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► **To cite this version:**

Sandrine Salmon, Jean-François Ponge. Species traits and habitats in springtail communities: a regional scale study. *Pedobiologia*, 2012, 55 (6), pp.295-301. 10.1016/j.pedobi.2012.05.003 . hal-00750242

HAL Id: hal-00750242

<https://hal.science/hal-00750242v1>

Submitted on 9 Nov 2012

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

3

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9 Running title: Trait-habitat relationships in springtails

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1 **Abstract**

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

24 **Keywords:** Collembola; species trait assemblages; habitats; trait-environment
25 relationships

1 **Introduction**

2 The indicative power of species trait assemblages has been intensively studied in
3 plants, birds and beetles and most species traits could be clearly related to habitat
4 preferences of species in these groups (Graves and Gotelli 1993; Ribera et al.
5 2001; Cornwell and Ackerly 2009; Mayfield et al 2009; Pavoine et al. 2011).
6 Surprisingly, although this is common sense and was reported for a long time in soil
7 zoology (Bornebusch 1930), few studies questioned whether the extraordinary diversity
8 of species traits which prevail in soil animal communities could be explained, and
9 potentially could have been selected, by differences in habitat use (Vandewalle et al.
10 2010; Decaëns et al. 2011; Bokhorst et al. 2011). Moreover, these studies focused either
11 on a restricted number of traits, or a restricted number of habitats which does not allow
12 providing general trends in relationships between species traits and habitat use.

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

16 Among soil invertebrates, we selected springtails (Hexapoda, Collembola) as an
17 abundant and diversified monophyletic group for which a great deal of work has been
18 devoted to the study of species/environment relationships at the community level (Poole
19 1962; Hågvar 1982; Ponge 1993; Chagnon et al. 2000; Auclerc et al. 2009). The Sénart
20 forest (Ile-de-France, northern France) and its vicinity were selected because they
21 display a great variety of soil and soil-related habitats (e.g. woodland, heathland,
22 grassland, ponds, paths, tree trunks) composing a little more than 3,000 ha of
23 heterogeneous landscape, now totally included in the Paris area. Data collected from
24 1973 to 1977, at a time when agriculture was still practiced both inside and outside the

1 forest, were revisited for a statistical analysis taking into account species
2 trait/environment relationships. The same pool of data (370 samples, 127 species) has
3 been already used in several studies dealing with species/environment relationships
4 (Ponge 1980, 1983, 1993) and was included in the COLTRAIT data base
5 [<http://www.bdd-inee.cnrs.fr/spip.php?article51&lang=en>], which also comprises data
6 about twelve morphological and life-history traits of more than 300 collembolan
7 species.

8 **Materials and Methods**

9 Site description

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

1 underlying impervious clay strata (permanent water tables). More details were given in
2 previously published papers (Ponge 1980, 1983, 1993).

3 Sampling procedure

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

21 Samples were taken with the help of a shovel for soil, and with fingers for above-
22 ground samples, care being taken not to lose too many jumping animals in particular
23 when sampling aerial parts of erected plants. No attempt was done to force a corer into
24 the soil. Samples were immediately put in plastic bags then transported to the nearby

1 laboratory, to be extracted on the same day. Extraction was done by the dry funnel
2 (Berlese) method over 10 days, using 25 W bulb lamps in order to avoid too rapid
3 desiccation of the samples, known to prevent slowly moving animals from escaping
4 actively the samples (Nef 1960). Animals were collected and preserved in 95% ethyl
5 alcohol in plastic jars. A total of 310 samples were collected and kept for the analysis.

6 Species identification

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

21 Trait data

22 Twelve traits, mostly extracted from the COLTRAIT data base and collected
23 from numerous identification keys or synopses, describe morphology and reproductive
24 mode of the 128 species used in the analysis. Attributes of each trait (Table 3) were

1 considered as variables, and were coded as binary (dummy) variables, resulting in a list
2 of 30 attributes: mode of reproduction (parthenogenesis dominant, sexual reproduction
3 dominant), body size (small, medium, large), body form (cylindrical body, stocky body,
4 spherical body), body color (pale-colored, bright-colored, dark-colored), scales (absent,
5 present), antenna size (short, long), leg size (short, long), furcula size (absent or
6 vestigial, short, long), eyenumber (0, 1-5, > 5), pseudocella (absent, present), post-
7 antennal organ (absent, simple, compound), and trichobothria (absent, present).
8 Antennae, eyes, post-antennal organs and trichobothria are supposed to play a sensory
9 role (Hopkin 1997).

10 Species habitat data

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

18 Statistical treatment of the data

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

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

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

3 **Results**

4 The rarefaction curve of the 128 observed species showed that sampling had
5 approached an asymptote. Estimating the number of missing species according to Chao
6 (1987) put the expected total number of species for the Sénart forest to 133 and
7 indicated that the sampling was relatively exhaustive.

8 Canonical Correspondence Analysis (CCA) with species trait attributes as
9 explained variables and species habitats as explanatory variables showed that traits were
10 significantly explained by habitats (number of permutations = 500, pseudo-F = 0.94, $P <$
11 0.0001). Constrained variance (variance of species traits explained by species habitats)
12 represented 72.9% of the total variance.

13 The first two canonical components of CCA extracted 54% of the constrained
14 (explained) variance (40% and 14% for F1 and F2, respectively). The projection of trait
15 attributes and species in the F1-F2 plane is shown in Figures 1a and 1b, respectively.
16 Both species and trait attributes were distributed along three dimensions. Species with
17 pseudocella and post-antennal organ present (of compound type), parthenogenesis
18 dominant, regressed locomotory (furcula, legs) and sensorial organs (eyes, antennae,
19 thichobothria), and pale color were opposed to species displaying opposite attributes
20 along F1. According to principal coordinates of species habitats (Table 2) this
21 corresponded to opposite habitats: woodland vs grassland and depth versus surface, from
22 negative to positive sides of F1. Heathland was in an intermediate position between
23 woodland and grassland (Table 2). Mineral soil, organo-mineral soil, humus (organic),
24 litter, plant aerial parts ranked in this order along F1. Sunlight was projected on the

1 positive side of F1 (open environments). The second canonical component F2 was more
2 specifically linked to corticolous microhabitats (trunks, wood and associated mosses
3 and lichens): associated trait attributes were short furcula, stocky and dark-colored
4 body, eyes present but in regressed number (1-5), post-antennal organ present but
5 simple. Acidity and humus type, as well as water, did not exhibit any pronounced
6 influence on species trait attributes. Partial CCA, allowing only water and soil acidity
7 (including humus type) to vary, showed that they did not influence the distribution of
8 trait attributes (pseudo-F = 0.17, P = 0.99).

9 **Discussion**

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

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

22 Despite clear trends of trait/habitat relationships exhibited by our results,
23 possible biases due to escape movements during sampling, in particular from the part of
24 big-size animals with long furcula, should not be overlooked. If such biases differ from
25 a habitat to another, this may flaw trait/habitat relationships. However, concerning the

1 association between big size and agricultural environments, which is novel to science, it
2 must be highlighted that it was less easy to collect vary motile specimens in the absence
3 of litter (i.e. in agricultural areas) than when litter was present (i.e. in forest areas),
4 stemming in a bias in quite opposite direction to the observed association. This made us
5 confident that such biases were not present in our dataset.

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

23 The fact that we did not discern any association between traits and obvious
24 factors such as water and soil acidity (or humus type) does not preclude any further
25 scrutiny of such relationships. Two reasons could be invoked. First, that, in its present

1 state, our database did not cover the traits needed to establish this relationship. Ponge
2 (2000b) showed that acidophilic and acidophobic species cohabited within the same
3 lineage, pointing to corresponding traits as mainly based on physiology (mechanisms
4 counteracting oxidative stress) rather than on anatomy and reproduction mode. Traits
5 associated with aquatic life concern mainly the form and size of claws (Gisin 1960), and
6 of course physiology (resistance to desiccation), which were not considered here.
7 Second, in the particular case of the Senart forest, traits adapting species to habitats
8 varying in terms of water availability and/or soil acidity could be masked by landuse or
9 vertical stratification effects, pointing to the need for studying trait/habitat relationships
10 on a wider geographic scale, as suggested by Lepetz et al. (2009).

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

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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 |

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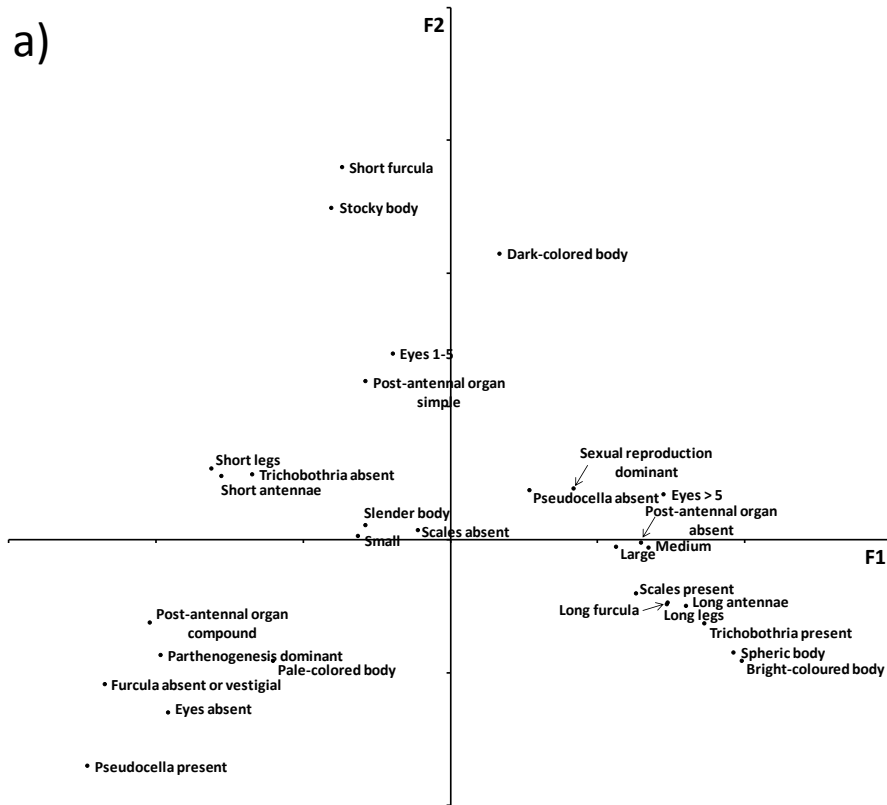
2

1 **Figure legends**

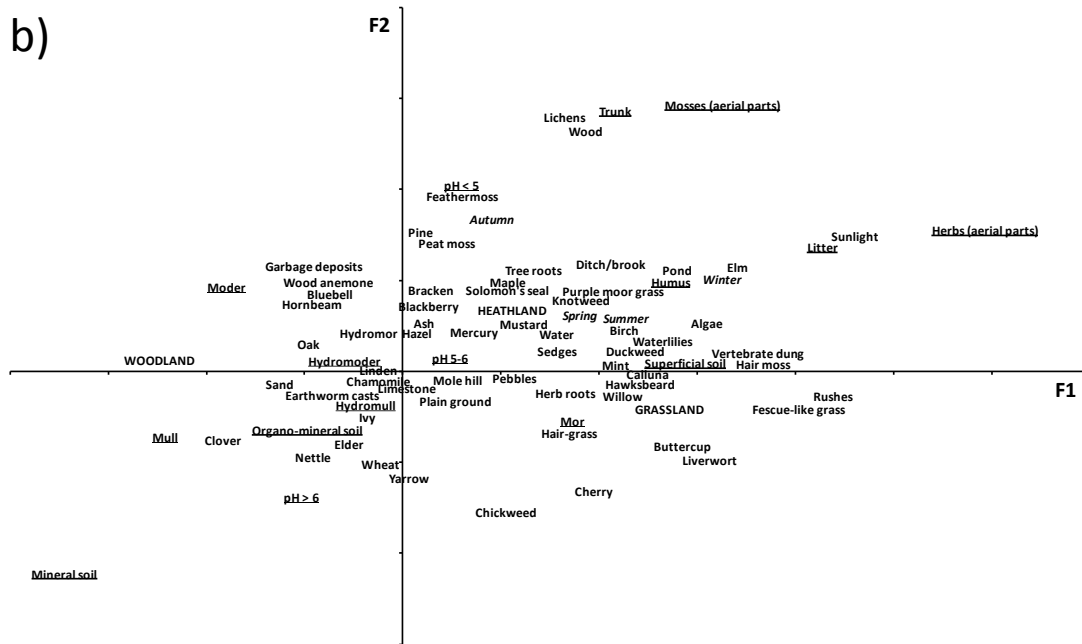
2 **Figure 1.** Canonical correspondence analysis of species trait attributes: projection of
3 traits (a) and habitat indicators (b) in the plane of the first two canonical factors
4 F1 and F2.

5

a)



b)



1

2 Fig. 1