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1 **Spatial and taxonomic correlates of species and species trait**
2 **assemblages in soil invertebrate communities**

3

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8

9 Running title: Spatial and taxonomic patterns of soil animal communities

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1 **Abstract**

2 Whether dispersal limitation and phylogenetic conservatism influence soil species
3 assemblages is still a debated question. We hypothesized that spatial and phylogenetic
4 patterns influence communities in a hump-backed fashion, maximizing their impact at
5 intermediate spatial and phylogenetic distances. Species-environment relationships are blurred
6 by dispersal limitation and restricted habitat choice at long and short spatial distances,
7 respectively (Hypothesis 1). Co-occurrence of species/traits is limited by divergent evolution
8 of species/traits and competitive exclusion at long and short phylogenetic distances,
9 respectively (Hypothesis 2). Springtails were sampled over a wide array of environmental
10 gradients, between-sample distance varying from a few cm to several km. We compared
11 communities using species composition, habitat features, and geo-localization. We compared
12 species using co-occurrence, habitat preference, traits and phylogeny. Mantel tests allowed
13 discerning which factors contributed the best to species/traits assemblages. Within the studied
14 area, species composition was influenced by habitat more than space. Traits displayed a
15 strong phylogenetic signal, but they contributed less than habitat preferences to species co-
16 occurrence. Species-environment relationships were better displayed within 200 m distance,
17 supporting Hypothesis 1. Occurrence-habitat preference relationships were better displayed at
18 family level, supporting Hypothesis 2.

19 **Keywords:**Collembola, habitat preferences, phylogeny, species traits, spatial distance

20

21 **Introduction**

22 A great deal of studies questioned the way species and/or species traits assemble
23 themselves and addressed rules which govern their assembly at both regional and local level
24 (reviewed in Weiher et al. 2011). Metacommunity approaches and concepts (patch dynamics,

1 species sorting, mass effects, and neutral dynamics) helped to discern processes acting at
2 various spatiotemporal scales (Leibold et al. 2004). At regional level dispersal and
3 emigration/immigration rates have a prominent influence on the composition and species
4 richness of communities (Erdmann et al. 2012). At local level two broad categories of
5 assembly processes have been proposed: *(i)* habitat filters that restrict the range of viable
6 strategies according to ecological requirements of species, and *(ii)* competitive exclusion and
7 niche partitioning that limits the similarity of coexisting species (Cornwell and Ackerly 2009).
8 The balance between ‘space’ and ‘environment’ in the assembly rules of communities is thus
9 strongly dependent of the scale used for the study (Belmaker and Jetz 2011).

10 Phylogenetic biology has allowed refining assembly rules, raising the importance of
11 evolutionary processes such as phylogenetic conservatism and convergence in the assemblage
12 of traits/species at community level (Cavender-Bares et al. 2009). Broadly speaking,
13 phylogenetic relationships of species may dictate whether they compete or not, whether they
14 share the same ecological requirements or not, and thus whether they cohabit or not.

15 Based on these various paradigms, spatial and phylogenetic correlates of species/trait
16 assemblages have been successfully used to predict changes in species composition along
17 environmental gradients (Lovette and Hochachka 2006), in the course of natural succession
18 (Brändle et al. 2003), and when and where communities are faced to global change
19 (Barnagaud et al. 2011) or anthropic pressure (Ozinga et al. 2009).

20 Several soil invertebrate studies questioned whether *(i)* species/environment
21 relationships are influenced by the spatial distribution of habitats, and if yes to which extent
22 (Winkler and Kampichler 2000), *(ii)* species/environment relationships are revealed at
23 different spatial scales (Terauds et al. 2011), *(iii)* habitat preferences and traits of co-occurring
24 species are influenced by their taxonomic relationships (Prinzing 2003). Erdmann et al.

1 (2012) stressed the importance of regional factors, compared to local factors in
2 Central European oribatid mite communities, pointing to ‘space’ having more importance
3 than ‘environment’. Ingimarsdóttir et al. (2012) showed that both species sorting (local effects
4 of the environment) and mass effects (regional effects of dispersal limitation) shaped
5 collembolan and oribatid mite communities in nunataks (deglaciated land). Kounda-Kiki et al.
6 (2009) showed that within-thicket (3 m) overwhelmed between-thicket (30 m) variation in
7 soil invertebrate communities on a tropical inselberg, pointing to ‘environment’ having more
8 influence than ‘space’. Lindo and Winchester (2008, 2009) embraced in the same study a
9 variety of scales ranging from the ‘local’ scale, at which most soil organisms interact with
10 their environment, to the ‘regional’ scale at which land use change may impact soil animal
11 communities. The interest of such a multilevel approach, focusing on how organisms perceive
12 landscape units, has been stressed by Chust et al. (2003).

13 Among soil invertebrates, we selected springtails (Hexapoda, Collembola) as a
14 monophyletic group for which a great deal of work has been devoted to community-level
15 assessment of species/environment relationships (reviewed by Rusek 1998 and Van Straalen et
16 al. 2008), and for which taxonomy is stable and fairly well supported by molecular
17 investigations (Porco and Deharveng 2009). Van Straalen et al. (2008) showed that these
18 wingless basal hexapods were a good model to test general biological principles. Ponge
19 (1993) showed that a limited number of ecological factors could explain the distribution of
20 Collembola species when collected in the same geographical context. Vertical distribution is
21 the main gradient along which most springtail species are distributed at the ‘local’
22 scale (Ponge 2000; Krab et al. 2010), followed by other factors such as water availability
23 (Verhoef and Van Selm 1983), soil acidity (Loranger et al. 2001), and land use (Salmon and
24 Ponge 2012), at ‘regional’ and intermediate scales.

1 In the present study we attempt to discern whether factors of variation other than
2 discernible environmental gradients might exist in the composition of springtail
3 communities. First, we will question the importance of spatial scale in species/environment
4 relationships. We already showed on the same data set that species (Ponge 1993) and traits
5 (Salmon and Ponge 2012) are distributed according to habitat requirements of species. In the
6 present paper, we make substantial additions to this knowledge, pointing to the importance of
7 spatial scale, which was not taken into account so far on this data set. On the base of
8 aforementioned regional versus local influences on species composition we hypothesize that at
9 ‘regional’ scale the selection of habitats is limited by dispersal capacities of species while at
10 ‘local’ scale it is limited by the number of habitats at disposal. As a consequence,
11 species/environment relationships should be better expressed at intermediate scales
12 (Hypothesis 1).

13 Second, we question the importance of phylogenetic relationships in
14 species/environment and trait/environment relationships. We hypothesize that (i) coexisting
15 species are less phylogenetically distant (and thus share more trait attributes) than segregating
16 species, i.e. display underdispersion (Weiher and Keddy 1995), but also that (ii) at low
17 taxonomic levels the relationship between phylogenetic proximity and co-occurrence is
18 traded-off by competitive exclusion. Thereby, phylogenetic distance will better influence co-
19 occurrence at not too high and not too low taxonomic levels (Hypothesis 2).

20 **Materials and methods**

21 **Origination of the data**

22 The Sénart forest (Ile-de-France, northern France, 48° 40’ N, 2° 29’ E) and its vicinity
23 were selected because they display a great variety of soil and soil-related habitats (woodland,
24 heathland, grassland, ponds, paths, tree trunks, ...) composing a little more than 3,000 ha of

1 variegated landscape, now totally included in the Paris area. Data collected from 1973 to
2 1977, at a time when agriculture was still in usage both inside and outside the forest, were
3 revisited for a statistical analysis taking into account spatial and phylogenetic influences on
4 species/environment relationships, still poorly addressed by soil biologists at the time of
5 sampling. The same pool of data (370 samples, 127 species) has been already used in a study
6 on species/environment relationships (Ponge 1993) and was included in the COLTRAIT data
7 base, which also comprises data for twelve morphological and life-history traits of more than
8 300 Collembola species. The COLTRAIT database is still not implemented on a website but a
9 short presentation is available at [<http://www.bdd-inee.cnrs.fr/spip.php?article51&lang=en>]
10 and a research report is available (in French only) at [[http://hal.archives-
11 ouvertes.fr/docs/00/60/78/37/PDF/Enrichissement_de_la_base_de_donnA_es_COLTRAIT.pd
12 f](http://hal.archives-ouvertes.fr/docs/00/60/78/37/PDF/Enrichissement_de_la_base_de_donnA_es_COLTRAIT.pdf)]. The COLTRAIT database has been used in a previous paper devoted to trait/environment
13 relationships (Salmon and Ponge 2012).

14 Site description

15 The Sénart state forest (3,000 ha) is located 20 km south-east of Paris on the western
16 border of the Brie plateau, delineated by a meander of river Seine and by a tributary, the river
17 Yerres, at an altitude ranging from 50 to 87 m a.s.l. At the time of sampling it was mainly
18 bordered by urbanized areas (communes of Quincy-sous-Sénart, Boussy-Saint-Antoine,
19 Brunoy, Yerres, Montgeron, Draveil) on its western and northern sides, and by agricultural
20 areas (communes of Soisy, Étiolles, Tigery, Lieusaint, Combs-la-Ville) on its eastern and
21 southern sides. Nowadays, the forest is totally included in the metropolitan area of Paris.
22 Private peripheral woods and agricultural areas (cultures and meadows) were included in the
23 study. Since the time of sampling most private woods have been incorporated to the state
24 forest, but agricultural areas have been built or transformed into golf courses or other

1 recreational areas. More details about climate, soils and vegetation are given in Salmon and
2 Ponge (2012).

3 Looking at historical reviews (Chodron de Courcel 1930) and botanical censuses
4 (Gaume 1938) reveals that before World War II a large part of the western part of the forest,
5 in particular the Uzelles de Draveil ('uzelles' meaning commons in old French) were used for
6 extensive agriculture and were progressively afforested after agriculture abandonment, now
7 subsisting on a small surface in the form of a managed ericaceous heath. As soon as 1938
8 Gaume indicated that the Rû d'Oly (a brook flowing westward in the western part of the
9 forest) was losing its botanical richness, due to the abandon of pasture in the wet meadows
10 bordering it (Gaume 1938).

11 Sampling procedure and species identification

12 Sampling took place from 15th October 1973 to 10th October 1977 in every season and
13 every kind of weather, our purpose at that time being to embrace all climate conditions,
14 except when the soil was deeply frozen and could not be sampled at all. At each sampling
15 occasion, a point was randomly selected on a map and geo-referenced, around which, upon
16 visit, all kinds of habitats and micro-habitats potentially available to springtails were
17 investigated, from deep soil (leached mineral horizons) to tree trunks two meters aboveground
18 and to floating vegetation in water-filled ponds when present in the vicinity. In average, a
19 circle of ca. 10 m around the randomly selected point was scrutinized for the variety of
20 habitats, which varied to a great extent according to land use (from 5 to 15 habitats/micro-
21 habitats per sampling plot). By this procedure sampling was done only once in each of the 42
22 sites thus visited. Distances between samples were classified in seven classes: less than 2 cm
23 (607 couples), from 2 to 20 cm (288 couples), from 20 cm to 2 m (442 couples), from 2 to 20
24 m (1,594 couples), from 20 to 200 m (5,128 couples), from 200 m to 2 km (32,043), and from

1 2 to 20 km (75,118 couples). Mean sampling interval was 34 days, distributed among the four
2 seasons, summer being somewhat undersampled (28%, 32%, 26% and 14% of total number of
3 samples in autumn, winter, spring and summer, respectively). No effort was done to
4 standardize sampling, the only requirement being to collect enough animals to get an idea of
5 species distribution in each sample (ca. more than 30 specimens per sample):at that time the
6 aim of the study was just to compare samples on the base of species distribution, without any
7 standard requirement for surface or volume. The volume sampled varied from 100 mL for
8 moss cushions, which are particularly rich in springtails (Gerson 1982)to 1 L for bleached
9 mineral soil horizons which are strongly impoverished in fauna (Hågvar 1983). The total
10 number of samples was 370, which contained 127 species. Care was taken not to undersample
11 some poorly represented habitats, such as calcareous soilsand dumping places, which
12 necessitated some complementary sampling (48 and 11 samples, respectively). Such a
13 selection procedure, combining random selection of sampling sites and directed choice of
14 habitats and micro-habitats, allows environmental gradients to be more fully described
15 (Gillison and Liswanti 2004).

16 At the time of study the only key available for European springtails was that of Gisin
17 (1960), to which were added numerous detailed published studies at family, genus or species
18 level (complete list available upon request), and miscellaneous (unpublished) additions by
19 Gisin himself. Gisin's nomenclature was updated using Fauna Europaea 2011
20 [<http://www.faunaeur.org/>]. A total of 127 species were found (Appendix 1).

21 Habitat data

22 Field notes taken at the time of sampling were used to classify habitat/micro-habitat
23 features in 82 habitat indicators, including seasons and vertical stratification (Appendix 2). To
24 each sample was thus assigned a set of 82 binary variables (coded as 0 or 1) which describe

1 its main features at varying scales, from landscape (heathland, grassland, woodland) to
2 sampling plot (ditch, plain ground, pond, vegetation, soil pH...) then to sample scale (plant
3 parts, litter and soil horizons, earthworm casts,...). A zero value for an habitat indicator might
4 mean either that it could not be estimated (for instance pH does not mean anything for plant
5 aerial parts) or that it was mutually exclusive with another indicator (for instance if sampling
6 was done in autumn, then winter, spring and summer indicators were automatically given the
7 value 0). The only meaningful value for the association of a sample with a habitat indicator
8 was thus 1. In many instances the information given by habitat indicators could be at least
9 partly redundant (viz. limestone and mull) or nested (viz. pond and water), but full
10 redundancy was excluded. The same latitude and longitude values (extended Lambert
11 coordinates) were assigned to all samples collected in the vicinity of a pre-designed point.

12 Phylogeny/taxonomy data

13 In the absence of a complete phylogeny of Collembola, we used the Checklist of the
14 Collembola of the World [<http://www.collembola.org/>], which is the most refined and updated
15 taxonomic classification of springtails, incorporating most recent results of molecular and
16 morphological investigations on this monophyletic group of Hexapoda.

17 Trait data

18 Twelve traits, mostly extracted from the COLTRAIT data base and collected from
19 numerous identification keys or synopses, describe the morphology and reproductive mode of
20 the 127 species used in the analysis (Salmon and Ponge 2012). In particular, we selected traits
21 thought to be more responsive to distance and habitat: visual, mechanical and olfactory organs
22 (eyes, trichobothria, post-antennal organs, and antennae) and coloration allow animals to
23 select and/or withstand habitats/micro-habitats according to their physiological requirements,
24 reviewed in Hopkin (1997). More details on selection of traits and trait attributes are given in

1 Salmon and Ponge (2012). The 30 trait attributes were coded as binary (dummy) variables
2 (Appendix 3). Morphological traits related to the mobility of species (visual and jumping
3 apparatus, length of legs) were used to classify species in putative fast and slow dispersers
4 according to Ponge et al. (2006).

5 Statistical treatment of the data

6 Mantel tests were devised to partial out the spatial component of ecological variation
7 (Legendre 1989) and were used successfully in the study of species-environment relationships
8 in microarthropod communities (Borcard and Legendre 1994; Lindo and Winchester 2009). In
9 the present study we extended this method to the study of trait-environment relationships by
10 discarding the effect of phylogenetic variations, as an alternative to the use of phylogenetic
11 contrasts (Martins and Hansen 1997). Partial and simple Mantel tests were used to measure the
12 correlation between distance/dissimilarity matrices, with and without discarding the effect of
13 one of them on the two others, respectively.

14 Dissimilarities between samples were calculated on the base of species composition,
15 habitat indicators and space. The Spearman coefficient of dissimilarity $D = (1-r_s)/2$, r_s being
16 the Spearman's rank correlation coefficient, was used as a measure of dissimilarity between
17 samples based on species abundances. The Spearman rank correlation coefficient allowed
18 taking into account the large variation in population size which was observed between e.g.
19 moss cushions, a micro-habitat which harbors numerous springtails, and mineral soil
20 horizons, a micro-habitat strongly impoverished in these animals. This method based on ranks
21 rather than on pure or transformed data (see Anderson et al. 2006 for a review on similarity
22 indices) allows comparisons based on the whole community composition, whatever the
23 theoretical distributions of species abundances, and decreases the variability due to sample
24 size heterogeneity (Gauthier 2001). Dissimilarities between samples based on habitat

1 indicators (dummy variables taking 0 or 1 value) were calculated using the Jaccard distance,
2 i.e. one minus the number of habitat indicators shared by a couple of samples divided by the
3 total number of habitat indicators when both samples are pooled. The Jaccard distance varied
4 from 0 (identity) to 1 (complete dissemblance). This measure of habitat dissimilarity was used
5 to calculate an average between-sample habitat dissimilarity at varying scales.

6 Spatial distances between samples were estimated using an index varying according to
7 a logarithmic scale: 0 (< 2 cm), 1 (2 – 20 cm), 2 (20 cm – 2 m), 3 (2 – 20 m), 4 (20 – 200 m),
8 5 (200 m – 2 km) and 6 (2 – 20 km). We calculated a Mantel rank correlation coefficient
9 between habitat and composition at varying spatial scales, i.e. by increasing the distance over
10 which samples were compared. The finest scale used for this calculation was for samples
11 located at less than 2 m the one from the other, while the largest scale was for the whole set of
12 samples, i.e. less than 20 km.

13 Dissimilarities between species were calculated on the basis of occurrences
14 (abundance values in the different samples), traits, habitat preferences and phylogeny. Habitat
15 preferences were cross-calculated by multiplying the matrix of abundance values (127 species
16 x 370 samples) by the matrix of habitat features (370 samples x 82 features, coded as 0 or 1).
17 The resulting matrix (127 species x 82 habitat features) was divided by the total abundance of
18 each species, in order to compare them on the base of relative preferences (sum of habitat
19 preferences equal to 1 for each species, whether abundant or not).Dissimilarities between
20 species using occurrenceand habitat preference were calculated using the Spearman
21 dissimilarity coefficient, as explained above.Dissimilarities between species using traits were
22 calculated using the Jaccard distance, as explained above for samples using habitat indicators.

1 Taxonomic distances were calculated using as a numerical estimate, the rank level at
2 which taxa were associated: 1 (subspecies), 2 (species), 3 (subgenus), 4 (genus), 5 (tribe), 6
3 (subfamily), 7 (family), 8 (superfamily), and 9 (order).

4 In all calculations of dissimilarity/distance matrices between species, whether based on
5 occurrence, traits or taxonomy, rare and common species were given the same weight, in the
6 same manner as species-poor and species-rich samples were given the same weight in
7 between-samples matrices. This is justified by the fact that we do not have a priori reasons for
8 judging that species-rich samples (resp. common species) are more informative than species-
9 poor samples (resp. rare species).

10 Species accumulation curves were calculated to estimate the exhaustiveness of our
11 sampling method and to compare different geographical areas within the Sénart forest. In
12 particular we arbitrarily divided the Sénart forest (ca. 8 x 8 km) in a western and an eastern
13 part, each of them ca. 4 x 8 km, on the base of aforementioned suspected differences in past
14 landuse. The same method was also applied to a comparison of the number of environmental
15 indicators (habitat features) between both geographical areas. Species accumulation curves
16 and jackknife estimators were calculated using EstimateS (version 8.2.0). Each sample was
17 considered a unit, containing a number of specimens belonging to different species. A
18 cumulative curve displays the increase in number of species when the number of samples
19 increases, on the base of observed means. Confidence intervals around observed means were
20 calculated according to the Mao Tau model (Colwell et al. 2004). The number of missing
21 species was estimated according to Chao (1987). Comparisons between accumulation curves
22 were performed by Chi-square tests.

23 Fisher's exact test was used to compare the distribution of fast- and slow-dispersers
24 (present vs. absent) between western and eastern parts of the Sénart forest and to compare the

1 number of habitats (present vs. absent) between both areas. Sign test was used to compare the
2 distribution of species habitat preferences (explained above) between western and eastern
3 parts of the Sénart forest (only species common to both areas were taken into account).

4 All calculations (to the exception of accumulation curves) were done using XLSTAT®
5 (Addinsoft®, Paris, France).

6 **Results**

7 The spatial component of species-environment relationships

8 The accumulation curve of the 127 observed species over the 370 samples (Fig. 1a)
9 showed that sampling had approached an asymptote, indicating that sampling effort was
10 adequate to embrace collembolan biodiversity of the Sénart forest. The expected total number
11 of species was 133 or 137 according to Chao1 and Chao2 estimators. Accumulation curves for
12 the western and eastern parts of the Sénart forest differed to a significant extent: for the same
13 sampling effort there was a lesser number of species in the western part of the forest (Fig. 1b).

14 Mantel tests (Table 1) indicated that dissimilarities between samples according to
15 species composition and according to habitat indicators were positively correlated: the more
16 dissimilar were habitat indicators, the more dissimilar Collembola communities were in their
17 species composition. Although highly significant in both cases, this relationship was better
18 expressed when the effect of spatial distance was discarded, resulting in a higher Mantel
19 statistic. There was a positive and highly significant relationship between spatial distance and
20 compositional dissimilarity of samples, although this correlation was poorer than that between
21 composition and habitat: the more spatially distant were the samples, the more distinct they
22 were in their species composition. This correlation was much lesser although still highly
23 significant when the effect of habitat was discarded. At last, habitat dissimilarity and
24 spatial distance were positively and highly significantly correlated, the value of the Mantel

1 statistic (0.38) being higher than between space and species composition (0.17) but near equal
2 to that between habitat and species composition (0.36): the more spatially distant the samples,
3 the more they differed in habitat features. The positive correlation between habitat
4 dissimilarity and spatial distance explains why the positive correlation between compositional
5 and habitat dissimilarities increased when spatial effects were discarded: this correlation was
6 better expressed at short distance.

7 Taking the value of the Mantel statistic as a measure of species-environment
8 relationships over the range of studied spatial scales (Fig. 2a) it can be seen that a maximum
9 value was obtained at the 200 m scale (0.49), which was not far from the value obtained when
10 spatial effects were excluded from the total set of samples (0.55). At larger and finer scales,
11 r_M values were lower and became not significant below 20 m. This indicated that species-
12 environment relationships were blurred at distances higher than 200 m or shorter than 20 m.
13 The poor explanatory value of habitat features for more neighboring samples (r_M values not
14 significant at distances < 20 m) can be explained by a lack of variety of the environment at
15 short distance. This was verified by the average habitat dissimilarity between samples
16 (calculated on the base of between-sample dissimilarity of habitat indicators), which sharply
17 increased with scale amplitude (Fig. 2b): the larger the scale, the larger the variety of
18 habitats sampled.

19 Environmental variety cannot explain the abovementioned higher number of species
20 in the eastern part of the forest, as exemplified by accumulation curves of habitat indicators,
21 which did not differ between western and eastern parts of the forest (Fig. 1b). Accordingly,
22 habitat preferences of the 77 species common to both parts of the forest did not reveal any
23 difference between western and eastern parts (sign test, $P = 0.96$). The deficit in species
24 richness observed in the western part of the forest (27 species, minus 23%) was significant
25 (Fisher's exact test, $P < 0.0001$), and could not be explained either by a deficit in habitats

1 (Fisher's exact test, $P = 0.84$) or by unbalanced sampling effort (Fig. 3). A distinction
2 between slow vs fast dispersers (Fig. 4) showed that the balance between slow and fast
3 dispersers (ca. 76% in favor of slow dispersers in the eastern part of the forest) shifted to 50%
4 for species common to both parts of the forest or for species living only in the western part.

5 The taxonomic component of traits, habitat preference and species co-occurrence

6 Using taxonomic distances as a proxy to phylogenetic distances (Table 2), Mantel
7 testsshowed, apart from the trivial result that traitsand taxonomy were correlated, thattrait and
8 habitat preference dissimilarities were positively and highly significantly correlated,
9 evenwhen excluding taxonomy. The relationship between habitat preference dissimilarity and
10 taxonomic distance was also positive and significant, but significance vanished when traits
11 were excluded, pointing to traits mediating the observed effect of taxonomy on habitat
12 preference.

13 Other Mantel tests showed that species occurrence dissimilarity was positively and
14 significantly explained by habitat preference ($r_M = 0.48$) and, although to a lesser extent, by
15 traits ($r_M = 0.12$) and taxonomy ($r_M = 0.07$): species which occurred together in the same
16 samples exhibited similar habitat preferences and traits, and they were closely related from a
17 taxonomic point of view (Table 3). The use of partial Mantel tests, allowing discarding the
18 effect of one of these three factors, did not show major increases or decreases of these values,
19 to the exception of the relationship between occurrence dissimilarity and taxonomy: this
20 positive relationship totally disappeared when the influence of traits was discarded (partial r_M
21 = -0.001, $P = 0.97$) while it remained near unchanged when habitat preference effects were
22 discarded (partial $r_M = 0.05$, $P < 0.0001$), pointing to traits as the major component of the
23 influence of taxonomy on species occurrence dissimilarity.

1 We used Mantel tests between species occurrence and habitat preference dissimilarity
2 matrices at successive taxonomic levels to question whether the positive relationship between
3 occurrence and habitat preference dissimilarities (Table 3) varied according to taxonomic
4 level. Figure 5 showed that the Mantel statistic measuring the correlation between occurrence
5 and habitat preference dissimilarities displayed a humped-back pattern. The maximum value
6 was observed at family level, and decreased to non-significant values at genus and species
7 levels: species with similar habitat preferences had more opportunities to live together when
8 they belonged to the same family, this relationship being blurred to some extent at higher-
9 order taxonomic levels and disappearing totally (although being still positive) at genus and
10 species levels.

11 We wondered whether species taxonomically close and with similar habitat
12 preferences were dissimilar from the point of view of occurrence, as expected from
13 competitive exclusion. This was not supported by our results on couples of species belonging
14 to the same genus (Fig. 6): except for the couple *Folsomia manolachei*X*Folsomia*
15 *quadrioculata* couples of species with a high similarity in habitat preference exhibited a
16 positive, neutral or weakly negative occurrence similarity.

17 **Discussion**

18 Within the studied area, we showed that species composition was more influenced by
19 habitat than by space. However, we also showed that when samples to be compared were
20 separated by a distance shorter than 20 m or higher than 200 m, the explanatory value of
21 habitat indicators for species occurrence decreased, pointing to variation in the composition of
22 springtail communities which is not entirely explained by habitat selection at short and long
23 spatial distances, thereby supporting Hypothesis 1.

1 The western part of the Sénart forest was impoverished in species, in particular in
2 species with poor dispersal ability, which can be explained by recent (100-50 years) tree
3 encroachment in previous agricultural land. This is reminiscent of a study done in another
4 region by Ponge et al. (2006), showing that there was a deficit in species with poor-dispersal
5 capacity (corresponding to subterranean life) in areas where woody coverage changed
6 abruptly in the course of the last half century. Can we expect the occurrence of a similar
7 phenomenon in the studied forest? And did it correspond to the observed east-west gradient of
8 decreasing biodiversity, despite similar richness in habitats? The observed discrepancy
9 between both parts of the forest in the balance between slow and fast dispersers led us to
10 suspect some delay in the dispersal of slow-moving species when colonizing forested
11 environments issued from previous agricultural land. Such a delay in colonization success at
12 regional scale, resulting in a loss of biodiversity at local scale, has been coined mass effect in
13 the frame of metacommunity theory (Guélat et al. 2008), and colonization credit in the frame
14 of restoration science (Cristofoli et al. 2010).

15 Decrease in the explanatory value of habitat indicators for species co-occurrence
16 observed at short distance (< 20 m), expressed by non-significant Mantel correlation
17 coefficients between habitat and species occurrence dissimilarities, was ascribed to a
18 restricted array of habitats available for habitat selection, making species sorting
19 (environmental filters) not fully expressed at fine scale. This phenomenon is related to the
20 more general problem of nichewidth in motile organisms: the more habitats will be visited by
21 an animal, the more its choice will fit its requirements, resulting in a better match between
22 ecological traits and environmental characteristics (Edelaar et al. 2008).

23 In the present study we showed that taxonomically distant springtail species (*i*) were
24 more dissimilar in their anatomical and reproductive traits, which is expected since some of
25 these traits are used to classify them by systematians, but also (*ii*) tended to be spatially

1 segregated despite of the fact that habitat preference was the main determinant of species
2 occurrence. The weaker but significant and positive correlation between taxonomic distance
3 and occurrence dissimilarity (phylogenetic clustering sensu Cavender-Bares et al. 2004) did
4 not vary to a great extent when habitat preferences were discarded but near totally
5 disappeared when traits were excluded, indicating that phylogenetic correlates of species
6 assemblages were mediated by traits. This is supported by the disappearance of the correlation
7 observed between taxonomic distance and habitat preference dissimilarity when traits were
8 excluded, pointing to phylogenetic conservatism of species traits and to environmental
9 filtering of species through their traits (Cavender-Bares et al. 2009).

10 We showed that the positive relationship between occurrence and habitat preference
11 (species exhibiting similar habitat preferences tend to co-occur more than random) was
12 taxonomically sensitive. It was better expressed at the family level, and was no longer
13 significant (although still positive) at genus and species levels, supporting Hypothesis 2.
14 Environmental/physiological filtering or species sorting (occurrence explained by habitat
15 preference) culminates at family level, which might indicate that assembly rules based on
16 habitat preferences (species having similar habitat preferences tend to assemble) are blurred
17 by biological filtering (competitive exclusion) when species are closely related, and are
18 blurred (although to a weak extent) by convergent evolution and co-adaptation at higher
19 taxonomic levels. That closely related species tend to segregate because of competitive
20 exclusion (Cavender-Bares et al. 2004, but see Guélat et al. 2008) was not supported by our
21 results, except on one couple of congeneric species, but we cannot exclude that competition
22 might decrease species coexistence to some extent. Most congeneric species exhibited a
23 positive occurrence similarity and only the couple *Folsomia quadrioculata* *F. manolachei*
24 was spatially segregated (i.e. exhibited a negative occurrence similarity) while displaying

1 similar habitat preferences. All these results point to a phylogenetic signal in species co-
2 occurrence, traded-off by competition at low taxonomic levels (Helmus et al. 2007).

3 Overall, habitat indicators (for samples) and habitat preferences (for species) were two
4 main determinants of the composition of Collembola communities, with a small, although
5 significant contribution of spatial and phylogenetic variation, the latter being mediated by
6 species traits. The small influence of dispersal limitation on the composition of soil arthropod
7 communities, compared to environmental variability, has been already observed on naked
8 granite, where isolation between patches of variegated vegetation was near total and within-
9 patch variation was much higher than between-patch variation (Kounda-Kiki et al. 2009).
10 This property is shared by microbial communities, where Beijerinck's 'everything is
11 everywhere, but, the environment selects' is a still widely respected adage at world scale
12 (Queloz et al. 2011). However, soil animal groups with poorer dispersal distances than
13 springtails, such as oribatid mites (Åström and Bengtsson 2011), displays a prominent part of
14 species composition which is explained by dispersal limitation (Lindo and Winchester 2008,
15 2009).

16 The small influence of phylogenetic variation on species co-occurrence must be
17 compared with that of traits: both contribute to a low, although significant extent, to habitat
18 preference. This might indicate that either (i) other traits than those here considered must be
19 taken into account, or (ii) only a minor fraction of studied traits is involved in the observed
20 effects, or (iii) other factors than traits might influence the composition of soil springtail
21 communities, as suggested by Terauds et al. (2011). The fact that the better explanatory value
22 of habitat features for species composition takes place when samples are located between 20
23 m and 200 m might be explained by species moving around and then deciding to stay and
24 reproduce in better suited (or less worse) habitats (local metacommunity scale sensu Terauds

1 et al. 2011; regional scale sensu Winkler and Kampichler 2000), i.e. at a distance where
2 species poorly interact between them but are filtered by the environment.

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- 13

1 **Figure legends**

2

3 **Figure 1.** Accumulation curves of collembolan species collected in the Sénart forest and in
4 nearby agricultural areas from 1973 to 1977, with 95% confidence interval around
5 observed means according to Mao Tau model: (a) whole forest, (b) western and
6 eastern parts of the Sénart forest.

7 **Figure 2.** (a) Mantel rank correlation coefficients between compositional and habitat indicator
8 dissimilarity matrices between samples, with or without spatial distance as co-variable,
9 at increasing sampling spatial scales (five maximum spatial distances in a geometric
10 series); (b) Average habitat dissimilarity between samples at increasing sampling
11 spatial scales. N.S. = not significant at 0.05 level. **** = significant at 0.0001 level.

12 **Figure 3.** Accumulation curves of habitat indicators in Sénart East and Sénart West, with
13 95% confidence intervals.

14 **Figure 4.** Distribution of fast dispersal and slow dispersal traits within three categories of
15 springtail species: species common to western and eastern parts of the Sénart forest,
16 species only found in the western part and species found only in the eastern part.

17 **Figure 5.** Mantel rank correlation coefficients between occurrence and habitat preference
18 dissimilarity matrices between springtail species, at increasing taxonomic levels (from
19 species to order). N.S. = not significant at 0.05 level. * = significant at 0.05 level. ****
20 = significant at 0.0001 level.

21 **Figure 6.** Relationship between habitat preference and occurrence similarity among springtail
22 species belonging to the same genus.

23

Table 1. Results of simple and partial Mantel tests using distance/dissimilarity matrices between samples based on species composition, habitat indicators and spatial localisation. Significant values in bold type (significance level = 0.008 after Bonferroni correction)

	Mantel statistic	Probability
Composition x habitat	0.360	<0.0001
Composition x habitat, space excluded	0.548	<0.0001
Composition x space	0.172	< 0.0001
Composition x space, habitat excluded	0.040	< 0.0001
Habitat x space	0.376	< 0.0001
1 Habitat x space, composition excluded	0.342	< 0.0001

2

Table 2. Results of simple and partial Mantel tests using distance/dissimilarity matrices between species based on traits, habitat preference and taxonomy. Significant values in bold type (significance level = 0.008 after Bonferroni correction)

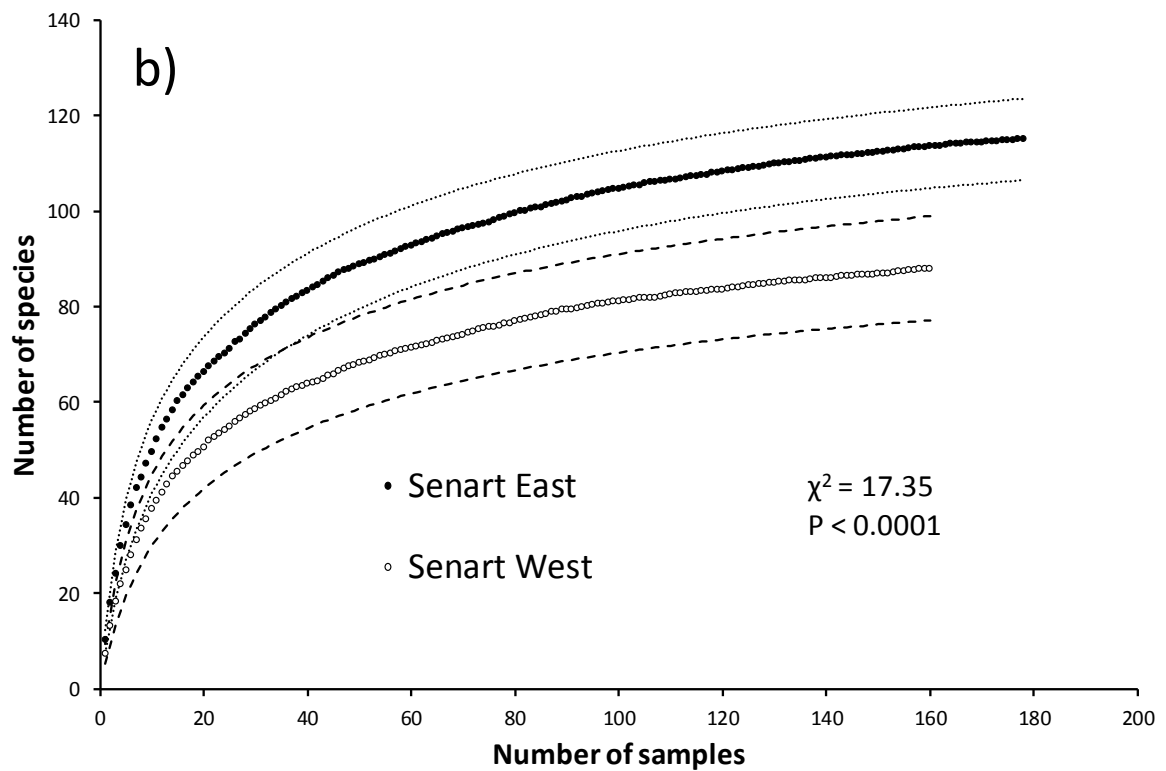
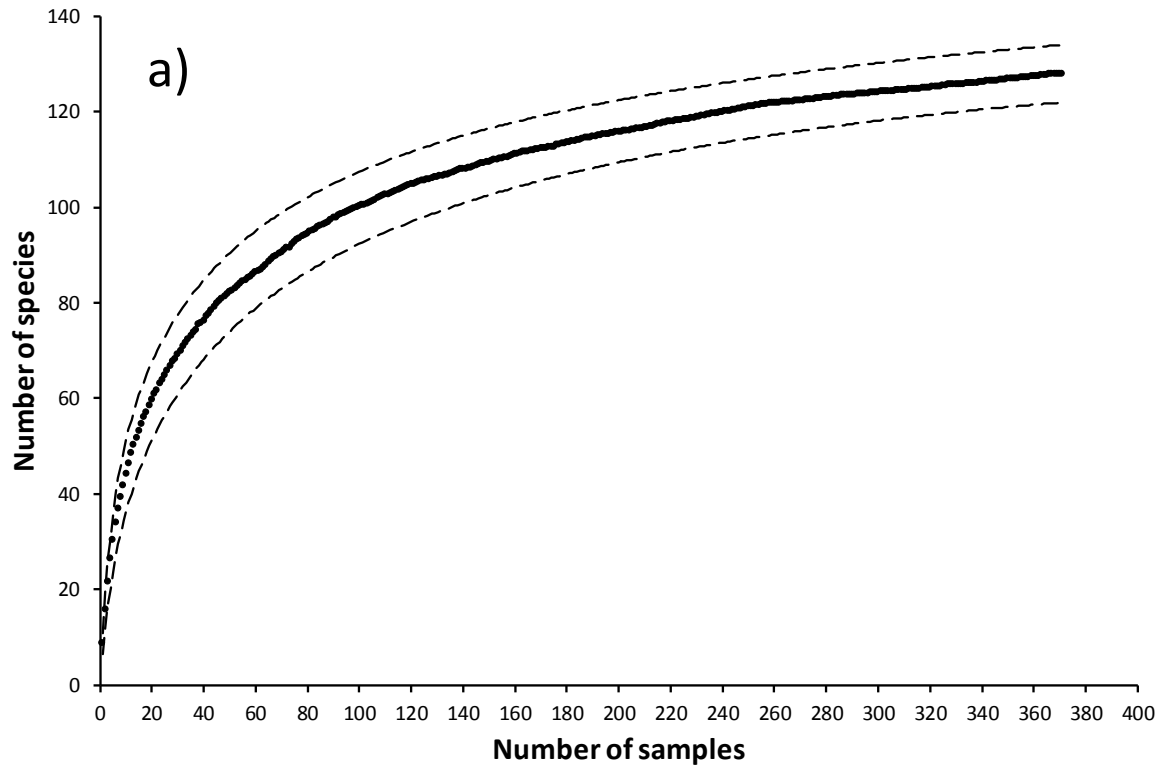
	Mantel statistic	Probability
Traits x taxonomy	0.563	<0.0001
Traits x taxonomy, habitat preference excluded	0.561	<0.0001
Traits x habitat preference	0.068	<0.0001
Traits x habitat preference, taxonomy excluded	0.049	<0.0001
Habitat preference x taxonomy	0.049	0.001
1 Habitat preference x taxonomy, traits excluded	0.013	0.23

2

Table 3. Results of simple and partial Mantel tests using distance/dissimilarity matrices between species based on occurrence, compared with habitat preference, traits and taxonomy. Significant values in bold type (significance level = 0.005 after Bonferroni correction)

	Mantel statistic	Probability
Occurrence x habitat preference	0.476	<0.0001
Occurrence x habitat preference, traits excluded	0.472	<0.0001
Occurrence x habitat preference, taxonomy excluded	0.474	<0.0001
Occurrence x traits	0.122	<0.0001
Occurrence x traits, habitat preference excluded	0.101	<0.0001
Occurrence x traits, taxonomy excluded	0.101	<0.0001
Occurrence x taxonomy	0.068	<0.0001
Occurrence x taxonomy, traits excluded	-0.001	0.97
1 Occurrence x taxonomy, habitat preference excluded	0.051	<0.0001

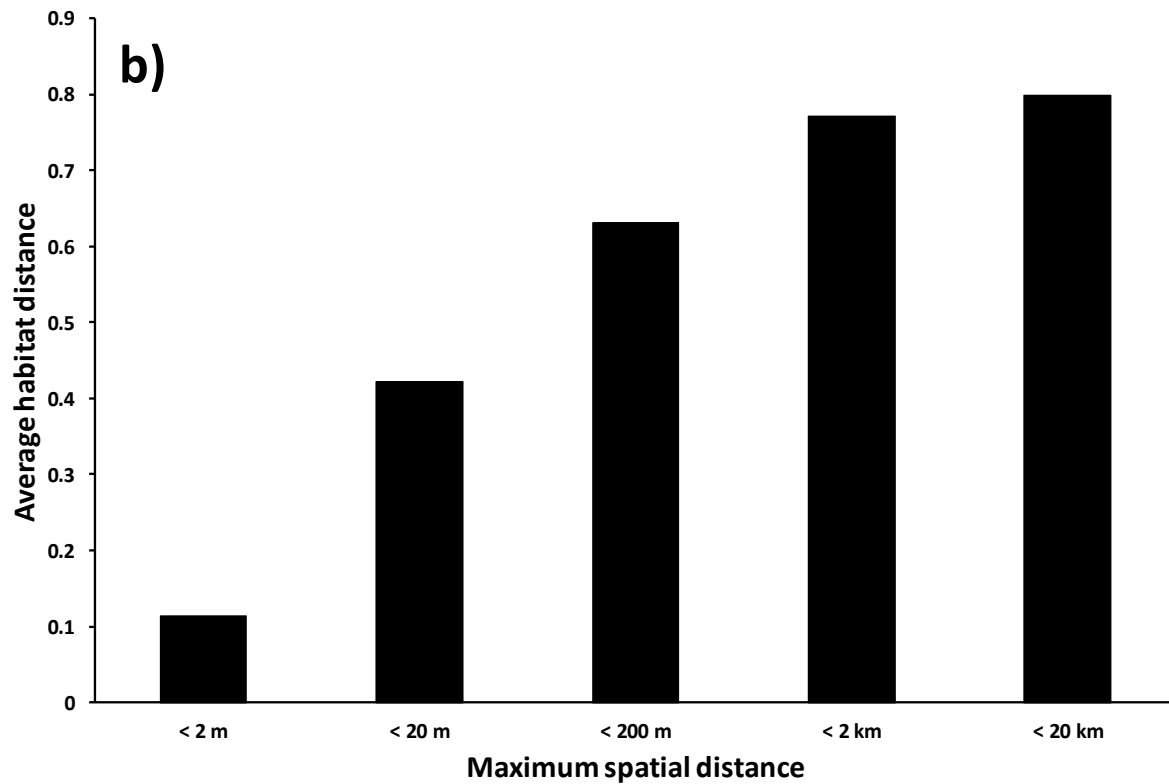
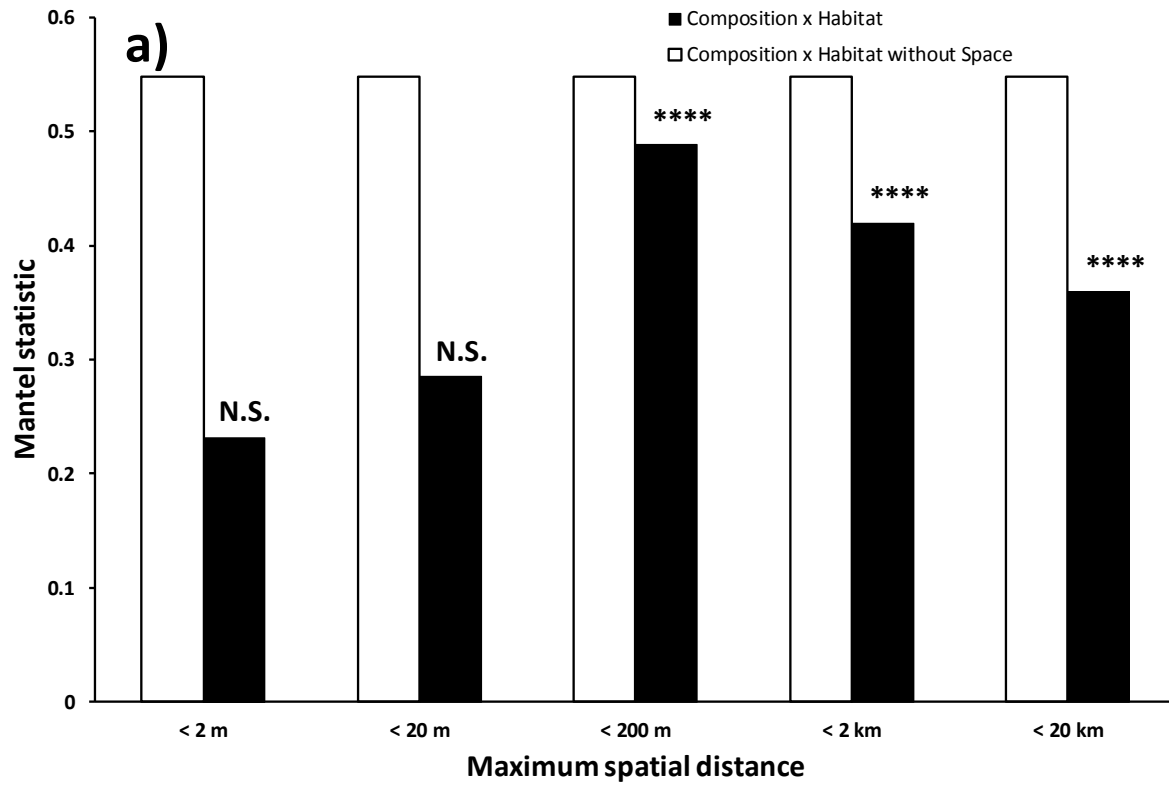
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2 Fig. 1

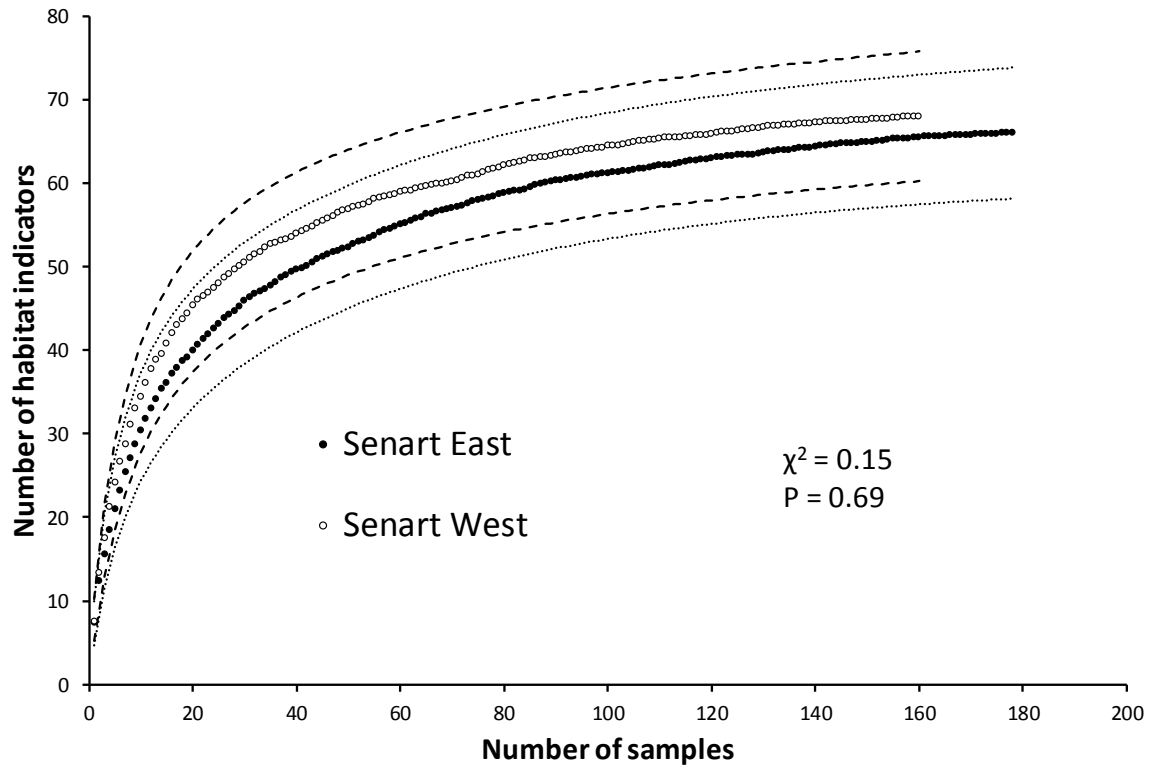
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2 Fig. 2

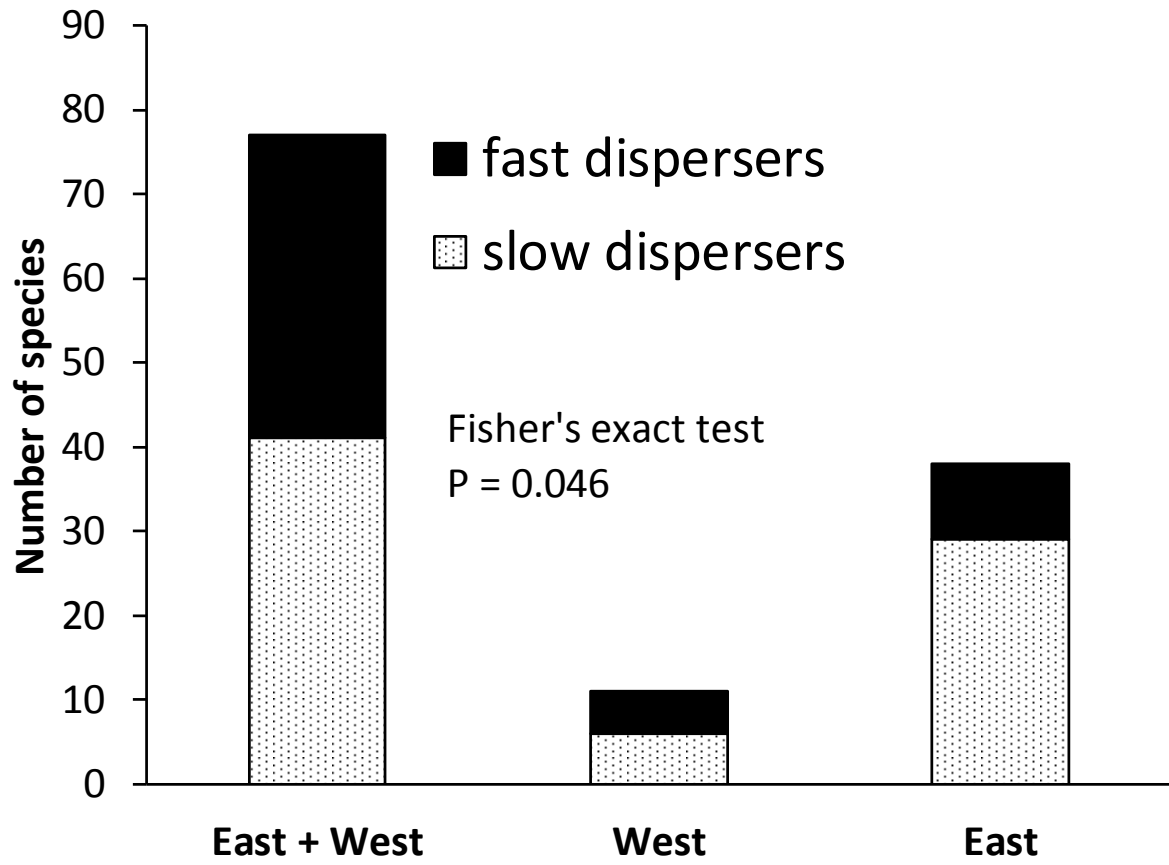
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2 Fig. 3

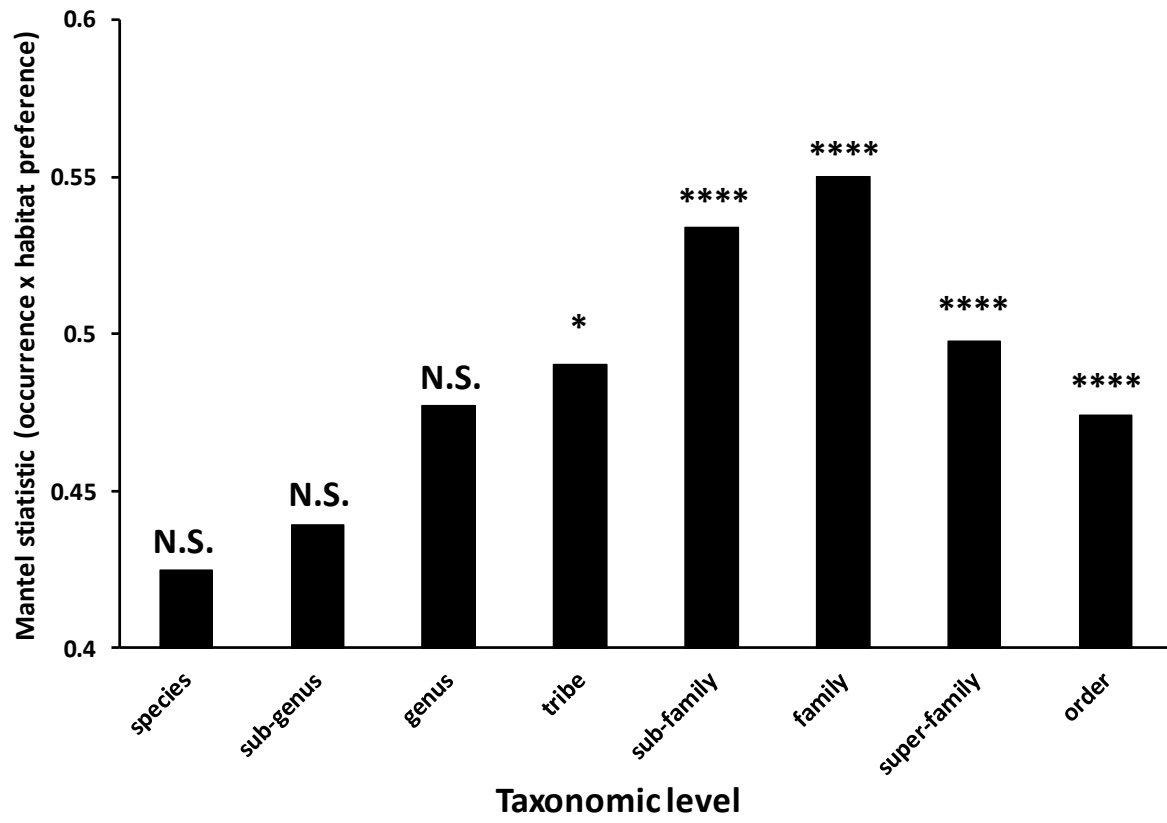
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2 Fig. 4

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2 Fig. 5

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Appendix 1. Codes and species names of springtails collected in the Senart forest from 1973 to 1977, total number of specimens (abundance) and number of samples where the species was found (frequency)

Latin name (original document)	Valid name (Fauna Europaea 2011)	Abundance	Frequency	Latin name (original document)	Valid name (Fauna Europaea 2011)	Abundance	Frequency
Order Poduromorpha				Order Entomobryomorpha (continued)			
Anurida brunsvigiensis	Anurida ellipsoides	12	4	Heteromurus major	Heteromurus major	594	71
Anurida sensillata	Micranurida sensillata	2	2	Heteromurus nitidus	Heteromurus nitidus	28	18
Bilobella grassei	Monobella grassei	32	14	Isotoma antennalis	Isotoma antennalis	1	1
Brachystomella parvula	Brachystomella parvula	1036	33	Isotoma bipunctata	Cryptopygus bipunctatus	2	1
Ceratophysella bengtssoni	Ceratophysella bengtssoni	436	4	Isotomiella minor	Isotomiella minor	2136	116
Ceratophysella denticulata	Ceratophysella denticulata	117	16	Isotoma notabilis	Parisotoma notabilis	6095	180
Friesea clavisetata	Friesea clavisetata	67	11	Isotoma olivacea	Desoria tigrina	1192	5
Friesea mirabilis	Friesea mirabilis	109	13	Isotomurus palustris	Isotomurus palustris	1483	101
Friesea truncata	Friesea truncata	361	57	Isotomodes productus	Isotomodes productus	4	1
Hypogastrura purpurescens	Hypogastrura purpurescens	1	1	Isotomodes sp.	Isotomodes sp.	2	2
Mesaphorura betschi	Mesaphorura betschi	12	6	Isotoma vridis	Isotoma vridis	54	13
Mesaphorura italica	Mesaphorura italica	21	9	Lepidocyrtus curvicolis	Lepidocyrtus curvicolis	72	26
Mesaphorura krausbaueri	Mesaphorura krausbaueri	813	69	Lepidocyrtus cyaneus	Lepidocyrtus cyaneus	889	35
Mesaphorura macrochaeta	Mesaphorura macrochaeta	2962	102	Lepidocyrtus lanuginosus	Lepidocyrtus lanuginosus	3399	160
Mesaphorura massoudi	Mesaphorura massoudi	31	2	Lepidocyrtus lignorum	Lepidocyrtus lignorum	565	63
Mesaphorura sylvatica	Mesaphorura hylophilia	633	42	Lepidocyrtus paradoxus	Lepidocyrtus paradoxus	2	2
Mesaphorura yosii	Mesaphorura yosii	158	13	Lepidocyrtus violaceus	Lepidocyrtus violaceus	4	4
Micranurida pygmaea	Micranurida pygmaea	829	72	Micranurophorus musci	Micranurophorus musci	5	1
Neanura muscorum	Neanura muscorum	115	53	Orchesella cincta	Orchesella cincta	1460	81
Neonaphorura duboscqi	Neonaphorura duboscqi	2	1	Oncopodura crassicomis	Oncopodura crassicomis	5	3
Neonaphorura novempina	Neonaphorura novempina	1	1	Orchesella villosa	Orchesella villosa	167	44
Neotullbergia ramicuspis	Neotullbergia ramicuspis	28	2	Pogonognathellus longicornis	Pogonognathellus longicornis	7	5
Odontella lamellifera	Superodontella lamellifera	4	3	Proisotoma minima	Proisotoma minima	156	25
Oligaphorura absoloni	Micraphorura absoloni	3	2	Proisotoma minuta	Proisotoma minuta	212	10
Onychiurus cebennarius	Deuteraphorura fimetaria	1	1	Pseudosinella alba	Pseudosinella alba	279	51
Onychiurus circulans	Onychiurus ambulans	2	2	Pseudosinella decipiens	Pseudosinella decipiens	7	6
Onychiurus jubilaris	Detriturus jubilaris	1	1	Pseudosinella mauii	Pseudosinella mauii	430	48
Onychiurus minutus	Micronychiurus minutus	1	1	Pseudosinella petterseni	Pseudosinella petterseni	1	1
Onychiurus pseudogranulosus	Onychiurides pseudogranulosus	347	13	Pseudosinella pongei	Pseudosinella pongei	12	4
Paratullbergia callipygos	Paratullbergia callipygos	430	53	Prorastriopes quinquefasciatus	Fasciosminthurus quinquefasciatus	2	2
Podura aquatica	Podura aquatica	410	7	Pseudisotoma sensibilibis	Pseudisotoma sensibilibis	1464	12
Protaphorura groupe armata (2+2)	Protaphorura aurantiaca	740	24	Tomocerus botanicus	Tomocerus botanicus	35	9
Protaphorura groupe armata (3+3)	Protaphorura subuliginata	193	20	Tomocerus minor	Tomocerus minor	312	45
Protaphorura groupe burmeisteri	Kalaphorura burmeisteri	30	5	Vertagopus arboreus	Vertagopus arboreus	788	31
Pseudachorutes parvulus	Pseudachorutes parvulus	229	35	Order Symphypleona			
Pseudachorutella asigillata	Pseudachorutella asigillata	16	5	Allacma fusca	Allacma fusca	1	1
Schaefferia sexoculata	Schaefferia sexoculata	1	1	Allacma gallica	Allacma gallica	5	2
Stenaphorura denisi	Stenaphorurella denisi	32	5	Arrhopalites caecus	Arrhopalites caecus	23	6
Stenaphorura quadrispina	Stenaphorurella quadrispina	7	3	Arrhopalites principalis	Arrhopalites principalis	9	7
Wankeliella pongei	Wankeliella pongei	2	1	Arrhopalites pygmaeus	Arrhopalites pygmaeus	13	7
Willemia anophthalma	Willemia anophthalma	577	35	Arrhopalites sericus	Arrhopalites sericus	24	8
Willemia buddenbrocki	Willemia buddenbrocki	5	3	Bourletella viridescens	Bourletella viridescens	50	15
Willemia intermedia	Willemia intermedia	1	1	Deuteromminthurus flavus	Deuteromminthurus flavus	7	5
Willowsia nigromaculata	Willowsia nigromaculata	3	1	Dicytoma fusca	Dicytoma fusca	34	19
Xenylla brevisimilis	Xenylla brevisimilis	2	1	Dicytoma minuta	Dicytoma minuta	56	30
Xenylla grisea	Xenylla grisea	361	19	Gisinianus flammeolus	Gisinianus flammeolus	98	6
Xenylla schillei	Xenylla schillei	18	5	Heterosminthurus claviger	Heterosminthurus claviger	3	1
Xenylla tullbergi	Xenylla tullbergi	4673	68	Heterosminthurus insignis	Heterosminthurus insignis	33	7
Xenylla xaveri	Xenylla xaveri	33	5	Lipothrix lubbocki	Lipothrix lubbocki	15	6
Order Entomobryomorpha				Sphaeridia pumilis	Sphaeridia pumilis	1566	107
Cyphoderus albinus	Cyphoderus albinus	3	2	Sminthurides aquaticus	Sminthurides aquaticus	1	1
Cryptopygus exilis	Cryptopygus exilis	4	3	Sminthurides assimilis	Sminthurides assimilis	78	12
Cryptopygus scapelliferus	Cryptopygus scapelliferus	22	3	Sminthurides malmgreni	Sminthurides malmgreni	591	43
Cryptopygus thermophilus	Cryptopygus thermophilus	13	2	Sminthurides schoetti	Sminthurides schoetti	401	44
Entomobrya albocincta	Entomobrya albocincta	120	17	Sminthurides parvulus	Sminthurides parvulus	82	13
Entomobrya lanuginosa	Entomobrya lanuginosa	39	13	Sminthurinus aureus	Sminthurinus aureus aureus	1054	75
Entomobrya multifasciata	Entomobrya multifasciata	166	11	Sminthurinus elegans	Sminthurinus elegans	95	21
Entomobrya muscorum	Entomobrya muscorum	17	15	Sminthurinus signatus	Sminthurinus aureus signatus	2407	97
Entomobrya nivalis	Entomobrya nivalis	74	8	Sminthurinus transversalis	Sminthurinus reticulatus	1	1
Entomobryoides purpurascens	Entomobryoides purpurascens	11	2	Sminthurus marginatus	Caprainea marginata	9	2
Folsomia candida	Folsomia candida	60	9	Sminthurus nigromaculatus	Sminthurus nigromaculatus	16	9
Folsomia nana	Folsomia manolachei	6274	101	Stenacidia violacea	Stenacidia violacea	6	2
Folsomides parvus	Folsomides parvulus	145	13	Order Neelipleona			
Folsomides pusillus	Subisotoma pusilla	82	5	Megalothorax incertus	Megalothorax incertus	12	9
Folsomia quadrioculata	Folsomia quadrioculata	1810	45	Megalothorax minimus	Megalothorax minimus	963	105

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Appendix 2. Environmental (habitat) indicators and total number of samples where indicators were quoted as 1 (frequency)

	Frequency		Frequency
Autumn	96	Hornbeam	42
Winter	108	Linden	22
Spring	88	Maple	8
Summer	46	Ash	8
Grassland	50	Cherry	9
Woodland	279	Elm	3
Heathland	9	Elder	3
Ditch/brook	44	Hazel	11
Pond	64	Pine	12
Plain ground	230	Calluna	6
Water	107	Blackberry	5
Sunlight	141	Ivy	4
pH < 5	32	Peat moss	18
pH 5-6	35	Hair moss	5
pH > 6	32	Feathermoss	8
Limestone	48	Liverwort	1
Sand	20	Lichens	4
Pebbles	23	Algae	3
Mull	57	Bracken	21
Moder	24	Purple moor grass	21
Mor	2	Hair-grass	5
Hydromull	6	Fescue-like grass	8
Hydromoder	3	Rushes	6
Hydromor	3	Waterlilies	10
Trunk	33	Hawksbeard	1
Herbs (aerial parts)	58	Sedges	4
Mosses (aerial parts)	74	Wood anemone	20
Superficial soil	17	Bluebell	20
Litter	80	Duckweed	1
Humus	41	Mustard	1
Organo-mineral soil	18	Chamomile	1
Mineral soil	68	Chickweed	9
Mole hill	4	Yarrow	4
Vertebrate dung	3	Nettle	5
Garbage deposits	11	Mercury	16
Wood	35	Solomon's seal	8
Earthworm casts	7	Wheat	7
Tree roots	5	Buttercup	1
Herb roots	8	Knotweed	1
Oak	142	Clover	5
Birch	41	Mint	1

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Appendix 3. Traits and trait attributes used to describe the 127 springtail species of the Sénart forest

Traits	Attributes
Reproduction type	Parthenogenesis dominant Sexual reproduction dominant
Body length	Small (< 2 mm) Medium (between 2 and 3 mm) Large (> 3 mm)
Body shape	Slender body Stocky body Spheric body
Body color	Pale-colored body Bright-colored body Dark-colored body
Presence of scales	Scales absent Scales present
Antennal length	Short antennae Long antennae
Leg length	Short legs (leg/thorax+abdomen < 0.3) Long legs (leg/thorax+abdomen \geq 0.3)
Furcula length	Furcula absent or vestigial Short furcula (anterior part of Abd II not reached) Long furcula (anterior part of Abd II reached)
Eye number	Ocella absent Ocella 1-5 Ocella > 5
Presence of pseudocella	Pseudocella absent Pseudocella present
Presence and complexity of the post-antennal organ	Post-antennal organ absent Post-antennal organ simple Post-antennal organ compound
Presence of trichobothria	Trichobothria absent Trichobothria present