_R ranges between 0.0 and b and is defined by $b_R = b \times (1 - R)$, where R, the resistance to metals, ranges between 0.0 and 1.0. As R approaches 1.0, b_R will decrease until the soil metal concentration has no effect on survival. Consequently,

$$S_R(C_y) = S(C_y) + C_y \times (b \times (1 - R) - b) =$$
$$S(C_y) - b \times C_y \times R.$$

As no independent data on the survival of *I. minor* is at hand, we assume that the two species have similar survival rates in unpolluted soil. This assumption is supported by observations made by Tranvik and Eijsackers (1989). Based on relative densities in the field gradient at Gusum, where the numbers of *I. minor* are 2500 individuals m^{-2} at the polluted site (here: C_3) and 5600 individuals m^{-2} at the unpolluted site (C_1) (Bengtsson and Rundgren 1988), the survival of *I. minor* in C_3 is approximated to 40% of the survival in C_1.

If individuals can adjust the direction of movement as a result of their capability to discriminate between habitats of different quality (Tranvik and Eijsackers 1989) and by sensing the direction of quality change, dispersal over a metal concentration gradient and the probability with which individuals move after the first stop may be influenced by this experience. We therefore assume that the probability to stop increases when the animal is confronted with a habitat of a higher metal concentration, $p(0)_{exp} \geq p(0)$. The maximum value of $p(0)$ is 1.0, so $p(0)_{exp}$ ranges between $p(0)$ and 1.0:
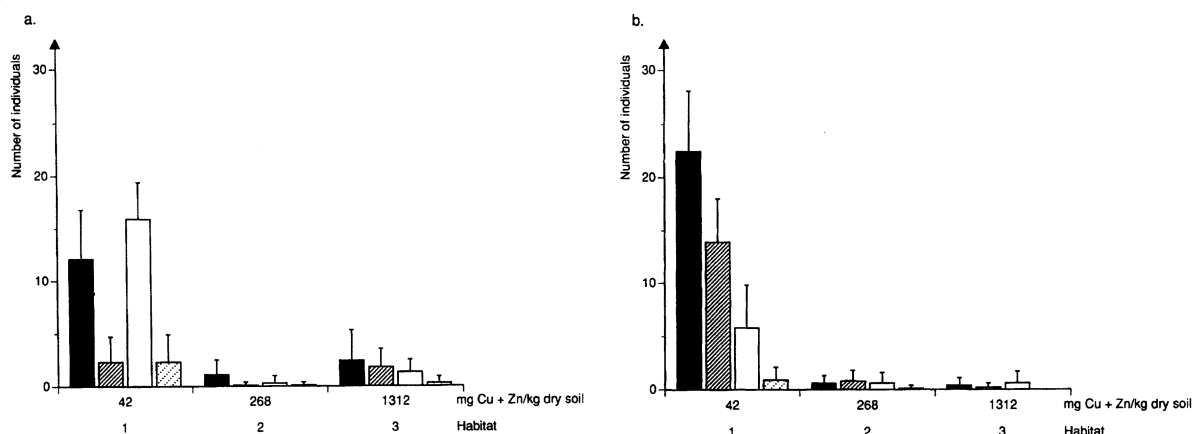
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Fig. 2. Distribution of adult *F. fimetarioides* and *I. minor* in the metal gradients after 2 wk (a) and 10 wk (b) of incubation. Ten specimens of one species or five specimens of each species were initially released in each habitat (see Fig. 1 for the combinations of species in the gradients). Bars represent mean and SD (n = 10).

$$p(0)_{exp} = p(0) + (1 - p(0)) \times \Delta C/(C_{max} - C_{min}),$$

where ΔC is the absolute difference in metal concentration that individuals from a certain habitat have experienced when moving from one habitat to another, whereas C_{min} and C_{max} are the lowest and highest metal concentrations in the gradient. Individuals released in the most polluted habitat have, by definition, a probability zero to stop there, so their experience of approaching habitat 3 from habitat 2 has no influence on $p(0)_{exp}$. Individuals dispersing from habitat 2 will have a previous experience of either a decreasing metal concentration, which will increase $p(0)_{exp}$ with $(1 - p(0)) \times \Delta C/(C_{max} - C_{min})$, or an increasing concentration, which will lower $p(0)$ with $p(0) \times \Delta C/(C_{max} - C_{min})$.

The models were written and implemented in the software package RS/1 (BBN Software Products Corporation, USA). Theoretical and experimental distributions were compared by the non-parametric Kolmogorov-Smirnov test to determine whether or not a model and observations were significantly different. Numbers of Collem-

Table 1. Spatial distribution of surviving juveniles expressed as individuals per inoculated adult (30 adults in separate and 15 of each species in mixed gradients) after 10 weeks of incubation. Mean and SD are given (n = 10).

Metal concentration (mg Cu + Zn/kg dry wt)	Type of gradient	Species	
		F. fimetarioides	I. minor
42	Separate	1.53 ± 1.20	0.14 ± 0.19
	Mixed	1.27 ± 1.10	0.04 ± 0.06
268	Separate	0.03 ± 0.04	0.01 ± 0.02
	Mixed	0.02 ± 0.03	0.01 ± 0.00
1312	Separate	0.01 ± 0.03	< 0.01 ± 0.01
	Mixed	0.01 ± 0.03	0

bola in different treatments were compared using a t-test or an ANOVA.

Results

Population persistence and dispersal distribution

After 2 wk of incubation 50–60% of the individuals persisted in the gradients when the species were kept separately and another 25–30% disappeared when *I. minor* and *F. fimetarioides* were mixed (Fig. 1). Even fewer *I. minor* were left after 10 wk, whereas the *F. fimetarioides* population had increased, resulting in a significant (t-test, p < 0.001) difference in persistence of the two species. Fewer *I. minor* were recovered when reared together with *F. fimetarioides* than when they were kept separately, both after 2 and 10 wk, whereas the number of *F. fimetarioides* observed after 10 wk in presence of *I. minor* was the greatest recorded.

The spatial distributions of *I. minor* were similar after 2 and 10 wk (Fig. 2). The distribution pattern of *F. fimetarioides* differed, however, between the two sampling occasions, and more specimens were found in habitat 3 after 2 wk than after 10 wk when they were kept separately (Kolmogorov-Smirnov two-sample test p < 0.01) and when mixed with *I. minor* (Kolmogorov-Smirnov, p < 0.001). This difference suggests that *F. fimetarioides* either responded slower than *I. minor* to high concentrations of copper and zinc and/or dispersed slower along the gradient. Also, a significantly higher proportion of *F. fimetarioides* stayed in the most polluted soil after 2 wk in the presence of *I. minor* than in its absence (Kolmogorov-Smirnov, p < 0.05). Interspecific competition for resources, for example preferred fungal species, should be more intense during the first weeks

F. fimetarioides from an unpolluted site
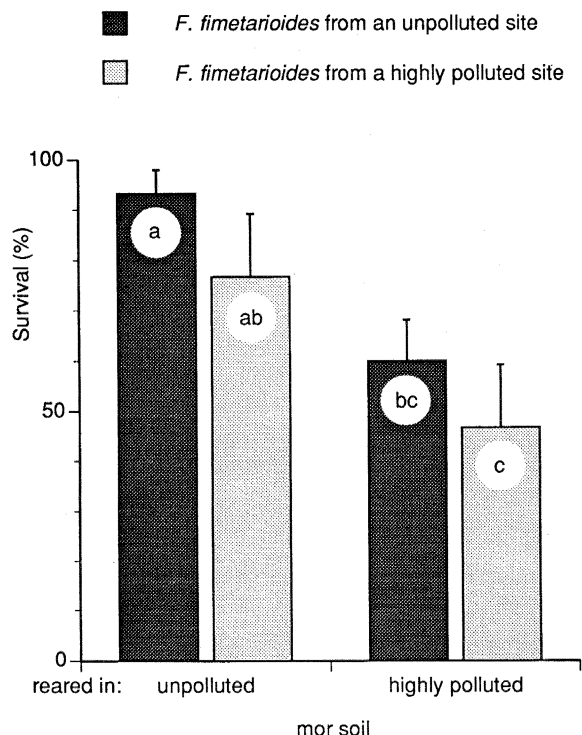
F. fimetarioides from a highly polluted site

Fig. 3. Survival (mean, SD) of adult *F. fimetarioides* sampled at an unpolluted and a highly polluted field site after 9 wk of incubation in 10 ml of either soil (n = 3). Different letters indicate significant difference (ANOVA F = 8.2 p = 0.008).

Persistence of F. fimetarioides

Both populations of *F. fimetarioides* were reduced by approximately 35% in polluted soil compared with the unpolluted one (Fig. 3). The population deriving from the polluted field site was, however, superior in both types of soil with respect to reproduction and produced 2.5 times more juveniles than the population from the unpolluted site in unpolluted soil (Fig. 4). The population from the unpolluted site completely ceased to reproduce when reared in soil from the polluted site, whereas the population from the polluted site produced almost three juveniles per ten adults.

Predicted dispersal distributions

The distribution of collembolans dispersing in the gradient in a linear response to the metal concentration depends on the probability to stop, p(0) (Fig. 5a). With p(0) = 0.0 the greatest number of individuals will be found in the most polluted habitat, but as p(0) approaches 1.0 more individuals tend to stop in habitats 1 and 2. Under the assumption of $p(C_x)$ decreasing linearly with increasing metal concentration, the aggregation of individuals in habitat 2 was the result of two circumstances, namely the relatively small difference in metal concentration between habitat 1 and 2 and the restricted number of habitats the animals faced on their one-way trip. When the probability to stop decreased exponentially with in-

since more *I. minor* were found in habitat 1 after 2 than after 10 wk and the outcome of competition is assumed to be density dependent. Assuming that the fungus grows continuously, replacing devoured biomass, during the whole incubation time, this would lead to a higher percentage of *F. fimetarioides* in habitat 3. Since most survivors aggregated in the least polluted habitat, population density in that habitat increased by 20% *(F. fimetarioides)* and 50% *(I. minor)* relative to the densities at start.

Few juvenile *F. fimetarioides* (0.4 ± 0.7) were found after 2 wk of incubation, but after 10 wk their numbers had increased by at least three times, to 1.5 juvenile per introduced adult (Table 1). 97% of the juveniles were found in the unpolluted soil. Juvenile *F. fimetarioides* were ten times more numerous along the gradient than juvenile *I. minor* (ANOVA F = 8.95 p = 0.0001). No interspecific effect on the distribution of juveniles was observed in either species after 10 wk. The reproduction of *I. minor* almost ceased when reared together with *F. fimetarioides,* while the latter species still produced 1.3 juveniles per adult. It should, however, be noted that *I. minor* is more sensitive to handling, which may partly explain the discrepancy between its dominance in the unpolluted field sites and its low persistence in the simulated gradients.
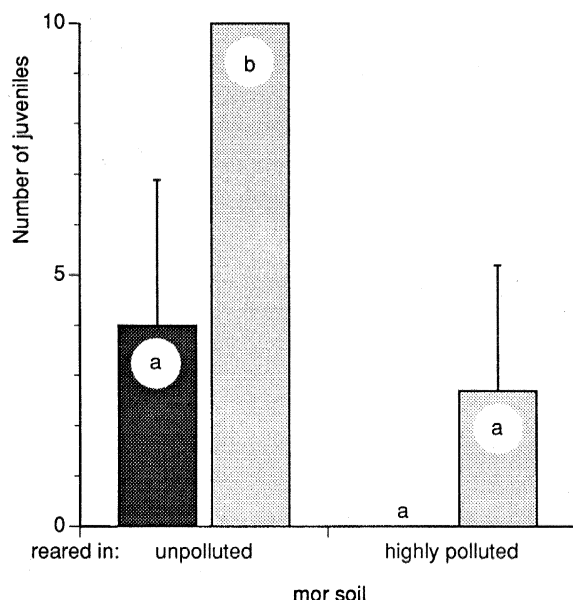

Fig. 4. The total number of surviving juvenile *F. fimetarioides* produced by 10 adults deriving from an unpolluted and a highly polluted field site after 9 wk of incubation in soil from either site (see legends Fig. 3). Bars show mean and SD (n = 3). Different letters indicate significant difference (ANOVA F = 9.6 p = 0.005).
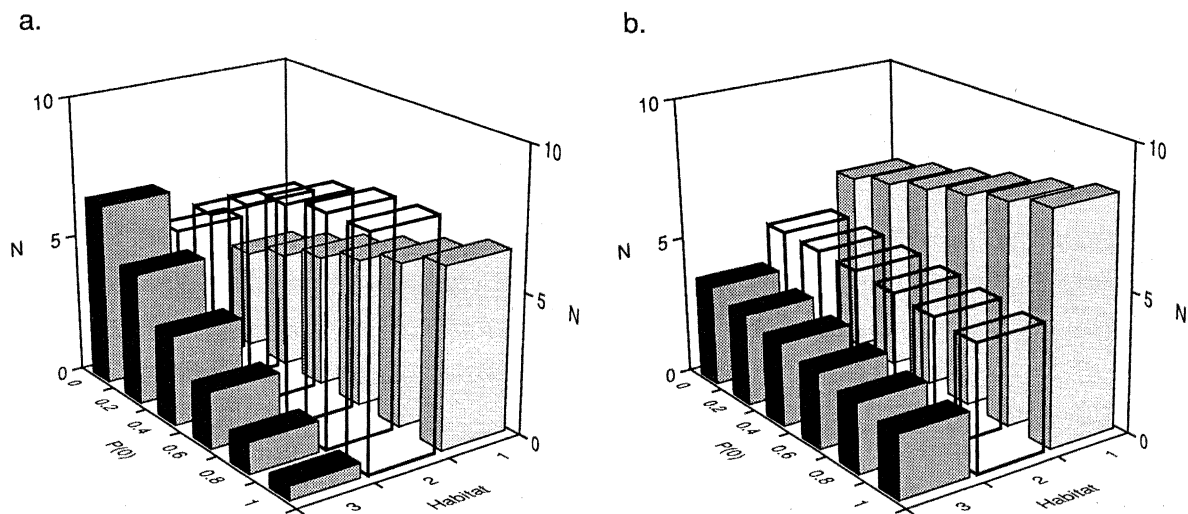
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a.

b.

Fig. 5. Distribution of collembolans in a metal gradient (habitat 1: 42, habitat 2: 268, habitat 3: 1312 mg Cu + Zn/kg dry wt) as a function of the probability to stop, p(0), in the habitat where they were released. p(0) is assumed to decrease linearly (a) or exponentially (b) with metal concentration. The distributions were obtained by the release of five specimens of either species in each habitat.

creasing metal concentration, variations in p(0) had only a marginal influence on the dispersal distribution (Fig. 5b). Since this dispersal mode reinforces the effect of small increases of metal concentration on the probability to stop and weakens the effect of large ones, more individuals will stop in the least polluted habitat (1) than they would if a linear dispersal mode was adopted.

Interspecific competition would tend to force *F. fimeta-*

rioides to move to the most polluted soil. When for instance $p(C_x)$ for both species decreases exponentially in response to metal concentration and $p(0) = 0.9$, the abundance of *F. fimetarioides* will increase in habitat 3 and decrease in habitat 1 as the competition coefficient, α, approaches 1.0 (Fig. 6). However, if the observed survival of mixed *F. fimetarioides* and *I. minor* is considered (Fig. 1a), competition makes less difference to the dispersal distribution of *F. fimetarioides* along the gradient.
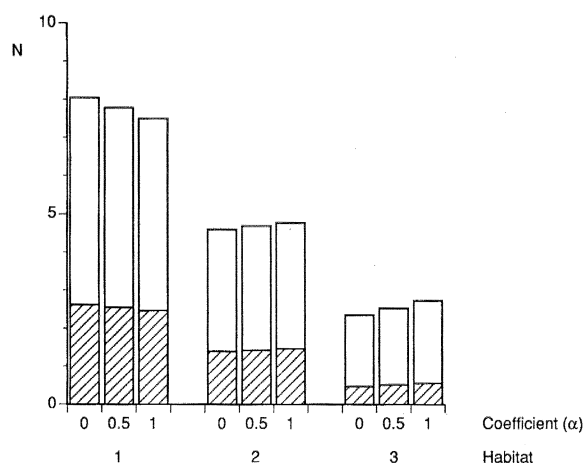

Fig. 6. Simulated distribution of persisting *F. fimetarioides* in a metal gradient when affected by competition and when $p(0) = 0.9$ and $p(C_x)$ decreases exponentially with increasing metal concentration (whole bars). The interspecific competition with *I. minor* is expressed by a competition coefficient, α, that varies between 0.0 and 1.0. Hatched part of bars shows the distribution after dispersal and mortality (values for *F. fimetarioides* after 2 wk of incubation in gradients together with *I. minor* are used (Fig. 1a)).
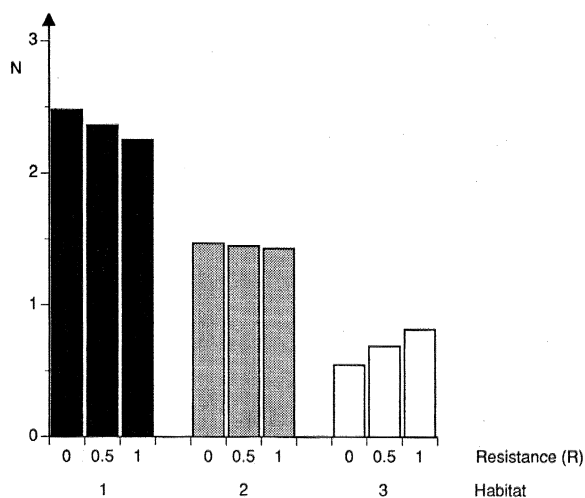

Fig. 7. Simulated distributions of three collembolan populations differing in metal resistance (R = 0.0, 0.5, 1.0) and subject to dispersal and habitat specific mortality in the soil gradient. The survival of *F. fimetarioides* in the gradient after 2 wk in the presence of *I. minor* (Fig. 1a) is used to run the model. P(0) = 0.9 and $p(C_x)$ decreases exponentially with metal concentration.
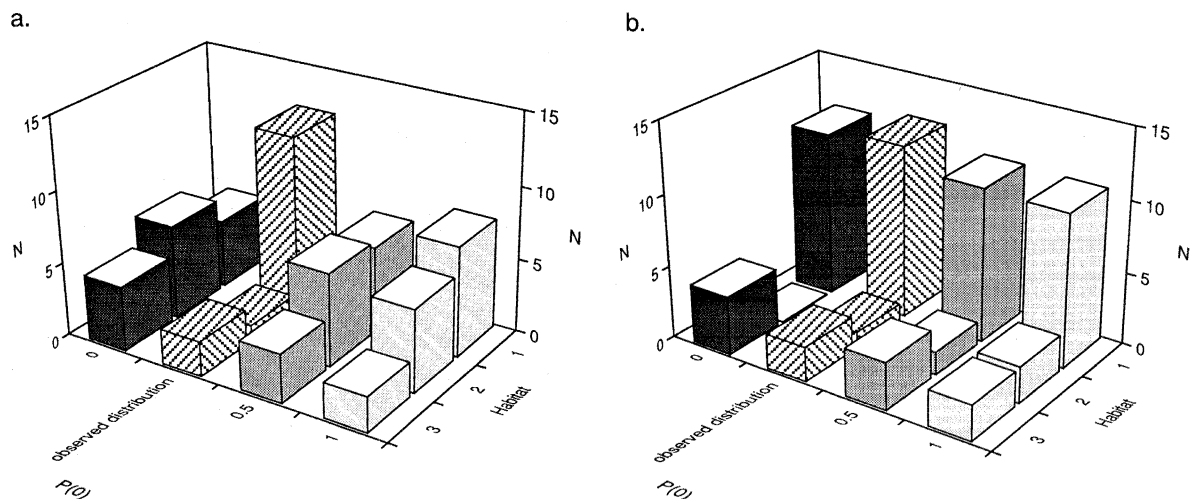
Fig. 8. Observed distribution of *F. fimetarioides* after 2 wk of incubation in a one-species gradient compared with the simulated distributions in which the individuals were allowed to disperse twice. It is assumed that their second dispersal was independent of (a) or dependent on (b) earlier experiences gained in the metal gradient. $P(C_x)$ decreases exponentially with metal concentration and resistance (R) is 0.0.

Competitive reduction of *F. fimetarioides* in habitat 1 will be compensated for by immigration of individuals from habitats 2 and 3, where metal concentrations rather than competition have a major impact on dispersal.

From the independent data in Fig. 3, survival of *F. fimetarioides* originating from the unpolluted field site and incubated in unpolluted soil (corresponding to habitat 1) or highly polluted soil (corresponding to habitat 3) was determined to $S(C_1) = 0.933$ and $S(C_3) = 0.600$, respectively. As a linear relation was assumed between survival and metal concentration the constants a and b could be calculated (a = 0.944 and b = -2.622×10^{-4}), and the survival in C_2 estimated to 0.874. If the same proportionality between $S(C_y)$ was assumed to hold for the survival of *F. fimetarioides* in the gradient experiments, the mortality observed after 2 wk of incubation (Fig. 1a) could be partitioned between the habitats. These values were used

to predict the distribution of individuals that survived after dispersing to a certain habitat with a probability that decreased with its metal concentration (Fig. 7). Metal resistance will tend to change the survival proportionality so that equal numbers of individuals survive in all habitats when R = 1.0. Consequently, resistance will redistribute the individuals towards the most polluted habitat, and the ratio of individuals in habitat 1 to those in habitat 3 will decrease by nearly 50% as R increases from 0.0 to 1.0 (Fig. 7). Resistance could also be expressed as an enhanced production or survival of offspring rather than as an increased survival of adults, as indicated by the experiment with *F. fimetarioides*. This would result in the rather inconsistent values of R for the best fitting simulations.

Individuals that disperse and settle in a habitat, where they survive for a certain period of time, will eventually

Table 2. Values of simulation variables for the best fit between observed and predicted distributions (Kolmogorov-Smirnov). The best fitting model includes dispersal, mortality and a second dispersal using gained experience in all cases and p(0) decreasing exponentially with metal concentration. N is the total number of surviving individuals in all replicates of the experimental distributions, D the Kolmogorov-Smirnov test statistics, and p the probability that predicted and observed distributions are identical. The predicted distributions differ in the probability to stop where released, p(0), interspecific competition, α, and resistance to metals, R.

Type of gradient	Time (wk)	Species	N	D	p	p(0)	α	R
Separate	2	*I. minor*	158	0.16800	<0.01	0.0	–	1.0
		F. fimetarioides	156	0.07115	ns	0.3	–	1.0
Separate	10	*I. minor*	70	0.13286	ns	0.4	–	1.0
		F. fimetarioides	235	0.22723	<0.01	0.0	–	1.0
Mixed	2	*I. minor*	26	0.14154	ns	0.2	–	0.0
		F. fimetarioides	36	0.15778	ns	0.0	0.2	0.0
Mixed	10	*I. minor*	10	0.22090	ns	0.5	–	0.0
		F. fimetarioides	149	0.21007	<0.01	0.4	0.0	1.0

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disperse again. If we let the survivors disperse and stop in a habitat with a probability that decreases with increasing metal concentration of the habitat, the distribution of the dispersal distances will vary with $p(0)$. When the probability to stop is maximal, most individuals will settle in habitat 1 and fewest in habitat 3, whereas most individuals will be found in habitat 2 when $p(0) = 0.0$ (Fig. 8a). This makes sense since most survivors were associated with habitat 1. If $p(0) = 1.0$ few survivors will leave habitat 1, whereas if $p(0) = 0.0$ most survivors will leave their habitat and stop in the adjacent one. However, regardless of the value chosen for $p(0)$, the theoretical distributions inadequately describe the observed distribution of *F. fimetarioides* after 2 wk of incubation. When the stopping probability of the second dispersal event was guided by the steepness of the metal concentration gradient experienced by the individual after the first stop, the majority of the collembolans would be found in habitat 1 and the minority in habitat 2, regardless of $p(0)$ (Fig. 8b). This mode of dispersal gave a distribution of dispersal distances that was close to that observed for *F. fimetarioides* after 2 wk (Fig. 8b), as well as to those observed for all combinations of species and incubation times (Table 2). The observed dispersal distances were generally best described by $p(0) < 0.5$, indicating that both species had a high tendency to disperse in the gradient under the conditions examined. The competition component required to describe dispersal of *F. fimetarioides* in combination with *I. minor* was weak, whereas dispersal distances of *F. fimetarioides* could only be described in conjunction with a strong resistance component (Table 2). The exception was the distribution of *F. fimetarioides* after 2 wk in the presence of *I. minor*, when the survivors were too few at any rate to indicate any metal resistance.

Discussion

Species distributions along a gradient of some environmental variable may be controlled by proximate factors, for instance present interactions with other species, or ultimate factors, for instance past adaptations to a range of levels of an environmental variable. If the distributions of *I. minor* and *F. fimetarioides* in the gradient of metal concentrations are controlled by interspecific interactions, each species would be expected to occupy the less polluted range of habitats in large numbers in the absence of the other. If, on the other hand, the distributions are a consequence of adaptation to a particular range of the environmental variable, the distribution of one species would be independent of the other. The experiments with the condensed soil gradient indicate that the distributions are, at least to some extent, controlled by proximate factors as well as ultimate. The factors enhancing mortality of *I. minor* in the presence of *F. fimetarioides* and vice versa and reducing abundance of *F. fimetarioides* in habitat 1 compared with habitat 3 in the presence of *I. minor*

are unknown. The different distributions of *F. fimetarioides* in the presence and absence of *I. minor* may result from competition, as anticipated in the model of the distribution of dispersal distances. The contribution of the competition coefficient, α, to the theoretical distribution pattern of *F. fimetarioides* was, however, small (Table 2), perhaps reflecting the low numbers of rather evenly distributed *I. minor* along the gradient. Competition was further relaxed after 10 wk of incubation, probably as a result of the low numbers of *I. minor*. Intraspecific competition was not addressed by the model or in the experiment but has been implicated as a driving force for dispersal of some avian and mammalian species (Waser 1985).

A significant adaptive control of the distributions was also observed with twice as many *F. fimetarioides* as *I. minor* residing in the most polluted habitat after 2 wk of incubation independent of absence or presence of the other species (Fig. 2a). The model, which calculated the abundance of *F. fimetarioides* based on data on survival of the population collected in the unpolluted field soil, clearly addresses this phenomenon, since the best description of the distribution of dispersal distances is achieved at a maximum of metal resistance (Table 2). Resistance also effectively explains the distribution of *I. minor*, but the result may be biased by the indirect method of estimating the survival rate of this species from its relative abundance in the field. The evolutionary consequences of the field gradient on the distribution of *F. fimetarioides* are demonstrated by the independent study of survival. The populations visualized in Fig. 4 can be taken to represent two distinct phenotypes adapted to either of the two extreme, coarse-grained environments in the field gradient. However, within each of the extremes but especially within the polluted site, the animals experience a mosaic of fine-grained patches with respect to metal concentration. We can expect that a population at the polluted site will be monomorphic if the difference in metal concentration between the fine-grained patches is small and polymorphic if the habitat is more diverse, as generally shown by Levene (1953). Even if patches of low metal concentrations would be rare within the polluted habitat, the capability of *F. fimetarioides* to perceive concentration differences could help it to reduce the selection pressure by moving, resulting in genetic changes that are suboptimal for the average metal concentration of the habitat.

The dispersal tendency clearly overrides both competition and metal adaptation as a factor controlling the distribution of collembolans in the experimental gradient. The probability to settle in the habitat where released is generally < 0.5 (Table 2), indicating that both species are exploratory rather than sedentary. The high dispersal tendency is not simply a consequence of an instantaneous escape from experimental manipulations since the distribution after 10 wk, when juveniles had hatched in the gradient, is similar to that after 2 wk. Both species seem to lay their eggs in the least polluted soil available or the

juveniles themselves find their way there. Presence of the other species reduces reproduction and/or juvenile persistence in both species, the most in *I. minor,* where only 1/3 as many juveniles were found in gradients with two species. Since the number of adult *F. fimetarioides* increased in both types of gradients, some early hatched juveniles must have reached adult size. This means that the difference between the two species in reproductive rate is even greater than observed from the number of juveniles.

The dispersal behaviour of collembolans in an environmental gradient of the kind described is apparently not a simple function of the characteristics of a specific site of the gradient, site-related mortality rates, or adaptation to a gradient range, but a combination of these factors and a system for receiving information about the steepness of the gradient through one or more receptor systems. The animals process this information into a prediction of future environments and respond to the prediction by adjusting the direction and rate of dispersal. This tendency for active dispersal will reduce the effects of selection for variable gradient conditions at a site explored in a fine-grained manner. Directional changes to selection in a specific patch will likely be ephemeral, and as animals move among the patches, local adaptive modifications, for example, to patches with low metal concentrations in environments with high average concentrations, will tend to be washed out. It is, however, doubtful whether an active dispersal, without a vector, of soil-living collembolans will suffice to influence selection for metal resistance along a field gradient of several km in distance. Potential dispersal vectors, such as moles, badgers, and small microtine rodents, may be helpful in accidental long-distance (from the Collembola point of view) dispersal, and constrain adaptive improvements especially in low-density populations at the most stressful end of a gradient.

The combination of a model for the theoretical distribution of dispersal distances and a microcosm simulating an environmental gradient offers an opportunity to gain a better understanding of the ecological and evolutionary factors underlying dispersal across habitats varying in one or more quality characteristics. This study demonstrates that adaptation and behavioural quality assessment influence the probability to stop in an experimental gradient of environmental stress. Such information is also useful in adopting dispersal patterns of soil animals as a potential tool in environmental hazard assessment.

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