Species traits and habitats in springtail communities: a regional scale study

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Running title: Trait-habitat relationshipsin springtails

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Abstract

Although much work has been done on factors patterning species trait assemblages in emblematic groups such as plants and vertebrates, more remains to be done in belowground invertebrate species. In particular,relationships between species traits and habitat preferences are still a matter of debate. Springtails were sampled in a heterogeneous landscape centered on the Sénart forest, near Paris (northern France), embracingthe largest possible array of five environmental gradients (humus forms, vegetation, moisture, vertical strata, and seasons) over which Collembola are known to be distributed. Distances between samples varied from a few cm to several km. Canonical correspondence analysis using species (128) as observations and species trait attributes (30) and habitat indicators (82) as dependent and independent variables, respectively, allowed to discern whether species habitats and species trait assemblages were related and which trends could be found in trait/environment relationships. It was concluded that, within the studied area, species habitatswere significantly associated with species trait assemblages. The main gradient explaining the distribution of species traits combined the vertical distribution of habitats (from the mineral soil to plant aerial parts), and the openness of the environment, i.e. a complex of many ecological factors. In the ecological traits of Collembola, this gradient corresponded to anincreasing contribution of sensory and locomotory organs, bright color patterns, size and sexual reproduction, all attributes associated with aboveground life under herbaceous cover. Another important, although secondarycontrast concerned traits associated with habitats far from soil but concealed (corticolous vs all other habitats). Soil acidity and water did not contribute significantly to trait distribution, at least within the limits of our database.

Keywords: Collembola; species trait assemblages; habitats; trait-environment relationships

Introduction

The indicative power of species trait assemblages has been intensively studied in plants, birds and beetles and most species traits could be clearly related to habitat preferences of species in these groups (Graves and Gotelli 1993; Ribera et al. 2001;Cornwell and Ackerly 2009; Mayfield et al 2009; Pavoine et al. 2011). Surprisingly, although this is common sense and was reported for a long time in soil zoology (Bornebusch 1930), few studies questioned whether the extraordinary diversity of species traits which prevail in soil animal communities could be explained, and potentially could have been selected, by differences in habitat use (Vandewalle et al. 2010; Decaëns et al. 2011; Bokhorst et al. 2011).Moreover, these studies focused either on a restricted number of traits, or a restricted number of habitats which does not allow providing general trends in relationships between species traits and habitat use.

The aim of our study was to determine trends that emerge from trait-environment relationships, i.e. how species traits vary along environmental gradients (e.g. vegetation, soil, depth).

Among soil invertebrates, we selected springtails (Hexapoda, Collembola) as an abundant and diversifiedmonophyletic group for which a great deal of work has been devoted to the study of species/environment relationships at the community level (Poole 1962; Hågvar 1982; Ponge 1993; Chagnon et al. 2000; Auclerc et al. 2009). The Sénart forest (Ile-de-France, northern France) and its vicinity were selected because they display a great variety of soil and soil-related habitats (e.g. woodland, heathland, grassland, ponds, paths, tree trunks) composing a little more than 3,000 ha of heterogeneous landscape, now totally included in the Paris area. Data collected from 1973 to 1977, at a time when agriculture was still practiced both inside and outside the forest, were revisited for a statistical analysis taking into account species trait/environment relationships. The same pool of data (370 samples, 127 species) has been already used in several studies dealing with species/environment relationships (Ponge 1980, 1983, 1993) and was included in the COLTRAIT data base [http://www.bdd-inee.cnrs.fr/spip.php?article51&lang=en], which also comprises data about twelve morphological and life-history traits of more than 300 collembolan species.

Materials and Methods

Site description

The Sénart state forest (3,000 ha) is located 20 km south-east of Paris on the western border of the Brie plateau, delineated by a meander of river Seine and by a tributary, the river Yerres, at an altitude ranging from 50 to 87 m a.s.l. At the time of sampling it was mainly bordered by urbanized areas (communes of Quincy-sous-Sénart, Boussy-Saint-Antoine, Brunoy, Yerres, Montgeron, Draveil) on its western and northern parts, and by agricultural areas (communes of Soisy, Étiolles, Tigery, Lieusaint, Combs-la-Ville) on its eastern and southern parts. Nowadays, the forest is totally included in the metropolitan area of Paris. Private peripheral woods and agricultural areas (cultures and meadows) were included in the study. Most of them have now been incorporated into the state forest, to the exception of peripheral agricultural areas which have been built or transformed into golf courses or other recreational areas.A number of soil types can be observed in the Sénart forest, varying according to the nature of quaternary deposits (loess or gravels) and permanent or seasonal waterlogging resulting from clay migration (perched water tables) or underlying impervious clay strata (permanent water tables). More details were given in previously published papers (Ponge 1980, 1983, 1993).

Sampling procedure

Sampling took place from 15th October 1973 to 10th October 1977 in every season and every kind of weather, our purpose being to embrace all climate conditions, except when the soil was deeply frozen and could not be sampled at all. At each sampling time, a point was randomly selected, around which all visible sitespotentially available to springtails were investigated, from deep soil (leached mineral horizons) to tree trunks two meters aboveground and to floating vegetation in water-filled ponds. No effort was made to standardize sampling, the only requirement being to collect enough litter (at all stages of decomposition), vegetation (aerial and subterranean parts), bark (naked or covered with lichens or mosses) or soil (organo-mineral to mineral horizons) to have enough animals as possible in each sample, the aim of the study being to know which species were living together in the same micro-habitat and which species were not.The volume sampled varied from 100 mL for moss cushions, which are particularly rich in springtails (Gerson 1982) to 1 L for bleached mineral soil horizons which are strongly impoverished in fauna (Hågvar 1983). Care was taken not to undersample some poorly represented habitats. For that purpose some additional sampling was done in agricultural areas, calcareous soils and dumping places. This procedure allows environmental gradients to be better described (Gillison and Liswanti 2004).

Samples were taken with the help of a shovel for soil, and with fingersfor above-ground samples, care being taken not to lose too many jumping animals in particular when sampling aerial parts of erected plants. No attempt was done to force a corer into the soil. Samples were immediately put in plastic bags then transported to the nearby laboratory, to be extracted on the same day. Extraction was done by the dry funnel (Berlese) method over 10 days, using 25 W bulb lamps in order to avoid too rapid desiccation of the samples, known to prevent slowly moving animals from escaping actively the samples (Nef 1960). Animals were collected and preserved in 95% ethyl alcohol in plastic jars. A total of 310 samples were collected and kept for the analysis.

Species identification

Animals were sorted in Petri dishes filled with ethyl alcohol then springtails were mounted and cleared in chloral-lactophenol to be identified under a light microscope at x 400 magnification. At the time of study the only key available for European springtails was that of Gisin (1960), to which were added numerous detailed published studies at family, genus or species level (complete list available upon request), and miscellaneous (unpublished) additions by Gisin himself. Color patterns were noted before animals were discolored in chloral-lactophenol. Young specimens, when not identifiable to species level, were allocated to known species by reference to adults or subadults found in the same sample, or in samples taken in the vicinity. For instance in the genus *Mesaphorura*, where several species may cohabit and diagnostic characters are not revealed in the first instar (Rusek 1980), unidentified juveniles were proportionally assigned to species on the base of identified specimens found in the same sample. Gisin's nomenclature was updated using Fauna Europaea 2011 [http://www.faunaeur.org/]. A total of 128 species were found (Table 1).

Trait data

Twelve traits, mostly extracted from the COLTRAIT data base and collected from numerous identification keys or synopses, describe morphology and reproductive mode of the 128 species used in the analysis. Attributes of each trait (Table 3) were considered as variables, and were coded as binary (dummy) variables, resulting in a list of 30 attributes: mode of reproduction (parthenogenesis dominant, sexual reproduction dominant), body size (small, medium, large), body form (cylindrical body, stocky body, spherical body), body color (pale-colored, bright-colored, dark-colored), scales (absent, present), antenna size (short, long), leg size (short, long), furcula size (absent or vestigial, short, long), eyenumber (0, 1-5, > 5), pseudocella (absent, present), post-antennal organ (absent, simple, compound), and trichobothria (absent, present). Antennae, eyes, post-antennal organsand trichobothria are supposed to play a sensory role (Hopkin 1997).

Species habitat data

Field notes were used to classify habitat features (sensu lato, including micro-habitat and season) in 82 categories (Table 2). To each sample was thus assigned a set of 82 habitat indicators which describe its main features at varying scales, from landuse (heathland, grassland, woodland) to sampling plot (e.g. ditch, plain ground, pond, vegetation, soil pH) then to within-plot scale (e.g. plant part, litter, earthworm casts, mineral soil). Species presence was indicated by dummy variables (coded as 0 or 1) for each of the 82 habitat categories.

Statistical treatment of the data

Canonical correspondence analysis was used to analyze trait-habitat relationships (species as observations, species trait attributes as dependent variables, species habitatsas constraining variables), permutation tests being used to test trait-habitat associations.

Rarefaction curves were calculated to estimate the exhaustiveness of our sampling method.Rarefaction curves and jacknife estimators were calculated using

EstimateS (version 8.2.0).All other calculations were done using XLSTAT® (Addinsoft®, Paris, France).

Results

The rarefaction curve of the 128 observed species showed that sampling had approached an asymptote. Estimating the number of missing species according to Chao (1987) put the expected total number of species for the Sénart forest to 133 and indicated that the sampling was relatively exhaustive.

Canonical Correspondence Analysis (CCA)with species trait attributes as explained variables and species habitats as explanatory variables showed that traits were significantly explained by habitats (number or permutations = 500, pseudo-F = 0.94, P < 0.0001). Constrained variance (variance of species traits explained by species habitats) represented 72.9% of the total variance.

The first two canonical components of CCA extracted 54% of the constrained (explained) variance (40% and 14% for F1 and F2, respectively). The projection of trait attributes and species in the F1-F2 plane is shown in Figures 1a and 1b, respectively. Both species and trait attributes were distributed along three dimensions. Species with pseudocella and post-antennal organ present (of compound type), parthenogenesis dominant, regressed locomotory (furcula, legs) and sensorial organs (eyes, antennae, thichobothria), and pale color were opposed to species displaying opposite attributes along F1. According to principal coordinates of species habitats (Table 2) this corresponded to opposite habitats: woodland vs grasslandand depth versus surface, from negative to positive sides of F1. Heathland was in an intermediate position between woodland and grassland (Table 2). Mineral soil, organo-mineral soil, humus (organic), litter, plant aerial parts ranked in this order along F1. Sunlight was projected on the positive side of F1 (open environments).The second canonical component F2 was more specifically linked to corticolous microhabitats (trunks, wood and associated mosses and lichens): associated trait attributes were short furcula, stocky and dark-colored body, eyes present but in regressed number (1-5), post-antennal organ present but simple. Acidity and humus type, as well as water, did not exhibit any pronounced influence on species trait attributes. Partial CCA, allowing only water and soil acidity (including humus type) to vary, showed that they did not influence the distribution of trait attributes (pseudo-F = 0.17, P = 0.99).

Discussion

Previous studies showed that a limited number of ecological factors could explain the distribution of collembolan species when collected in the same geographical context, at a regional scale (Ponge 1993; Ponge et al. 2003). Vertical distribution is the main gradient along which most springtail species are distributed (Hågvar 1983; Faber and Joosse1993; Ponge 2000a), followed by the contrast between woodland and grassland (Ponge et al. 2003), and other factors such as water availability (Verhoef and Van Selm 1983) and soil acidity (Loranger et al. 2001). We showed that grassland and epigeic habitats were mostly characterized by traits adapting species to surface life: big size, high mobility, protection against desiccation by round shape or cuticular clothing (Kaersgaard et al. 2004), avoidance of predation by flight and color signaling, and sexual reproduction (Fig. 1, Table 2, F1 component, positive side). On the oppositeside, woodland and endogeic habitats were mostly characterized by traits associated with subterranean life: small size, small locomotory appendages, poor protection from desiccation, avoidance of predation by toxic excreta (pseudocella), and parthenogenesis.

Much life in woodland is more concealed than in grassland: smaller forms, more sensitive to environmental stress because of a higher surface/volume ratio (Kærsgaard et al. 2004;Bokhorst et al. 2012), and less motile species (Auclerc et al. 2009), can find in woodland better conditions for survival and reproduction. Mebes and Filser (1997) showed that surface dispersal of Collembola was much more intense in agricultural fields compared to adjoining shrubby fallows where litter began to accumulate, and Alvarez et al. (1997, 2000) highlighted the role of hedgerows as temporary refuges for species living at the surface of arable fields.Sexual reproduction needs easy-to-visit sites for the deposition of spermatophores by males (Chahartaghi et al. 2006), and movement in search of mating partners using olfactory or tactile clues (Chernova et al. 2010), which is easier in surface than in depth, in the same sense as escape from predators needs visual or tactile sensory organs to detect their presence (Baatrup et al. 2006) and needs jumping movements (ensured by furcula acting as a spring) for fleeing away (Bauer and Christian 1987). The fractionation of space within leaf or needle litter horizons makes the forest floor improper to rapid surface movements (Bauer and Christian 1987), while protecting soil-dwelling animals from surface predation by carabids and vertebrates (Hossie and Murray 2010) and offering a variety of food resources such as fungal colonies and animal excreta (Bengtsson et al. 1991; Salmon and Ponge 2001). Other predators are subterranean and cannot be avoided through active movements, hence the use of chemical repellents excreted by pseudocella (Dettner et al. 1996; Negri 2004).

Despite clear trends of trait/habitat relationships exhibited by our results, possible biases due to escape movements during sampling, in particular from the part of big-size animals with long furcula, should not be overlooked. If such biases differ from a habitat to another, this may flaw trait/habitat relationships. However, concerning the association between big size and agricultural environments, which is novel to science, it must be highlighted that it was less easy to collect vary motile specimens in the absence of litter (i.e. in agricultural areas) than when litter was present (i.e. in forest areas), stemming in a bias in quite opposite direction to the observed association. This made us confident that such biases were not present in our dataset.

The second canonical component of trait-environment relationships (Fig. 1, Table 2, F2 component) distinguishes traits associated with life in bark and associated mosses and lichens: the combination of short furcula, dark color, stocky body, eyes present but in limited number is an original adaptation to life in concealed environments (hence small size and limited movements) but far from soil (hence the need to be protected from UV radiation through pigmentation and possibilities offered by vision). The structure of the post-antennal organ, opposing simple to compound structure (more typical of edaphic habitat) is worthy of note, since no other studies considered its ecological correlates. The exact role played by this organ is still unknown, but anatomical observations on the innervation of these pitted porous plates located not far from the protocerebrum point to sensory activity (Altner and Thies 1976). Differences between simple and compound post-antennal organs concern the number of dendritic branches, which are more numerous in compound organs (Altner and Thies 1976), suggesting that compound post-antennal organs are more sensitive to chemical features of the immediate environment. The higher sensitivity of the compound post-antennal organ could be more adapted to deeper horizons by compensating the reduction or the complete absence of other sense organs such as eyes.

The fact that we did not discern any association between traits and obvious factors such as water and soil acidity (or humus type) does not preclude any further scrutiny of such relationships. Two reasons could be invoked.First, that, in its present state, our database did not cover the traits needed to establish this relationship. Ponge (2000b) showed that acidophilic and acidophobic species cohabited within the same lineage, pointing to corresponding traits as mainly based on physiology (mechanisms counteracting oxidative stress) rather than on anatomy and reproduction mode. Traits associated with aquatic life concern mainly the form and size of claws (Gisin 1960), and of course physiology (resistance to desiccation), which were not considered here. Second, in the particular case of the Senart forest, traits adapting species to habitats varying in terms of water availability and/or soil acidity could be masked by landuse or vertical stratification effects, pointing to the need for studying trait/habitat relationships on a wider geographic scale, as suggested by Lepetz et al. (2009).

References

Altner, H., Thies,G., 1976. The post-antennal organ: a specialized unicellular sensory input to the protocerebrum in apterygotan insects (Collembola). Cell Tissue Res. 167, 97-110.

Alvarez, T., Frampton, G.K., Coulson,D., 1997. Population dynamics of epigeic Collembola in arable fields: the importance of hedgerow proximity and crop type. Pedobiologia 41, 110-114.

Alvarez, T., Frampton, G.K., Coulson,D., 2000.The role of hedgerows in the recolonisation of arable fields by epigeal Collembola.Pedobiologia 44, 516-526.

Auclerc, A., Ponge, J.F., Barot, S., Dubs,F., 2009. Experimental assessment of habitat preference and dispersal ability of soil springtails. Soil Biol. Biochem. 41, 1596-1604.

Baatrup, E., Bayley, M.,Axelsen,J.A., 2006.Predation of the mite *Hypoaspisaculeifer* on the springtail *Folsomia fimetaria* and the influence of sex, size, starvation, and poisoning.Entomol. Exp. Appl. 118, 61-70.

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

Bengtsson, G., Hedlund, K., Rundgren, S., 1991. Selective odor perception in the soil Collembola *Onychiurusarmatus*.J. Chem. Ecol. 17, 2113-2125.

Bokhorst, S., Phoenix, G.K., Bjerke, J.W., Callaghan, T.V., Huyer-Brugman, F., Berg, M.P., 2012. Extreme winter warming events more negatively impact small rather than large soil fauna: shift in community composition explained by traits not taxa. Glob. Change Biol 18, 1152-1162.

Bornebusch, C.H.,1930. The fauna of forest soil.Forstl.Forsøksv.Danmark11, 1-158.

Chagnon, M., Hébert, C., Paré, D., 2000.Community structures of Collembola in sugar maple forests: relations to humus type and seasonal trends. Pedobiologia 44, 148-174.

Chahartaghi, M., Scheu, S.,Ruess,L., 2006.Sex ratio and mode of reproduction in Collembola of an oak-beech forest.Pedobiologia 50, 331-340.

Chao, A., 1987. Estimating the population size for capture-recapture data with unequal catchability. Biometrics 43, 783-791.

Chernova, N.M., Potapov, M.B., Savenkova, Y.Y.,Bokova,A.I., 2010.Ecological significance of parthenogenesis in Collembola.Entomol. Rev. 90, 23-38.

Cornwell, W.K., Ackerly, D.D., 2009. Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. Ecol. Monogr. 79, 109-126.

Decaëns, T., Margerie P., Renault, J., Bureau, F., Aubert, M., Hedde, M., 2011. Niche overlap and species assemblage dynamics in an ageing pasture gradient in north-western France. ActaOecol. 37, 212-219.

Dettner, K., Scheuerlein, A.,Fabian, P.,Schulz, S.,Francke,W., 1996. Chemical defense of giant springtail *Tetrodontophorabielanensis* (Waga) (Insecta: Collembola). J. Chem. Ecol. 22, 1051-1074.

Faber, J.H., Joosse,E.N.G., 1993. Vertical distribution of Collembola in a *Pinus nigra* organic soil.Pedobiologia 37, 336-350.

Gerson, U., 1982. Bryophytes and invertebrates.In:Smith, A.J.E. (Ed.), Bryophyte Ecology Chapman and Hall, London, pp. 291-332.

Gillison, A.N., Liswanti,N., 2004. Assessing biodiversity at landscape level in northern Thailand and Sumatra (Indonesia): the importance of environmental context.Agr. Ecosyst. Environ. 104, 75-86.

Gisin, H., 1960. CollembolenfaunaEuropas. Muséum d'Histoire Naturelle, Geneva.

Graves, G.R., Gotelli, N.J., 1993.Assembly of avian mixed-species flocks in Amazonia. P. Natl Acad. Sci. USA 90, 1388-1391.

Hågvar, S., 1982.Collembola in Norwegian coniferous forest soils. I. Relations to plant communities and soil fertility. Pedobiologia 24, 255-296.

Hågvar, S., 1983.Collembola in Norwegian coniferous forest soils. II. Vertical distribution. Pedobiologia 25, 383-401.

Hopkin, S.P., 1997. Biology of the Springtails (Insecta: Collembola). Oxford University Press, Oxford.

Hossie, T.J., Murray, D.L., 2010. You can't run but you can hide: refuge use in frog tadpoles elicits density-dependent predation by dragonfly larvae. Oecologia 163, 395-404.

Kærsgaard, C.W., Holmstrup, M.,Malte, H., Bayley,M.,2004.The importance of cuticular permeability, osmolyte production and body size for the desiccation resistance of nine species of Collembola. J. Insect Physiol. 50, 5-15.

Lepetz, V., Massot, M., Schmeller, D.S., Clobert, J., 2009. Biodiversity monitoring: some proposals to adequately study species' responses to climate change. Biodivers.Conserv. 18, 3185-3203.

Loranger, G., Bandyopadhyaya, I., Razaka, B., Ponge,J.F., 2001. Does soil acidity explain altitudinal sequences in collembolan communities? Soil Biol. Biochem. 33, 381-393.

Mayfield, M.M., Boni, M.F., Ackerly, D.D., 2009. Traits, habitats, and clades: identifying traits of potential importance to environmental filtering. Am. Nat. 174, E1-E22.

Mebes, K.H.,Filser,J., 1997. A method for estimating the significance of surface dispersal for population fluctuations of Collembola in arable land.Pedobiologia 41, 115-122.

Nef, L., 1960. Comparaison de l'efficacité de différentes variantes de l'appareil de Berlese-Tullgren. Z. Angew. Entomol. 46, 178-199.

Negri, I., 2004. Spatial distribution of Collembola in presence and absence of a predator.Pedobiologia 48, 585-588.

Pavoine, S., Vela, E.,Gachet, S.,de Bélair, G.,Bonsall,M.B.,2011. Linking patterns in phylogeny, traits, abiotic variables and space: a novel approach to linking environmental filtering and plant community assembly.J. Ecol. 99, 165-175.

Ponge, J.F., 1980. Les biocénoses des collemboles de la forêt de Sénart. In Pesson, P. (Ed.),Actualités d'Écologie Forestière.Gauthier-Villars, Paris, pp. 151-176.

Ponge, J.F., 1983. Les collemboles, indicateurs du type d'humus en milieu forestier: résultats obtenus au sud de Paris. ActaOecol.Oec. Gen. 4, 359-374.

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

Ponge, J.F., 2000a. Vertical distribution of Collembola (Hexapoda) and their food resources in organic horizons of beech forests. Biol. Fert. Soils 32, 508-522.

Ponge, J.F., 2000b. Acidophilic Collembola: living fossils? Contr. Biol. Lab. Kyoto Univ. 29, 65-74.

Ponge, J.F., Gillet, S., Dubs, F., Fedoroff, E., Haese, L., Sousa, J.P. Lavelle, P., 2003. Collembolan communities as bioindicators of land use intensification. Soil Biol. Biochem. 35, 813-826.

Poole, T.B., 1962. The effect of some environmental factors on the pattern of distribution of soil Collembola in a coniferous woodland. Pedobiologia 2, 169-182.

Ribera, I., Doledec, S.,Downie, I.S. Foster,G.N.,2001.Effect of land disturbance and stress on species traits of ground beetle assemblages. Ecology 82, 1112-1129.

Rusek, J., 1980. Morphology of juvenile instars in two Mesaphoruraspecies (Collembola: Tullbergiinae). Rev. Ecol. Biol. Sol17, 583–589.

Salmon, S., Ponge,J.F., 2001. Earthworm excreta attract soil springtails: laboratory experiments on *Heteromurus nitidus* (Collembola: Entomobryidae). Soil Biol. Biochem. 33, 1959-1969.

Vandewalle, M., de Bello, F.,Berg, M.P.,Bolger, T.,Dolédec, S.,Dubs, F.,Feld, C.K.,Harrington, R.,Harrison, P.A.,Lavorel, S.,da Silva, P.M., Moretti, M., Niemelä, J., Santos, P., Sattler, T., Sousa, J.P., Sykes, M.T., Vanbergen, A.J., Woodcock,B.A., 2010. Functional traits as indicators of biodiversity response to land use changes across ecosystems and organisms. Biodivers.Conserv. 19, 2921-2947.

Verhoef, H.A., Van Selm,A.J., 1983. Distribution and population dynamics of Collembola in relation to soil moisture.Holarctic. Ecol. 6, 387-394.

Table 1. Codes and species names of springtails collected in the Senart forest from 1973 to 1977, total abundance, and number of samples in which the species was found. Species names according to Fauna Europaea 2011

Code	Species name	Abundance	Number of samples	Code	Species name	Abundance	Number of samples
ACA	Arrhopalites caecus	23	6	MKR	Mesaphorura krausbaueri	813	69
AEL	Anurida ellipsoides	12	4	MMA	Mesaphorura macrochaeta	2962	102
AFU	Allacma fusca	1	1	MMI	Megalothorax minimus	963	105
AGA	Allacma gallica	5	2	MMS	Mesaphorura massoudi	31	2
APR	Arrhopalites principalis	9	7	MMT	Micronychiurus minutus	1	1
APY	Arrhopalites pygmaeus	13	7	MMU	Micranurophorus musci	5	1
ASE	Arrhopalites sericus	24	8	MPY	Micranurida pygmaea	829	72
BPA	Brachystomella parvula	1036	33	MSE	Micranurida sensillata	2	2
BVI	Bourletiella viridescens	50	15	MYO	Mesaphorura yosii	158	13
CAL	Cyphoderus albinus	3	2	NDU	Neonaphorura duboscqi	2	1
CBE	Ceratophysella bengtssoni	436	4	NMU	Neanura muscorum	115	53
CBI	Cryptopygus bipunctatus	2	1	NNO	Neonaphorura novemspina	1	1
CDE	Ceratophysella denticulata	117	16	NRA	Neotullbergia ramicuspis	28	2
CEX	Cryptopygus exilis	4	3	OAM	Onychiurus ambulans	2	2
CMA	Caprainea marginata	9	2	OCI	Orchesella cincta	1460	81
CSC	Cryptopygus scapelliferus	22	3	OCR	Oncopodura crassicornis	5	3
CTH	Cryptopygus thermophilus	13	2	OPS	Onychiuroides pseudogranulosus	347	13
DFL	Deuterosminthurus flavus	7	5	OVI	Orchesella villosa	167	44
DFI	Deuteraphorura fimetaria	1	1	PAL	Pseudosinella alba	279	51
DFU	Dicyrtoma fusca	34	19	PAQ	Podura aquatica	410	7
DJU	Detriturus jubilarius	1	1	PAS	Pseudachorutella asigillata	16	5
DMI	Dicyrtomina minuta	56	30	PAU	Protaphorura aurantiaca	740	24
DTI	Desoria tigrina	1192	5	PCA	Paratullbergia callipygos	430	53
EAL	Entomobrya albocincta	120	17	PDE	Pseudosinella decipiens	7	6
ELA	Entomobrya lanuginosa	39	13	PLO	Pogonognathellus longicornis	7	5
EMA	Entomobrya multifasciata	166	11	PMA	Pseudosinella mauli	430	48
EMU	Entomobrya muscorum	17	15	PMI	Proisotoma minima	156	25
ENI	Entomobrya nivalis	74	8	PMU	Proisotoma minuta	212	10
EPU	Entomobryoides purpurascens	11	2	PNO	Parisotoma notabilis	6095	180
FCA	Folsomia candida	60	9	PPA	Pseudachorutes parvulus	229	35
FCL	Friesea claviseta	67	11	PPE	Pseudosinella petterseni	1	1
FMA	Folsomia manolachei	6274	101	PPO	Pseudosinella pongei	12	4
FMI	Friesea mirabilis	109	13	PSE	Pseudisotoma sensibilis	1464	12
FPA	Folsomides parvulus	145	13	PSU	Protaphorura subuliginata	193	20
FQU	Folsomia quadrioculata	1810	45	SAQ	Sminthurides aquaticus	1	1
FQS	Fasciosminthurus quinquefasciatus	2	2	SAS	Sminthurides assimilis	78	12
FTR	Friesea truncata	361	57	SAU	Sminthurinus aureus aureus	1054	75
GFL	Gisinianus flammeolus	98	6	SDE	Stenaphorurella denisi	32	5
HCL	Heterosminthurus claviger	3	1	SEL	Sminthurinus elegans	95	21
HIN	Heterosminthurus insignis	33	7	SLA	Superodontella lamellifera	4	3
HMA	Heteromurus major	594	71	SMA	Sminthurides malmgreni	591	43
HNI	Heteromurus nitidus	28	18	SNI	Sminthurus nigromaculatus	16	9
HPU	Hypogastrura purpurescens	1	1	SPA	Sminthurides parvulus	82	13
IAN	Isotomurus antennalis	1	1	SPS	Subisotoma pusilla	82	5
IMI	Isotomiella minor	2136	116	SPU	Sphaeridia pumilis	1566	107
IPA	Isotomurus palustris	1483	101	SQU	Stenaphorurella quadrispina	7	3
IPR	Isotomodes productus	4	1	SSC	Sminthurides schoetti	401	44
ISP	Isotomodes sp.	2	2	SSE	Schaefferia sexoculata	1	1
IVI	Isotoma viridis	54	13	SSI	Sminthurinus aureus signatus	2407	97
KBU	Kalaphorura burmeisteri	30	5	STR	Sminthurinus reticulatus	1	1
LCU	Lepidocyrtus curvicollis	72	26	SVI	Stenacidia violacea	6	2
LCY	Lepidocyrtus cyaneus	889	35	TBO	Tomocerus botanicus	35	9
LLA	Lepidocyrtus lanuginosus	3399	160	TMI	Tomocerus minor	312	45
LLI	Lepidocyrtus lignorum	565	63	VAR	Vertagopus arboreus	788	31
LLU	Lipothrix lubbocki	15	6	WAN	Willemia anophthalma	577	35
LPA	Lepidocyrtus paradoxus	2	2	WBU	Willemia buddenbrocki	5	3
LVI	Lepidocyrtus violaceus	4	4	WIN	Willemia intermedia	1	1
MAB	Micraphorura absoloni	3	2	WNI	Willowsia nigromaculata	3	1
MBE	Mesaphorura betschi	12	6	WPO	Wankeliella pongei	2	1
MGR	Monobella grassei	32	14	XBR	Xenylla brevisimilis	2	1
MHG	Mesaphorura hygrophila	1	1	XGR	Xenylla grisea	361	19
MHY	Mesaphorura hylophila	633	42	XSC	Xenylla schillei	18	5
MIN	Megalothorax incertus	12	9	XTU	Xenylla tullbergi	4673	68
MIT	Mesaphorura italica	21	9	XXA	Xenylla xavieri	33	5

Table 2. Habitat indicators, number of samples where indicators were quoted as 1 and principal coordinates along the two first components of CCA. F1 component (40% of explained variance) is linked to landuse and depth. F2 component (14% of explained variance) is linked more specifically to corticolous micro-habitats

	Number of samples	F1	F2		Number of samples	F1	F2
Autumn	96	0.045	0.084	Hornbeam	42	-0.046	0.037
Winter	108	0.162	0.051	Linden	22	-0.012	0.001
Spring	88	0.091	0.035	Maple	8	0.053	0.049
Summer	46	0.109	0.030	Ash	8	0.011	0.026
Grassland	50	0.136	-0.021	Cherry	9	0.097	-0.066
Woodland	279	-0.124	0.006	Elm	3	0.170	0.057
Heathland	9	0.064	0.029	Elder	3	0.112	-0.012
Ditch/brook	44	0.106	0.059	Hazel	11	-0.027	-0.040
Pond	64	0.140	0.056	Pine	12	0.007	0.021
Plain ground	230	0.027	-0.011	Calluna	6	0.009	0.076
Water	107	0.078	0.023	Blackberry	5	0.124	-0.002
Sunlight	141	0.230	0.074	Ivy	4	0.013	0.036
pH < 5	32	0.030	0.102	Peat moss	18	0.022	0.071
pH 5-6	35	0.024	-0.003	Hair moss	5	0.183	0.008
pH > 6	32	-0.052	-0.069	Feathermoss	8	0.030	0.102
Limestone	48	0.002	-0.009	Liverwort	1	0.156	-0.041
Sand	20	-0.062	-0.009	Lichens	4	0.082	0.140
Pebbles	23	0.057	-0.004	Algae	3	0.155	0.023
Mull	57	-0.121	-0.036	Bracken	21	0.014	0.044
Moder	24	-0.090	0.046	Purple moor grass	21	0.108	0.039
Mor	2	0.086	-0.027	Hair-grass	5	0.084	-0.028
Hydromull	6	-0.019	-0.019	Fescue-like grass	8	0.201	-0.016
Hydromoder	3	-0.030	0.004	Rushes	6	0.219	-0.013
Hydromor	3	-0.017	0.021	Waterlilies	10	0.132	0.021
Trunk	33	0.108	0.143	Hawksbeard	1	0.121	-0.003
Herbs (aerial parts)	58	0.296	0.077	Sedges	4	0.078	0.016
Mosses (aerial parts)	74	0.163	0.146	Wood anemone	20	-0.037	0.045
Superficial soil	17	0.146	0.003	Bluebell	20	-0.037	0.045
Litter	80	0.213	0.068	Duckweed	1	0.121	0.007
Humus	41	0.136	0.043	Mustard	1	0.062	0.024
Organo-mineral soil	18	-0.049	-0.032	Chamomile	1	-0.013	-0.008
Mineral soil	68	-0.172	-0.111	Chickweed	9	0.053	-0.078
Mole hill	4	0.028	-0.007	Yarrow	4	0.003	-0.051
Vertebrate dung	3	0.181	0.010	Nettle	5	-0.046	-0.047
Garbage deposits	11	-0.045	0.058	Mercury	16	0.036	0.022
Wood	35	0.093	0.132	Solomon's seal	8	0.053	0.049
Earthworm casts	7	-0.036	-0.013	Wheat	7	-0.011	-0.051
Tree roots	5	0.067	0.053	Buttercup	1	0.142	-0.041
Herb roots	8	0.083	-0.006	Knotweed	1	0.091	0.037
Oak	142	-0.048	0.015	Clover	5	-0.091	-0.038
Birch	41	0.113	0.026	Mint	1	0.123	0.001

Table 3. Trait attributes of the 128 springtail species collected in the Sénart forest, and number of species where attributes were found

Trait	**Attribute**	**Number of species**
Mode of reproduction	Parthenogenesis dominant	36
	Sexual reproduction dominant	89
Body size	Small	86
	Medium	28
	Large	14
Body form	Slender	92
	Stocky	6
	Spheric	30
Body color	Pale-coloured	60
	Bright-coloured	30
	Dark-coloured	38
Scales	Absent	109
	Present	19
Antenna size	Short	65
	Long	63
Leg size	Short	61
	Long	67
Furcula size	Absent or vestigial	35
	Short	25
	Long	68
Eye number	0	42
	1-5	24
	> 5	62
Pseudocella	Absent	105
	Present	23
Post-antennal organ	Absent	69
	Simple	21
	Compound	38
Trichobothria	Absent	72
	Present	56

Figure legends

Figure 1. Canonical correspondence analysis of species trait attributes: projection of traits (a) and habitat indicators (b) in the plane of the first two canonical factors F1 and F2.

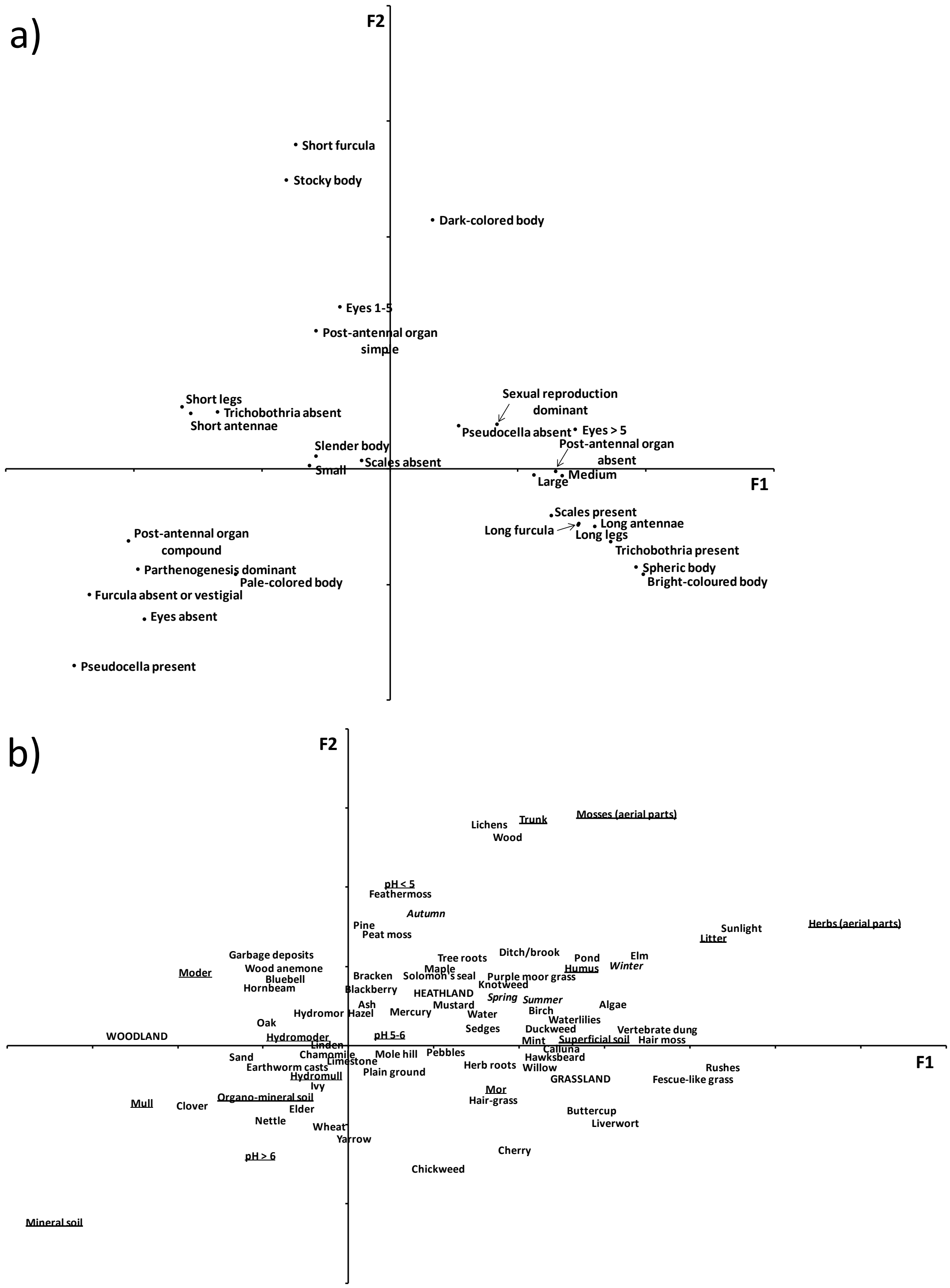
a)
F2
F1
Short furcula
Stocky body
Dark-colored body
Eyes 1-5
Post-antennal organ simple
Short legs
Trichobothria absent
Short antennae
Slender body
Small
Scales absent
Sexual reproduction dominant
Pseudocella absent
Eyes > 5
Post-antennal organ absent
Large
Medium
Scales present
Long furcula
Long antennae
Long legs
Trichobothria present
Spheric body
Bright-coloured body
Post-antennal organ compound
Parthenogenesis dominant
Pale-colored body
Furcula absent or vestigial
Eyes absent
Pseudocella present
b)
F2
F1
Lichens
Trunk
Mosses (aerial parts)
Wood
pH < 5
Feathermoss
Autumn
Pine
Peat moss
Sunlight
Litter
Herbs (aerial parts)
Garbage deposits
Wood anemone
Moder
Bluebell
Hornbeam
Tree roots
Ditch/brook
Pond
Elm
Maple
Humus
Winter
Bracken
Solomon's seal
Purple moor grass
Blackberry
Knotweed
HEATHLAND
Spring
Summer
Ash
Mustard
Algae
Hydromor
Hazel
Mercury
Water
Birch
Oak
Waterlilies
Sedges
Duckweed
Vertebrate dung
WOODLAND
Hydromoder
pH 5-6
Mint
Superficial soil
Hair moss
Linden
Calluna
Sand
Chamomile
Mole hill
Pebbles
Hawksbeard
Limestone
Earthworm casts
Herb roots
Willow
Rushes
Hydromull
Plain ground
GRASSLAND
Fescue-like grass
Ivy
Mor
Organo-mineral soil
Hair-grass
Mull
Clover
Elder
Buttercup
Nettle
Liverwort
Wheat
Yarrow
Cherry
pH > 6
Chickweed
Mineral soil

Fig. 1