



Experimental assessment of habitat preference and dispersal ability of soil springtails

A. Auclerc^a, J.F. Ponge^{a,*}, S. Barot^b, F. Dubs^b

^a Muséum National d'Histoire Naturelle, CNRS UMR 7179, 4 avenue du Petit-Chateau, 91800 Brunoy, France

^b Institut de Recherche pour le Développement, UMR 7618 Bioemco, 32 avenue Henri-Varagnat, 93143 Bondy Cédex, France

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ABSTRACT

Beside biotic interactions, habitat preference and dispersal ability of species play a prominent role in the building of animal species assemblages. However, these traits are usually very poorly documented for soil organisms. A soil transfer experiment was designed to study habitat preference (including land-use and soil preference) and dispersal ability of soil springtail species living in a meadow and in an adjoining deciduous forest. The study was performed in the Morvan Regional Natural Park (Central France), using untreated or defaunated soil blocks, transferred to another land-use or replaced in their original land-use. Land-use preference was quantified in untreated and untransferred samples from meadow and forest. Dispersal ability was estimated from the time at which species colonized defaunated samples in their own habitat. Soil preference was estimated from the colonization rate of defaunated samples by comparing transferred and untransferred soil blocks. Results showed that in the community, 6% of species were land-use generalists, 30% were soil generalists and 36% recolonized defaunated soil blocks within a week. Land-use preference, soil preference and dispersal ability were largely independent components of species characteristics. Although our experiment dealt only with small-scale colonization, comparisons between species showed that the dispersal type based on anatomical features (legs, antenna, furcula, visual apparatus) does not allow predicting the dispersal ability of these species. Discrepancies between land-use preference and soil preference suggest that other habitat features must be relevant for Collembola, and that a trade-off exists between eco-physiological and biotic interactions (including food requirements).

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1. Introduction

According to theories in community ecology (Drake, 1990; Hunter and Price, 1992; Clobert et al., 2001; Weiher and Keddy, 2001; Tews et al., 2004), the composition of species assemblages can be explained by three processes, the former two acting at the species level, the third one acting at the community level: (1) habitat preference, (2) dispersal, (3) biotic interactions (positive and negative). These interconnected processes filter regional biodiversity, shaping species assemblages at the local level (Keddy, 1992; Zobel, 1997; Rajaniemi et al., 2006). Knowledge on habitat preference and dispersal ability is necessary to understand the distribution of species both at local and regional scales. Species belonging to the same community and thought to have similar or at least compatible ecological requirements may disperse at varying rates, and thus may respond differently to environmental change

and heterogeneity (Ribera et al., 2001; Ponge et al., 2006). Indeed, dispersal ability and habitat preference constrain species capability to reach and occupy different parts of an ecosystem mosaics. Species with high dispersal ability are able to reach more easily all patches of the landscape and will respond to environmental and land-use change, while species with low dispersal ability might not reach some patches (depending on habitat connectivity) even those suitable in habitat requirements (Dunning et al., 1992; Andrén et al., 1997). Similarly, species with narrow habitat requirements are constrained to live in particular patches, which can also impede them to reach some patches (again depending on landscape structure).

Springtails are an integral part of healthy soils and play a critical role in ecosystem services such as dissemination and control of microbial communities (Rusek, 1998). They also influence litter decomposition by the control they have on microbial diversity (Hättenschwiler et al., 2005; Lavelle and Spain, 2005). Despite of their prominent role in structuring communities (see above), habitat preferences and dispersal abilities are still imperfectly known in this group. Moreover, documenting these traits could

* Corresponding author. Tel.: +33 6 78930133; fax: +33 1 60465009.
E-mail address: ponge@mnhn.fr (J.F. Ponge).

help understanding some features of Collembolan spatial distribution. For example, as many other soil invertebrates, they are poorly sensitive to habitat fragmentation at local scale (1 m²) (Rantalainen et al., 2008) even though they are sensitive to fragmentation at the landscape scale (1 km²) (Sousa et al., 2006) and they may suffer from land-use change due to poor active dispersal (Ponge et al., 2006) even if some species are known for their high passive dispersal ability (Van der Wurff et al., 2003). All these results show that (1) it is worth studying further the factors which shape Collembolan species assemblages in mosaics of land-uses and (2) documenting species characteristics such as dispersal and habitat preference would allow to better understand mechanisms hidden behind patterns of species distribution.

To do so, in situ transfer of soil blocks between a forest and a nearby meadow was performed to directly assess in the same experiment habitat preferences and dispersal abilities of all species of Collembola found. With this in situ experiment we could also identify whether species preference for meadow or forest is due to a preference for soil quality. As we documented different species characteristics, we could also test for significant correlations between them. For example we tested whether (1) land-use specialists (restricted to a given habitat) are also specialized in the soil type of their land-use, (2) habitat generalists have higher dispersal ability than habitat specialists.

2. Materials and methods

This field experiment was established in the Morvan Regional Natural Park (Central France) from December 2005 to June 2006 and was similar to the shorter-term and simpler experimental approach by Ponge et al. (2008).

2.1. Study site

The Morvan Regional Natural Park (Central France) is under submontane-atlantic climate with continental influence, with a mean annual rainfall of 1000 mm, and a mean temperature of 9 °C. The parent rock is granite (Adolphe and Desmanèges-Lorenz, 1977). Soils are weakly to strongly acidic (Fedoroff and Arousseau, 1981), with a humus form sensu Brêthes et al. (1995) varying from Eumull to Dysmoder (Ponge et al., 2003).

The forest contains hundred-year-old beeches (*Fagus sylvatica* L.) and oaks [*Quercus petraea* (Matt.) Liebl]. The soil is an Acrisol and the humus form is a Dysmoder. The nearby meadow was mowed each year at the end of spring and then grazed by cattle in autumn. The soil is a Cambisol and the humus form is a Eumull. There is a sharp transition between the forest and the meadow.

2.2. Experimental design

On December 2005, 60 circular soil blocks (15 cm diameter × 10 cm depth) were dug in both land-use plots along 10 evenly spaced transects (25 m between transects), with 6 blocks in each transect (50 cm between blocks located in the same transect). Transects were perpendicular to the forest edge and started 10 m from it both in the forest and the meadow. Sixty soil blocks among 120 were dug ten days before start of the experiment then kept frozen to –20 °C in order to get rid of fauna, the other 60 being left undisturbed until start of the experiment.

In each land-use plot 15 untreated and 15 defaunated blocks were transferred to the other site while the remaining 15 untreated and 15 defaunated blocks were replaced in their original land-use plot. Meadow blocks were transferred with their original grass, without any further pre-treatment. In the same manner, forest blocks were transferred with their thick litter but with no ground

vegetation (except some mosses). Taken together, eight treatments were implemented (Fig. 1), according to the initial presence or absence of fauna (W with fauna, O without fauna), land-use plots from which blocks have been taken (F forest, M meadow), and land-use plots where blocks have been replaced (F forest, M meadow). In each treatment (15 blocks), five blocks were sampled randomly one week after start of the experiment (December 2005), five others after 1 month (January 2006) and the remaining five after 6 months (June 2006). The following treatment codes were used in the experimental design: OFF = blocks without fauna taken in the forest and replaced in the forest; OFM = blocks without fauna taken in the forest and replaced in the meadow; OMM = blocks without fauna taken in the meadow and replaced in the meadow; OMF = blocks without fauna taken in the meadow and replaced in the forest; WFF = blocks with fauna taken in the forest and replaced in the forest; WFM = blocks with fauna taken in the forest and replaced in the meadow; WMM = blocks with fauna taken in the meadow and replaced in the meadow; WMF = blocks with fauna taken in the meadow and replaced in the forest.

Samples were immediately taken to the laboratory to be extracted over 10 days in a Berlese–Tullgren apparatus with a 15 W bulb lamp suspended over each sample. Extracted micro-arthropods were preserved in 95% ethyl alcohol until sorting and identification. Springtails were identified to species level under a binocular microscope (50×) and a light microscope (400×) using keys by Gisin (1960), Zimdars and Dunger (1994), Potapow (2001), Thibaud et al. (2004) and Hopkin (2007).

2.3. Characterization and statistical validation of classes of dispersal ability

For each of the springtail species which were present in the 60 blocks replaced in their original environment (WFF, WMM, OFF, OMM), dispersal ability was defined by the time at which the species reappeared in the defaunated blocks (OFF, OMM). This allowed us to classify springtail species in four classes of dispersal ability, either in the forest or the meadow. Indeed, the dispersal ability of a species could well be different in the two land-use types (noted F in the forest and M in the meadow): species for which the first individuals colonized defaunated blocks (1) within a week (F1 or M1), (2) after a week and within a month (F2 or M2), (3) after a month and within six months (F3 or M3), (4) species which did not colonize defaunated blocks after six months but were found in untreated blocks (F4 or M4). When species were never found in the land-use under investigation, we noted them M0 in the meadow and F0 in the forest.

To test the relevance of our four classes of dispersal ability, we tested the effect of the interaction between time and dispersal ability on the presence/absence of species using Generalized Linear Models (GLM) with binomial models for presence/absence of species (Pinheiro and Bates, 2000). We used OFF and OMM treatments for dispersal ability. All statistics were implemented using R software (Crawley, 2007).

2.4. Characterization of species land-use preference and statistical validation of preference classes

To define land-use preference we used the IndVal index (Dufrene and Legendre, 1997) which combines the specificity of a species for a habitat type (a species is found only in a defined habitat) and its fidelity to this habitat (a species is found in all samples of a defined habitat):

$$I_{ij} = A_{ij} \times B_{ij} \times 100, \text{ where}$$

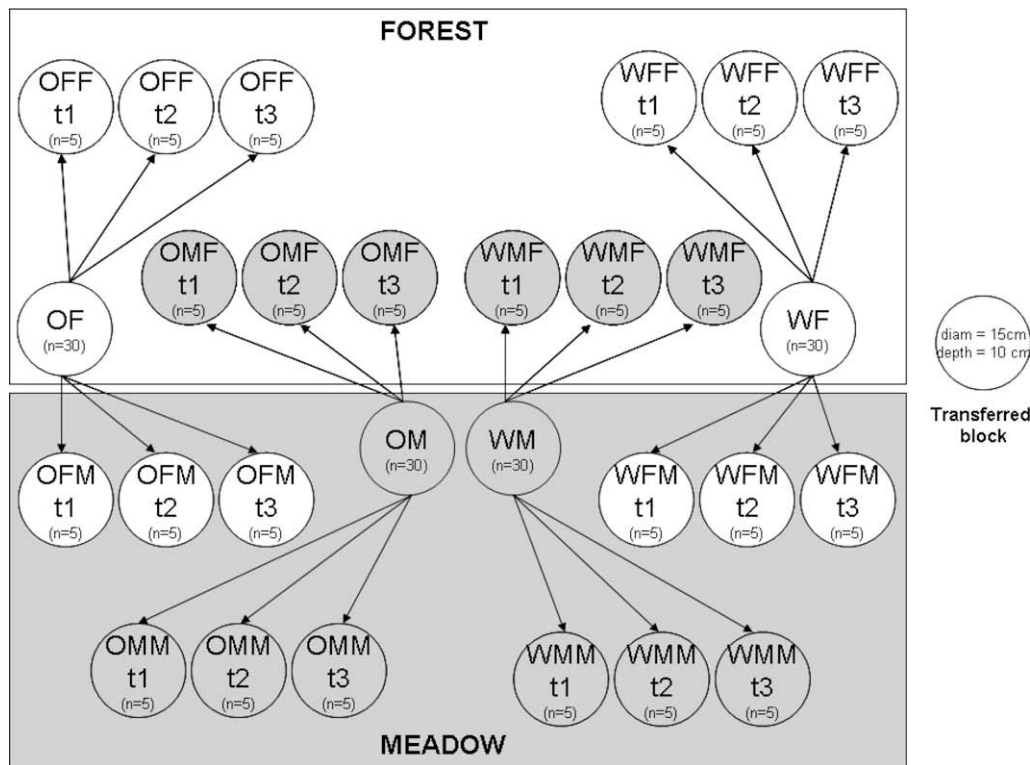


Fig. 1. Experimental design of soil block transfer between a forest and a nearby meadow. Grey arrows represent soil blocks transferred in the other land-use. Upper case letters indicate treatment codes (refer to text in Section 2.2 for symbols).

A_{ij} = average abundance of species i in blocks of habitat j /
average abundance of species i

B_{ij} = number of blocks of habitat j where species i is present/
number of blocks of habitat j

I_{ij} reaches its maximum value (100) when species i is present in all soil blocks from habitat j and absent in blocks from all other habitats. Here only two land-uses (forest and meadow) were considered. For the calculation of the IndVal index, we only used untreated blocks that were replaced in their original land-use plot, i.e. WFF and WMM treatments.

For each species, we calculated forest and meadow IndVal indices using the 'duleg' function of the 'labdsv' package from R software (Ihaka and Gentleman, 1996). Then we classified the species in five groups according to their affinity for one or both land-uses: (1) forest-specialists or strict-forest species (F), (2) forest-preferring species (FP), (3) meadow-specialists or strict-meadow species (M), (4) meadow-preferring species (MP), (5) generalists (G).

To test the relevance of our classes of land-use preference, we tested the effect of the interaction between land-use preference and land-use category on the abundance and on the presence/absence of species using Generalized Linear Models (GLM) with approximate Poisson error for species abundance or binomial models for presence/absence of species (Pinheiro and Bates, 2000). We used WFF and WMM treatments to validate classes of land-use preference.

2.5. Characterization of soil preference and statistical validation of preference classes

To characterize the preference of species for soil types we compared defaunated or untreated soil blocks from a land-use with defaunated or untreated blocks transferred from the other land-

use. For each species we run a Generalized Linear Model with approximate Poisson error to test for the effect of block transfer on species abundances. When this test was significant, the block type in which the species was the more abundant was considered as the preferred soil of the species. For strict-forest, forest-preferring and generalist species, we used OFF–OMF and WFF–WMF treatments and for strict-meadow, meadow-preferring and generalist species, we used OMM–OFM and WMM–WFM treatments. Indeed, a meadow-soil-preferring species will be more abundant in OMM or OMF blocks, while a forest-soil-preferring species will be more abundant in OFF or OFM blocks. When the type of soil had no significant effect on the abundance of species, the species were considered as soil-generalist. Otherwise, the parameters estimated from the GLM model indicated the soil preference of the species: (i) meadow-soil preferential species (MS), (ii) forest-soil preferential species (FS) and (iii) soil-generalist species (SG).

2.6. Relationship between land-use preference, soil preference and dispersal ability

The relationship between the land-use preference and the dispersal ability of species was tested by a Fisher's exact test based on two-way contingency tables with classes of land-use preference (forest-specialist or meadow-specialist species depending on the land-use where dispersal was examined, forest- or meadow-preferring and generalist species) and classes of dispersal ability (species colonizing defaunated blocks within a week, within a month, within six months or more than six months) as entries. The relationships between soil preference and land-use preference or dispersal ability were tested in the same way with all land-use preferences and all dispersal abilities for soil preference modalities, except for the species for which there were not enough specimens to run the model (NR, Table 1). Finally, the relationship between

dispersal abilities in two land-uses (forest and meadow) was also tested by the Fisher's exact test not taking into account species absent from the land-uses tested (modality M0 in the meadow and F0 in the forest).

3. Results

In the 120 soil blocks a total of 80,119 springtails were identified to species; 57 species were found in this study but only 49 species in untreated and untransferred blocks (WMM and WFF) for which dispersal ability and land-use preference were established (Table 1, Fig. 2).

Species could be classified according to their dispersal ability (Table 1). We found 18 species which dispersed within a week (nine in the forest, four in the meadow and five in both land-uses), one which dispersed after a week and within a month (in the forest), five which dispersed after a month and within six months (two in the forest and three in the meadow) and seven which did not disperse after six months (five in the forest and two in the meadow). However, as estimated from the colonization of defaunated blocks, dispersal abilities varied with the land-use (Table 1) and forest-preferring and meadow-preferring species could have different abilities to disperse depending on land-use (Table 2).

Table 1

Land-use preference, dispersal ability and nature of soil preference for springtail species used in the soil transfer experiment. **Land-use preference:** F = forest-specialist or strict-forest species, FP = forest-preferring species, M = meadow-specialist or strict-meadow species, MP = meadow-preferring species, G = land-use generalist species. **Dispersal ability in meadow:** M0 = species absent in the meadow, M1 = species which colonized meadow defaunated blocks within a week, M2 = species which colonized meadow defaunated blocks after a week and within a month, M3 = species which colonized meadow defaunated blocks after a month and within six months, M4 = species which did not colonize meadow defaunated blocks within six months. **Dispersal ability in forest:** F0 = species absent in the forest, F1 = species which colonized forest defaunated blocks within a week, F2 = species which colonized forest defaunated blocks after a week and within a month, F3 = species which colonized forest defaunated blocks after a month and within six months, F4 = species which did not colonize forest defaunated blocks within six months. **Soil preference:** FS = forest-soil-preferring species, MS = meadow-soil-preferring species, SG = soil-generalist species. NR: not enough specimens to run the model.

Species name	Species code	Land-use preference	Dispersal ability		Soil preference	Dispersal type (from Ponge et al., 2006)	Habitat preference (from Ponge et al., 2006)
			in the meadow	in the forest			
<i>Allacma fusca</i>	All_fus	F	M0	F4	NR	Fast	Woodland
<i>Arrhopalites principalis</i>	Arr_pri	F	M0	F4	MS		
<i>Arrhopalites sericus</i>	Arr_ser	FP	M4	F1	MS		
<i>Ceratophysella denticulata</i>	Cer_den	MP	M1	F4	MS		
<i>Ceratophysella recta</i>	Cer_rec	FP	M4	F3	MS		
<i>Deuteraphorura inermis</i>	Deu_ine	FP	M4	F1	MS		
<i>Deuterostminthurus sulphureus</i>	Deu_sul	M	M3	F0	MS	Fast	Agricultural land
<i>Dicyrtomina minuta</i>	Dic_min	F	M0	F1	FS	Fast	Agricultural land
<i>Entomobrya multifasciata</i>	Ent_mul	F	M3	F4	NR	Fast	Agricultural land
<i>Folsomia listeri</i>	Fol_lis	M	M4	F0	NR		
<i>Folsomia manolachei</i>	Fol_man	M	M1	F0	MS		
<i>Folsomia quadrioculata</i>	Fol_qua	FP	M1	F1	MS	Slow	Woodland
<i>Friezea truncata</i>	Fri_tru	F	M0	F1	SG	Slow	Woodland
<i>Gisinius flammeolus</i>	Gis fla	F	M0	F4	NR		
<i>Heteromurus nitidus</i>	Het_nit	M	M1	F0	MS	Slow	Agricultural land
<i>Isotoma anglicana</i>	Iso_ang	MP	M1	F4	MS		
<i>Isotomiella minor</i>	Iso_min	F	M0	F1	MS	Slow	Woodland
<i>Lepidocyrtus cyaneus</i>	Lep_cya	M	M1	F0	SG	Fast	Agricultural land
<i>Lepidocyrtus lanuginosus</i>	Lep_lan	G	M1	F1	SG	Fast	Woodland
<i>Lepidocyrtus lignorum</i>	Lep_lig	G	M1	F1	SG	Fast	Agricultural land
<i>Lipothrix lubbocki</i>	Lip_lub	F	M0	F2	FS	Fast	Woodland
<i>Megalothorax minimus</i>	Meg_min	MP	M1	F3	MS	Slow	Woodland
<i>Mesaphorura florae</i>	Mes_flo	M	M3	F0	MS		
<i>Mesaphorura macrochaeta</i>	Mes_mac	G	M2	F1	MS	Slow	Woodland
<i>Micranurida pygmaea</i>	Mic_pyg	MP	M4	F3	NR	Slow	Woodland
<i>Micraptorura absoloni</i>	Mic_abs	F	M0	F4	NR	Slow	Woodland
<i>Neanura muscorum</i>	Nea_mus	F	M0	F3	SG	Slow	Woodland
<i>Orchesella cincta</i>	Orc_cin	F	M0	F3	MS	Fast	Woodland
<i>Paratullbergia callipygos</i>	Par_cal	F	M0	F4	NR	Slow	Woodland
<i>Parisotoma notabilis</i>	Par_not	MP	M1	F1	SG	Slow	Agricultural land
<i>Pogonognathellus flavescens</i>	Pog fla	F	M0	F1	SG	Fast	Woodland
<i>Protaphorura aurantiaca</i>	Pro_aur	MP	M1	F4	SG		
<i>Pseudachorutes parvulus</i>	Pse_par	F	M0	F1	SG	Slow	Woodland
<i>Pseudosinella alba</i>	Pse_alb	MP	M1	F4	SG	Slow	Agricultural land
<i>Pseudosinella terricola</i>	Pse_ter	F	M0	F1	SG		
<i>Sminthurides parvulus</i>	Smi_par	M	M3	F0	SG	Fast	Agricultural land
<i>Sminthurides schoetti</i>	Smi_sch	MP	M2	F4	MS	Fast	Agricultural land
<i>Sminthurinus aureus</i>	Smi_aur	MP	M1	F1	MS	Fast	Agricultural land
<i>Sminthurinus signatus</i>	Smi_sig	F	M0	F1	SG	Fast	Woodland
<i>Sminthurus viridis</i>	Smi_vir	M	M1	F0	MS	Fast	Agricultural land
<i>Sphaeridia pumilis</i>	Sph_pum	M	M4	F3	FS	Fast	Agricultural land
<i>Stenaphorura denisi</i>	Steph_de	M	M4	F0	NR	Slow	Agricultural land
<i>Stenognathellus denisi</i>	Stegn_de	F	M0	F1	FS		
<i>Subisotoma pusilla</i>	Sub_pus	F	M3	F4	NR		
<i>Vertagopus arboreus</i>	Ver_arb	FP	M1	F4	MS	Fast	Woodland
<i>Willemia anophthalma</i>	Wil_ano	FP	M4	F2	FS	Slow	Woodland
<i>Willemia denisi</i>	Wil_den	FP	M4	F3	MS	Slow	Woodland
<i>Xenylla grisea</i>	Xen_gri	F	M0	F1	SG	Slow	Woodland
<i>Xenylla tullbergi</i>	Xen_tul	FP	M4	F1	SG	Slow	Woodland

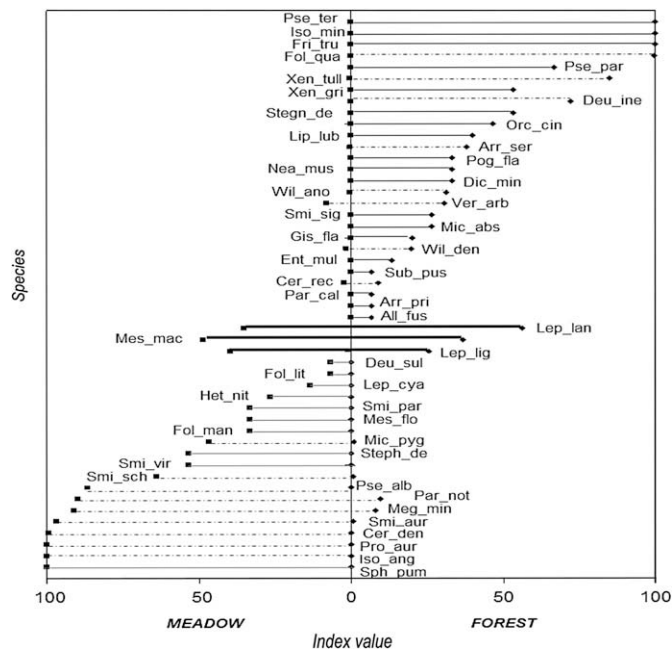


Fig. 2. Graphical representation of the distribution of Collembolan species between the forest and the meadow according to IndVal values for meadow (light grey) and forest (black). Full light grey lines indicate species specialist of the meadow and full black lines indicate species specialist of the forest. Dotted and dashed light grey lines indicate species preferential of the meadow and black ones the same for the forest. Full dark grey lines indicate generalist species, i.e. species did not displaying any preference for one or the other land-use.

Species could be classified in decreasing affinity to the meadow and increasing affinity to the forest, using respective IndVal values (Fig. 2). Only three species did not exhibit any preference for one habitat: *Mesaphorura macrochaeta* (Mes_mac), *Lepidocyrtus lignorum* (Lep_lig) and *Lepidocyrtus lanuginosus* (Lep_lan). A total of 19 species were forest-specialists, ten were meadow-specialists, nine were meadow-preferring and eight were forest-preferring species (Table 1).

Species could be classified according to their soil type preferences (Table 1). Five species were forest-soil-preferring, twenty were meadow-soil-preferring species and fifteen had no preference (i.e. soil generalists). For nine species, the total abundance of each species was too low to allow us running the analysis to determine their soil preference (i.e. NR modality in Table 1).

Our classes of land-use preference were validated: there is a significant interaction between sampling land-uses and land-use preference classes when taking into account the abundance of species or their presence/absence in WFF and WMM soil blocks (GLM, ANOVA test $p < 0.01$). A similar validation was achieved on classes of dispersal ability: there is a significant interaction between time of sampling and classes of dispersal ability when taking into account the presence/absence of species in OFF and OMM blocks (GLM, ANOVA test $p < 0.01$). Soil preference classes were directly validated by the GLM procedure that was used to build these classes.

There was a significant relationship between land-use preference and dispersal ability of species in the meadow (Table 3, Fig. 3a, Fisher's exact test, $p < 0.05$) but not in the forest (Table 3, Fig. 3b, Fisher's exact test, $p > 0.05$): the meadow soil was colonized more rapidly by meadow species than by forest species. Among forest species (forest-specialist and forest-preferring species), 4.1% (two species among a total of 49) colonized the blocks within a week in the meadow and 26.5% (13 species among 49) in the forest

Table 2

Crossed relationships between categories of land-use preference and dispersal ability. Data are numbers of species belonging to each crossed category. Marginal totals are indicated in italic type. Same codes for categories as in Fig. 3.

Dispersal ability in the forest (F0–F4) and in the meadow (M0–M4)						
	M0	M1	M2	M3	M4	
F0	0	4	0	3	2	9
F1	9	5	1	0	3	18
F2	1	0	0	0	1	2
F3	2	1	0	0	4	7
F4	5	5	1	2	0	13
	<i>17</i>	<i>15</i>	<i>2</i>	<i>5</i>	<i>10</i>	<i>49</i>
Dispersal ability of land-use preference categories in the meadow						
	M0	M1	M2	M3	M4	
F	17	0	0	2	0	19
FP	0	2	0	0	6	8
M	0	4	0	3	3	10
MP	0	7	1	0	1	9
G	0	2	1	0	0	3
	<i>17</i>	<i>15</i>	<i>2</i>	<i>5</i>	<i>10</i>	<i>49</i>
Dispersal ability of land-use preference categories in the forest						
	F0	F1	F2	F3	F4	
F	0	9	1	2	7	19
FP	0	4	1	2	1	8
M	9	0	0	1	0	10
MP	0	2	0	2	5	9
G	0	3	0	0	0	3
	<i>9</i>	<i>18</i>	<i>2</i>	<i>7</i>	<i>13</i>	<i>49</i>

(Table 2), while among meadow species (meadow-specialist and meadow-preferring species) 22.4% (11 species among 49) did so in the meadow and 10.2% (five species among 49) in the forest. However, 47% forest-specialist and 50% forest-preferring species dispersed within a week in the forest while only 25% forest-preferring species did it in the meadow and 40% meadow-specialist and 77% meadow-preferring species dispersed within a week in the meadow while only 22% meadow-preferring species did it in the forest (Table 2). This confirmed that recolonization was more rapid in the meadow than in the forest.

There was no significant relationship between land-use preference and soil preference of species (Fig. 3c, Fisher's exact test, $p > 0.05$): when transferred into the other land-use, forest as well as meadow species preferred the meadow soil. Only four among the 21 forest-specialist and forest-preferring species that could be tested showed a preference for the forest soil, while nine preferred the meadow soil and eight were indifferent (Table 1). Among the 16 meadow-specialist and meadow-preferring species that could be tested, ten showed a preference for the meadow soil, only one preferred the forest soil and five were indifferent. There was no significant relationship between soil preference and dispersal

Table 3

Links between land-use preference, dispersal ability and nature of soil preference for springtail species tested by Fisher's exact test. LUP: Land-use preference. DAM: Dispersal ability in the meadow. DAF: Dispersal ability in the forest. SP: Soil preference. (1) Modalities used: M = meadow-specialist species, MP = meadow-preferring species, G = land-use generalist species. (2) Modalities used: F = forest-specialist species, FP = forest-preferring species, G = habitat generalist species. (3) All modalities used except species for which there were not enough specimens to run the model. (4) All modalities used except M0 = species absent in the meadow and F0 = species absent in the forest. * = Significant at 0.05 level. NS = not significant.

	LUP	DAM	DAF
DAM	(1)*		
DAF	NS (2)	NS (4)	
SP	NS (3)	NS (3)	NS (3)

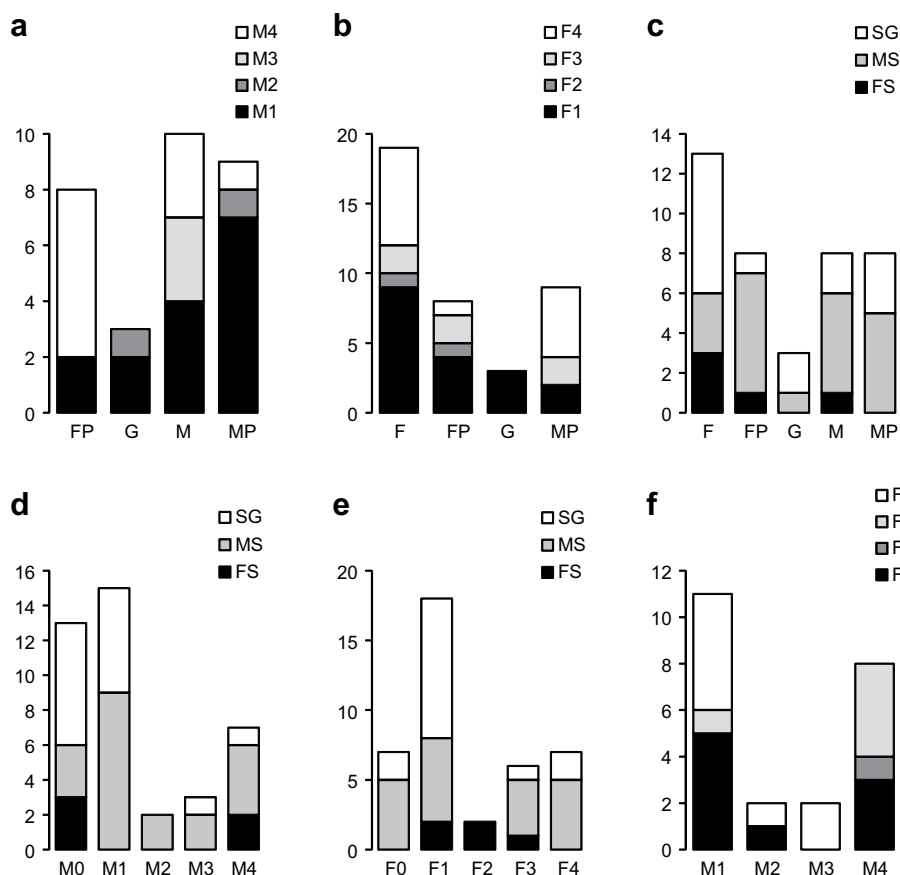


Fig. 3. Distribution of species according to different response traits. Trait classes in abscissa, number of species in ordinate (refer to text or to Table 1 for symbols). (a) Land-use preference. (b) Dispersal ability in the meadow. (c) Dispersal ability in the forest. (d) Soil preference. (e) Dispersal ability in the forest. (f) Dispersal ability in the meadow.

ability of species in the meadow and in the forest (Table 3, Fig. 3d and e, Fisher's exact test, $p > 0.05$) and there was no significant relationship between the dispersal abilities of species in the meadow and in the forest (Table 3, Fig. 3f, Fisher's exact test, $p > 0.05$).

4. Discussion and conclusion

By transferring soil blocks with and without their fauna between a forest and a meadow, we showed that habitat preference and dispersal ability of springtail species could be estimated, and that soil preference could be distinguished from land-use preference. We found 19 forest-specialist, eight forest-preferring, ten meadow-specialist, nine meadow-preferring and three generalist species. Concerning soil preference, we found five forest-soil-preferring, 20 meadow-soil-preferring and 15 soil-generalist species (nine were not categorized as they were too scarce). Within a week 17 species recolonized soil blocks in the meadow and 18 did it in the forest, while ten did not recolonize the blocks after six months in the meadow and 13 did not it in the forest. Land-use preference, soil preference and dispersal ability were largely independent from each other.

4.1. Dispersal ability

Given that they live in a dense and movement-impeding environment, litter- and soil-dwelling springtail species could be suspected at first sight to have low dispersal abilities (Rantalainen et al., 2008). However, our results showed that 37% of the species

colonized 15 cm wide soil blocks in less than a week. Ponge et al. (2006) estimated the dispersal ability of 88 springtail species of the Morvan Natural Regional Park using several anatomical features: species with long legs and antennae, a functional jumping apparatus (furcula) and complete eye spots (eight ommatidies) were considered as able to disperse rapidly by their own means (Hopkin, 1997). Our results invalidate the overall principle of these predictions as there was no link between anatomical features and dispersal ability classes for half of the species (Table 1). For example, species such as *M. macrochaeta*, *Xenylla grisea* and *Friesea truncata*, which have short legs and do not possess any functional jumping apparatus and thus were classified as slow-dispersal species by Ponge et al. (2006), were observed to colonize defaunated blocks within a week. Vannier (1975) studied the colonization rate of springtails in soil columns of varying particle size distribution. Rapid colonization (less than a week) was mostly observed for species with long legs and antennae, developed furcula and complete visual apparatus. However, Neelidae (most probably *Megalothorax minimus*) were also shown to colonize rapidly soil columns. *M. minimus* was classified by Ponge et al. (2006) as a poorly dispersing species on the base of its anatomical features. In our experiment it was also shown to colonize the meadow soil (which it preferred) within a week (Table 1). Ojala and Huhta (2001) performed a microcosm experiment in which dispersal rates of springtail species could be measured at several distances of a colonization source. They found that springtail species with high dispersal rates belonged to very different taxonomic groups: both Tullbergiinae (short legs and antennae, no furcula, no eyes) and Sminthuridae (opposite features) were active

migrants. Dunger et al. (2002) followed experimentally over a year the colonization of open-cast mine dumps by Collembola. The first immigrant was a species with long legs, antenna and furcula and complete visual apparatus, *Bourletiella pistillum*, but the second immigrant was *Mesaphorura florum* a Tullbergiinae. In our study *M. macrochaeta* (Tullbergiinae) exhibited high dispersal ability (colonization in less than a week) in the forest habitat. Discrepancies between aptitude for jump and walk and observed dispersal ability could be partially explained by passive dispersal which, however, has never been measured directly but was inferred from genetic exchange between distant populations of the epigeic springtail *Orchesella cincta* (Van der Wurff et al., 2003). Rightly, Dunger et al. (2002) did not attribute to passive dispersal by wind a prominent influence, except for the first immigrant, *B. pistillum*. We cannot rule out that other mechanisms of passive dispersal such as phoresy or egg transport could help some poorly mobile species to reach remote places, as this has been shown in aquatic invertebrates (Frisch et al., 2007), which might explain discrepancies between predicted (on the base of anatomy) and observed colonization rates by springtail species.

4.2. Land-use preference

For 85% of the species we sampled there was a fairly good correspondence between land-use preferences estimated in our experiment and already published results (Table 1). However, some species (*Arrhopalites principalis*, *Dicyrtomina minuta*, *Entomobrya multifasciata*, *Folsomia manolachei*, *F. truncata*, *Isotomiella minor*, *Neanura muscorum*, *O. cincta*, *Paratullbergia callipygos*, *Pogonognathellus flavescens*, *Pseudochorutes parvulus*, *Sphaeridia pumilis*, *Subisotoma pusilla*) were classified in our study as forest- or meadow-specialists while, according to literature, they can be found in both habitats (Ponge, 1980, 1993; Rusek, 1989; Dombos, 2001; Ponge et al., 2003, 2006; Petersen et al., 2004; Kuznetsova, 2006; Chauvat et al., 2007) and should be classified as preferring or generalist but not specialist species. This could be due to local environmental peculiarities that did not allow these species to live in both habitats, such as differences in soil condition (humus form). It should also be noted that in the present study land-use preferences were estimated from a limited set of IndVal values and thus cannot be extrapolated to a variety of environments, contrary to studies cited above.

4.3. Soil preference

Species known for their strong affinity to acid soils, such as *Lipothrix lubbocki* and *Willemia anophthalma* (Ponge, 1980, 1993; Hågvar and Abrahamsen, 1984) exhibited a preference for the forest soil, in accordance with its Dysmoder humus form. Conversely, species which are repelled by soil acidity, such as *Sminthurinus aureus* and *Heteromurus nitidus* (Ponge, 1980, 1993; Salmon and Ponge, 1999) preferred the meadow soil, in accordance with its Eumull humus form. However, the preference for the forest soil exhibited by *S. pumilis*, a species which we classified as meadow-specialist according to its distribution in our sites (the present study), seems to be contradictory. However, as this species, according to its distribution observed by Ponge et al. (2003) in the same regional context, should be meadow-preferring rather than meadow-specialist, the result obtained here is probably due to a stochastic effect of its lower abundance in the forest. Together with our results on land-use preference (see above), this study points to other, still imperfectly explored, environmental features that could be meaningful for Collembola. Microclimate, which differs to a great extent between forest and meadow (Morecroft et al., 1998), has a decisive influence on the survival of these

moisture-sensitive tiny arthropods (Betsch and Vannier, 1977; Tsiafouli et al., 2005). Biotic interactions such as competition are also thought to influence species distribution (Hågvar, 1990; Christiansen et al., 1992; Theenhaus et al., 1999; Salmon and Ponge, 2001; Krivtsov et al., 2003; Salmon et al., 2005). Hågvar (1990) suggested that oribatid species living commonly in Dysmoder (acid-tolerant species) dominate in forest soils, not because they are attracted to acidity, but rather because they compete better with acid-intolerant species. Indeed, competition with resident species can impede a local patch to be colonized by dispersing individuals of other species: competition can thus decrease the realized niche of species (Shigesada and Kawasaki, 1997). Hints on the effect of inter-specific competition could be given in the future by the comparison of our defaunated and untreated blocks.

To the present state of our knowledge it is not possible to establish a link between habitat preference (including soil preference) and morphological traits of Collembola, although Ponge (2000) noted that extant springtail species or species groups with ancestral anatomical characters exhibited a higher tolerance to soil acidity, as ascertained by their present-day distribution.

4.4. Interactions between dispersal ability, land-use preference and soil preference

The attractiveness of the meadow soil (Fig. 3c) for a majority of forest as well as meadow-specialist and preferring species needs to be interpreted. The meadow humus form was a Eumull, which contrasts with the Dysmoder into which it was transferred in our experiment. It has been demonstrated that soils with high earthworm activity, such as our meadow soil, are attractive for many arthropod species and particularly for Collembolan species (Hamilton and Sillman, 1989; Loranger et al., 1998; Salmon and Ponge, 1999; Maraun et al., 1999). Earthworm activity, which is usually high in Eumull (Brêthes et al., 1995), provides food and habitat for many subterranean organisms, mainly through bioturbation and redistribution of organic matter in the topsoil (Scheu, 1987), and protection against predation offered by earthworm burrows (Salmon et al., 2005). That forest species could be attracted to Eumull (with prominent earthworm activity) while they are commonly living in Dysmoder with poor earthworm activity (Brêthes et al., 1995), and are absent from the nearby meadow, might indicate that their achieved distribution is due to a trade-off between (i) their preference for soils with more favourable biotic interactions (food included) and (ii) their eco-physiological constraints (sensitivity to desiccation, waterlogging, frost) which can be more easily fulfilled in sheltered woodland microclimate conditions.

Although we did not detect any link between dispersal ability in the forest and the type of land-use preference (Fig. 3b), there was a significant correlation between dispersal ability in the meadow and the type of land-use preference (Fig. 3a): in the meadow, meadow-specialist and meadow-preferring species disperse more quickly than forest-preferring species. This suggests that dispersal in the meadow was easier than in the forest. An explanation could be that the meadow represents a disturbed habitat for Collembola, so that meadow species need to be more mobile to persist in this land-use. Indeed, forests are more stable habitats as the establishment of a mature forest takes several decades (Ponge et al., 1998) whereas a meadow is usually ploughed and replanted each ten years. Temperature range and soil compression due to cattle trampling are higher in meadow than in forest (Friberg et al., 2008). Thus forest Collembolan species would not have evolved towards high dispersal abilities because their environment was stable, thereby confirming previous results obtained by Ponge et al. (2008). The absence of correlation between dispersal ability in the

forest and land-use preference would be explained by the lack of attractiveness of the forest soil for most species (see above). In the light of our results and according to Mysrerud and Ims (1998), it can be suggested that (1) Collembolan species can be attracted to another soil than that of their current habitat, (2) this does not impede them to persist in this habitat if food is abundant enough. In the example of *Vertagopus arboreus*, tree trunks are known to be favoured temporary habitats, in both disturbed and undisturbed environments (Ponge, 1993; Prinzing, 2001).

We did not detect any link between dispersal ability, either in the meadow or in the forest, and soil preference. However, as noticed above, we found a link between land-use preference and dispersal ability in the meadow. If we combine these results with the abovementioned attractiveness of the meadow soil, and the fact that we did not detect any significant relationship between meadow- and forest-dispersal abilities, this points to species-specific barriers to colonization, which do not necessarily match soil preferences. The freezing procedure which was used to deprive the blocks from their original fauna could make the forest soil somewhat distasteful for some species: it has been shown that freezing, by splitting macromolecular assemblages, may increase the toxicity of carbon-rich sediments (Geffard et al., 2004).

4.5. Working hypotheses and perspectives

Our results do not support the hypothesis that land-use specialist species are also soil-specialists of the corresponding soil. However the meadow soil was more attractive whatever the land-use preference of the species, suggesting that food resources must be an important dispersal-triggering stimulus. This is supported by Bengtsson et al. (1994) who experimentally showed that the dispersal rate decreased as food resources increased in Collembolan populations. Our results do not fully support our second hypothesis that land-use generalists have higher dispersal ability than specialists. This hypothesis was supported for dispersal in the meadow but the idea that dispersal is not counter-selected for habitat specialists (and vice versa) is not supported. However, the selection of more mobile species in the more disturbed land-use (the meadow) supports the hypothesis that dispersal and habitat-preference strategies of species have been selected to allow them to recolonize quickly soil patches after a disturbance. It would also be interesting to further investigate whether disturbed habitats have led to the selection of species that can survive disturbances. Indeed, temperature variability is stronger in meadows than in forests (Friberg et al., 2008) and Collembola are known to be sensitive to temperature (Betsch and Vannier, 1977). Moreover, springtails have already been shown to have evolved different eco-physiological strategies to resist disturbance by selecting species-specific traits such as, among others, diapausing eggs (Leinaas and Bleken, 1983) and light avoidance (Salmon and Ponge, 1998). More generally, the absence of relationship between species traits (i.e. dispersal ability, land-use preference and soil preference), except in the case of land-use preference and dispersal in the meadow, suggests that these species characteristics were selected mostly independently. Because Collembolan life-history is probably constrained by many trade-offs (Tully et al., 2006), this might also mean that more traits have to be documented to find a general pattern.

More investigations are needed to better understand the determinants and stimuli of active dispersal for springtails. Indeed, there are still very few studies on dispersal in Collembola but existing ones suggest that Collembolan movements influence their population dynamics (Bengtsson et al., 1994, 2002). For example, dispersal can be a way to avoid intra-specific competition. Moreover, if the role of facilitation or competitive exclusion is established as a mechanism structuring local species assemblages

(Connell and Slatyer, 1977), the role of inter-specific competition was never tested for springtails. The design of our experimental protocol will allow us to investigate further these issues.

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