

Linking species, traits and habitat characteristics of Collembola at European scale

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1 **Abstract**

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3 Although much work has been done on factors which influence the patterning of species and
4 species trait assemblages in a variety of groups such as plants, vertebrates and invertebrates,
5 few studies have been realized at a broad geographic scale. We analyzed patterns of
6 relationships between species, species trait distribution/assembly, and environmental variables
7 from the west of Europe to Slovakia, Poland and Sweden. We created a database by compiling
8 traits and occurrence data of European collembolan species, using literature and personal field
9 studies embracing a large range of environmental gradients (vertical stratification, habitat
10 closure, humus form, soil acidity and moisture, temperature, rainfall, altitude) over which
11 Collembola are supposed to be distributed. Occurrences of the 58 best-documented species,
12 environmental variables and species traits allowed us to (i) show which environmental
13 variables impact the distribution of the 58 species at broad scale and (2) document to what
14 extent environmental variables and species trait assemblages are related and which trends
15 could be found in trait/environment relationships. The impact of vertical stratification, habitat
16 closure, humus form, soil acidity, soil moisture, temperature, and to a lesser extent rainfall
17 and altitude on species distribution, firstly revealed by indirect gradient analysis
18 (correspondence analysis, CA), was further shown to be significant by direct gradient analysis
19 (canonical correspondence analysis, CCA). RLQ analyses were performed to find linear
20 combination of variables of table R (environmental variables) and linear combinations of the
21 variables of table Q (species traits) of maximum covariance weighted by species occurrence
22 data contained in table L. RLQ followed by permutation tests showed that all tested
23 environmental variables apparently contributed significantly to the assemblages of the twelve
24 species traits studied. A convergence was observed between traits related to vertical
25 stratification and those related to habitat closure/aperture. Well-developed locomotory organs

1 (furcula, legs), presence of sensorial organs sensitive to air movements and light (e.g.
2 trichobothria and eye spots), spherical body, large body size, pigmentation (UV protection
3 and signalling) and sexual reproduction largely occur in epigeic and open habitats, while most
4 of woodland and edaphic habitats are characterized by short locomotory appendages, small
5 body size, high number of defense organs (pseudocelli), presence of post-antennal organs and
6 parthenogenesis. Climate and especially temperature exert an effect on the assemblage of
7 traits that are mostly present above-ground and in open habitats. The contribution of
8 combinations of some environmental variables to the occurrence of each species trait was
9 tested by linear, logistic or multinomial regression (Generalized Linear Models). Vertical
10 stratification, followed by temperature, played a dominant role in the variation of the twelve
11 studied traits. Relationships between traits and environment tested here shows that it is
12 possible to use some traits as proxies to identify potential ecological preferences or tolerances
13 of invertebrate species. However, a significant part of species distribution remained
14 unexplained, probably partly because some traits, like ecophysiological ones, or traits
15 involved in biotic interactions (e.g. competition) were unavailable. The present work is thus a
16 first step towards the creation of models predicting changes in collembolan communities.
17 Further studies are required to inform ecophysiological traits, in order to complete such
18 models. Moreover the niche width of species will have to be determined.

19

20 **Keywords:** Collembola; environmental filtering; habitats; broad scale distribution; species
21 traits; species assemblages; sensory organs

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1 **1. Introduction**

2
3 Identifying the main factors that drive the composition of communities and the
4 distribution of species is a fundamental goal in community ecology and is of particular
5 importance for predicting biodiversity responses to environmental changes (Belyea and
6 Lancaster, 1999). Selection of species by habitat constraints (deterministic process) is one of
7 the four classes of processes that influence patterns in the composition and diversity of
8 species (Vellend, 2010). Functional traits, (named “traits” hereafter), are well-defined,
9 measurable properties of organisms, used comparatively across species, and that strongly
10 influence organismal performance (McGill et al., 2006). Focusing on the selection of species
11 functional traits rather than only on species identity, allows to (1) identify mechanisms
12 implied in the distribution of species and in the dynamics of biodiversity, (2) understand the
13 mechanisms that shape communities comprised of many species (3) identify general patterns
14 and hence, help to predict potential changes in the composition of communities, and
15 consecutive ecosystem functioning, following disturbance (McGill et al., 2006, Vellend,
16 2010). The use of functional traits of species allowed to understand species responses to
17 varied disturbances such as fragmentation, land use change or agricultural practices (Cole et
18 al., 2002; Barbaro and van Halder, 2009; Ozinga et al. 2009, Vandewalle et al., 2010). For
19 example, Ozinga et al. (2009) showed that differences between plant species in characteristics
20 (traits) involved in dispersal processes contribute significantly to explaining losses in plant
21 diversity in response to habitat degradation.

22 Species traits of diverse communities (plants, carabids, butterflies, birds, spiders) also
23 have been shown to vary with environmental factors such as habitat fragmentation (Barbaro
24 and van Halder, 2009), presence of planted hedgerows in highway verges (Le Viol et al.,
25 2008), post-fire age (Langlands et al., 2011), salinity (Pavoine et al., 2011), agricultural land

1 use and urbanisation (Vandewalle et al., 2010). Nevertheless, the role of habitat constraints
2 and dispersal abilities as filters, allowing only species with similar traits to assemble, has
3 never been demonstrated at broad spatial scales, due to lack of suitable data, especially in soil
4 invertebrates (Barbaro and van Halder, 2009; Decaëns et al., 2011; Makkonen et al., 2011;
5 Pavoine et al., 2011). This may bias to a great extent the relationships between habitat
6 preferences and species traits. Because the overall species response to habitat constraints
7 involves trade-offs (Uriarte et al., 2012) between responses to different environmental factors
8 (e.g. bedrock and climate, habitat openness and humidity, or temperature, or soil pH), it is
9 easy to correlate erroneously a trait to an environmental factor. For example, the collembolan
10 species *Heteromurus nitidus*, thought to strictly depend on soil pH since it was never found in
11 soils at pH <5 in North and West of France (Ponge, 1980, 1993), was later found in soils at
12 pH <4 in south-western mountains of France (Cassagne et al., 2003, 2004). One way of
13 avoiding this error risk is to determine habitat preferences of species over a wide range of
14 habitats, encompassing a variety of temperature and altitude levels, at a scale close to the
15 geographic distribution range of the species.

16 Moreover, despite the abundance, high diversity and essential functional role of soil
17 invertebrates (Hopkin, 1997; Coleman et al., 2004), trait-based approaches were not explicitly
18 used to study species/environment patterns and processes in these animal groups (Vandewalle
19 et al 2010). Only studies focusing either on a restricted number of traits (especially dispersal),
20 or of habitats have been made to assess the effects of land-use disturbance or climate change
21 on soil communities (Ponge et al., 2006; Vandewalle et al., 2010; Decaëns et al., 2011;
22 Makkonen et al., 2011; Bokhorst et al., 2012).

23 The taxonomic Class of Collembola is a good model to address such questions,
24 because it comprises a high number of species, occupying highly diverse habitats over a broad
25 biogeographic area (Hopkin, 1997). Moreover, some authors have hypothesized, from field

1 observations, the existence of five or more “eco-morphological groups” based on conspicuous
2 morphological differences among Collembola living in diverse habitats (Gisin, 1943;
3 Delamare-Deboutteville, 1951; Rusek, 2007). They classified collembolan species according
4 to the relationships between some morphological characteristics and different gradients of
5 vertical stratification (edaphic, hemiedaphic, epigeic) and soil moisture (hydrophilic,
6 xerophilic), but no attempt was made to rely statistically morphological characteristics (traits)
7 to environmental variables. Europe, as a wide area including a high diversity of landscape
8 and vegetation types, is a favourable terrain for exploring multivariate relationship between
9 species trait values, assembly processes, and environmental factors.

10 In this study, we asked the following questions: (1) What is the pattern of relationships
11 between species assemblages and environmental variables at broad geographic scale? (2)
12 Which environmental variables are associated with trait variation in Europe and which
13 environmental variables contribute to the assemblage of local communities?

14 To this end, we compiled a large volume of data about species traits and
15 environmental characteristics of sites where species have been collected throughout Europe.
16 To enable this, we created ‘Coltrait’, a database collating traits and occurrence data of
17 European collembolan species across a wide range of habitats, mostly from Northwest
18 Europe. Occurrence data and associated descriptions of samples and sampling sites were
19 either provided by our own studies, or collected in the literature. For traits, we selected
20 collembolan characteristics expected to explain the distribution of species and the subsequent
21 composition of species communities through three processes that drive patterns of community
22 composition, namely (1) Abiotic components of habitat, (i.e. environmental variables)
23 adaptation/selection (e.g. sensorial organs, cuticle protection, reproduction type); (2)
24 Dispersal ability (e.g. locomotory appendages); (3) Biotic components of habitat selection
25 (predator defence, e.g. detection by sensory organs, excretion of repulsive substances).

1 We firstly analyzed the impact of environmental variables on the distribution of species in
2 Europe, and then we analyzed patterns of trait/environment relationships.

3 4 **2. Materials and methods**

5 6 *2.1. Data collection*

7 8 2.1.1. Habitat characteristics and species occurrences

9 The Coltrait database comprises four tables that were used for the present study: a
10 species traits table, a sample description table (environmental variables observed in samples
11 or in sample sites to determine habitat characteristics), an occurrence/sample table and a
12 bibliography table.

13 Habitat characteristics and occurrences of collembolan species in these habitats were
14 provided either by our own studies (Arpin et al., 1984, 1985, 1986; Ponge, 1980, 1993; da
15 Gama et al., 1994, 1997; Ponge, 2000; Loranger et al., 2001; Ponge et al., 2003; Gillet and
16 Ponge, 2005) or were extracted from articles dealing with field studies on collembolan
17 communities (e.g. Hågvar, 1982; Rusek, 1989, 1990; da Gama et al., 1994, 1997; Cassagne et
18 al., 2003, 2004; Dunger et al., 2004; Chauvat et al., 2007; see Appendix 1 for the complete list
19 of references). We selected habitat characteristics (environmental variables) that were
20 described for a large amount of samples, proved to be linked to the composition of
21 communities at local scale in previous studies and/or were susceptible to “filter” species traits.

22 We collected qualitative and quantitative data regarding site and sample descriptions
23 (i.e. habitat characteristics) of 926 samples. Quantitative data (temperature and rainfall,
24 altitude, soil pH and C/N) were directly incorporated in the data base (Table 1). We
25 aggregated qualitative data into binary classes, assigning each sample to one of two classes

1 for each modality of a given habitat: “1” if sampling occurred in the modality (e.g. close
2 habitat, mull humus...), “0” if sampling did not occur in the modality and this for each field
3 study. Modalities were (1) for habitat closure “close” (forest, wood), “open” (pasture,
4 grassland, meadow, cultivated field) and “intermediate” (hedgerow, forest clearing, forest
5 edge, heathland), (2) for soil characteristics “mull”, “moder” and “mor” humus, “peat” and
6 “cultivated” soil, “organic” and “organo-mineral” horizons and “hydromorphic” soils, (3) for
7 vertical stratification “edaphic” (soil), “hemiedaphic” (litter), “epigeic-1” (ground surface and
8 mosses), “epigeic-2” (herb layer, boulder), “epigeic-3” (tree trunk and canopy) (Table 1).

9 These data allowed us determining the occurrence of species and their traits along
10 several environmental gradients: vertical stratification, habitat closure, soil acidity,
11 decomposition rate (humus form and C/N), moisture, minimum annual air temperature
12 (hereafter named “temperature”), minimum annual rainfall (hereafter named “rainfall”) and
13 altitude.

14 As sampling strategies varied between different studies and was not always precisely
15 described regarding every sampling area, volume or depth of soil, we only compiled the
16 presence/absence of species and not their abundance. We selected species that were recorded
17 in at least 10 studies and 20 samples, providing a list of 58 most frequent collembolan species
18 in Europe (Table 2). Habitat and species occurrence data covered the following countries:
19 Germany, United Kingdom, Austria, Belgium, Denmark, Spain, Finland, France, Italy,
20 Norway, the Netherlands, Poland, Portugal, Czech Republic, Slovakia, Sweden, two thirds of
21 samples being from France. Available data from Greece were discarded because the 58
22 selected species were generally present in the 17 above-cited countries while 33 species out of
23 58 were not recorded in Greece according to Fauna Europaea. Consequently, in our analysis,
24 biogeographic segregation does not bias species distribution.

25

2.1.2 Species traits

We first listed traits that were most likely to influence community assembly either through habitat characteristics, dispersal abilities, or biotic interactions. We then eliminated traits for which detailed and complete information was not available for a high number of species. This selection step provided a set of 11 morphological traits and one life-history trait (reproduction mode). Physiological traits would have been highly relevant, however, as far as we are aware this information is only available for a few species reared in laboratory conditions. In the same way, life-history traits were poorly informed except for reproduction mode.

Traits were collected from a number of specified synopses and identification keys (Gisin, 1960; Jordana et al., 1997; Fjellberg, 1998, 2007; Bretfeld, 1999; Potapow, 2001; Thibaud et al., 2004; Chahartaghi et al., 2006; Hopkin, 2007; Chernova et al., 2009; Dunger and Schlitt, 2011). Visual and jumping apparatus and leg lengths are supposed to be related to dispersal abilities of species (Ponge et al., 2006). Antennal length, eye (ocelli) number, presence of trichobothria and presence and complexity of post-antennal organs play a role in sensory functions (Hopkin, 1997) and are expected to vary between close versus open, and epigeic versus endogeic habitats. Body pigmentation and presence of scales are involved in UV protection, thermodynamic buffering and signalling (Hopkin, 1997) and are also suspected to vary with habitat characteristics, as well as body shape and length and length of jumping apparatus. Pseudocelli are circular structures allowing Collembola to extrude repulsive fluids from specialized glands (Hopkin, 1997; Rusek and Weyda, 1981) and thus play a role in protection against predation (Rusek and Weyda, 1981). At last sexual/parthenogenetic reproduction is associated to survival or colonizing strategy (Chernova et al., 2009; Lavelle et al., 1987). Most of these traits are species- or clade- (e.g. pseudocelli) specific and we did not consider here intra-specific variability since data on

1 morphometric variation over broad geographical areas are unavailable in Collembola. Data
2 may be quantitative (e.g. body length), binary (e.g. presence/absence of scales), or semi-
3 quantitative (e.g. furcula length, see Table 3). We computed traits of the 58 selected
4 collembolan species. All trait attributes (e.g. furcula length categories) were issued from
5 precise definitions (Table 3) and not from expert appreciations. Some of these traits, currently
6 in the Coltrait database, will be integrated in the BETSI database (Hedde et al., 2012).

7 8 2.2. *Statistical analyses*

9
10 Correspondence analysis (CA) was used to analyze species-environment relationships without
11 constraining species distribution (samples as observations, species as active variables,
12 environmental variables as passive variables). As an explanatory step, CA allowed us to
13 visualize patterns of species distribution with environmental variables superposed on the
14 revealed gradients.

15 Canonical correspondence analysis (CCA) and Monte Carlo permutation tests were
16 used to verify whether species distribution was significantly explained by environmental
17 factors and to know the importance of each factor. The type of horizon (organo-mineral or
18 organic) and the C/N ratio were discarded because they were not available for a high number
19 of samples. As Spearman correlation tests revealed that some environmental variables or
20 levels of environmental variables were correlated we discarded some of them and we tested
21 only the effect of temperature and rainfall (for climate), soil pH, hydromorphy and only some
22 modalities of habitat closure (Open), vertical stratification (Hemi, Epi-1, Epi-2, Epi-3), and
23 humus forms (Mull, Moder). Missing values were estimated by the nearest neighbor method.
24 Seven partial CCAs were then performed to test the effect of above-mentioned variables
25 while discarding the effect of one of them on species distribution.

26 RLQ analyses (Dolédec et al., 1996) were performed to assess whether species traits
27 distribution was significantly correlated with environmental variables, and to determine

1 patterns observed when variables were constrained. RLQ analysis allows to perform a double
2 inertia analysis of two arrays (R: environmental variables, and Q: species traits) with a link
3 expressed by a contingency table (L: species occurrences). We discarded C/N, organo-mineral
4 and organic horizons and soil pH, that were not sufficiently informed. As missing
5 observations were deleted when variables (e.g. mull, moder) were not fully informed (Table
6 1), and as informed variables varied among studies (either humus form, or climate) we
7 performed two RLQs to minimize the loss of data in each analysis. We transformed
8 quantitative data (temperature, altitude and rainfall, leg and furcula lengths, ocelli and PAO
9 vesicle numbers) into semi-quantitative data with three or two classes each. This
10 transformation was performed by discretizing data over two classes when the trait might be
11 absent and consequently it comprises a class "0" (e.g. ocelli, PAO vesicle numbers) in
12 addition to the two classes created by the discretization. Discretization was performed over
13 three classes for the other traits (e.g. lengths). To limit deleting observations we pulled
14 together samples taken either in edaphic or in hemiedaphic levels (S.Soil), creating a vertical
15 stratification category gathering samples taken either from the soil or from the litter. We also
16 created another level of vertical stratification (S.Soil-Epi) that includes moss cushions or
17 grass tufts with adhering humus or soil. Other variables were the same as those used in CA
18 (Table 3). The first RLQ tested the interaction of traits with climate, vertical stratification,
19 habitat closure, and soil moisture, while the second RLQ tested the interaction of traits with
20 humus form, habitat closure, and soil moisture.

21 At last, traits were analyzed separately using statistical models to test the effect of
22 environmental variables highlighted by RLQ. We first calculated the percent occurrence of
23 each species for each level of binary environmental variables (e.g. edaphic level, hemiedaphic
24 level, mull humus, moder humus, etc...), and for continuous environmental variables (soil
25 pH, altitude, temperature and rainfall) we selected minimum or maximum values for each

1 species. We then implemented linear models on continuous trait values, binary logit models
2 on binary traits, and a multinomial logit model on pigmentation which included three
3 categories. We excluded variables with a variance inflation factor (VIF) higher than four to
4 avoid multi-collinearity. We selected models with contributive variables that significantly
5 explained the greatest part of trait variability (i.e. with highest adjusted R^2 and log-likelihood
6 for linear and logit models, respectively). All variables bringing significant information to the
7 model were included, even if their impact was not significant when evaluated separately
8 (Type III analysis). In order to fulfill linear model assumptions, some variables had to be log-
9 transformed. As pseudocelli number did not follow a normal distribution even after
10 transformation, we analyzed their presence/absence with a binary logit model.

11
12 RLQ analysis was performed with the package “ade4” in R software (R Development
13 Core Team, 2010). CA, CCA, general linear models (GLM) and other calculations (e.g. data
14 normalization, discretization) were done using XLSTAT[®] (Addinsoft[®], Paris, France).

15

16 **3. Results**

17

18 *3.1. Species and environmental variables*

19 The relationship between species, environmental variables and traits was first analyzed by CA
20 using samples as observations, species as active variables and environmental variables as
21 passive variables (Figs. 1a, 1b). The first three components of CA extracted 17.4% of the total
22 variance (6.3%, 5.9% and 5.2% for F1, F2 and F3, respectively). The projection of species
23 and environmental variables along axes 1 and 2 (Fig. 1a) shows that species are spread along
24 axis 1 mainly according to humus form, soil hydromorphy and habitat opening/closure and to
25 a lesser extent soil acidity, temperature and altitude. Along axis 2, species are distributed
26 according to vertical stratification, and to a lesser extent habitat closure/opening, soil
27 hydromorphy, organic matter, and temperature. In the upper left side of the biplot, we find

1 edaphic and hemiedaphic species living in acid soils with a low rate of organic matter
2 decomposition (peat, mor, moder): *Micraptorura absoloni*, *Mesaptorura tenuisensillata*,
3 *Willemia denisi*, *Willemia anophthalma*, *Mesaptorura yosii*, *Micranurida pygmaea*, *Folsomia*
4 *quadrioculata*, *Protaptorura armata* and *Pogonognathellus flavescens*. Opposed to this
5 group along axis 1, we find edaphic and hemiedaphic species living in mull on calcareous or
6 neutroacidocline soils: *Stenaptorura denisi*, *Mesaptorura hylophila*, *Mesaptorura*
7 *krausbaueri*, *Heteromurus nitidus*, *Mesaptorura italica*, *Paratullbergia callipygos*, and
8 *Pseudosinella alba*.

9 Opposed along axis 2 to these two groups of edaphic and hemi-edaphic species, we
10 find epigeic species living on the soil surface (epigeic-1), herb layers and boulders (epigeic-2)
11 and trees (epigeic-3) (Figs 1a, 1b): *Orchesella cincta*, *Heteromurus major*, *Xenylla tullbergi*
12 *Lepidocyrtus curvicollis*, *Xenylla grisea*, *Brachystomella parvula*, *Isotomurus palustris*,
13 *Sminthurinus elegans*, *Sminthurides schoetti*, *Entomobrya multifasciata* and *Tomocerus*
14 *minor*. Species distribution according to soil characteristics (humus form, acidity) thus occurs
15 mainly for endogeic and hemiedaphic species.

16 Epigeic species are separated along axis 1 by low temperature levels and hydromorphy
17 gradients, *O. cincta*, *H. major*, *X. tullbergi*, *X. grisea* and *L. curvicollis* occurring more often
18 in slightly drier and/or warmer habitats (Temp), while *B. parvula*, *S. elegans*, *E. multifasciata*,
19 *I. palustris* and *L. cyaneus* prefer hydromorphic soils (Hydro). Forests (close) and open
20 habitats are better separated by axis 3 (Fig. 1b) that opposes epigeic species living
21 preferentially in herb layers or exceptionally on boulders (epigeic-2) in open habitats (*S.*
22 *elegans*, *B. parvula*, *L. cyaneus*, *E. multifasciata*, *S. schoetti*, *I. palustris*), to epigeic species
23 living either at the soil surface (epigeic-1) or on trees (epigeic-3) in forests (*X. tullbergi*, *O.*
24 *cincta*, *L. curvicollis*, *Entomobrya nivalis*, *X. grisea*, *Allacma fusca*). Species segregation
25 according to habitat closure thus mainly occurs for epigeic species. *Parisotoma notabilis*

1 shows no preferences for the studied factors, like the very common species *Isotomiella minor*,
2 which tends nevertheless to be observed more frequently in non-acidic soils.

3 CCA indicated that the bulk of tested environmental variables, i.e. humus form, habitat
4 closure, vertical stratification, hydromorphy, temperature, rainfall and soil pH significantly
5 impacted species distribution (Table 4). The seven partial CCAs computed without either
6 vertical stratification (Hemie, Eda, Epi1, Epi2, Epi3), or humus form (Mull, Moder), or
7 habitat closure (Open), or hydromorphy, or rainfall, or temperature, or soil pH showed that
8 remaining factors impacted significantly the distribution of species (all $p < 0.0001$) but with a
9 decrease in the rate of constraint inertia. This indicates that all factors impacted the
10 distribution of species directly and not only through interactions with other factors. However,
11 discarding the effect of one or the other variable did not affect to the same extent the
12 constrained inertia (12.5% for total CCA): 5.2%, 8.0%, 10.5%, 10.6%, 10.6%, 11.5%, and
13 11.6% of the total inertia were explained when discarding vertical stratification, humus form,
14 rainfall, temperature, habitat closure, hydromorphy and pH effect, respectively.

15

16 3.2. *Traits and environmental variables*

A first RLQ analysis was applied to climate (temperature and rainfall), altitude, vertical stratification, habitat closure, soil moisture, and traits (Figs. 2a, 2b). Axis 1 separates levels of rainfall, temperature, vertical stratification, soil hydromorphy, and to a lesser extent, altitude. Axis 2 separates modalities of the same factors than for axis 1 in addition to habitat opening/closure. Traits mostly represented in deep soil and closed habitats (on the positive side of axes 1 and 2) are the absence of pigmentation, furcula, ocelli, trichobothria and scales, the presence of a post-antennal organ (PAO) comprising a great number of vesicles, of pseudocelli (defense organs), short legs and antennae and small body length. These habitats also display a parthenogenetic dominant reproduction. On the soil surface, the

number of ocelli and furcula length increased slightly. When habitats are less edaphic, more open and in less favorable climatic conditions (higher altitude, associated to low temperature levels positive side of axis 1 and negative side of axis 2) the following trait modalities are more frequent: stocky body, variable pigmentation, PAO present but less developed, and furcula, present but usually regressed and not fully functional. In epigeic habitats and more favorable climatic conditions (i.e. high and intermediate temperature levels and lower altitude, negative side of axis 1) most common traits are larger body size, elongated legs and antennae, spherical and pigmented body, well-developed eyes, presence of trichobothria and scales, and absence of PAO and pseudocella, with sexual reproduction dominant.

A second RLQ tested the relationships between humus forms and soil types, habitat closure, soil moisture, and traits (Figs. 3a, 3b). Axis 1 separates closed and open habitats while axis 2 separates humus forms. Open habitats (positive side of axis 1) hosted species displaying traits previously mostly observed in epigeic and favorable climate conditions: increased body, leg and antennae length, spherical and pigmented body, with scales and trichobothria, well-developed eye spots, absence of pseudocelli, absence or reduction of PAO vesicles, and dominance of sexual reproduction. Furcula may be either very long or regressed. Near the positive end of axis 1, higher body length is found in well moistened soils. Closed (forest) and intermediate (heathland and scrub) habitats (negative side of axis 1) are separated along axis 2 according to humus form and thickness of organic horizon. Small body, leg and antennae length, with pseudocella and well developed PAO, but no pigmentation, scales and trichobothria, are observed in both mull and moder humus (negative side of axis 1 and axis 2). Some traits varied along axis 2 in relation to the humus form, especially the increase in organic horizon thickness. From mull to moder the following changes are observed: mixed reproduction shifts towards parthenogenesis, absence of eye towards simple eye, absence of furcula towards mean-length furcula. In humus forms with

thickest organic layers (Mor and Peat) particular traits are observed, e.g. stocky body, short furcula and variable pigmentation. This change of traits from mull with thin organic layers to humus forms with thicker organic layers (moder, then mor and peat) coincides with the passage from deep organo-mineral horizons with small interconnected pores (earthworm galleries, allowing Collembola to go deeper in the soil as in mull) to upper thick organic horizons that offer more space, allowing the movement of large bodies and the use of a medium-size or short furcula, while eyes are larger in relation to a little more light.

Monte-Carlo tests based on 1000 replicates were highly significant ($p < 0.001$) for the two RLQs, indicating a significant relationship between traits and environmental variables.

1 Linear and logistic models showed that environmental variables explained antenna,
2 leg, body and furcula lengths, number of eyes and PAO vesicles, reproduction mode,
3 spherical and cylindrical body shape, and presence of trichobothria, pseudocelli, scales and
4 pigment to significant levels (Tables 5 and 6). Only the stocky body shape (McFadden $R^2 =$
5 0.099 ; $\text{Chi}^2 = 3.362$; $p\text{-value} = 0.067$) was not significantly explained by environmental
6 variables. Logistic and linear regressions corroborated that temperature plays a significant
7 part in the explanation of most trait variation (Tables 5 and 6). Antenna, furcula, leg, and
8 body lengths, number of ocelli, sexual reproduction, spherical body shape, and presence of
9 trichobothria were significantly and positively explained by minimum temperatures. Some of
10 these traits tended to be (body length) or were (trichobothria) negatively explained by altitude.
11 Vertical stratification (mostly through epigeic and hemiedaphic levels) contributed to the
12 explanation of all traits (except stocky body). Both the number of PAO vesicles and the
13 presence of pseudocelli were significantly and negatively explained by minimum
14 temperatures and epigeic-1 level, and were positively explained by soil pH. Humus form and

1 habitat openness contributed to explain variations of only five and two traits, respectively, and
2 this contribution was significant in two cases only (peat and mor explained trichobothria
3 presence and antenna length, respectively).

4 5 6 **4. Discussion**

7 8 *4.1. Species and environmental variables*

9 We showed that the distribution of species is conditioned, first by vertical stratification, then
10 by humus form, air temperature, rainfall, and habitat closure. Soil moisture and acidity were
11 also shown to affect species distribution but more indirectly, probably through the effect of
12 humus form (Ponge et al., 2002; Cassagne et al., 2004), while the effect of altitude was
13 correlated to air temperature and rainfall (and more probably to insolation). These results arise
14 from an analysis performed at a broad scale, that covers most part of the biogeographic
15 distribution area of species. The multiplicity of sites over such a broad geographical scale
16 allows to overcome eventual interactions between spatial autocorrelation and environmental
17 variables that could arise at lower scales, e.g. at the scale of habitat (e.g. a forest) or
18 microhabitat (e.g. soil characteristics) (Caruso et al., 2012).

19
20 Our results show that these habitat constraints contributed in structuring collembolan
21 communities to an extent of about 12%. Consequently, at least 12% collembolan species
22 assemblies were explained in a deterministic way (Streit et al., 1985; Weiher and Keddy,
23 1995) while about 88% species distribution remained unexplained. A part of this unexplained
24 variation is probably due to the lack of data about biotic interactions like competition (McGill
25 et al., 2006; Comita et al., 2009).

1 We characterized habitat preferences for many species (see section 3.1.). The three
2 levels of epigeic species were well separated between soil surface (epige-1), herb layers and
3 boulders (epige-2) and trees (epige-3) while hemiedaphic species were closely related to
4 edaphic species. This could in part be due to the fact that some samples contained a mixture
5 of litter and organo-mineral or even mineral soil (soil), leading to a connection of species
6 living in one or the other level, but also to the vertical movement of animals through horizons
7 (Hassall et al., 1986). The distribution of species in the three epigeic levels was related to
8 habitat closure, above-ground species that live in forests being preferentially located either at
9 the soil surface (epige-1) or on trees (epige-3), contrary to above-ground species living in
10 open areas which are located preferentially in herb layers or on boulders (epige-2). Species
11 segregation according to habitat closure thus especially occurs for epigeic species because
12 they are living far from the protection ensured by soil/litter layers, and occupy different
13 substrata, some of them being more frequent in forests (trees) or in open environments (herb
14 layers). Edaphic species appear in both closed and open habitats while hemiedaphic species
15 seem more linked to closed habitats (due to thicker litter layers). However, their central
16 location on the F2-F3 biplot of CA makes hemiedaphic habitats more difficult to interpret in
17 terms of relationships with habitat closure. Edaphic species were actually segregated
18 according to humus form and acidity.

19 Our results support studies done at a more local scale on the vertical distribution of
20 species (Delamare-Deboutteville, 1951; Hale, 1966; Hågvar, 1983; Ponge, 2000), preferences
21 for humus forms and soil acidity levels (Ponge, 1983; Hågvar and Abrahamsen, 1984;
22 Loranger et al., 2001), and comparisons between forests and open habitats (Ponge, 1993).
23 They reveal an impact of the minimum annual air temperature at which species have been
24 found as well as the segregation of epigeic species among the three levels of epigeic habitats
25 (see above). However, as our analysis encompasses a broad spatial area, and consequently

1 more diverse levels of environmental factors, we found some contrasted results compared to
2 more local studies. For example *Mesaphorura macrochaeta*, previously observed in more
3 relative abundance in acidic soils in a more local study (Ponge, 1993), is here found not really
4 responding to acidity level, and even tending to occur more often in subacidic or non-acidic
5 soils. The collembolan *H. nitidus*, proved to prefer edaphic and hemiedaphic habitats in mull
6 humus and calcareous or neutroacidocline soils (see 2.2 Results) on a broad scale, was able to
7 live in acidic soil in some places (Cassagne et al., 2003, 2004). Such contrasted responses of
8 species to varied environmental conditions show that the response (reaction norm) of species
9 results from trade-offs between preferences for a variety of environmental factors and varies
10 according to the value of each factor (Fry, 2003; Uriarte et al., 2012). They also highlight that
11 in spite of marked habitat preferences, the studied collembolan species were able to live in
12 extremely diverse conditions. Consequently, the niche width will remain to be defined for the
13 present 58 species in order to determine precisely the habitat limits of each species and thus
14 provide a tool that could be used for eventual predictions of changes in collembolan
15 communities. Nevertheless, we have to keep in mind that some species appearing in our study
16 as ubiquitous, such as *Parisotoma notabilis* or *Isotomiella minor*, might in fact be species
17 complexes composed of two or more species with narrower niches as suggested by recent
18 sequencing of a barcode DNA fragment (5' end of COI gene) (Porco et al, 2012).

19

20 4.2. Traits and environmental variables

21

22 RLQ and GLM analyses showed that all tested environmental variables contributed to
23 the assemblage of species traits. Vertical stratification followed by annual air temperature
24 play a dominant role in the explanation of variation of the 12 studied traits.

25 The relationship between traits and vertical distribution of species, which was
26 previously hypothesized by Collembola specialists (Gisin, 1943; Delamare-Deboutteville,

1 1951; Hågvar, 1983; Rusek, 2007) on the basis of their observations, is now statistically
2 tested over a wide range of ecosystems. The contribution of habitat closure/openness and
3 humus form to traits assemblages is showed at broad scale for the first time. We also showed
4 that traits of species living in open habitats (e.g. grassland) or above-ground are both adapted
5 to surface life, i.e. to light, a potentially dry environment and a wide space: high mobility
6 (long legs and furcula), big size often associated with spherical body, scales, pigments
7 (protection against UV), sensorial organs sensitive to air and light (trichobothria, ocelli and
8 antennal organs), and sexual reproduction. On the opposite side, traits that are dominant in
9 woodland are quite similar to those observed in hemiedaphic and edaphic levels and are
10 mostly associated with subterranean concealed life or at least with a stable microclimate (litter
11 in forests): small size, small locomotory appendices, toxic excreta (pseudocelli), post-antennal
12 organs as main sensorial organs, and parthenogenesis. Such variation of trait modalities
13 between open habitats and forests probably explain the higher soil fauna diversity (γ -
14 diversity) observed in landscapes composed of a mixture of forests and open habitats in
15 regard to homogeneous landscapes (Vanbergen et al, 2007).

16 The convergence of traits observed along gradients of habitat closure and of vertical
17 distribution is explained by a higher incidence of environmental stress (drought, UV and
18 wind) in less protected open as well as aboveground habitats. Among species previously
19 recorded as drought-sensitive (Lindberg and Bengtsson, 2005), many appears here as being
20 edaphic and woodland species (*Micraptorura absoloni*, *Willemia anophthalma*, *Micranurida*
21 *pygmaea*, *Mesaptorura macrochaeta*), while drought-tolerant species are found to be epigeic
22 (*Lepidocyrtus spp.*, *Entomobrya nivalis*).

23 The relatively large body size of epigeic species is a protection strategy against frost
24 and desiccation (Kaersgaard et al., 2004, Bokhorst et al., 2012). Moreover, open unstable and
25 stressful environments like agricultural fields require higher motility (long legs and furcula)

1 than shrubby fallows where litter begins to accumulate or woodland (Mebes and Filser, 1997).
2 Escaping from predators aboveground also relies on jumping, ensured by long furcula acting
3 as a spring (Bauer, 1987), as well as visual (ocelli) or tactile (trichobothria) sensorial organs
4 to detect their presence (Baatrup et al., 2006). In epigeic and open habitats longer antennae,
5 bearing specialized tactile and chemosensory setae and vesicles, also allow detecting
6 chemicals and air vibration at a higher distance (Hopkin, 1997). Increased ocelli number and
7 furcula, antenna and body lengths were also used by Rusek (2007) to propose two epigeic
8 collembolan “life form groups”, namely “Macrophytobionts” and “Microphytobionts”,
9 corresponding to epigeic levels 2 and 3, respectively, in our study. Conversely, reduced
10 pigmentation, furcula length and number of ocelli fit generally well with the “Euedaphobiont
11 life form group” (Rusek, 2007). Ocelli number, antenna and furcula lengths had also
12 previously been shown to be correlated with change in the vertical distribution of species in
13 response to tree plantation affecting litter quality and quantity (Vandewalle et al., 2010).

14 Pseudocelli, mostly present in edaphic species, probably compensate for the difficulty
15 to escape predators through active movement in deep soil by excreting chemicals that repel
16 predators (Negri, 2004). In the same way the presence of post-antennal organs (PAO) in
17 edaphic and hemiedaphic species only, support the hypothesis raised by Salmon and Ponge
18 (2012) that these organs could compensate for the absence of other sensorial organs that are
19 adapted to air (trichobothria), light (ocelli) and spacious environments (sensory organs on
20 long antennae), PAO being supposed to be composed of thermo-, hygro-, or chemosensitive
21 receptor cells (Altner, 1976). At last, the reproductive insurance hypothesis (Jain, 1976)
22 predicts that parthenogenesis is favored in populations where mates are difficult to find. This
23 hypothesis can explain the higher rate of parthenogenesis observed among euedaphic species,
24 living in deep soil horizons and faced to deficit of space and need to explore narrow soil pore
25 networks for mating (Chahartaghi et al., 2006; Chernova et al., 2009).

1 The effect of climate, and especially of temperature, on the distribution of traits is
2 mostly observed in aboveground and open habitats, i.e. in least protected and more unstable
3 environments. Moreover, as climate drives vegetation patterns and humus forms (Ponge et al,
4 2011), the effect of climate seems tightly linked to that of humus forms.

5 In this way, less favorable climatic conditions (high altitude associated with low
6 temperature levels), when they allow vegetation development, often generate mor humus and
7 peat, i.e. humus with thick organic horizons made of undecayed plant fragments where
8 collembolan species with stocky body can move more easily than in small soil pores, and are
9 impeded to go deep in the soil by waterlogging. Such conditions favor traits that are
10 intermediate between strictly edaphic and epigeic life (pigmentation variable, PAO present
11 but less developed, and short or regressed furcula). Species traits observed under more
12 favorable climate conditions (moderately high temperature and moisture and low altitude), are
13 the same as those present in epigeic levels because such conditions are favorable to epigeic
14 life and because species adapted to drought can live above-ground in open habitats (see
15 above; Siepel, 1996). This is supported by the positive correlation of the activity of epigeic
16 Collembola with temperature in agricultural soils (Frampton et al., 2001). At last, the post-
17 antennal organ seems more complex (larger numbers of vesicles, in relation to the number of
18 dendritic branches of neural systems; Altner and Thies, 1976) in most species of mull humus
19 and edaphic levels than in moder humus and hemiedaphic levels. This suggests that complex
20 post-antennal organs, supposed to be more sensitive to chemical features of the immediate
21 environment (Altner and Thies, 1976), could compensate for the complete absence of eyes
22 and reduction of other sensory organs observed in euedaphic species, providing better
23 adaptation to deeper soil layers. Nevertheless, although the presence of PAO was essentially
24 observed in edaphic and hemiedaphic species, only a study of the variation of PAO

1 complexity in relation to habitat depth of each species along one or several lineages will be
2 able to state on the importance of PAO complexity for adaptation to subterranean life.

3 Our results support some of the relationships between traits and environmental factors
4 observed in a previous study realized at a more local scale (Salmon and Ponge, 2012).
5 Nevertheless, some differences have to be noted since the cited study did not allow discerning
6 a clear correlation between traits and humus types associated to soil acidity. The larger dataset
7 used here allowed us to demonstrate such relationships.

8 The present study, by showing the change of traits along environmental gradients supports the
9 importance of niche-based environmental filtering in the assembly of Collembolan species
10 (McGill et al., 2006, Weiher et al, 2011). However, models showed that environmental
11 variables explained 23% (cylindrical body) to 71% (pseudocelli; Table 6) of trait variation,
12 meaning that a high part of trait and species assembly variation is explained by other factors.
13 Community phylogenetics will probably add an important contribution to the explanation of
14 species distribution and assembly as this has been shown for plant communities (Prinzing et
15 al., 2008; Pavoine et al., 2011). In addition, ecophysiological traits such as resistance to
16 desiccation, enzymatic equipment for food digestion, colonization rate, etc., were missing in
17 our analysis because they were only available for a few species (Hopkin, 1997) and lengthy
18 researches are needed to assess them in a meaningful number of species. At last, although
19 pseudocelli and furcula development allow taking into account repulsion to and escape from
20 predators, respectively, the effects of other biotic interactions such as competition, or
21 commensalism, known to be important drivers of community structuration (McGill et al.,
22 2006; Comita et al., 2009; Vellend, 2010), were not taken into account because of the little
23 amount of available data. Limits of models relating species range distributions to
24 environmental variables have been underlined, in particular when using species- or trait-
25 environment relationships to track large-scale effects of global change (Fridley and Wright,

1 2012; Urban et al., 2013; Zhu et al., 2014). We showed that within the studied group climate
2 effects concern mainly traits associated to aboveground habitats in open environments, and
3 that soil properties are the main driver of changes in belowground communities. However,
4 predictions about the response of collembolan trait/species distributions at local scale to
5 climate warming will have to take into account other factors like biotic interactions (Urban et
6 al., 2013) and ecophysiological traits.

7

8 **5. Conclusions**

9 Our study shows that collembolan species assembly at a broad scale is conditioned by a set of
10 interacting parameters including vertical stratification, humus form, habitat closure, air
11 temperature, soil moisture and acidity, and to a lesser extent rainfall and altitude. Our results
12 show that all these environmental factors significantly contributed to the assemblages of
13 twelve studied species traits. Combinations of certain environmental factors, especially
14 stratification level and air temperature, explain a large variety of species traits and are thereby
15 thought responsible for a great part of collembolan “species sorting”. A convergence was
16 observed between traits related to stratification level and habitat closure/openness, that we
17 interpreted as the effect of similar physiological and behavioral constraints. The action of
18 humus form would impact indirectly trait distribution/assembly through the interaction
19 between vertical stratification and habitat openness. Ecological preferences were identified for
20 the 58 studied collembolan species relatively to this set of traits, their niche width and their
21 degree of specialization remaining to be more precisely defined. Nevertheless, relationships
22 between traits and environments provide interesting proxies to identify ecological preferences

1 of Collembola, even when not identified to species level. Beyond Europe (where the
2 invertebrate fauna is relatively well-characterized), this approach may offer new insight, for
3 example with respect to tropical soil communities where most species are still unknown to
4 science, and will likely remain so in the near future.

5
6

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8

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11

1 **Figure captions**

2

3 **Fig. 1.** Correspondence analysis showing the distribution and assembly of species (active
4 variables) and environmental variables; a) Species and environmental variables along axes 1
5 and 2; b) Species and environmental variables along axes 2 and 3. See tables 1 and 2 for
6 abbreviations.

7

8 **Fig. 2.** RLQ testing the direct relationships between climate (temperature and precipitation),
9 altitude, vertical stratification, habitat closure and soil moisture, and traits. a) Environmental
10 variables; b) Traits. Environmental variable classes were altitude: Alt.low: $\leq 50\text{m}$, Alt.int:
11 $50\text{m} < x \leq 100\text{m}$, Alt.high $> 100\text{m}$; rainfall: Pre.Low $\leq 650\text{mm}$, Pre.Int $650\text{mm} < x \leq 800\text{mm}$,
12 Pre.High $> 800\text{mm}$; temperature: Tem.Low $2.8^\circ\text{C} < x < 8^\circ\text{C}$, Tem.Int $8^\circ\text{C} < x \leq 11^\circ\text{C}$, Tem.High
13 $> 11^\circ\text{C} < x < 15^\circ\text{C}$; habitat closure: close (H.Close), open (H.Open), intermediate (H.Int);
14 stratification: epigeic levels of soil surface (S.Epi1), herb layers and boulders (S.Epi2), trees
15 (S.Epi3), hemiedaphic and edaphic level (S.Soil) and soil and soil surface level (S.Epi.soil);
16 hydromorphic (Hydro.1) and non-hydromorphic soils (Hydro.0). See Table 3 for abbreviations
17 of species traits.

18

19 **Fig. 3.** RLQ testing the relationships between humus forms and soil types, habitat closure, soil
20 moisture and traits. a) Environmental variables; b) Traits. Environmental variable classes
21 were: habitat closure: close (H.Close), open (H.Open), intermediate (H.Int); stratification:
22 epigeic levels of soil surface (S.Epi1), herb layers and boulders (S.Epi2), trees (S.Epi3),
23 hemiedaphic and edaphic level (S.Soil) and soil and soil surface level (S.Epi.soil);
24 hydromorphic (Hydro.1) and non-hydromorphic soils (Hydro.0); humus forms: mull (S.Mul),
25 moder (S.Mod), mor (S.Mor), peat (S.Peat), mull or moder (S.MuMo), cultivated soil
26 (S.Cult). See Table 3 for abbreviations of species traits.

Table 1

Modalities, abbreviations, information level, and data type of environmental variables.

Environmental variables	Modalities	Abbreviations for CA graphics	Information level (%)	Data type (units)
Habitat closure	Close habitat	Close	100	0/1
	Open habitat	Open	100	0/1
	Intermediate habitat	Int	100	0/1
Stratification	Epigeic 1 (soil surface and mosses)	Epi-1	100	0/1
	Epigeic 2 (herb layers and boulders)	Epi-2	100	0/1
	Epigeic 3 (trees)	Epi-3	100	0/1
	Soil (edaphic and/or hemiedaphic)	Soil	100	0/1
	Hemiedaphic (litter)	Hemi	84	0/1
	Edaphic (A, H, B, E and layers deeper than 3 cm)	Eda	84	0/1
Humus form	Peat	Peat	100	0/1
	Mull	Mull	65	0/1
	Moder	Mod	63	0/1
	Mor	Mor	63	0/1
	Cultivated soil	Cult	95	0/1
Geoclimatic features	Mean annual temperature	Temp	58	value (°C)
	Annual rainfall	Pre	78	value (mm/year)
	Altitude	Alt	80	value (m)
	Hydromorphy	Hydro	100	0/1
Soil chemistry	Soil pH	pH	61	0/1
	Organic layer	Org	49	0/1
	Organo-mineral layer	OM	47	0/1
	C/N ratio	C/N	42	value

Table 2

Name, abbreviations for CA analysis, and number of observations of the 58 most commonly recorded collembolan species.

Species name	Abbreviation	Number of observations	Species name	Abbreviation	Number of observations
<i>Allacma fusca</i> (Linnaeus, 1858)	Afu	43	<i>Mesaphorura tenuisensillata</i> Rusek, 1974	Mte	97
<i>Brachystomella parvula</i> (Schäffer, 1896)	Bpa	66	<i>Mesaphorura yosii</i> (Rusek, 1967)	Myo	106
<i>Ceratophysella armata</i> (Nicolet, 1841)	Car	57	<i>Metaphorura affinis</i> (Börner, 1902)	Maf	20
<i>Ceratophysella denticulata</i> (Bagnall, 1941)	Cde	88	<i>Micraphorura absoloni</i> (Börner, 1901)	Mca	87
<i>Dicyrtoma fusca</i> (Lubbock, 1873)	Dfu	69	<i>Micranurida pygmaea</i> Börner, 1901	Mpy	255
<i>Dicyrtomina minuta</i> (O. Fabricius, 1783)	Dmi	53	<i>Neanura muscorum</i> (Templeton, 1835)	Nmu	147
<i>Entomobrya multifasciata</i> (Tullberg, 1871)	Emu	54	<i>Oncopodura crassicornis</i> Shoebbotham, 1911	Ocr	35
<i>Entomobrya nivalis</i> (Linnaeus, 1758)	Eni	75	<i>Orchesella cincta</i> (Linnaeus 1758)	Oci	111
<i>Folsomia candida</i> Willem, 1902	Fca	36	<i>Paratullbergia callipygos</i> (Börner, 1902)	Pca	363
<i>Folsomia manolachei</i> Bagnall, 1939	Fma	268	<i>Parisotoma notabilis</i> (Schäffer, 1896)	Pno	598
<i>Folsomia quadrioculata</i> (Tullberg, 1871)	Fqu	310	<i>Pogonognathellus flavescens</i> (Tullberg, 1871)	Pfl	77
<i>Friesea mirabilis</i> (Tullberg, 1871)	Fmi	103	<i>Protaphorura armata</i> (Tullberg 1869)	Par	161
<i>Friesea truncata</i> Cassagnau, 1958	Ftr	239	<i>Proisotoma minima</i> (Absolon 1901)	Pmi	66
<i>Heteromurus major</i> (Moniez, 1889)	Hma	124	<i>Proisotoma minuta</i> (Tullberg 1871)	Pminu	38

Table 2 (continued)

<i>Heteromurus nitidus</i> (Templeton, 1835)	Hni	68	<i>Pseudosinella alba</i> (Packard, 1873)	Pal	222
<i>Isotomiella minor</i> (Schäffer, 1896)	Imi	642	<i>Pseudachorutes parvulus</i> Börner, 1901	Ppa	96
<i>Isotomurus palustris</i> (Müller, 1776)	Ipa	73	<i>Pseudisotoma sensibilis</i> (Tullberg, 1876)	Pse	61
<i>Isotoma viridis</i> Bourlet, 1839	Ivir	92	<i>Sminthurinus aureus</i> (Lubbock, 1862)	Sau	208
<i>Lepidocyrtus curvicollis</i> Bourlet, 1839	Lcu	51	<i>Sminthurinus elegans</i> (Fitch, 1863)	Sel	44
<i>Lepidocyrtus cyaneus</i> Tullberg, 1871	Lcy	119	<i>Sminthurides schoetti</i> Axelson, 1903	Ssc	52
<i>Lepidocyrtus lanuginosus</i> (Gmelin, 1788)	Lla	459	<i>Sminthurinus signatus</i> (Krausbauer, 1898)	Ssi	152
<i>Lepidocyrtus lignorum</i> (Fabricius, 1793)	Lli	207	<i>Sphaeridia pumilis</i> (Krausbauer, 1898)	Spu	221
<i>Lepidocyrtus violaceus</i> (Geoffroy, 1762)	Lvi	30	<i>Stenaphorurella denisi</i> (Bagnall, 1935)	Sde	93
<i>Lipothrix lubbocki</i> (Tullberg, 1872)	Llu	69	<i>Tomocerus minor</i> (Lubbock, 1862)	Tmi	79
<i>Megalothorax minimus</i> Willem, 1900	Mmi	453	<i>Willemia anophthalma</i> Börner, 1901	Wan	197
<i>Mesaphorura hylophila</i> Rusek, 1982	Mhy	161	<i>Willemia denisi</i> Mills, 1932	Wde	87
<i>Mesaphorura italica</i> (Rusek, 1971)	Mit	76	<i>Willemia intermedia</i> Mills, 1934	Win	38
<i>Mesaphorura krausbaueri</i> Börner, 1901	Mkr	174	<i>Xenylla grisea</i> Axelson, 1900	Xgr	45
<i>Mesaphorura macrochaeta</i> Rusek, 1976	Mma	513	<i>Xenylla tullbergi</i> Börner, 1903	Xtu	107

Table 3

Modalities of traits, abbreviations for RLQ and models, type of data, number of species for each category of categorical and binary traits and mean* for discrete and continuous data.

Trait	Trait modalities	Types of data for RLQ and models	Number of species per category or mean* for all species	Abbreviation of classes for RLQ	Abbreviation for regression models
Reproduction mode	Parthenogenesis	0/1	10	Repro.part	Repro.part
	Sexual reproduction	0/1	41	Repro.sex	Repro.sex
	Mixed reproduction	0/1	7	Repro.mix	Repro.mix
Body shape	Spherical body	0/1	10	Body.sphe	Body.sphe
	Cylindrical body	0/1	42	Body.cyl	Body.cyl
	Stocky body	0/1	6	Body.stock	Body.stock
Body length	Body length (RLQ)	Categories (RLQ) : -1: less than 2mm	9	Body.L.1	-
		-2: between 2 and 3mm.	7	Body.L.2	
		-3: more than 3mm	42	Body.L.3	
	Body length (models)	Length in mm	1.82*	-	Body-L
Locomotory organs	Furcula length	Categories : -4 : reaches the anterior limit of abd 2 when folded along body	29	Furca.L.4	
		-3 : reaches the anterior limit of abd 3	5	Furca.L.3	Furcula-L
		-2 :does not reach the anterior limit of abd 3	6	Furca.L.2	
		-1 : rudimentary, not functional	3	Furca.L.1	
	-0 :absent	5	Furca.L.0		
Leg length	Ratio leg length / body length	0.36*	Leg.L.1 Leg.L.2 Leg.L.3	Legs-L	
Sensory or sense-related organs	Antenna length	Ratio antenna length /head diagonal length	1.17*	Ant.L.1 Ant.L.2 Ant.L.3	Antenna-L

Table 3 (continued)

Trait	Trait modalities	Types of data for RLQ and models	Number of species per category or mean* for all species	Abbreviation of classes for RLQ	Abbreviation for regression models
Sensory or sense-related organs	Number of ocelli	Number from 0 to 8	4-5*	Ocel.0 Ocel.1 Ocel.2	Ocelli
	Max number of PAO vesicles	Number from 0 to 40	8*	PAO.ves.0 PAO.ves.1 PAO.ves.2	PAO vesicles-max
	Trichobothria	Absent:0 Present :1	24	Tricho.0 Tricho.1	Tricho
Protective features	Scales	Absent:0 Present :1	11	Scale.0 Scale.1	Scales
	Pigmentation	Absent:0 Present :1 Presence variable (RLQ only)	36	Pigment.0 Pigment.1 Pigment.var	Pigment
Defense against predators	Pseudocelli	Absent:0 Present :1	11	Pseudo.0 Pseudo.1	Pseudo

Table 4

Results of CCA followed with permutation tests with species occurrence as active variables and environmental factors as constraining variables. Humus form: Mull, Moder; Habitat closure: Open; Vertical stratification: Hemiedaphic, Epigeic-1, Epigeic-2, Epigeic-3; Hydromorphy, pH: soil pH, Climate: minimum Temperature and Precipitation.

		Habitat closure-Vertical stratification-Humus form-Hydromorphy-Climate-pH	
	Totale	4.987	100
Inertia	Constrained (%)	0.625	12.528
	No-constrained (%)	4.362	87.472
Permutation test	Permutation number		900
	Pseudo F		0.680
	p-value		< 0.0001

Table 5

Results of linear models (R^2 , F, p-value) and type III analysis of sum of squares (p-value) between discrete and continuous trait values, respectively and species occurrence in binary environmental variables or minimum values of continuous environmental variables (values in bold type indicate significant effect: $p < 0.05$; see Tables 1 and 3 for abbreviations).

	Antenna-L	Furcula-L	Ocelli	Legs-L	Log(Body-L)	Log(PAO vesicles-max)
R^2	0.352	0.328	0.437	0.405	0.454	0.430
F	5.543	6.337	10.085	6.937	4.983	7.710
Pr > F	0.000	0.000	<0.0001	<0.0001	0.000	<0.0001
Alt-min		0.359		0.285	0.057	0.378
Pre-min	0.062				0.041	
Temp-min	0.016	0.034	0.023	0.099	0.107	0.001
Moder					0.054	
Mor	0.009					
Eda	0.001			0.043		
Hemi			0.809	0.004		0.692
Epi-1		0.001	<0.0001		0.001	0.001
Epi-2				0.006	0.040	
Epi-3					0.034	
pH-min	0.067	0.054	0.152		0.081	0.001

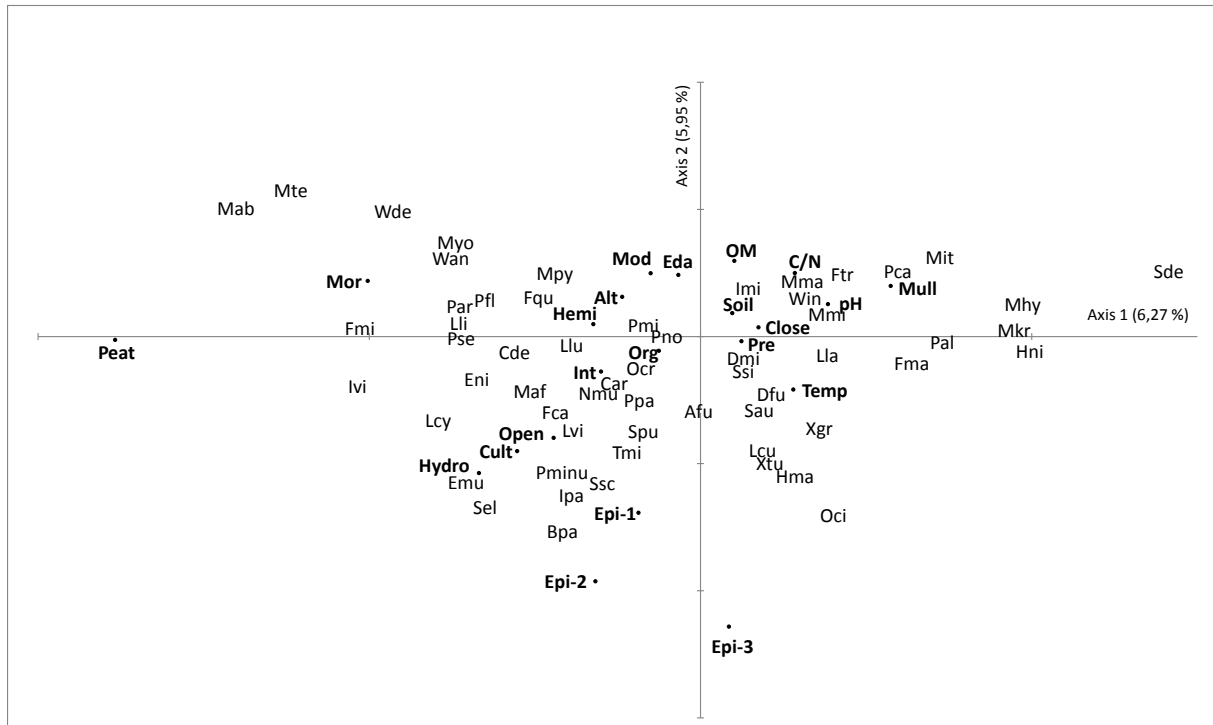
Table 6

Results of logistic models (Mc Fadden R², Khi², p-value) and type III analysis (p-value) between binary and qualitative trait values, respectively and species occurrence in binary environmental variables or minimum values of continuous environmental variables (values in bold type indicate significant effect: p <0.05; see Tables 1 and 3 for abbreviations).

	Scale	Pseudo	Repro.sex	Repro.part	Body.sphe	Body.cyl	Tricho	Pigment
R ²	0.084	0.707	0.316	0.348	0.310	0.229	0.447	0.547
McFadden	4.756	39.842	22.207	18.572	16.556	15.211	35.152	49.431
Khi ²	0.029	<0.0001	0.000	0.001	<0.005	0.019	<0.0001	<0.0001
p-value								
Alt-min							0.000	
Pre-min						0.533		
Temp-min		0.000	0.030	0.030	0.077		0.014	
Mull						0.666		
Moder		0.623						
Open			0.217	0.698				
Peat							0.004	
Eda	0.029				0.172	0.068		0.169
Hemi			0.095		0.002	0.010	0.148	0.295
Epi-1		<0.0001		0.197	0.142			<0.0001
Epi-2			0.003		0.009	0.024	0.000	
Epi-3				0.053		0.070		
pH-min		0.001	0.281					

Fig. 1

a)



b)

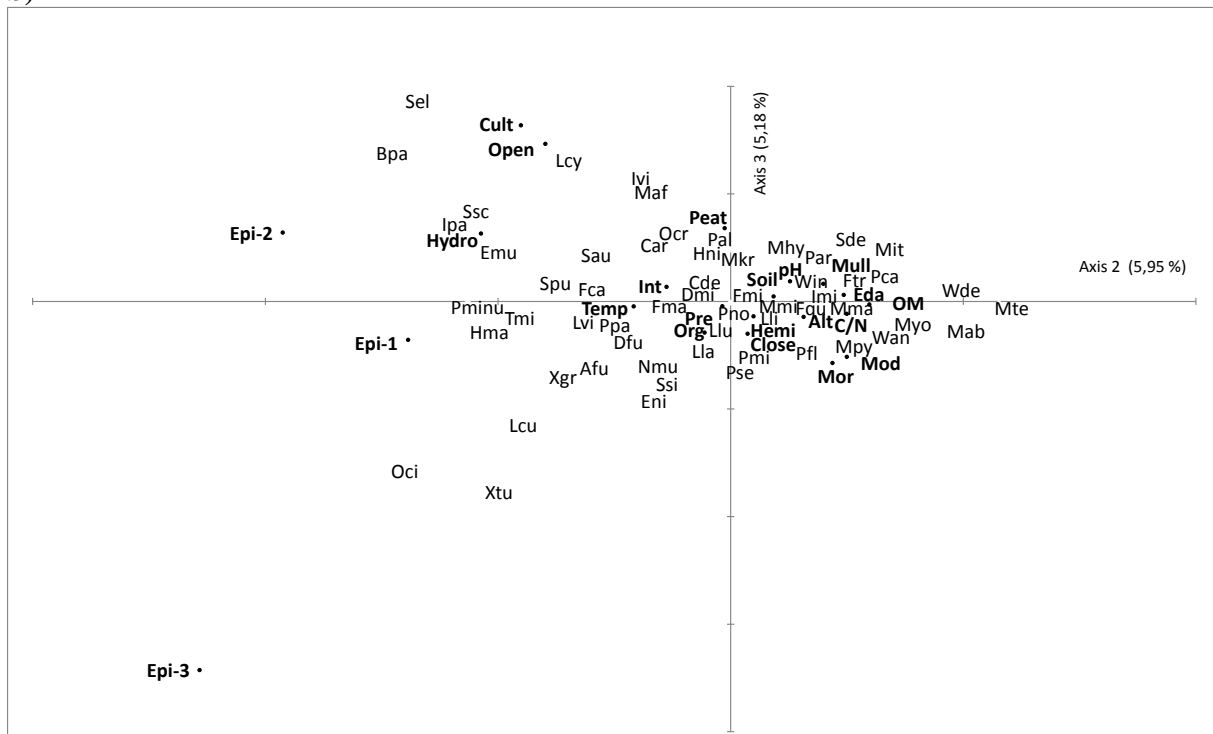
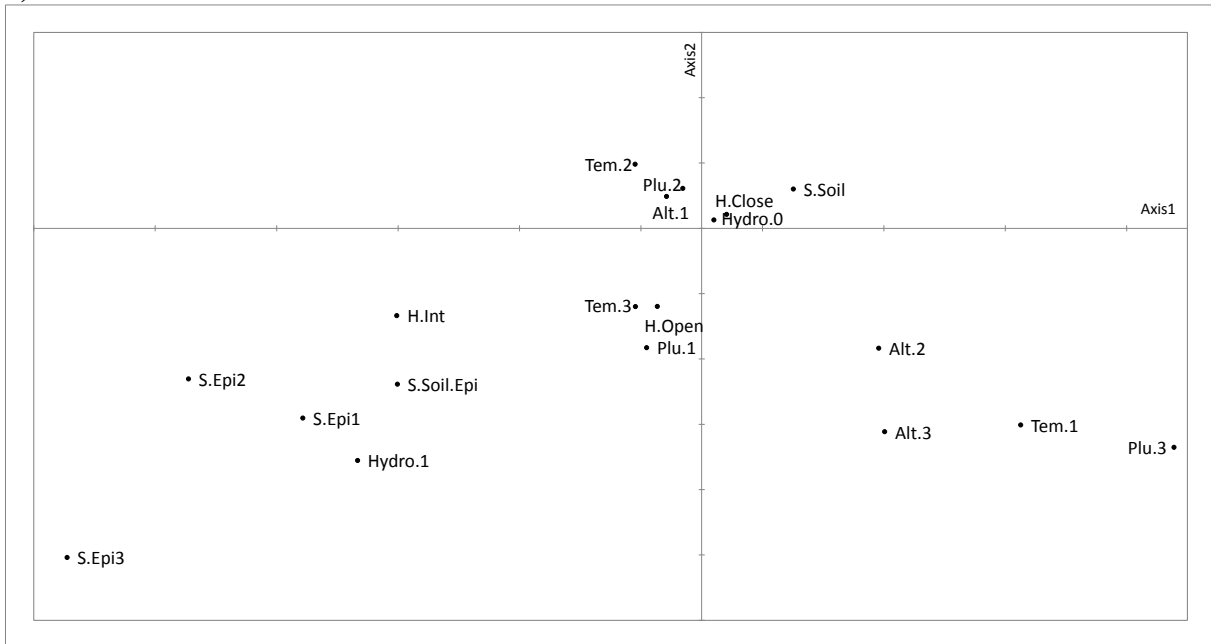


Fig. 2

a)



b)

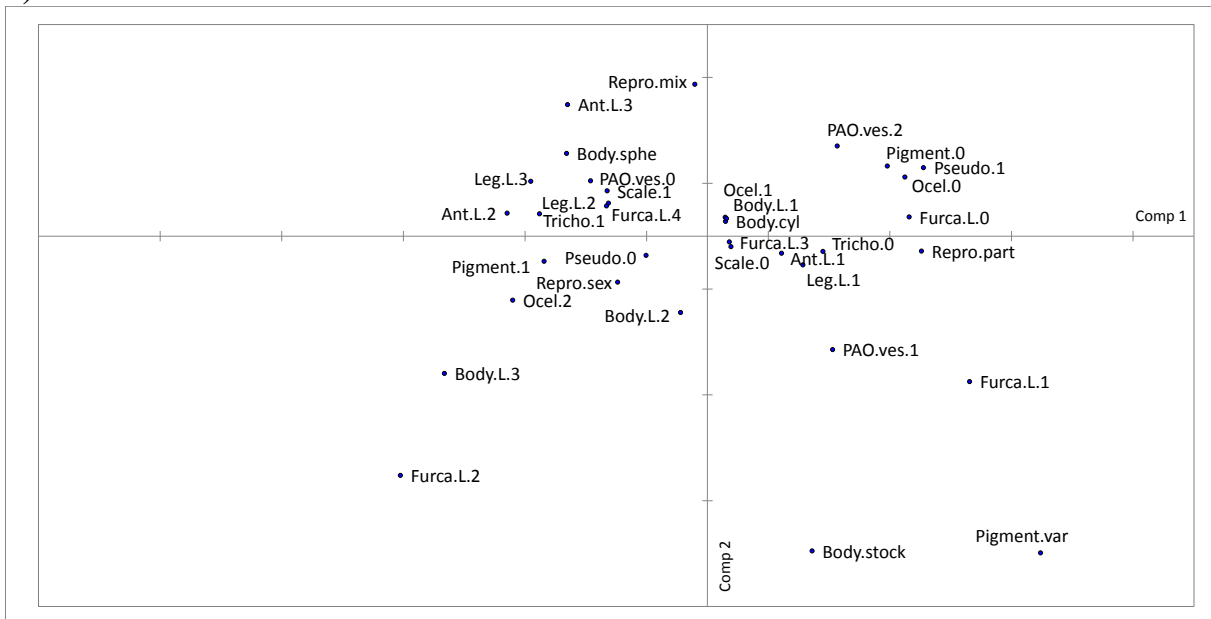
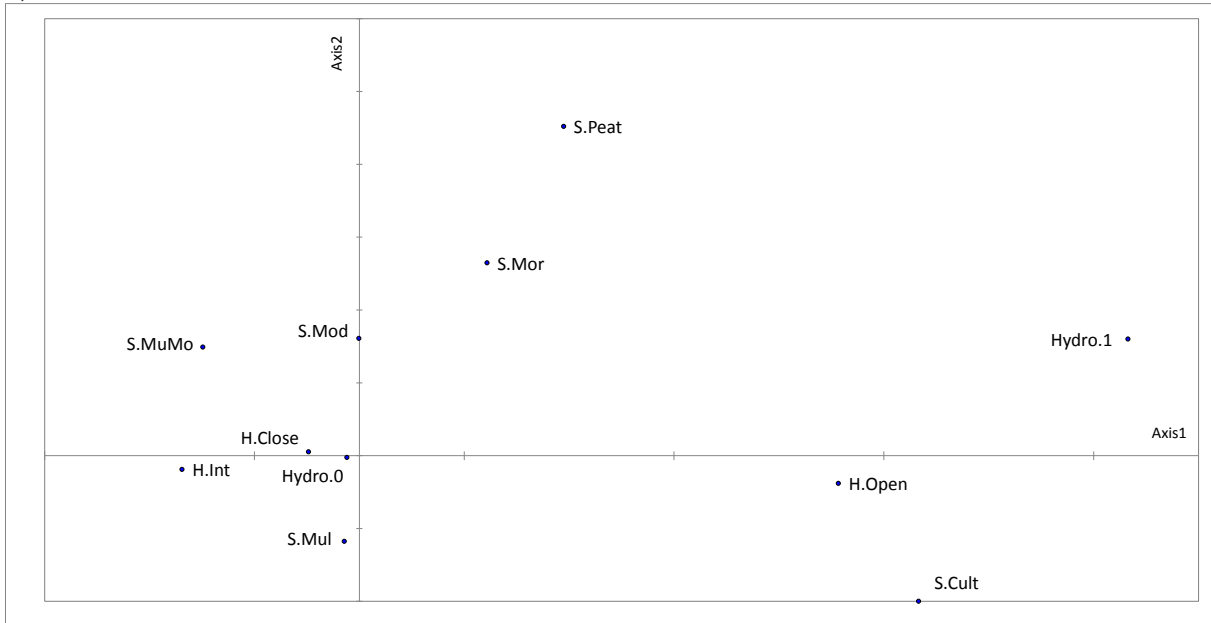
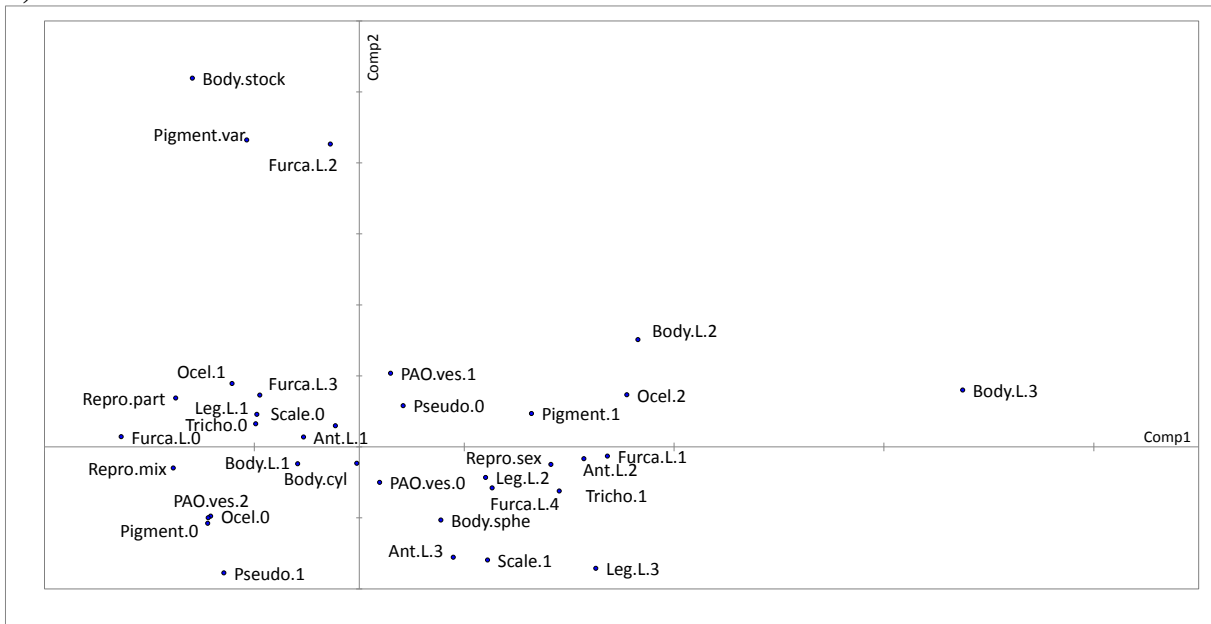


Fig. 3

a)



b)



Appendix 1

References dealing with field studies on collembolan communities and used to compile occurrences of collembolan species in diverse habitats and the description of these habitats in Coltrait database.

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