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Soil Biology & Biochemistry 38 (2006) 1158–1161

Soil Biology & Biochemistry

www.elsevier.com/locate/soilbio

Short communication

Decreased biodiversity in soil springtail communities: the importance of dispersal and landuse history in heterogeneous landscapes

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Received 28 June 2005; received in revised form 2 September 2005; accepted 13 September 2005
Available online 8 November 2005

Abstract

In previously published papers it had been demonstrated that at the local level the species richness of soil springtail communities was negatively influenced by landuse diversity. When the dispersal rate of soil animals was taken into account, quite opposite trends were displayed by species having poor or high dispersal capabilities. At the local level, species with short legs, non functional jumping apparatus and reduction of visual organs were distinguished against by landuse diversity, while species with long legs, functional jumping apparatus (furcula) and complete eyes, thus able to disperse at the soil surface, were not. It was verified, through aerial photographs taken 50 years ago, that landuse changes, expected to be more frequent in heterogeneous landscapes, may contribute to explain this phenomenon.

Keywords: Landuse intensification; Springtails; Landuse diversity; Dispersal rate

In a previous study conducted within the BioAssess EC program, we have shown that the springtail species richness of core samples (local biodiversity) was inversely related to landuse diversity along a gradient of landuse intensification (Ponge et al., 2003), while an opposite trend was displayed by plant species (Fédoroff et al., 2005). We hypothesized that, in the studied region, heterogeneous landscapes were most subject to changes in landuse history, to which soil animals were lesser adapted than plant forms. To test this hypothesis we decided to revisit our data set, by taking into account the dispersal abilities of the different springtail species, and the landuse changes that occurred over the last half century.

Sampling took place in the Morvan Regional Nature Park (western Burgundy, Centre of France). Six landuse units (LUUs), one square kilometer each, have been chosen on the basis of aerial photographs, taking into account the distribution of forested areas (coniferous, deciduous), meadows and agricultural crops. LLUs 1–6 depicted a gradient of increasing influence of human activities. Soil and climate conditions, as well as landuses, were described in two previously published papers (Ponge et al., 2003; Fédoroff et al., 2005). The distribution of landuse types in the six LUUs is shown in Table 1. In each LUU the diversity of landuse types was expressed by the Shannon Index.

Using aerial photographs, a grid of 16 regularly spaced plots (200 m) was identified in each of the six LUUs. Sampling of Collembola took place in June 2001. Methods used for sampling, extraction, sorting and identification of Collembola at the species level were detailed in Ponge et al. (2003). One sample was discarded for extraction, because of waterlogging at the time of sampling.

Collembolan species were classified in two groups, according to their ability to disperse actively or not (Table 2). Species with long legs and antenna, a developed jumping apparatus (furcula) and complete visual apparatus (8 ocella per eye spot) were considered able to disperse rapidly by their own means (Hopkin, 1997). All other species, because of a reduction in motion or vision organs, were considered as having poor dispersal capabilities. It has been demonstrated that fully functional visual organs allow springtails to move directionally over long distances (Hågvar, 1995). Conversely, springtails showing a reduction in their eye number, even when fully motile, exhibit negative phototaxis and thus cannot disperse easily (Salmon and Ponge, 1998).

Ecological requirements of Collembolan species were derived from the distribution of species over all samples

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0038-0717/$ - see front matter © 2006 Elsevier Ltd. All rights reserved.
doi:10.1016/j.soilbio.2005.09.004

Table 1
Distribution of land use types among the six land use units (LUUs), ordered according to increasing landuse diversity

	LUU 1	LUU 2	LUU 6	LUU 3	LUU 5	LUU 4
Deciduous forest	16	1	0	8	3	0
Coniferous forest	0	14	0	2	2	3
Clear-cut	0	1	0	0	0	1
Hedgerow	0	0	0	0	1	0
Hay meadow	0	0	0	4	4	4
Pasture	0	0	2	1	6	3
Fallow	0	0	5	0	0	1
Arable crop	0	0	9	1	0	3
Not sampled	0	0	0	0	0	1
Shannon Index	0	0.67	1.37	1.88	2.11	2.42

Sixteen samples were taken in each LUU, except LUU 4 with fifteen samples only.

($n=95$), which was studied by multivariate analysis (Ponge et al., 2003). Axis 1 coordinates of correspondence analysis (CA) in Ponge et al. (2003) were used to separate forest from agricultural species (Table 2). It should be noted that the environmental gradient depicted by the first axis of CA was a combination of all factors, which contrasted woodland and agricultural land, humus type included.

Ancient aerial photographs (1948 IGN campaign) were examined for each LUU, in order to identify the landuse type, which prevailed at the place where sampling took place in 2001. Black and white photographs easily distinguished woodland, agricultural land, and hedgerows, but could not be used for finer resolution. Thus, landuse types were gathered into two gross categories, namely woodland (deciduous and coniferous forests) and agricultural land (hay meadows, pastures, arable crops, recent fallows). Hedgerows (one sample) and clear-cuts (two samples) were not taken into account in the census. Afforested land was comprised of 10- to 50-yr-old coniferous plantations (Douglas fir, Norway spruce) and old fields (wooded fallows).

When landuse units were ordered according to increasing landuse diversity (Table 1), the balance between the two springtail categories changed markedly (Fig. 1). Slow-dispersal species were largely dominant in forested areas, decreasing from LUU 1 to LUU 4, while the fast-dispersal species increased. In the most diverse landscape (LUU 4) fast-dispersal and slow-dispersal species were at the same richness level. In areas dominated by agriculture (LUU 5 and LUU 6), slow-dispersal species were also dominant, but to a lower extent than in areas dominated by forests (LUU1 and LUU2). The mean species richness of slow-dispersal Collembola was negatively correlated with landuse diversity ($r=-0.93$, $P=0.003$), while fast-dispersal species were positively, but poorly correlated with landuse diversity ($r=0.68$, $P=0.07$).

Examination of past landuse revealed that some changes took place over the last half century. Eight samples were taken in places where there was a shift from agricultural land to woodland (afforestation), while two samples were taken in places where woodland was replaced by agricultural land (deforestation). Calculation of the impact of landuse change on local species richness of springtail communities was only possible in afforested sites. It revealed a deficit of species richness in sites where agricultural land was afforested (8.4 ± 1.1), compared to stable woodland (13.2 ± 0.6, Mann–Whitney $U=54.5$, $P=0.001$). When springtail species were separated in two dispersal groups, still clearer features appeared. In afforested land, the richness of slow-dispersal species was equal to that of the original agricultural land (i.e. near half that of woodland), while the richness of fast-dispersal species decreased to the level typical of woodland, i.e. near half that of agricultural land. While dominance of slow- over fast-dispersal species was prominent in woodland as well as agricultural land, afforested land displayed the reverse phenomenon. The examination of ecological requirements of species (forest vs. agricultural species) showed that in afforested land fast-dispersal species were shared between forest (57%) and agricultural species (43%), while nearly all slow-dispersal species were still those typical of agricultural soils (88%).

We found that (i) the heterogeneity of the landscape exerted a negative influence on slow-dispersal collembolan species, (ii) at least part of these effects could be explained by time-related processes, acting differentially on organisms with distinct life habits.

Soil collembolan communities are negatively affected by deforestation as well as afforestation and this impact was shown to be durable (Jordana et al., 1987; Deharveng, 1996). The contrast between closed and open habitats is one of the chief complex of factors, which govern the species composition of most soil animal groups (Nordström and Rundgren, 1974; Ponge, 1993). Soil and climate factors are in play in the influence of landuse change on soil animal communities, more especially when agricultural land shifts to woodland, or the reverse. However, in the present state of our knowledge of ecological requirements and dispersal abilities of Collembola, only cursory explanation can be found for the observed changes in species composition and diversity, which are summarized below.

In the present study, the passage from agricultural land to woodland was accompanied by soil acidification (Ponge et al., 2003). In mixed landscapes, the higher acidity of the soil in woody areas is not solely due to the acidifying influence of forest growth (Nilsson et al., 1982) but also to (i) the choice of more fertile (thus less acidic) soils for agriculture and (ii) the fertilization associated with the permanent use of land for agriculture (Brady and Weil, 1999). Soil acidity and associated factors influence the species composition of most soil animal communities (Nordström and Rundgren, 1974; Wauthy, 1982; Ponge, 1993), but they affect primarily species in permanent contact with humified organic matter (Ponge, 1993).

Micro-climate changes affect primarily soil animal species living at the soil surface or not far from it, with agricultural land exhibiting more contrasting thermic and hygric conditions than woodland at the ground surface (Coffin and Urban, 1993). In springtails, it has been demonstrated that the first instar, i.e. the first stage of development following egg hatching, was more sensitive to desiccation that further instars and that this phenomenon was more pronounced in woodland than in agricultural land species (Betsch and Vannier, 1977).