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

Jean-François Ponge, Florence Dubs, Servane Gillet, José Paulo Sousa, Patrick Lavelle

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

Jean-François Ponge*[1], Florence Dubs[2], Servane Gillet[1], Jose Paulo Sousa[3], Patrick Lavelle[2]

[1]*Muséum National d'Histoire Naturelle, CNRS UMR 5176, 4 avenue du Petit-Chateau, 91800 Brunoy, France*

[2]*Institut de Recherche pour le Développement, UMR 137 BioSol, 32 rue Henri Varagnat, 93143 Bondy Cédex, France*

[3]*Universidade de Coimbra, Instituto do Ambiente e Vida, Lg. Marquês de Pombal, 3004-517 Coimbra, Portugal*

* Correspondence: Jean-François Ponge, Muséum National d'Histoire Naturelle, CNRS UMR 5176, 4 avenue du Petit-Chateau, 91800 Brunoy, France. E-mail: jean-francois.ponge@wanadoo.fr

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 aparatus 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 fifty 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 to 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 (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).

Slow-dispersal Collembola, contrary to fast-dispersal species, are favoured by forest environments. Most of them need a protection towards desiccation, because they are badly equipped for jumping rapidly from a micro-site to another in a changing environment (Bauer and Christian, 1987). Most species classified in the slow-dispersal category are soil-dwelling species, to the exception of small surface species, such as *Xenylla* spp. and *Brachystomella parvula*, which live under the protection of mosses and lichens or exhibit anhydrobiosis (André, 1976; Poinsot-Balaguer, 1976).

In a complex landscape where forest and agricultural land are intimately mixed, two categories of underground biodiversity should be considered apart: those organisms which are able to disperse at the scale of landscape heterogeneity (these communities will be positively or not affected by heterogeneity, here fast-dispersal springtails), and those unable to do that, which will be negatively affected except those tolerant of landuse changes. Examination of literature shows that most springtail species which are considered of particular interest, because they are endemic or rare, fall into the slow-dispersal category, thus are threatened by landuse changes (Barrocas et al., 1998; Deharveng, 1996; Lauga-Reyrel and Deconchat, 1999).

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References

André, H., 1976. Introduction à l'étude écologique des communautés de microarthropodes corticoles soumises à la pollution atmosphérique. Bulletin d'Écologie 7, 431-444.

Barrocas, H.M., da Gama, M.M., Sousa, J.P., Ferreira, C.S., 1998. Impact of reafforestation with *Eucalyptus globulus* Labill. on the edaphic collembolan fauna of Serra de Monchique (Algarve, Portugal). Miscellània Zoològica 21.2, 9-23.

Bauer, T., Christian, E., 1987. Habitat dependent differences in the flight behaviour of Collembola. Pedobiologia 30, 233-239.

Betsch, J.M., Vannier, G., 1977. Caractérisation de deux phases juvéniles d'*Allacma fusca* (Collembole, Symphypleona) par leur morphologie et leur écophysiologie. Zeitschrift für Zoologische Systematik und Evolutionsforschung 15, 124-141.

Brady, N.C., Weil, R.R., 1999. The Nature and Properties of Soils, 12th edn. Prentice Hall, Upper Saddle River.

Coffin, D.P., and Urban, D.L., 1993. Implications of natural history traits to system-level dynamics: comparisons of a grassland and a forest. Ecological Modelling 67, 147-178.

Deharveng, L., 1996. Soil Collembola diversity, endemism, and reforestation: a case study in the Pyrenees (France). Conservation Biology 10, 74-84.

Fédoroff, E., Ponge, J.F., Dubs, F., Fernández-González, F., Lavelle, P., 2005. Small-scale response of plant species to land-use intensification. Agriculture, Ecosystems and Environment 105, 283-290.

Hågvar, S., 1995. Long distance, directional migration on snow in a forest collembolan, *Hypogastrura socialis* (Uzel). Acta Zoologica Fennica 196, 200-205.

Hopkin, S.P., 1997. Biology of the Springtails. Oxford University Press, Oxford.

Jordana, R., Arbea, J.I., Moraza, L., Montenegro, E., Mateo, M.D., Hernandez, M.A., Herrera, L., 1987. Effect of reafforestation by conifers in natural biotopes of middle and South Navarra (Northern Spain). Revue Suisse de Zoologie 94, 491-502.

Lauga-Reyrel, F., Deconchat, M., 1999. Diversity within the Collembola community in fragmented coppice forests in south-western France. European Journal of Soil Biology 35, 177-187.

Nilsson, S.I., Miller, H.G., Miller, J.D., 1982. Forest growth as a possible cause of soil and water acidification: an examination of the concepts. Oikos 39, 40-49.

Nordström, S., Rundgren, S., 1974. Environmental factors and lumbricid associations in southern Sweden. Pedobiologia 14, 1-27.

Poinsot-Balaguer, N., 1976. Dynamique des communautés de Collemboles en milieu xérique méditerranéen. Pedobiologia 16, 1-17.

Ponge, J.F., 1993. Biocenoses of Collembola in atlantic grass-woodland ecosystems. Pedobiologia 37, 223-244.

Ponge, J.F., Gillet, S., Dubs, F., Fédoroff, E., Haese, L., Sousa, J.P., Lavelle, P., 2003. Collembolan communities as bioindicators of landuse intensification. Soil Biology and Biochemistry 35, 813-826.

Salmon, S., Ponge, J.F., 1998. Responses to light in a soil-dwelling springtail. European Journal of Soil Biology 34, 199-201.

Wauthy, G., 1982. Synecology of forest soil oribatid mites of Belgium (Acari, Oribatida). III. Ecological groups. Acta Oecologica, Oecologia Generalis 3, 469-494.

Table 1. Distribution of land use types among the six land use units (LUUs), ordered according to increasing landuse diversity. Sixteen samples were taken in each LUU, except LUU 4 with fifteen samples only

	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

Table 2. List of collembolan species found in the study sites, classified according to their ability ot disperse (estimated by appendage and eye development). F = forest species. A = agricultural species

Slow-dispersal		Fast-dispersal	
A	*Anurida granaria*	F	*Allacma fusca*
A	*Anurida uniformis*	A	*Deuterosminthurus sulphureus*
F	*Arrhopalites bifidus*	A	*Dicyrtoma fusca*
F	*Arrhopalites sp.*	A	*Dicyrtomina minuta*
A	*Brachystomella parvula*	A	*Dicyrtomina ornata*
F	*Ceratophysella armata*	A	*Entomobrya multifasciata*
A	*Ceratophysella denticulata*	F	*Entomobrya nivalis*
F	*Ceratophysella luteospina*	A	*Fasciosminthurus quinquefasciatus*
A	*Cyphoderus albinus*	A	*Isotoma antennalis*
A	*Folsomia candida*	A	*Isotoma tigrina*
A	*Folsomia fimetaria*	A	*Isotoma viridis*
F	*Folsomia quadrioculata*	A	*Isotomurus palustris*
F	*Friesea claviseta*	A	*Lepidocyrtus cyaneus*
F	*Friesea mirabilis*	F	*Lepidocyrtus lanuginosus*
F	*Friesea truncata*	A	*Lepidocyrtus lignorum*
A	*Heteromurus nitidus*	F	*Lipothrix lubbocki*
F	*Isotomiella minor*	F	*Orchesella cincta*
F	*Isotomodes productus*	A	*Orchesella quinquefasciata*
A	*Kalaphorura burmeisteri*	A	*Orchesella villosa*
F	*Megalothorax minimus*	F	*Pogonognathellus flavescens*
F	*Mesaphorura betschi*	F	*Pseudisotoma sensibilis*
F	*Mesaphorura jevanica*	A	*Sminthurides parvulus*
F	*Mesaphorura leitzaensis*	A	*Sminthurides schoetti*
F	*Mesaphorura macrochaeta*	A	*Sminthurinus aureus*
F	*Mesaphorura yosii*	A	*Sminthurinus niger*
F	*Micranurida pygmaea*	F	*Sminthurinus signatus*
F	*Micranurida sensillata*	A	*Sminthurus nigromaculatus*
F	*Micraphorura absoloni*	A	*Sminthurus viridis*
F	*Neanura muscorum*	A	*Sphaeridia pumilis*
F	*Neelides minutus*	A	*Stenacidia violacea*
A	*Neotullbergia ramicuspis*	F	*Tomocerus minor*
F	*Oncopodura crassicornis*	F	*Vertagopus arboreus*
F	*Onychiuroides pseudogranulosus*	A	*Willowsia nigromaculata*
F	*Onychiurus cebennarius*		
A	*Onychiurus jubilarius*		
F	*Paratullbergia callipygos*		
A	*Parisotoma notabilis*		
F	*Proisotoma minima*		
A	*Protaphorura armata*		
A	*Protaphorura meridiata*		
A	*Protaphorura prolata*		
F	*Pseudachorutes parvulus*		
A	*Pseudanurophorus binoculatus*		
A	*Pseudosinella alba*		
A	*Pseudosinella illiciens*		
F	*Pseudosinella mauli*		
A	*Spinonychiurus edinensis*		
A	*Stenaphorura denisi*		
A	*Stenaphorura quadrispina*		
F	*Willemia anophthalma*		
F	*Willemia denisi*		
F	*Willemia intermedia*		
F	*Xenylla grisea*		
F	*Xenylla tullbergi*		
F	*Xenyllodes armatus*		

Figure captions

Fig. 1. Local species richness of fast- and slow-dispersal springtail communities along a gradient of increasing landuse diversity. The two springtail categories were compared at each LUU by Mann-Whitney non-parametric tests. N.S. = not significant, ** = $P<0.01$, *** = $P<0.001$. Bars are standard errors of the means. Within each category, LUUs were compared by repeated Mann-Whitney non-parametric tests, the significance of differences between groups (at P 0.05) being indicated by common letters (a, b for fast-dispersal species, x, y, z for slow-dispersal species)

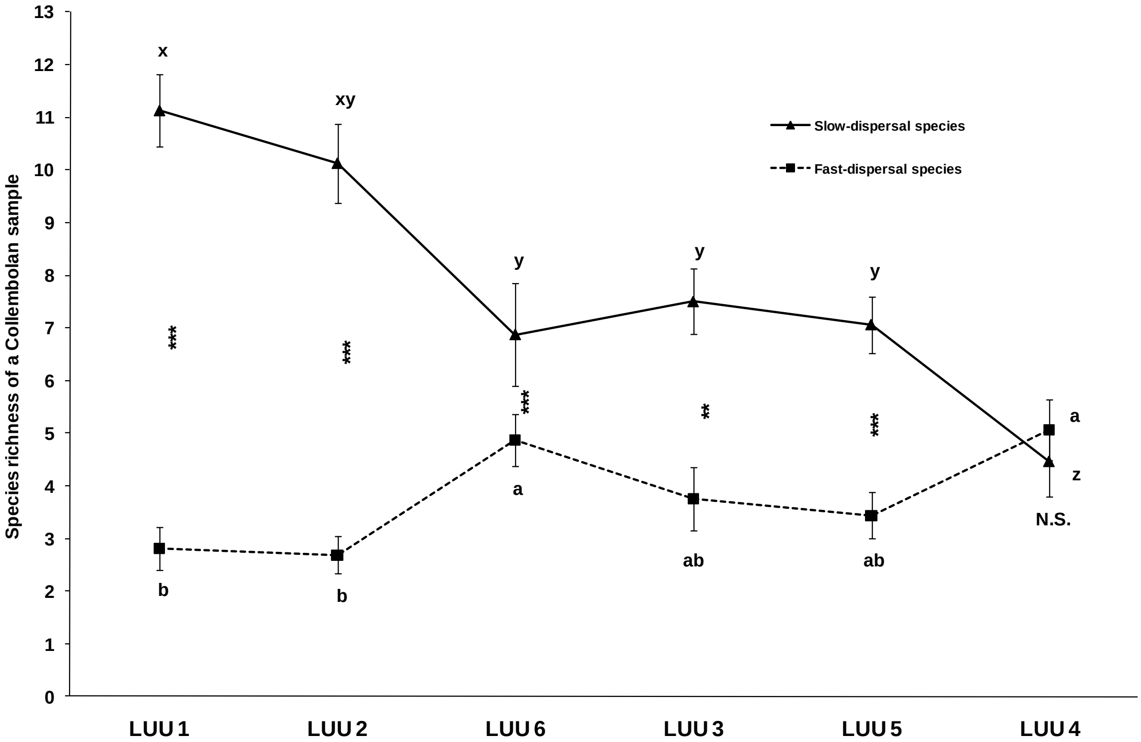
Species richness of a Collembolan sample
13
12
11
10
9
8
7
6
5
4
3
2
1
0
Slow-dispersal species
Fast-dispersal species
x
xy
y
y
y
z
b
b
a
ab
ab
a
***
***
***
*
***
N.S.
LUU 1
LUU 2
LUU 6
LUU 3
LUU 5
LUU 4

Fig. 1