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### ► To cite this version:

Benoît Vanhee, Sandrine Salmon, Cédric Devigne, Alain Leprêtre, Louis Deharveng, et al.. The ‘terril’ effect: coal mine spoil tips select for collembolan functional traits in post-mining landscapes of northern France. *Applied Soil Ecology*, 2017, 121, pp.90-101. 10.1016/j.apsoil.2017.09.027 . hal-01600784

**HAL Id: hal-01600784**

**<https://hal.science/hal-01600784v1>**

Submitted on 2 Oct 2017

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1 **The ‘terril’ effect: coal mine spoil tips select for collembolan functional traits**  
2 **in post-mining landscapes of northern France**

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13 **ABSTRACT**

14 We sampled collembolan communities in 11 coal mine spoil tips (locally called ‘terrils’) from the  
15 North of France, and their surroundings, in various stages of vegetation development (bare soil, herb,  
16 shrub and tree vegetation). We wondered whether species, functional trait (Community Weighted  
17 Mean trait or CWM) composition and trait diversity (Rao’s quadratic entropy) responded to the  
18 particular environment of coal mine spoil tips (here called ‘terril’ effect) and to successional effects  
19 and which of these three sets was the best indicator of soil and vegetation effects, taking into  
20 account that spoil tips were spatially distant and idiosyncratic (e.g. varying in height, area, past

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1 history and surrounding environment). We showed that species, but not traits, were strongly  
2 influenced by site effects, while traits were influenced by both 'terril' and successional effects to a  
3 significant extent, making traits more robust than species when trying to discern patterns of  
4 community response to soil and vegetation changes. Functional diversity did not show any significant  
5 multi-trait response to either 'terril' or successional effects, but several functional traits showed an  
6 increase in diversity with succession. The overall response of trait diversity was intermediate  
7 between species and trait responses. The 'terril' effect was mainly mediated by a coarser soil texture  
8 (51% coarse sand compared to 14% in the surrounding environment) which, combined with harsher  
9 microclimate conditions, stems in a better representation of functional traits linked to subterranean  
10 life, such as shorter body length and increased representation of parthenogenesis. Successional  
11 effects (in particular the increase in diversity shown by several functional traits varying with vertical  
12 distribution) were mediated by the increasing development of organic horizons but other factors like  
13 microclimate were seemingly involved, too. More generally this study showed that shift to  
14 subterranean life was an adapted response of collembolan communities to harshness of the  
15 environment and that vertically stratified ecosystems allow a more complete expression of their  
16 functional diversity.

17 *Keywords:* coal mine spoil tips; Hauts de France; collembolan communities; functional traits;  
18 functional diversity; vegetation succession

19

## 1 **1. Introduction**

2 Environmental filtering has been considered as a prominent source of variation of plant and  
3 animal communities at a level intermediate between regional species pools and species interactions  
4 (Rajaniemi et al., 2006). Coal mine spoil tips are thought to play the role of environmental filters for  
5 regional species pools (Molyneux, 1963; Kirmer et al., 2008), as could also be observed for instance in  
6 the colonisation of glacier moraines (Ingimarsdóttir et al., 2012). The need to adapt to such  
7 environments, known for their harsh microclimate and soil conditions and strong seasonal contrasts  
8 (Whitlock et al., 2015), can be expected to select for functional traits (sensu Pey et al., 2014) which  
9 might differ to a great extent from those of the surrounding woodland, agricultural or urban land  
10 (Frouz et al., 2013; Tischew et al., 2014). Vegetation succession, whether natural (primary  
11 succession) or under landscaping activities, superimposes changes in soil and microclimate which  
12 may impact in turn the composition of communities (Alday et al., 2011; Piekarska-Stachowiak et al.,  
13 2014; Markowicz et al., 2015). Thus coal mine soil tips, characterized by both strong selection  
14 pressure and strong heterogeneity (Whitlock et al., 2015), could be considered as good models for  
15 studying at community level the response of functional traits to environmental forcing (Piekarska-  
16 Stachowiak et al., 2014).

17 Colliery waste heaps (also called coal mine spoil tips) are in high contrast with the flat  
18 surrounding agricultural or urban environment (Molyneux, 1963; Lemoine, 2012). Although their  
19 shape may vary according to present or past usages they generally look like conical hills made of  
20 waste deposits (more generally shale and/or sandstone) extracted from the subsoil while tunnelling  
21 it for coal extraction. Their height, generally between 50 and 100 m, may exceptionally reach 200 m  
22 or more, with unstable slopes as steep as 100%. Steep slope, darkness and coarse texture of  
23 extracted rock debris make the microclimate of coal mine spoil tips warmer and drier than the  
24 surrounding environment, as attested by the thermophilic nature of spontaneous vegetation, with  
25 strong analogies with coastal dune environments (Petit, 1980; Lemoine, 2012). Subterranean

1 spontaneous and self-sustained combustion often occurs by places, because of the presence of coal  
2 remains in admixture with other deposits (Bell et al., 2001). After abandonment soil develops in the  
3 course of time, together with plant succession from pioneer mosses and lichens to woody plants  
4 (Down, 1973). The encroachment of natural vegetation is often artificially hastened by sowing grasses  
5 and planting trees, for recreation purposes and to prevent erosion.

6           Collembola are among the most abundant soil animal groups (Rusek, 1998) and their  
7 functional importance has been acknowledged from their involvement in bacterial- and fungal-based  
8 soil food webs (Filser, 2002; Chahartaghi et al., 2005; Murray et al., 2009), the translocation of litter  
9 carbon to soil (Chamberlain et al., 2006), the control of fungal pathogens (Mitschunas et al., 2006)  
10 and the dispersal of microbial and plant diaspores (Cronberg et al., 2006), giving them the status of  
11 “ecosystem engineers” (Bispo et al., 2009). Species traits are known to vary vertically according to  
12 the stratification of ecosystems (Prinzing and Woas, 2003; Rusek, 2007; Krab et al., 2010; Salmon et  
13 al., 2014) and horizontally according to land-use changes (Salmon and Ponge, 2012; Santorufo et al.,  
14 2015; Martins da Silva et al., 2016; Winck et al., 2017) and other environmental influences (Salmon et  
15 al., 2014). Soil collembolan communities have been already inventoried in coal mine spoil tips  
16 (Hutson, 1980; Moore and Luxton, 1986), as well as in other types of mining activities, such as  
17 reclaimed lignite strip-mining sites (Dunger et al., 2001, 2004; Dunger and Voigtländer, 2005), but  
18 nothing is known in terms of trait responses to environmental factors.

19           We needed to ascertain in the studied region to which extent collembolan communities of  
20 coal mine spoil tips differed from their surrounding environment (a contrast here collectively called  
21 ‘terril’ effect) and varied according to vegetation development. We hypothesized (Hypothesis H1)  
22 that trait modalities linked to subterranean life such as short appendages, absence of pigmentation  
23 and of sexual reproduction (Hopkin, 1997) were favourable to survival in warmer and drier  
24 environments, i.e. were increased in representation by the ‘terril’ effect, like in coastal dune and  
25 desert soils (Wallwork, 1972; Koehler et al., 1995), and were also favoured by the concomitant

1 development of soil and vegetation, as observed when comparing 'open' and 'closed' areas (Salmon  
2 et al. 2014). The use of functional traits, which directly express the adaptation of species to a given  
3 environment (Bokhorst et al., 2012; Santorufo et al., 2015) was justified by the need to discern  
4 environmental drivers of community change, above variation due to spatial and historical patterns,  
5 here grouped under the 'site' effect. We also wanted to know whether the natural or artificial  
6 development of vegetation on abandoned coal tips (from bare soil to trees, passing by herbaceous  
7 and shrubby stages), known to increase the vertical stratification of the soil niche (Salmon et al.,  
8 2014), would increase in turn the functional diversity of collembolan communities (Hypothesis H2). If  
9 it is known that functional diversity increases with species richness in plant communities (Petchey  
10 and Gaston, 2002), and if it is known that collembolan species richness increases with stand  
11 development (Addison et al., 2003), nothing such is known as yet for functional diversity. At last we  
12 wonder whether species, traits and trait diversities had their own specificities when assessing  
13 environmental effects on collembolan communities. We hypothesized that functional traits, being  
14 directly influenced by environmental effects (Santorufu et al., 2015), are more robust than species to  
15 assess environmental effects at community level, and that trait diversity, being driven by processes in  
16 which both species and traits are involved (Mayfield et al., 2010), are intermediate in robustness  
17 (Hypothesis H3).

18 For this study we selected 11 'terrils' located in the North of France, the use of which  
19 declined progressively from 1960 on and was definitely abandoned in 1990 (Ladoucette, 2004).

## 20 **2. Material and methods**

### 21 *2.1. Study sites*

22 Nineteenth and 20<sup>th</sup> centuries knew a dramatic expansion of industrial activities based on  
23 coal mining as the dominant source of energy (Hubbert, 1956). Coal mining activities ceased  
24 progressively in the second half of the 20<sup>th</sup> century, leaving a flat landscape punctuated by cone-  
25 shaped coal spoil tips (colliery spoil heaps), locally called 'terrils'. These artificial hills were later left

1 untouched for most of them or reworked for recreational purposes (Lemoine, 2012). Given their  
2 richness in rare thermophilic plant and animal species these ‘terrils’ got a conservation status and  
3 were studied by university scientists (Petit, 1980, 1983; Godin, 2002). In 2012 the Nord Pas-de-  
4 Calais Mining Basin has been included in its entirety in the UNESCO World Heritage List (UNESCO,  
5 2012).

6           Eleven sites, including spoil tips and their immediate environment, were sampled (Appendix  
7 A). They are representative of the western part of the Nord Pas-de-Calais Mining Basin. Coal mine  
8 spoils were mostly made of shale and sandstone deposits of varying texture, with a dominance of  
9 coarse sand in the 2-mm sieved fraction (Table 1). Their edification started in the first half of the 20<sup>th</sup>  
10 century. The end of edification is difficult to establish rigorously, given that mining activities declined  
11 over ca. 30 years (1960-1990) with temporary recovery during the 70s, and some former conical spoil  
12 tips were partly exploited for various purposes after mining activities have ceased, stemming in  
13 truncated or flat appearance. Primary succession took place after abandonment, at a rate and a  
14 species composition highly influenced by the local species pool, as commonly observed in similar site  
15 conditions (Kirmer et al., 2008; Alday et al., 2011; Tischew et al., 2014). Three types of land use were  
16 considered to describe the surrounding environment: urban (included in the city), rural (included in  
17 an agricultural landscape) and woodland (Appendix A). Several stages of vegetation development,  
18 from bare soil to herbaceous then to shrub and to tree vegetation (mainly silver birch, *Betula*  
19 *pendula* Roth.) are still already visible today and were selected for sampling, when present (bare soil  
20 or woody vegetation can be lacking). Colonization by birch was more rapid and occurred over higher  
21 areas when this wind-dispersed tree species was present in the immediate environment (woodland  
22 environment). Some ‘terrils’ were revegetated (mainly with silver birch) and landscaped for  
23 recreational purposes. Combinations of surrounding landscapes and successional stages result in  
24 various environmental conditions at local level. Sampling was done in order to reflect the variety of  
25 conditions found in the mining basin, taking also into account the immediate environment where  
26 bare soil, herb, shrub and tree vegetation (when present) were sampled for the sake of comparison.

1 In total 81 sample points were selected, shared in 37 for spoil tips and 44 for the surrounding  
2 environment (Appendix E). Note that sampling reflected the fact that the distribution of the four  
3 successional stages was naturally unbalanced between spoil tips and their environment, impeding  
4 any orthogonal treatment of the data.

## 5 *2.2. Sampling and extraction*

6 Sampling took place at each sampling point by forcing a cylindrical core (8 cm diameter,  
7 11 cm depth) in the soil. This operation was duplicated in order to obtain ca. one cubic decimetre of  
8 soil, which was carried in polythene bags back to the laboratory. Extraction was achieved in 7 days in  
9 Berlese-type funnels, below which soil animals escaping drying soil samples were collected in a  
10 mixture of ethyl alcohol (70 %) and ethylene glycol (30 %). Collembola were mounted in lactic acid  
11 then were counted and identified using various keys (Gisin, 1960; Bretfeld, 1999; Potapow, 2001;  
12 Thibaud et al., 2004; Hopkin, 2007; Dunger and Schlitt, 2011; Jordana, 2012).

## 13 *2.3. Soil features*

14 At each sampling point two additional soil samples were taken then sent to soil analytical  
15 laboratory for measurement of pH (ISO, 2005), organic matter (ISO, 1995a), total nitrogen (ISO,  
16 1995b), carbon/nitrogen ratio and particle size distribution (ISO, 2009). All analytical results are  
17 presented in Appendix E.

## 18 *2.4. Data collection and treatment*

19 Species functional traits were taken from the Coltrait database (Salmon et al., 2014) and  
20 were transformed in a small number of non-overlapping modalities, ranging from 2 to 4 depending  
21 on traits (Table 2, Appendix B). A small number of species (less than 10 %) could not be found in the  
22 database, for which original diagnoses were used to complete the table for the 107 species collected  
23 during the study. When building the Coltrait database species traits were directly measured on adults  
24 or taken from published diagnoses. We are aware that not taking into account within-species trait



1 variation, in particular ontogenetic changes, could impact our results, as this has been demonstrated  
2 in vegetation studies when saplings and adult trees were confounded (Spasojevic et al., 2014). In our  
3 dataset only body length will be impacted by this simplification, because other traits (body shape and  
4 colour, eye number, presence of trichobothria, ocelli, and anal spines, relative lengths of  
5 appendages) do not change to a great extent along a springtail's life (Hopkin, 1997), or are relative to  
6 a whole springtail's life (reproduction mode).

7         In a first step we performed an indirect gradient analysis, here Principal Components Analysis  
8 (PCA), of species occurrences, using presence/absence in place of abundance and Spearman (rank) in  
9 place of Pearson (linear) as a measure of correlation between variables. This multivariate method has  
10 been already used to analyse binary data (Debinski and Brussard, 1994; Troia et al., 2012) and was  
11 judged better than correspondence analysis (a multivariate method adapted to count data) when  
12 searching for gradients (Kenkel, 2006). For this analysis we used only species present in more than  
13 two samples, letting 74 species as active variables. Explanatory variables (nine soil parameters as  
14 listed in Table 1 and Appendix E, spoil tip versus surrounding environment, the three kinds of  
15 surrounding environment, the four successional stages) were added as passive variables, using the  
16 same measure of distance (rank correlation coefficient) than active variables. Functional traits were  
17 also added as passive variables, affecting a score to each trait according to scaled modalities (Table 2,  
18 left column). For each trait the score varied from 1 (absence) to 2, 3 or 4, affecting an arbitrary  
19 number to each step of the corresponding scale. These values were averaged for each sample, after  
20 each species has been weighted by its relative abundance (Appendix E), thus giving the same trait  
21 value to all individuals belonging to the same species. This community assessment of trait values has  
22 been called Community Weighted Mean (CWM) trait by Garnier et al. (2004) and has been used for  
23 studying the response of soil animal communities to environmental change (Moretti and Legg, 2009;  
24 Bokhorst et al., 2012; Malmström, 2012). CWMs were calculated on the whole set of species, thus  
25 including those present in more than two samples.

1           The rationale for the use of species rather than functional traits as active variables was that  
 2   PCA was used as a preliminary step, allowing us to discern all environment gradients of potential  
 3   influence on collembolan communities. An even more important reason was that the set of  
 4   functional traits used in an ecological study is only a subset of the complete set of traits (including  
 5   the so-called ‘hard traits’) needed to assess community responses to environmental change (Lavorel  
 6   and Garnier, 2002; Garnier et al., 2004). In particular, concerning springtails, we are still in need of  
 7   physiological traits explaining the response of species to factors such as soil acidity, one of the most  
 8   complex (although highly influential) ecological determinants of species occurrence (Hågvar, 1990;  
 9   Loranger et al., 2001; Salmon et al., 2002).

10           We also added measurements of functional diversity for single traits (here called ‘trait  
 11   diversity’) and a multi-trait measurement of functional diversity (here called ‘functional diversity’).  
 12   For these purposes the diversity of modalities of each trait in each sample was estimated by Rao’s  
 13   quadratic entropy (Rao, 1982), using relative abundance values for each species present in a sample  
 14   and squared differences (squared Euclidean distances) between standardized CWM values (each trait  
 15   rescaled to vary between 0 and 1) as a measurement of dissimilarity between species (Appendix E).  
 16   The diversity of modalities for trait A in a community (sample), measured by Rao’s quadratic entropy,  
 17   is:

$$Q = \sum_i \sum_j D_{ij} \times p_i \times p_j$$

18    $p_i$  et  $p_j$  are the relative frequencies of species  $i$  et  $j$ , respectively

$$D_{ij} = (A_i - A_j)^2$$

19    $A_i$  and  $A_j$  are the values of trait A for species  $i$  et  $j$ , respectively

20

21           We demonstrated that the calculation can be simplified to a great extent when using  
 22   standardized CWMs, i.e. when  $0 \leq A_i \leq 1$  and  $0 \leq A_j \leq 1$ . In this case Rao’s quadratic entropy is

1 rigorously equal to trait variance (Appendix C). We also showed that when traits have only two  
2 modalities (for instance presence versus absence) Rao's quadratic entropy (or trait variance) is a  
3 quadratic function of standardized CWM, passing by a maximum for a value of 0.5 (Appendix C).  
4 Rao's multi-trait functional diversity (Botta-Dukát, 2005; Schleuter et al., 2010) was calculated using  
5 the Euclidean distance between species (i.e. the sum of single-trait squared differences) as a  
6 measure of their dissimilarity (Champely and Chessel, 2002).

7           In a second step we tested whether soil features, species traits and trait diversity varied  
8 according to the 'terril' effect (spoil tip versus surrounding environment) and the successional stages  
9 (bare, herb, shrub, and tree). For that purpose we used Kruskal-Wallis rank tests followed by Dunn  
10 tests with Bonferroni adjustment for multiple comparisons among groups (Tables 1-3). Rank  
11 correlation coefficients between the first two components of PCA, soil variables, CWM values and  
12 trait diversities were also calculated (Appendix F).

13           In a third step we used Redundancy Analysis (RDA), a direct gradient multivariate method  
14 complementary to PCA (Van den Wollenberg, 1977), to test for site, the 'terril', succession, land use,  
15 and soil effects on species (presence/absence), functional traits (CWM-RDA, Kleyer et al., 2012) and  
16 multi-trait functional diversity (Rao's quadratic entropy). Tests were performed with Monte-Carlo  
17 simulation (500 permutations). Partial RDA was used to partial out several components of the whole  
18 effect (Økland, 1996) and combinations of partial and simple RDAs were used to address some  
19 specific questions, in particular whether site specificity may mask or not overall effects of soil and  
20 vegetation development. For this purpose we included or not some factors in the model, and fixed  
21 them (as co-variate or confounding factor) or not. As an example of reasoning we wanted to ask  
22 whether the 'terril' effect was mediated or no by soil effects when all other effects were discarded:  
23 for this purpose we performed two tests with site, successional stage, and surrounding land-use as  
24 fixed factors, one (1) with soil not included in the model and thus allowed to vary, and the other (2)  
25 with soil included in the model but fixed (testing for pure 'terril' effect because all other factors are

1 fixed). If test (1) is significant while test (2) is not, it means that the 'terril' effect was mediated by  
2 soil.

3 All calculations were done with XLSTAT® version 18.07 (Addinsoft®, Paris, France).

### 4 **3. Results**

5 The first two principal components of PCA extract 13.2% of the total variation in species  
6 composition (6.8 and 6.4% for PC1 and PC2, respectively), a low value quite expected in indirect  
7 gradient analyses with a high number of active variables (74 species) and observations (81 samples).  
8 The projection of samples and species in the PC1-PC2 scatterplot shows a fairly good spread along  
9 both axes, without any visible horseshoe (curvilinear distortion) effect (Appendix D).

10 The projection of explanatory variables (Fig. 1) shows that PC1 mainly represents the 'terril'  
11 effect, as shown by ST, ST bare, ST herb, ST shrub and ST tree having positive scores, while ENV, ENV  
12 bare, ENV herb, ENV shrub have negative scores and ENV tree has a nil score. PC2 mainly represents  
13 the successional effect, with ST bare, ENV bare, ST herb and ENV herb having negative scores while  
14 ST tree, ENV tree and ENV shrub have positive scores. The only exception is ST shrub with weakly  
15 negative scores along PC2. Anyhow, whether in spoil tips or in their surrounding environment, early  
16 successional stages (bare, herb) have lower scores along PC2 than late successional stages (shrub,  
17 tree). The significance of PC1 and PC2 according to 'terril' and successional effects, respectively, has  
18 been verified by Kruskal-Wallis rank tests (Table 1). The 'terril' effect is mainly displayed by PC1 ( $P <$   
19  $0.0001$ ) while PC2 mainly represents the successional effect ( $P < 0.0001$ ), but some (although  
20 weaker) contrast between spoil tips and the surrounding environment is also represented by PC2 at a  
21 lower level of confidence ( $P < 0.01$ ), while a contrast between successional stages is also represented  
22 by PC1 ( $P < 0.0001$ ), as already suggested by Figure 1. This indicates that both factors are not strictly  
23 independent, although a similar successional trend (involving the same species replacements) can be  
24 evidenced in spoil tips and in their surrounding environment. The projection of the variable 'Species  
25 richness' in the PC1-PC2 scatterplot shows that sample species richness is mainly correlated with

1 PC2, thus with plant succession and associated changes in soil resources and habitats. It has been  
2 verified that species richness of the samples increases with plant succession, near doubling from 7.4  
3 species in bare soil to 14 species under trees ( $P < 0.0001$ ) but does not differ between spoil tips and  
4 their environment (11.5 and 12.3, respectively).

5         Some explanatory variables are projected far from the origin in the PC1-PC2 scatterplot,  
6 thereby indicating a strong correlation with the first two PCA components. This is the case of pH,  
7 which exhibits a strong negative correlation with PC2 ( $r_s = -0.42$ ,  $P < 0.001$ , Appendix F), and thus  
8 decreases with plant succession, but not with PC1 ( $r_s = -0.072$ ,  $P = 0.52$ , Appendix F), and thus does  
9 not seem to differ between spoil tips and their surrounding environments. This has been verified by  
10 non-parametric tests (Table 1): pH decreases from 7.7 in bare soil to 6.2 under trees (1.5 unit less, i.e.  
11 30 times less protons), but does not vary between spoil tips (6.9) and their surrounding environment  
12 (6.8). Figure 1 and Table 1 show that the soil nitrogen content near doubles along the successional  
13 gradient (from 2.5 to 4.5‰) but only slightly decreases from spoil tips (3.6‰) to surrounding  
14 environments (3.1‰). Similar variations have been also observed in the organic matter content, with  
15 a doubling from 41 to 81‰ according to succession, and a 68 to 50‰ decrease from spoil tip to  
16 environment. Nitrogen and organic matter contents are strongly and positively correlated ( $r_s = 0.77$ ,  
17  $P < 0.001$ , Appendix F). The C/N ratio does neither show 'terril' nor successional effect, indicating  
18 that the increase in nitrogen content is only due to the increase in organic matter, not to a change in  
19 organic matter quality. Among soil textural classes, PC1 shows a strong contrast between fine  
20 textural classes with strongly negative scores (clay, fine and coarse silt), and coarse sand with  
21 strongly positive scores, fine sand being in an intermediary position, with a slightly positive score.  
22 Non-parametric tests (Table 1) show that, to the exception of fine sand, there is a high contrast ( $P <$   
23  $0.0001$ ) between spoil tips (with coarse texture) and their environment (with fine texture).  
24 Woodland, urban and rural land uses are projected far from the origin in the PC1-PC2 scatterplot  
25 (Fig. 1). This shows that they contribute to explain the species composition of collembolan  
26 communities, with a contrast between urban and woodland land uses along PC2, i.e. in the direction

1 of plant succession, with agricultural land in an intermediary position. This suggests that the  
2 influence of land use is probably indirect, plant succession seemingly reaching sooner (and thus more  
3 often) the tree stage when spoil tips are inserted in a forested landscape. This has been verified by  
4 the examination of aerial photographs (data not shown). At last, the existence of a site effect is  
5 revealed by the spread of the different sites in the PC1-PC2 scatterplot (Fig. 1). However, it must be  
6 noticed that the spread of sites is not due only to their own respective characteristics, as detailed in  
7 Appendix A, but also and most probably only to the unbalanced distribution of vegetation types  
8 among them, resulting in unbalanced sampling of associated collembolan communities between  
9 bare, herb, shrub and tree successional stages. Overall results depicted in Figure 1 and Table 1 show  
10 that the species composition of collembolan communities responds to a variety of more or less  
11 correlated environmental factors ('terril' effect, plant succession, soil features, surrounding land use).  
12 They also suggest that soil and land use effects can be at least partly explained by 'terril' and  
13 successional effects.

14         Based on the interpretation of PC1 and PC2 as 'terril' and successional effects on collembolan  
15 communities, respectively, the projection of species functional traits in the PC1-PC2 scatterplot (Fig.  
16 2) shows that most traits, to the exception of body colour and body shape which are projected not  
17 far from the origin, are influenced by one or the other factor or most often by both of them. Most  
18 pronounced variation along PC1 (as deduced from arrow lengths on Fig. 2) is decreasing body length,  
19 furcula and antenna relative lengths, decreasing presence of trichobothria and scales, decreasing  
20 ratio of sexual reproduction and decreasing eye number on one hand, increasing complexity of post-  
21 antennal organs and increasing presence of anal spines and pseudocelli on the other hand. All CWM  
22 trait values, to the exception of body colour, are significantly correlated with PC1 (Appendix F). The  
23 association of these trends with the 'terril effect' (Table 2) has been verified for antenna length ( $P <$   
24 0.001), trichobothria ( $P < 0.001$ ), body length ( $P < 0.01$ ), post-antennal organ ( $P < 0.01$ ), scales ( $P <$   
25 0.01), reproduction type ( $P < 0.05$ ), and furcula length ( $P < 0.05$ ). Typically, according to our results

1 Collembola living in spoil tips are smaller, with shorter jumping and sensorial appendages, without  
2 scales and trichobothria, with developed post-antennal organs, and parthenogenetic.

3 Most pronounced variation along PC2 was decreasing relative leg and furcula lengths,  
4 decreasing ratio of sexual reproduction and eye number, decreasing presence of trichobothria and  
5 scales, and increasing body length. The association of these traits with plant succession has been  
6 verified by Kruskal-Wallis test for reproduction type ( $P < 0.0001$ ), eye number ( $P < 0.0001$ ), leg length  
7 ( $P < 0.05$ ), furcula length ( $P < 0.05$ ) and trichobothria ( $P < 0.05$ ). Only one discrepancy occurs  
8 between the association of functional traits with successional stages according to PCA (Fig. 2) and  
9 non-parametric tests (Table 2). It concerns antenna length, which is poorly associated with PC2 (Fig.  
10 2, Appendix F) while it significantly decreases under trees (Table 2). Typically, according to our results  
11 Collembola living in open environments (in bare areas or under herbaceous vegetation) have a sexual  
12 reproduction, large eye spots, trichobothria and long furcula and legs, while those living in woody  
13 environments (under shrubs or trees) exhibit opposite trait modalities.

14 Figure 3 shows that trait diversity is influenced by factors represented by PC1 and PC2. The  
15 diversities of trichobothria and scale presence, body length, body shape, and eye number decrease  
16 along PC1 (see Appendix F for sign and significance of correlation coefficients). It has been verified  
17 (Table 3) that all these trait diversities decrease from the surrounding environment to spoil tips, with  
18 the highest level of significance ( $P < 0.0001$ ) being displayed by trichobothria diversity. Typically,  
19 Collembola living in spoil tips exhibit a lower diversity for trichobothria, scales, body length, body  
20 shape and eye number. They are thus morphologically more similar than those living in the  
21 surrounding environment. However, some variation in trait diversity is displayed by PCA but not  
22 confirmed by non-parametric tests. This is the case for the increasing diversities along PC1 shown by  
23 anal spines, pseudocelli, and leg and furcula lengths (Fig. 3, Table 3).

24 The diversity of antennal length, body colour, reproduction type, anal spines, leg length,  
25 furcula length and pseudocelli increases, while that of body length decreases along PC2 (see

1 Appendix F for sign and significance of correlation coefficients). The relationship with successional  
2 stage has been verified for antennal length, body colour, anal spines, furcula length, pseudocelli, and  
3 body length diversity (Table 3). Multi-trait functional diversity increases along PC2 ( $r_s = 0.30$ ,  $P < 0.01$ ,  
4 Appendix F) but the relationship with successional stages is not significant (Table 3). With the  
5 exception of body size, it can be said that Collembola living in open environments of the study site  
6 are morphologically more similar than those living in woody environments.

7 It should be noted that Rao's trait diversity (= trait variance) is strongly related to  
8 standardized CWM (Appendix C). The two parabolic curves (Rao's trait diversity and trait variance)  
9 show that trait diversity increases from 0 when all species are similar, whether by the common  
10 presence or absence of a trait, to a maximum of 0.25 when CWM has a standardized value of 0.5 (all  
11 trait modalities equally distributed around the mean value).

12 Redundancy analysis (RDA) shows that combined site, 'terril', successional, land use and soil  
13 effects explain from 39 to 43% of total variation in species composition, CWM and trait diversity  
14 (Table 4, test 1). When site effects are discarded, these percentages fall to values from 16 to 25%,  
15 trait diversity being most affected (Table 4, test 2). Pure site effects (all other factors fixed) represent  
16 14 to 16% of total variation in species, CWM and trait diversity, without reaching significance level on  
17 CWM (Table 4, test 3), while shared site effects increase slightly from 16 to 19% of total variation,  
18 here too without reaching significance level on CWM (Table 4, test 4). Thus species composition is  
19 highly influenced by the site effect (whether pure or shared), trait diversity also, although to a lower  
20 extent, while CWM is not influenced at all.

21 We wanted to test whether site effects are at least partly mediated by the dominant land use  
22 surrounding the spoil tips. When allowing the land use to vary while all other factors are included  
23 and fixed, site effects (Table 4, test 5) are roughly the same as when land use is fixed (Table 4, test 3).  
24 Species strongly respond to the site effect, while CWMs do not, and trait diversities show an  
25 intermediate (although significant) response, whether land use is allowed to vary or not, pointing to



1 a negligible influence of this factor on the site effect. However, we may ask whether the surrounding  
2 landscape can have a more direct influence on collembolan communities, i.e. is not just a surrogate  
3 of site effect. For that purpose we discarded the site effect from the model and fixed all factors to  
4 the exclusion of the land use effect (Table 4, test 6). Only species composition can be explained by  
5 this factor, and that highly significantly, despite the poor 4% of variance explained.

6 We wanted to test whether 'terril' and successional effects are mediated (or not) by the soil  
7 effect, since we showed that soil features vary according to the 'terril' effect (spoil tips have a  
8 coarser soil texture, Table 1) and to the successional stage (organic matter and nitrogen increase and  
9 pH decreases along succession, Table 1). When soil is not included in the model while site,  
10 successional and land use effects are included and fixed (Table 4, test 7), species and CWMs are  
11 significantly influenced by the 'terril' effect while trait diversity is not. When soil is fixed (Table 4, test  
12 8) species and trait diversity are significantly influenced by the 'terril' effect while CWMs are not.  
13 Thus 'terril' effects on functional traits are seemingly mediated by soil, while species composition is  
14 affected by soil but also by other factors, and trait diversity is affected only (although to a much  
15 lower extent than species) by other factors than soil.

16 Contrary to the 'terril' effect, successional effects do not differ to a great extent when site,  
17 'terril' and land use effects are fixed while soil is allowed to vary or not (Table 4, tests 9 and 10,  
18 respectively). Species, CWMs and trait diversities are all affected by successional effects, whether soil  
19 varies or not, pointing to other influences than soil physical-chemical properties as factors mediating  
20 successional effects.

21 At last, we wondered whether pure soil effects (all other potential effects discarded,  
22 including the soil-mediated 'terril' effect) can explain species, CWM and trait diversity effects. The  
23 corresponding model (Table 4, test 11) shows that species do not react at all to soil itself, while trait  
24 and trait diversities do, although at a low level of significance.

#### 25 **4. Discussion**

1 *4.1. Functional traits of collembolan communities differ according to 'terril' and successional effects,*  
2 *despite site-specific variation*

3 Hypothesis H1 was fully verified: functional traits of collembolan communities differ  
4 according to 'terril' and successional effects, despite site-specific variation. We showed that  
5 functional traits are not influenced by the site effect, contrary to species composition. Widenfalk et  
6 al. (2015) pointed to the interest of traits, better than species, when comparing spatially distant sites  
7 sharing similar environmental conditions. Reasons advocated are that (i) species with similar  
8 ecological requirements share the same traits, thereby similar environments will harbour the same  
9 suites of traits (Lavorel and Garnier, 2002), and (ii) species are submitted to stochastic influences,  
10 such as species-specific source-sink dynamics (Hertzberg 1997; Kirmer et al., 2008; Ingimarsdóttir et  
11 al., 2012) and checkerboard distributions resulting from negative interactions (Widenfalk et al.,  
12 2016), which do not affect functional traits or affect them to a much lower extent than species  
13 (Mayfield et al., 2010).

14 *4.2. Functional traits and the 'terril' effect*

15 We showed that at community level, traits are affected by the 'terril' effect and that this  
16 effect is mediated by soil factors. Traits negatively affected by the 'terril effect' are body size, sexual  
17 reproduction, jumping appendages and sensorial organs, scales and trichobothria, indicating an  
18 adaptation to belowground life (eu-edaphic life-form) where space is limited for movements,  
19 including search for food (Auclerc et al., 2010) and sexual partners (Chahartaghi et al., 2006;  
20 Chernova et al., 2010), escape of predators (Salmon et al., 2005), and aggregation (Verhoef et al.,  
21 1977; Negri, 2004). Conversely, the development of compound post-antennal organs, the sensorial  
22 role of their vesicles has been deduced from anatomical investigations (Altner and Thies, 1976), is  
23 typical of soil-dwelling groups such as Tullbergiidae, Onychiuridae and many Hypogastruridae  
24 (Hopkin, 1997). Salmon et al. (2014) confirmed on a wide array of samples (926) recorded at  
25 European level that collembolan traits associated to deep soil are the absence of pigmentation,

1 furcula, ocelli, trichobothria and scales, the presence of compound post-antennal organs and  
2 pseudocelli, and the reduction of body size, legs and antenna, to the notable exception of some  
3 common eu-edaphic species such as *Isotomiella minor*. In our dataset all these traits responded  
4 similarly to the 'terril' effect, to the exception of body colour (Table 2). It is well-known that most  
5 soil-dwelling springtails are depigmented, a trait often used to sort this functional group without  
6 resorting to species identification (Rusek, 2007). This discrepancy might indicate that either (i) body  
7 pigmentation, ensuring UV-protection (Leinaas, 2002), displays a high level of phylogenetic inertia  
8 and thus can be conserved even when unnecessary as already known from plant pigments (Lee,  
9 2002), or (ii) trade-offs exist with other adaptive traits (Roff and Fairbairn, 2007). Both processes may  
10 result in pale colours shared with springtails living at or near the surface, such as for instance the  
11 epigeous pale-yellow *Entomobrya lanuginosa* (Ponge, 1993), and dark-coloured springtails having a  
12 wide vertical range distribution, such as the predatory *Friesea truncata* (Ponge, 1993, 2000).  
13 Similarly, pseudocelli, known as chemical defence organs in collembolan species which cannot  
14 escape predation by jumping (Usher and Balogun, 1966; Dettner et al., 1996), were not preferentially  
15 associated with spoil tips (Table 1). We cannot address more accurately these issues with our data,  
16 given that our sampling was not vertically stratified (Berg et al., 1998).

17 We showed that the soil of studied colliery spoil tips has a coarser texture, resulting in a  
18 better developed 'porosphere' (Vannier, 1987), and is in average richer in nitrogen and organic  
19 matter than the surrounding soil (Figure 1, Table 1), thus allocating space and nutrients to the  
20 animals which avoid the harsh conditions prevailing at the ground surface (Kent, 1982). The fact that  
21 trait modalities associated with belowground life (small size, reduced or absent sensorial and  
22 jumping organs, parthenogenesis) characterize spoil tips at community level (CWM) indicates that  
23 species living at or near the surface are only secondary components of spoil tip collembolan  
24 communities, whatever the soil is covered or not with vegetation. It should be noted that the  
25 adaptation to subterranean life is also accompanied by an increased tolerance to high carbon dioxide  
26 concentrations (Zinkler and Platthaus, 1996), a 'hard' trait (sensu Violle et al., 2007) probably of

1 utmost importance in or near spontaneous combustion zones with burning charcoal remnants (Kent,  
2 1982). It should also be highlighted that according to the QBS index (Parisi et al., 2005), the  
3 dominance of suites of traits associated with subterranean life indicates a good soil quality inasmuch  
4 as species richness remains at a 'normal' level in spoil tips (Table 1).

5           We may wonder why the 'harsh' environmental conditions of coal mine spoil tips do not  
6 favour traits associated with stress tolerance, such as those reported in alpine environments (Zettel,  
7 2000) and following extreme temperature events (Van Dooremalen et al., 2013), with cold and heat  
8 hardiness being the privilege of dark-coloured, motile aboveground-living collembolan species. It  
9 must be argued that there exist two 'strategies' by which an animal can escape stressful conditions:  
10 either it must move to find rapidly a refuge at the ground surface (Ponge et al., 2006; Salmon and  
11 Ponge, 2012) or dip in the soil, using pore networks between mineral particles or earthworm galleries  
12 when present (Salmon et al., 2005). Given that environmental conditions prevailing in the soil are  
13 more stable than above it (Vannier, 1987; Van Dooremalen et al., 2013) soil is expected to constitute  
14 an efficient refuge for the more fragile species, provided (i) these species are adapted to  
15 subterranean life, i.e. harbour small size, reduced or absent sensorial and jumping organs,  
16 parthenogenesis, (ii) there is a well-developed porosphere (Vannier, 1987). In the absence of one or  
17 the other of these two conditions, only the first strategy (surface movement) will be feasible. This is  
18 the case in permanently or seasonally frozen or waterlogged soils (Chang et al., 2013), or when the  
19 soil is compact (Larsen et al., 2004).

#### 20 *4.3. Functional traits and the successional effect*

21           We showed that at community level functional traits are affected by successional effects (the  
22 shift from bare soil to herbaceous then to shrub and finally to tree cover) but also that, contrary to  
23 the 'terril effect', factors other than soil are also in play. Traits which vary according to plant  
24 succession are eye number, leg and furcula length, and trichobothria, which all decrease in CWM  
25 value with vegetation development, and reproduction type (increased representation of

1 parthenogenesis with succession). All these trends are related to the passage from open to close  
2 environments, with associated shifts in trait representation (Salmon and Ponge, 2012; Salmon et al.,  
3 2014; Santorufo et al., 2015; Martins da Silva et al., 2016), like in the abovementioned ‘terril’ effect.  
4 Both climate and soil are involved in the contrast between open and close environments, the effects  
5 of both factors on collembolan communities having been experimentally disentangled by transfers of  
6 soil blocks between forest and pasture (Heiniger et al., 2015). The buffering effect of woodland  
7 against wind, frost and aridity (Ashcroft et al., 2012) allows less mobile species (with short  
8 appendages and/or asexual reproduction) and more sensitive species (with a lower tolerance to  
9 desiccation) to find a refuge in forested environments (Chernova et al., 2010; Van Dooremalen et al.,  
10 2013). Changes in CWMs along successional seres have been the object of investigations by plant  
11 ecologists (Kahmen and Poschlod, 2004), coal mine spoil tips included (Piekarska-Stachowiak et al.,  
12 2014), and that from the seminal work by Garnier et al. (2004) who showed that species with  
13 contrasting characteristics (called ‘biological markers’) were replaced along successional trajectories.

#### 14 *4.4. Does the diversity of collembolan functional traits increase with the development of vegetation?*

15 We showed that trait diversity increased with plant succession for a number of functional  
16 traits (Fig. 3, Table 3) but this effect was trait-specific, resulting in the absence of a statistically  
17 significant multi-trait trend. Thus our hypothesis H2 was only partially supported by our dataset.  
18 Traits the variety of which increased with the successional stage were body length, antenna and  
19 furcula length, pseudocelli number, anal spines, and body colour. It is worth to notice that body  
20 length did not respond to the successional stage when expressed as mean trait value (CWM) but did  
21 it when expressed as trait variety. Conversely, some traits the average value of which varied  
22 according to plant succession (reproduction type, eye number, leg length, trichobothria) did not vary  
23 in variety according to this factor. This suggests at first sight that discrepancies exist between CWM  
24 values and trait diversity values, which do not follow the same laws and are thus complementary in  
25 the search for assembly rules (Ricotta and Moretti, 2011). The increase in organic matter content

1 from bare soil to tree cover (Table 1) and the concomitant increase in the number of soil horizons  
2 within and underneath litter from early to late successional stages (Emmer and Sevink, 1994)  
3 suggests that the number of potential niches for collembolan communities increases with plant  
4 succession (Berg et al., 1998). This results in an increasing number of species per sample (Greenslade  
5 and Majer, 1993; Rusek, 2004), as verified in the present study (Table 1), but also in an increase in  
6 functional trait diversity as ascertained by Martins da Silva et al. (2016) from grassland to forest,  
7 which was verified here only on a subset of functional traits.

8           The absence of an overall trend of increasing functional diversity suggests that other factors  
9 than niche variety (thought to act on the whole set of traits) could be involved, too, and that with  
10 some degree of trait specificity. It has been shown that functional diversity varies according to (i) the  
11 number of micro-niches to be occupied by species with different trait modalities, as expected from  
12 the adaptive value of functional traits (Massicotte et al., 2014; Bobrov et al., 2015) but also (ii) direct  
13 species interactions leading to trait overdispersion and underdispersion (by comparison with null  
14 models) for negative and positive interactions, respectively (Widenfalk et al., 2016). Both processes  
15 (within-sample environmental filtering and cooperation/competition) are not mutually exclusive,  
16 because any increase in the number of available niches would contribute to decrease the intensity of  
17 competition through niche partitioning (Anderson, 1978), pointing to some incertitude in the balance  
18 between both processes (and thus some confusion in the conclusions) in the absence of precise  
19 measurements of niche variety within samples and of niche overlapping between species (Astor et  
20 al., 2014). The impact of predation on functional diversity has been neglected in soil community  
21 ecology, although selective predation and competition release are known as routes for negative and  
22 positive top-down effects of predation on functional diversity, respectively (Helenius et al., 2015).

23           We also observed increases in trait diversity from spoil tips to their surrounding  
24 environments (Fig. 3, Table 3). In particular, trichobothria diversity showed a strong increase, at a  
25 very high level of significance ( $P < 0.0001$ ), independent of successional stages (where no change was

1 observed). This urged us to analyse this trend with more precision. As developed in Appendix C, we  
2 showed that trait diversity was not independent of mean trait values (CWM) and thus should be  
3 interpreted with care. Trait diversity decreases when CWMs approach either minimum or maximum  
4 values, with a maximum at medium CWM values. This means that trait diversity gives erroneous  
5 information when species share medium trait modalities in a community: trait diversity will be  
6 always higher at medium values of CWM. In the above example of the presence/absence of  
7 trichobothria, the increase in trait diversity between spoil tips and their surrounding environment  
8 (Table 3) is related to the high contrast in CWM values for this trait between spoil tips (0.14, not far  
9 from 0, indicating the dominant contribution of endogeic life forms) and their surrounding  
10 environment (0.21, farther from 0, indicating a higher contribution of epigeic life forms).

11 *4.5. Which criteria are better for the assessment of environmental effects on collembolan*  
12 *communities: species, CWMs, or trait diversities?*

13 We showed that species were influenced to a great extent by the site effect while CWMs  
14 were not, thus supporting our Hypothesis H3 (Table 4). This result is worthy of notice as it might  
15 indicate that when environmental effects are to be tested on a variety of sites, even within a  
16 common regional species pool, results may be strongly influenced by spatial factors, blurring  
17 potential effects of environmental filters, hence the need for partialling out spatial variation by more  
18 or less sophisticated methods (Martins da Silva et al., 2012; Ingimarsdóttir et al., 2012; Gao et al.,  
19 2014). However, some studies showed that functional traits could be also affected by spatial factors,  
20 even to a higher extent than species (Widenfalk et al., 2016). This can be due either to spatially-  
21 anchored environmental variation (Widenfalk et al., 2015) or to dispersal limitation of some traits  
22 (Alday et al., 2011; Malmström, 2012). In the present study, the fact that traits did not reveal any  
23 significant variation among sites might indicate that spoil tips (and their surrounding environments)  
24 have already reached equilibrium from the point of view of mean trait values. This does not mean  
25 that species reached the equilibrium at community level, rather that the addition of new species will

1 probably not change mean functional trait values at community level, and thus most functional  
2 processes mediated by these traits (Malmström, 2012), and that despite of the fact that studied  
3 traits were only a subset of the complete set of functional traits.

4         A cursory examination of Table 4 clearly indicates that species display many more significant  
5 effects than traits: all tests with species, to the exception of test 11 (testing pure soil effects), were  
6 significant, and all at the highest level of significance ( $P < 0.0001$ ). The high sensitivity of species to all  
7 kinds of influences, whether spatial, environmental or historical (Ponge et al., 2003; Ingimarsdóttir et  
8 al., 2012; Maaß et al., 2015) should be acknowledged, but traits seem to be more robust than species  
9 to assess the effect of environmental parameters at community level, for instance in the presence of  
10 strong spatial influences (Fukami et al., 2005; Bokhorst et al., 2012). In our study, we were able to  
11 show (at least within the limits of our environmental records) that ‘terril’ effects on traits, and not  
12 successional effects, were mediated by soil (in particular coarser texture), which would have been  
13 more difficult to show with the only help of species composition. Thus collembolan functional traits,  
14 despite still insufficient knowledge about trait/function relationships (Grubert et al., 2016), may  
15 allow disentangling spatial and environmental effects more easily than species.

16         Despite the abovementioned methodological (non-monotonous relationship with CWM) and  
17 conceptual (competition versus niche availability) limits in the interpretation of functional diversity,  
18 Table 4 suggests that trait diversity is more informative than community-level mean trait values  
19 (CWM), by the higher number of significant tests. It has been underlined in several instances in the  
20 Results section that trait diversities showed results intermediate between species presence/absence  
21 and CWMs. This means that functional diversity (whether single- or multi-trait) is driven by processes  
22 in which both species and traits are involved (Mayfield et al., 2010). It is well-known that most  
23 functional diversity indices increase with species richness even when they are built independently  
24 from it (Laliberté and Legendre, 2010; Mouchet et al., 2010), although exceptions occur (Mayfield et  
25 al., 2010; Villéger et al., 2010; Mouchet et al., 2010). This relationship was verified on our data



1 (Spearman rank test,  $r_s = 0.36$ ,  $P < 0.01$ ), meaning that functional diversity increases when species are  
2 added, whether abundant or not, while community-weighted mean trait values (CWM), being  
3 weighted by the relative abundance of species, are more sensitive to dominant than to subordinate  
4 species (Grime, 1998). In fact, average functional trait values (CWMs) are better indicators of actual  
5 environmental effects and ecosystem processes than trait diversity, while trait diversity better  
6 indicates the potential of the community to resist environmental hazards, in other words its  
7 resilience (Mason et al., 2005; Mayfield et al., 2010; Villéger et al., 2010).

## 8 **5. Conclusion**

9 Colliery heaps (or coal mine spoil tips) seem to be a good model for studying environmental filtering  
10 of traits and trait diversity at community level, by their high contrast with the surrounding  
11 environment, in particular concerning soil and microclimate conditions. They exert a high selection  
12 pressure, by forcing invertebrates to live in the soil rather than at the surface, favouring trait  
13 modalities linked to subterranean life, e.g. decreased size, absence or reduction of visual and  
14 jumping organs and reproduction by parthenogenesis. Parallel changes could be observed in spoil  
15 tips and their surrounding environment according to the concomitant development of vegetation  
16 and soil, with an increase in diversity for most (although not all) functional traits and in the  
17 representation of trait modalities linked to subterranean life. We also showed that a focus on traits  
18 rather than on species allows better discerning community responses to environmental factors at  
19 regional scale.

## 20 **Acknowledgements**

21 We warmly acknowledge the Métropole Européenne de Lille for its financial support, Mikhail  
22 Potapow for its help in the identification of Istomidae spp., Rafael Jordana and Enrique Baquero for  
23 their help in the identification of *Pseudosinella* spp., and Charles Gers, Frans Janssens, David Russel  
24 and Laszlo Danyi for their sharp advices.

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1 **Figure captions**

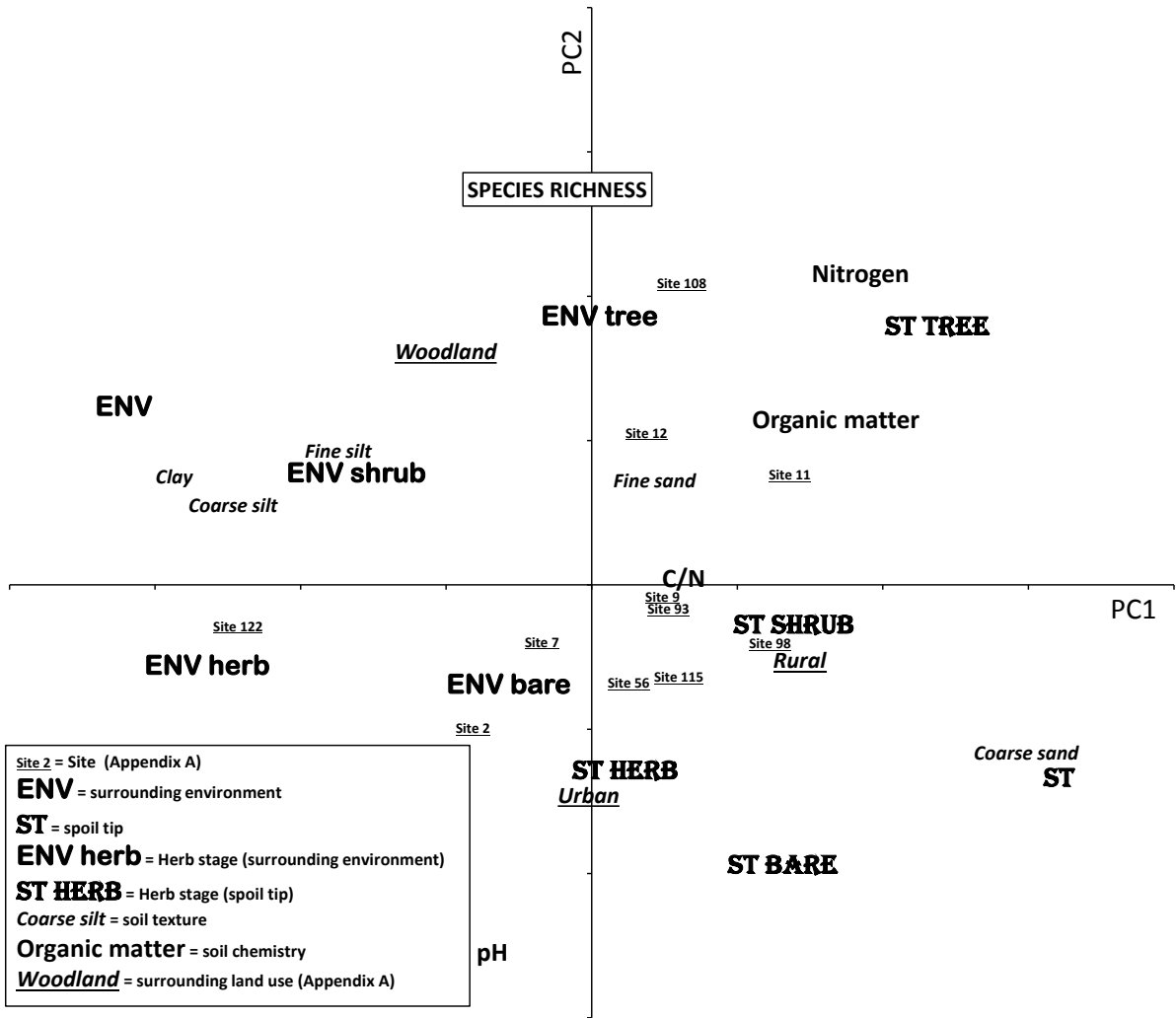
2 **Fig. 1.** Principal components analysis. Projection of environment descriptors in the plane of the first  
3 two principal components. ENV = surrounding environment; ST = spoil tip.

4 **Fig. 2.** Principal components analysis. Projection of CWMs (Community Weighted Mean traits) in the  
5 plane of the first two principal components. See Table 2 for the list of trait modalities and the  
6 numerical values assigned to each of them.

7 **Fig. 3.** Principal components analysis. Projection of single-trait diversities (Rao's quadratic entropy)  
8 and functional diversity (multi-trait diversity) in the plane of the first two principal  
9 components.

10

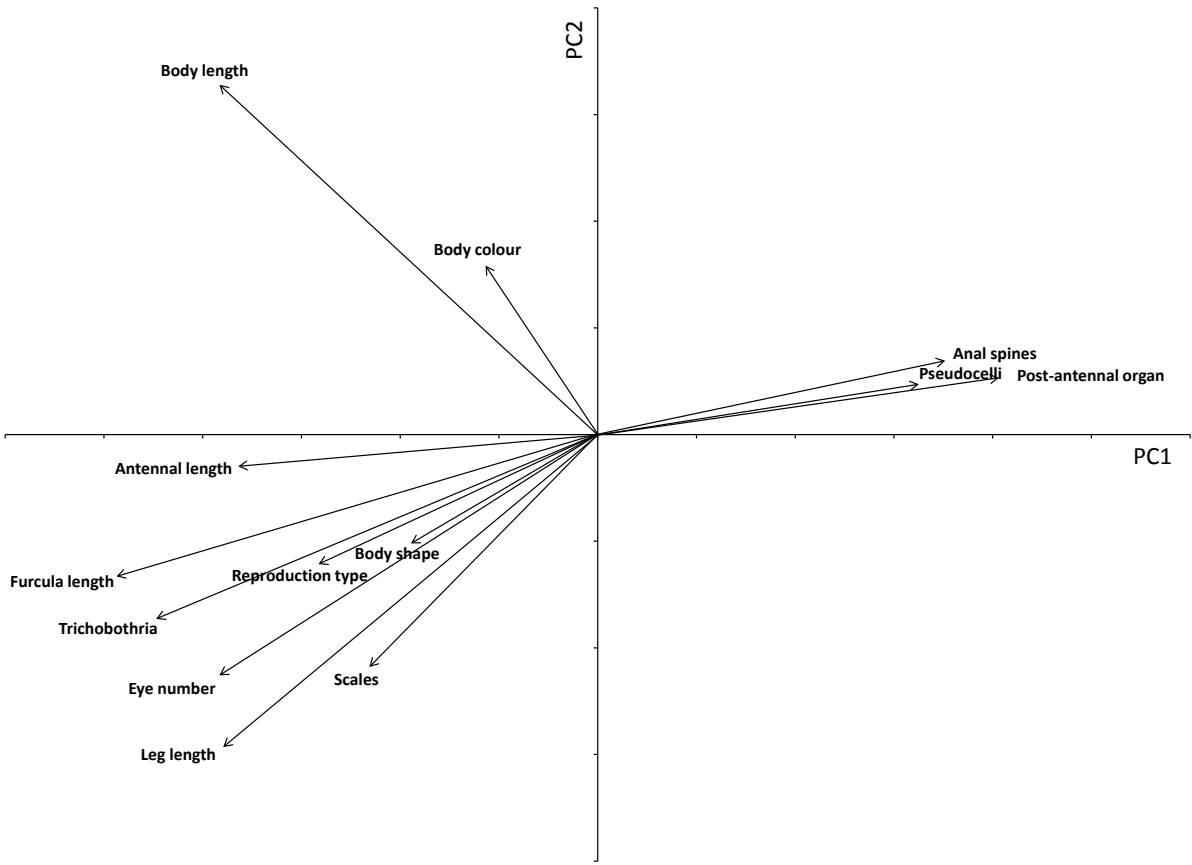




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2 Fig. 1

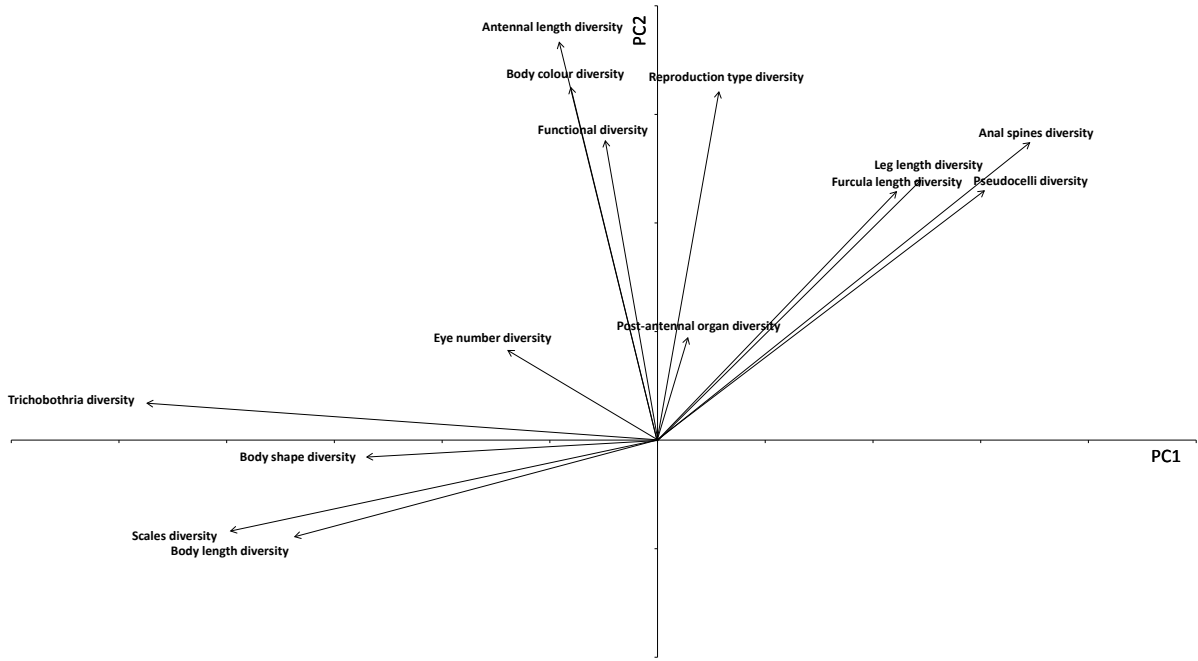
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2 Fig. 2

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2 Fig. 3

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**Table 1.** Mean values ( $\pm$  SE) of two first components of PCA (faunistic composition), numbers of species per sample (species richness) and main soil analyses according to primary (spoil tip versus environment) and secondary (successional stage) environmental factors. Comparisons among modalities were performed for each factor by Kruskal-Wallis rank tests (NS = not significant, \*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $p < 0.0001$ , \*\*\*\*  $P < 0.0001$ ) followed by Dunn tests (different letters indicate significant differences among modalities after Bonferroni adjustment for multiple comparisons).

	Spoil tip (n = 37)	Surrounding environment (n = 44)		Bare (n = 17)	Herb (n = 36)	Shrub (n = 9)	Tree (n = 22)	
PC1	<b>1.57<math>\pm</math>0.29<sup>a</sup></b>	<b>-1.32<math>\pm</math>0.26<sup>b</sup></b>	****	<b>0.64<math>\pm</math>0.34<sup>ab</sup></b>	<b>-1.15<math>\pm</math>0.27<sup>c</sup></b>	<b>-0.65<math>\pm</math>1.04<sup>bc</sup></b>	<b>1.51<math>\pm</math>0.46<sup>a</sup></b>	****
PC2	<b>-0.59<math>\pm</math>0.38<sup>b</sup></b>	<b>0.50<math>\pm</math>0.30<sup>a</sup></b>	**	<b>-1.74<math>\pm</math>0.16<sup>c</sup></b>	<b>-0.68<math>\pm</math>0.23<sup>b</sup></b>	<b>0.62<math>\pm</math>0.36<sup>ab</sup></b>	<b>2.00<math>\pm</math>0.57<sup>a</sup></b>	****
Sample species richness	11.5 $\pm$ 0.8	12.3 $\pm$ 0.6	NS	<b>7.4<math>\pm</math>0.8<sup>b</sup></b>	<b>11.9<math>\pm</math>0.7<sup>a</sup></b>	<b>13.9<math>\pm</math>1.2<sup>a</sup></b>	<b>14.0<math>\pm</math>0.6<sup>a</sup></b>	****
pH	6.9 $\pm$ 0.2	6.8 $\pm$ 0.2	NS	<b>7.7<math>\pm</math>0.2<sup>a</sup></b>	<b>6.8<math>\pm</math>0.2<sup>b</sup></b>	<b>7.3<math>\pm</math>0.2<sup>ab</sup></b>	<b>6.2<math>\pm</math>0.2<sup>b</sup></b>	***
Organic matter (‰)	<b>68.3<math>\pm</math>6.5<sup>a</sup></b>	<b>50.1<math>\pm</math>3.7<sup>b</sup></b>	*	<b>40.8<math>\pm</math>6.4<sup>b</sup></b>	<b>50.0<math>\pm</math>4.2<sup>b</sup></b>	<b>62.1<math>\pm</math>8.9<sup>ab</sup></b>	<b>81.1<math>\pm</math>8.3<sup>a</sup></b>	****
Nitrogen (‰)	<b>3.59<math>\pm</math>0.22<sup>a</sup></b>	<b>3.10<math>\pm</math>0.26<sup>b</sup></b>	*	<b>2.52<math>\pm</math>0.23<sup>b</sup></b>	<b>2.94<math>\pm</math>0.23<sup>b</sup></b>	<b>3.06<math>\pm</math>0.27<sup>ab</sup></b>	<b>4.49<math>\pm</math>0.37<sup>a</sup></b>	***
C:N	9.8 $\pm$ 3.5	7.9 $\pm$ 0.8	NS	7.4 $\pm$ 1.3	8.0 $\pm$ 0.9	7.7 $\pm$ 0.9	11.2 $\pm$ 1.0	NS
Coarse sand (%)	<b>51.2<math>\pm</math>2.8<sup>a</sup></b>	<b>14.3<math>\pm</math>1.5<sup>b</sup></b>	****	<b>50.9<math>\pm</math>6.9<sup>a</sup></b>	<b>23.2<math>\pm</math>3.2<sup>b</sup></b>	<b>30.5<math>\pm</math>7.8<sup>ab</sup></b>	<b>31.6<math>\pm</math>4.4<sup>ab</sup></b>	**
Fine sand (%)	13.4 $\pm$ 0.5	15.8 $\pm$ 1.0	NS	13.6 $\pm$ 1.3	14.4 $\pm$ 0.8	13.9 $\pm$ 1.4	16.1 $\pm$ 1.5	NS
Coarse silt (%)	<b>14.3<math>\pm</math>1.9<sup>b</sup></b>	<b>24.7<math>\pm</math>1.5<sup>a</sup></b>	****	<b>9.4<math>\pm</math>1.4<sup>b</sup></b>	<b>23.7<math>\pm</math>2.0<sup>a</sup></b>	<b>21.2<math>\pm</math>3.9<sup>a</sup></b>	<b>20.2<math>\pm</math>2.4<sup>a</sup></b>	****
Fine silt (%)	<b>12.6<math>\pm</math>0.7<sup>b</sup></b>	<b>25.5<math>\pm</math>1.7<sup>a</sup></b>	****	17.4 $\pm$ 3.7	21.5 $\pm$ 1.7	18.2 $\pm$ 3.5	18.3 $\pm$ 2.0	NS
Clay (%)	<b>8.6<math>\pm</math>0.7<sup>b</sup></b>	<b>19.7<math>\pm</math>1.0<sup>a</sup></b>	****	<b>8.7<math>\pm</math>2.1<sup>b</sup></b>	<b>17.2<math>\pm</math>1.2<sup>a</sup></b>	<b>16.2<math>\pm</math>3.2<sup>ab</sup></b>	<b>13.8<math>\pm</math>1.5<sup>ab</sup></b>	**

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**Table 2.** Mean values ( $\pm$  SE) of community-weighted mean (CWM) functional traits according to primary (spoil tip versus environment) and secondary (successional stage) environmental factors. Comparisons among modalities were performed for each factor by Kruskal-Wallis rank tests (NS = not significant, \*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ , \*\*\*\*  $P < 0.0001$ ) followed by Dunn tests (different letters indicate significant differences among modalities after Bonferroni adjustment for multiple comparisons).

Functional trait	Functions fulfilled	Spoil tip	Surrounding environment		Bare	Herb	Shrub	Tree	
		(n = 37)	(n = 44)		(n = 17)	(n = 36)	(n = 9)	(n = 22)	
Reproduction type (1: parthenogenetic; 2: sexual)	Reproduction	<b>1.60±0.04<sup>a</sup></b>	<b>1.73±0.03<sup>a</sup></b>	*	<b>1.70±0.08<sup>ab</sup></b>	<b>1.77±0.02<sup>a</sup></b>	<b>1.57±0.06<sup>ab</sup></b>	<b>1.54±0.05<sup>b</sup></b>	****
Body length (1: < 1 mm; 2: 1-2 mm; 3: 2-3 mm; 4: > 3 mm)	Feeding, excretion, active and passive dispersal, respiration	<b>2.12±0.05<sup>b</sup></b>	<b>2.35±0.04<sup>a</sup></b>	**	2.12±0.07	2.31±0.06	2.16±0.11	2.26±0.06	NS
Body shape (1: very slender; 2: slender; 3: stocky; 4: globular)	Passive dispersal (lift-to-drag ratio), protection against desiccation (surface/volume ratio)	2.14±0.06	2.20±0.04	NS	2.19±0.14	2.22±0.04	2.26±0.09	2.07±0.03	NS
Body colour (1: pale-coloured; 2: bright-coloured; 3: dark-coloured)	Protection against UV-radiation	2.18±0.09	2.24±0.05	NS	1.92±0.18	2.29±0.05	2.22±0.14	2.26±0.07	NS
Scales (1: absent; 2: present)	Protection against desiccation	<b>1.18±0.04<sup>a</sup></b>	<b>1.24±0.02<sup>a</sup></b>	**	1.34±0.08	1.22±0.03	1.17±0.04	1.13±0.02	NS
Antennal length (1: < head diagonal; 2: 1-2 head diagonals; 3: > 2 head diagonals)	Reception of olfactory, heat and tactile signals	<b>1.56±0.05<sup>b</sup></b>	<b>1.75±0.03<sup>a</sup></b>	***	<b>1.66±0.09<sup>ab</sup></b>	<b>1.76±0.03<sup>a</sup></b>	<b>1.63±0.08<sup>ab</sup></b>	<b>1.51±0.05<sup>b</sup></b>	**
Leg length (1: leg III/body < 0.3; 2: leg III/body $\geq$ 0.3)	Locomotion	1.68±0.04	1.75±0.03	NS	<b>1.74±0.08<sup>ab</sup></b>	<b>1.78±0.03<sup>a</sup></b>	<b>1.74±0.05<sup>ab</sup></b>	<b>1.61±0.05<sup>b</sup></b>	*
Furcula length (1: absent or vestigial; 2: Abd III anterior not reached; 3: Abd III anterior reached)	Jump (dispersal, predator avoidance)	<b>2.42±0.07<sup>b</sup></b>	<b>2.63±0.04<sup>a</sup></b>	*	<b>2.45±0.15<sup>ab</sup></b>	<b>2.65±0.05<sup>a</sup></b>	<b>2.57±0.08<sup>ab</sup></b>	<b>2.39±0.06<sup>b</sup></b>	*
Eye number (1: 0; 2: 1-5; 3: > 5)	Vision	2.18±0.07	2.35±0.05	NS	<b>2.14±0.15<sup>b</sup></b>	<b>2.51±0.04<sup>a</sup></b>	<b>2.17±0.07<sup>b</sup></b>	<b>2.02±0.04<sup>b</sup></b>	****
Pseudocecella (1: absent; 2: present)	Predator repellence	1.14±0.03	1.10±0.01	NS	<b>1.18±0.07<sup>ab</sup></b>	<b>1.07±0.01<sup>b</sup></b>	<b>1.08±0.02<sup>ab</sup></b>	<b>1.17±0.02<sup>a</sup></b>	**
Post-antennal organ (1: absent; 2: simple; 3: compound)	Reception of olfactory signals (still not fully known)	<b>1.87±0.07<sup>a</sup></b>	<b>1.68±0.04<sup>b</sup></b>	**	<b>1.70±0.14<sup>ab</sup></b>	<b>1.73±0.06<sup>b</sup></b>	<b>1.65±0.07<sup>ab</sup></b>	<b>1.90±0.04<sup>a</sup></b>	*
Trichobothria (1: absent; 2: present)	Reception of tactile signals	<b>1.27±0.04<sup>b</sup></b>	<b>1.43±0.03<sup>a</sup></b>	***	<b>1.44±0.09<sup>ab</sup></b>	<b>1.41±0.04<sup>a</sup></b>	<b>1.34±0.05<sup>ab</sup></b>	<b>1.23±0.03<sup>b</sup></b>	*
Anal spines (1: absent; 2: present)	Mechanical defense against predation	1.20±0.04	1.12±0.02	NS	<b>1.18±0.07<sup>ab</sup></b>	<b>1.12±0.03<sup>b</sup></b>	<b>1.12±0.03<sup>ab</sup></b>	<b>1.22±0.03<sup>a</sup></b>	**

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**Table 3.** Mean values ( $\pm$  SE) of trait diversities and multi-trait functional diversity (Rao's quadratic entropy) according to primary (spoil tip versus environment) and secondary (successional stage) environmental factors. Comparisons among groups were performed for each factor ('terril' effect and successional effect) by Kruskal-Wallis rank tests (NS = not significant, \*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ , \*\*\*\*  $P < 0.0001$ ) followed by Dunn tests (different letters indicate significant differences among modalities after Bonferroni adjustment for multiple comparisons).

	Spoil tip (n = 37)	Surrounding environment (n = 44)		Bare (n = 17)	Herb (n = 36)	Shrub (n = 9)	Tree (n = 22)	
Reproduction type	0.175 $\pm$ 0.014	0.165 $\pm$ 0.011	NS	0.123 $\pm$ 0.027	0.156 $\pm$ 0.013	0.218 $\pm$ 0.015	0.202 $\pm$ 0.010	NS
Body length	<b>0.052<math>\pm</math>0.007<sup>b</sup></b>	<b>0.081<math>\pm</math>0.007<sup>a</sup></b>	***	<b>0.033<math>\pm</math>0.009<sup>b</sup></b>	<b>0.093<math>\pm</math>0.008<sup>a</sup></b>	<b>0.061<math>\pm</math>0.015<sup>ab</sup></b>	<b>0.052<math>\pm</math>0.005<sup>b</sup></b>	****
Body shape	<b>0.030<math>\pm</math>0.004<sup>b</sup></b>	<b>0.046<math>\pm</math>0.005<sup>a</sup></b>	*	0.023 $\pm$ 0.006	0.047 $\pm$ 0.006	0.054 $\pm$ 0.010	0.030 $\pm$ 0.004	NS
Body colour	0.152 $\pm$ 0.010	0.175 $\pm$ 0.007	NS	<b>0.122<math>\pm</math>0.021<sup>b</sup></b>	<b>0.163<math>\pm</math>0.008<sup>ab</sup></b>	<b>0.176<math>\pm</math>0.018<sup>ab</sup></b>	<b>0.189<math>\pm</math>0.009<sup>a</sup></b>	*
Scales	<b>0.100<math>\pm</math>0.013<sup>b</sup></b>	<b>0.162<math>\pm</math>0.010<sup>a</sup></b>	**	0.146 $\pm$ 0.025	0.147 $\pm$ 0.014	0.131 $\pm$ 0.028	0.106 $\pm$ 0.013	NS
Antennal length	0.068 $\pm$ 0.006	0.070 $\pm$ 0.005	NS	<b>0.042<math>\pm</math>0.009<sup>b</sup></b>	<b>0.073<math>\pm</math>0.006<sup>a</sup></b>	<b>0.086<math>\pm</math>0.006<sup>a</sup></b>	<b>0.074<math>\pm</math>0.005<sup>a</sup></b>	***
Leg length	0.162 $\pm$ 0.013	0.153 $\pm$ 0.011	NS	0.119 $\pm$ 0.025	0.145 $\pm$ 0.011	0.175 $\pm$ 0.025	0.193 $\pm$ 0.013	NS
Furcula length	0.107 $\pm$ 0.011	0.103 $\pm$ 0.008	NS	<b>0.097<math>\pm</math>0.023<sup>ab</sup></b>	<b>0.084<math>\pm</math>0.008<sup>b</sup></b>	<b>0.124<math>\pm</math>0.020<sup>ab</sup></b>	<b>0.136<math>\pm</math>0.011<sup>a</sup></b>	**
Eye number	<b>0.087<math>\pm</math>0.008<sup>b</sup></b>	<b>0.112<math>\pm</math>0.007<sup>a</sup></b>	*	0.075 $\pm$ 0.014	0.110 $\pm$ 0.008	0.104 $\pm$ 0.019	0.100 $\pm$ 0.008	NS
Pseudocella	0.088 $\pm$ 0.012	0.082 $\pm$ 0.009	NS	<b>0.081<math>\pm</math>0.020<sup>ab</sup></b>	<b>0.062<math>\pm</math>0.010<sup>b</sup></b>	<b>0.071<math>\pm</math>0.015<sup>ab</sup></b>	<b>0.128<math>\pm</math>0.014<sup>a</sup></b>	**
Post-antennal organ	0.087 $\pm$ 0.007	0.097 $\pm$ 0.005	NS	0.085 $\pm$ 0.016	0.089 $\pm$ 0.005	0.097 $\pm$ 0.011	0.101 $\pm$ 0.008	NS
Trichobothria	<b>0.141<math>\pm</math>0.012<sup>b</sup></b>	<b>0.207<math>\pm</math>0.008<sup>a</sup></b>	****	0.148 $\pm$ 0.023	0.192 $\pm$ 0.011	0.206 $\pm$ 0.018	0.160 $\pm$ 0.014	NS
Anal spines	0.112 $\pm$ 0.013	0.096 $\pm$ 0.010	NS	<b>0.082<math>\pm</math>0.020<sup>b</sup></b>	<b>0.082<math>\pm</math>0.011<sup>b</sup></b>	<b>0.097<math>\pm</math>0.021<sup>ab</sup></b>	<b>0.152<math>\pm</math>0.014<sup>a</sup></b>	**
1 Functional diversity	1.36 $\pm$ 0.08	1.55 $\pm$ 0.05	NS	1.18 $\pm$ 0.17	1.44 $\pm$ 0.06	1.60 $\pm$ 0.15	1.62 $\pm$ 0.08	NS

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**Table 4.** Simple and partial redundancy analyses (RDA) used to ask some questions about site effect (11 sites), 'terril' effect (2 types: spoil tip, environment), plant successional effect (4 types: bare, herb, shrub, tree), surrounding land use effect (3 types: woodland, agriculture, urban) and soil physicochemistry (9 variables) on collembolan species presence/absence, Community Weighted Mean (CWM) trait values, and on trait diversity (Rao's quadratic entropy). \* =  $P < 0.05$ ; \*\* =  $P < 0.01$ ; \*\*\* =  $P < 0.001$ ; \*\*\*\* =  $P < 0.0001$ ; NS = not significant. Yes = included in the model as active factor; No = not included in the model; Fixed = included in the model as a confounding factor (effects discarded).

Number	Site effect	Terril effect	Successional effect	Land use effect	Soil effect	Species (% explained)	Traits (CWM) (% explained)	Trait diversity (% explained)
1	Yes	Yes	Yes	Yes	Yes	39.0 ****	40.8 **	42.8 ****
2	Fixed	Yes	Yes	Yes	Yes	24.8 ****	29.2 **	16.2 **
3	Yes	Fixed	Fixed	Fixed	Fixed	16.0 ****	13.6 NS	16.2 **
4	Yes	No	No	No	No	19.0 ****	16.4 NS	17.8 *
5	Yes	Fixed	Fixed	No	Fixed	19.4 ****	16.0 NS	18.7 *
6	No	Fixed	Fixed	Yes	Fixed	4.1 ****	2.7 NS	3.0 NS
7	Fixed	Yes	Fixed	Fixed	No	3.2 ****	5.4 **	2.6 NS
8	Fixed	Yes	Fixed	Fixed	Fixed	2.5 ****	1.8 NS	3.4 *
9	Fixed	Fixed	Yes	Fixed	No	9.0 ****	10.2 **	14.0 **
10	Fixed	Fixed	Yes	Fixed	Fixed	8.6 ****	9.0 *	13.6 ****
11	Fixed	Fixed	Fixed	Fixed	Yes	14.2 NS	16.5 *	16.6 *

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