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Population-level consequences of spatially heterogeneous exposure to heavy metals in soil: An individual-based model of springtails

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A B S T R A C T

Contamination of soil with toxic heavy metals poses a major threat to the environment and human health. Anthropogenic sources include smelting of ores, municipal wastes, fertilizers, and pesticides. In assessing soil quality and the environmental and ecological risk of contamination with heavy metals, often homogeneous contamination of the soil is assumed. However, soils are very heterogeneous environments. Consequently, both contamination and the response of soil organisms can be assumed to be heterogeneous. This might have consequences for the exposure of soil organisms and for the extrapolation of risk from the individual to the population level. Therefore, to explore how soil contamination of different spatial heterogeneity affects population dynamics of soil invertebrates, we developed a spatially explicit individual-based model of the springtail, *Folsomia candida*, a standard test species for ecotoxicological risk assessment. In the model, individuals were assumed to sense and avoid contaminated habitat with a certain probability that depends on contamination level. Avoidance of contaminated areas thus influenced the individuals' movement and feeding, their exposure, and in turn all other biological processes underlying population dynamics. Model rules and parameters were based on data from the literature, or were determined via pattern-oriented modelling. The model correctly predicted several patterns that were not used for model design and calibration. Simulation results showed that the ability of the individuals to detect and avoid the toxicant, combined with the presence of clean habitat patches which act as "refuges", made equilibrium population size due to toxic effects less sensitive to increases in toxicant concentration. Additionally, the level of heterogeneity among patches of soil (i.e. the difference in concentration) was important: at the same average concentration, a homogeneously contaminated scenario was the least favourable habitat, while higher levels of heterogeneity corresponded to higher population growth rate and equilibrium size. Our model can thus be used as a tool for extrapolating from short-term effects at the individual level to long-term effects at the population level under more realistic conditions. It can thus be used to develop and extrapolate from standard ecotoxicological tests in the laboratory to ecological risk assessments.

1. Introduction

Heavy metals are common soil contaminants resulting from anthropogenic activities such as smelting of ores, municipal wastes, use of fertilizers and pesticides (Leyval et al., 1997; Nursita et al., 2005). They pose a major threat to the continued capacity of soil to sustain its biological productivity, maintain the quality of the surrounding air and water environments, and promote plant, animal, and human health (Doran et al., 1996). To accurately evaluate this threat, just determining the total metal concentrations in soils is not sufficient since some of the metal may be in a form that is not available for uptake by organisms (Loureiro and Nogueira, 2005). Bioassays are therefore widely used for accurately assessing soil quality and potential toxicity of contaminants in that they measure the bio-available metal fraction (Boiteau et al., 2011). Standardized soil ecotoxicology tests have been developed using soil-dwelling invertebrates such as earthworms and collembolans (springtails) (Løkke et al., 1998). Collembolans are one of the most abundant groups of arthropods on Earth (Fountain and Hopkin, 2005). They play an important role in ecosystems functioning (Hopkin, 1997) and are vulnerable to soil contamination (Fountain and Hopkin, 2005; Crouau et al., 1999). The abundance and diversity of

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collembolans have been widely used to assess the environmental impacts of a range of pollutants on soils (Fountain and Hopkin, 2005; Crouau et al., 1999).

In particular, interest in the collembolan *Folsomia candida* Willem 1902 has been increasing in recent years. It is a very common species and has been found in a variety of habitats including soil, caves and glasshouses. *F. candida* has been used extensively as a model arthropod in many ecological and evolutionary studies (see Hopkin, 1997 and references therein). Moreover, it is used as a standard test organism for toxicity tests: a 28-day reproduction test (ISO, 1999; OECD, 2009) is included in the refinement options for ecological risk assessment of plant protection products to soil organisms (EC, 2009). However, one of the limitations of virtually all-standard toxicity tests with soil organisms is that soil contamination is assumed to be homogeneous, whereas the heterogeneous nature of soil is well known. Spatial heterogeneity in soils occurs at widely different scales, from continental and regional to micro aggregates within specific soil horizons. Common soil properties such as clay and organic matter concentrations often show clearly defined spatial patterns that vary depending on the scales at which they are considered (Lavelle and Spain, 2001). Moreover, contamination of soils is heterogeneous as well because the distribution of chemicals in soil depends on the source of contamination (i.e., point vs. non-point source) and on specific soil properties that result in different interactions between chemicals and soil particles.

Studies exploring the ecological relevance of local variability in soil conditions are rare. Palmqvist and Forbes (2008) examined the influence of contaminant spatial heterogeneity in sediment systems and found that contaminant hotspots led to lower equilibrium population sizes and longer recovery times compared to homogeneously contaminated sediment, despite that the total amount of contamination in the former scenario was less than the latter. Understanding such effects and predicting the consequences of spatially heterogeneous contamination are not straightforward. On the one hand, unpolluted patches in a matrix of polluted soil can be beneficial in order to sustain metapopulations. However, if soil organisms actively aggregate in unpolluted patches, and if such patches are small, density can become too high to sustain local populations.

Several studies have been conducted to investigate avoidance behaviour of *F. candida* in the presence of heterogeneously contaminated soil, and have had mixed results. For instance, *F. candida* does not avoid naphthalene (Boitaud et al., 2006), while (Aldaya et al., 2006) observed a good correlation between avoidance and toxicity for substrates with a high content of polycyclic aromatic hydrocarbon (PAH) compounds. Greenslade and Vaughan (2003) compared avoidance and reproduction for soils with heavy metal contamination and found that some substances, such as cadmium salts, were not perceived as repellent, and therefore were not avoided, whereas other metals, such as inorganic copper, were avoided by *F. candida* at concentrations below those having effects on reproduction. Similarly, Filser and Holscher (1997) observed that *F. candida* is capable of discriminating between Cu-contaminated and uncontaminated areas. A 2-day avoidance test with collembolans has also been proposed as an early screening tool to assess toxic effects of chemicals and soil contamination (da Luz et al., 2004).

To obtain a more comprehensive understanding of how behavioural responses such as avoidance affect population dynamics, population structure, and distribution of individuals in soils with heterogeneous contamination, population models can help to overcome the logistical constraints of short-term laboratory experiments. We therefore developed an individual-based model of laboratory populations of *F. candida* in heterogeneously contaminated soils. We used copper sulphate ($CuSO_4$) as a model contaminant. It is proven to have toxic effects on *F. candida* survival and reproduction, and to elicit behavioural responses like avoidance (Boiteau et al., 2011). Moreover, it is the main ingredient of Bordeaux mixture, a commonly used fungicide (Barker and Gimingham, 1911).

Our model, incorporating information on behaviour and life history, is designed to represent *F. candida* realistically enough to be used for evaluating and improving standard ecotoxicological tests based on this species. Parameter values were taken directly from the literature or determined inversely by making the model reproduce several patterns observed in laboratory populations at different scales and levels of biological organization ("pattern-oriented modelling"; Grimm et al., 2005; Grimm and Railsback, 2012; Railsback and Grimm, 2012). The structural realism of the model, i.e. its ability to make valid independent predictions, was tested. In this paper we focus on the design, parameterization, and understanding of the model, and present first results regarding the population-level effects of different levels of heterogeneity in soil contamination. More specific analyses related to ecotoxicological tests will be published elsewhere.

2. Methods

2.1. Biological background

The genus *Folsomia* includes species in the family *Isotomidae* that have a well-developed furca (springing organ), no anal spines, and an abdomen with the posterior three segments fused (Fountain and Hopkin, 2005). Like all other collembolans, *F. candida* has a pair of thin-walled, closely apposed, eversible vesicles on the ventral side of the first abdominal segment. This structure is commonly known as the ventral tube, or collophore, and is involved in fluid exchange with the external environment (Hopkin, 1997). The ventral tube is an important exposure route for chemicals dissolved in soil pore water (Lock and Janssen, 2003). Mature individuals of *F. candida* are 1.5–3.0 mm long; the species feeds preferably on fungal hyphae, and populations exclusively consist of parthenogenetic females. The species can inhabit caves and mines, agricultural systems, soils with a high level of organic matter, forests, and the edges of streams. *F. candida* is occasionally the dominant collembolan, and population densities commonly reach 10^5 m^{-2} in soil and leaf litter layers in many ecosystems. The average lifespan of a female at 15 °C under laboratory conditions is 240 days, but decreases when temperature increases (e.g. lifespan is 111 days at 24 °C: Marshall and Kevan, 1962). At 20 °C females reach sexual maturity around 15–20 days after hatching (Fountain and Hopkin, 2005; Krogh, 2008).

F. candida can be exposed to contaminants via the soil and/or food in a battery of tests that examine life-history parameters, bioaccumulation, and/or effects on behaviour. Such tests are used to assess the toxicity of a wide range of organic and inorganic pollutants and have been used as bioassays to monitor the success of remediation of contaminated soils (Fountain and Hopkin, 2005).

2.2. The model

The model description follows the ODD (Overview, Design concepts, Details) protocol for describing individual-based models (Grimm et al., 2006, 2010). The model was implemented in NetLogo 5.0 (Wilensky, 1999), a free software platform for implementing individual-based models.

2.2.1. Purpose

The purpose of the model is to simulate *F. candida* population dynamics and to investigate how they are affected by spatial distribution of toxic contamination in soil, with a special focus on interactions with food availability and local population density.