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11 **Title:** COLLEMBOLAN COMMUNITIES AS BIOINDICATORS OF LAND USE INTENSIFICATION

12

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27

1 **Abstract**

2

3 Springtail communities (Hexapoda: Collembola) were sampled in the Morvan Nature Regional

4 Park (Burgundy, France) in six land use units (LUUs) one square kilometer each, which had been

5 selected in order to cover a range of increasing intensity of land use. Human influence increased from

6 LUU 1 (old deciduous forest) to LUU 6 (agricultural land mainly devoted to cereal crops), passing by

7 planted coniferous forests (LUU 2) and variegated landscapes made of cereal crops, pastures, hay

8 meadows, conifer plantations and small relict deciduous groves in varying proportion (LUUs 3 to 5).

9 Sixteen core samples were taken inside each LUU, at intersections of a regular grid. Species

10 composition, species richness and total abundance of collembolan communities varied according to

11 land use and landscape properties. Land use types affected these communities through changes in

12 the degree of opening of woody landscape (woodland opposed to grassland) and changes in humus

13 forms (measured by the Humus Index). A decrease in species richness and total abundance was

14 observed from old deciduous forests to cereal crops. Although the regional species richness was not

15 affected by the intensification gradient (40 to 50 species were recorded in every LUU), a marked

16 decrease in local biodiversity was observed when the variety of land use types increased. In

17 variegated landscapes the observed collapse in local species richness was not due to a different

18 distribution of land use types, since it affected mainly woodland areas. Results indicated the

19 detrimental influence of the rapid afforestation of previous agricultural land, which did not afford time

20 for the development of better adapted soil animal communities.

21

22 **Keywords:**

23

24 Land use, biodiversity, Humus Index

25

26 **1. Introduction**

27

28 Collembolan communities have been shown to vary in abundance and species composition

29 according to changes in vegetation and soil conditions (Hågvar 1982; Ponge, 1993; Chagnon et al.,

30 2000). Soil acidity, mainly through associated changes in food and habitat, but also through chemical

1 composition or osmolarity of the soil solution, may favour or disfavour some species (Hågvar and
2 Abrahamsen, 1984; Vilkamaa and Huhta, 1986; Salmon and Ponge, 2001), and pH 5 has been noted
3 as a landmark between two distinct types of communities (Ponge, 1993). The opposition between
4 grassland and woodland can also be traced by the species composition of springtail populations
5 (Gisin, 1943; Rusek, 1989; Ponge, 1993). As a whole, Collembola are highly tolerant of a wide range
6 of environmental conditions, including agricultural and industrial pollution, but species differ strongly in
7 their sensitivity to environmental stress (Lebrun, 1976; Prasse, 1985; Sterzyńska, 1990). The
8 parthenogenetic collembolan *Folsomia candida* is now currently used as a standard in the assessment
9 of environmental risk (Riepert and Kula, 1996; Cortet et al., 1999; Crouau et al., 1999). In the search
10 for indicators of environmental change, more especially those affecting biodiversity, abundant, diverse
11 animal communities can be used to trace changes taking place at the landscape level, as this has
12 been demonstrated in other arthropod groups (Duelli et al., 1990; Halme and Niemelä, 1993).

13

14 The present study was undertaken within the European Community project BioAssess. Here
15 we present springtail results (Hexapoda: Collembola) from the French sites, which were located in the
16 Morvan Regional Nature Park (Burgundy). This central region was selected for its high variety of land
17 use types, ranging from large areas of old forests or cereal crops to variegated landscapes with
18 intricate deciduous and coniferous woodlands, pastures, hay meadows and agricultural fields
19 (Plaisance, 1986). We asked whether there was a response of collembolan communities to land use
20 intensification and, if yes, whether this effect was just a replacement of species or affected biodiversity
21 patterns.

22

23 **2. Material and methods**

24

25 *2.1. Study sites*

26

27 Sampling took place in the Morvan Regional Nature Park, which covers most of the northern
28 part of the Morvan natural region (western Burgundy, Centre of France). The climate is continental,
29 with an annual rainfall averaging 1000 mm and a mean temperature of 9°C. The parent rock is granite.

1 The soil trophic level is poor, but despite moderate to strong acidity, the dominant humus form is mull
2 (Perrier, 1997).

3

4 In the Morvan region, land use is shared between sylviculture (45%) and agriculture (55%).
5 Forested areas are comprised of coniferous stands (silver fir, Douglas fir, Norway spruce) with an
6 artificial intensive management system (45%), and deciduous stands (beech, oak) with a semi-natural
7 or a traditional management system (55 %). Agricultural areas are made up of grassland (80%, among
8 which 40% are permanent pastures and 40 % are temporary hay meadows) and crops (20%) with
9 dominance of cereals (wheat, barley) and conifer trees (Norway spruce, Douglas fir). Agricultural
10 management systems exhibit a wide range of disturbance intensity (use of mineral fertilizers and
11 pesticides to organic manure only). Several socio-economical and political driving forces influenced
12 dynamics and composition of the landscape during the last five decades (Plaisance, 1986). Many old
13 deciduous forests have been transformed to coniferous plantations and more recently forested areas
14 expanded by afforestation of previous agricultural land, using European subsidies.

15

16 Six land use units (LUUs), one square kilometer each, have been chosen on the basis of aerial
17 photographs, taking into account the distribution of forested areas (coniferous, deciduous), meadows
18 and agricultural crops. LUUs 1 to 6 depicted a gradient of increasing influence of human activities:

19

20 • LUU 1 is within an old (100-150 year) deciduous forest landscape managed by the French
21 National Office of Forests (public sector). This forested area is made of acidophilic
22 beechwoods (*Fagus sylvatica* L.), oakwoods [*Quercus petraea* (Mattus.) Liebl.] and mixed
23 stands, with holly (*Ilex aquifolium* L.) in the understory. The management system is based on
24 natural regeneration and selection by man. LUU 1 is made up of stands at different stages of
25 forest development.

26

27 • LUU 2 is within a more recent (20-50 year) coniferous forest landscape managed by the
28 French Forest National Office (public sector), mostly made of silver fir plantations (*Abies alba*
29 Mill.). Previous land use was deciduous forest. Where soils were too wet for coniferous growth
30 spontaneous vegetation was let to grow (willow, alder, birch). The management system of

1 coniferous stands is intensive and based on artificial regeneration (clear-cut followed by
2 plantation).

3

4 • LUU 3 is comprised of meadows within a forested landscape. Originally farmers cleared the
5 native forest. Currently, by the way of national subsidies for afforestation of agricultural land,
6 Douglas fir [*Pseudotsuga menziesii* (Mirb.) Franco] and Norway spruce [*Picea abies* (L.)
7 Karst.] were planted fifty years ago on previous agricultural land purchased by private
8 insurance companies. Remains of the old deciduous forest (now managed as beech and oak
9 coppice) are also present, as well as a few cereal crops.

10

11 • LUU 4 is a mixed land use mosaic characterised by the presence of wet meadows. The
12 agricultural system is based on organically manured meadows and intensive cereal crops
13 (recently converted to organic farming). Some plots were afforested with Douglas fir and
14 Norway spruce about thirty years ago.

15

16 • LUU 5 is a meadow landscape. The dominant agricultural system is based on organic farming.
17 A few plantations of Douglas fir or Norway spruce (20-50 years old) are also present, as well
18 as a few relict deciduous thickets pastured by livestock.

19

20 • LUU 6 is an agricultural landscape dominated by cereal crops. The agricultural system is
21 intensive with a range of intensity levels depending on the farmer, but pesticides and mineral
22 fertilizers are used currently. Some plots are prescribed fallow, some others have recently
23 turned to short rotation conifer crops (Christmas trees). Recently abandoned land (scrub) is
24 also present.

25

26 2.2. Sampling procedure

27

28 Using aerial photographs, a grid of 16 regularly spaced plots (200 m) was identified in each of
29 the six LUUs, and their position in the field was found by their spatial coordinates, given by a
30 calibrated GPS system. Each sampling plot was indicated by a central post. Litter and soil springtails

1 were sampled by taking a core (5 cm diameter, 10 cm depth) at a three-meter distance from the
2 central post, in a northerly direction. Soil and litter were immediately sealed in a polythene bag then
3 transported within three days to the laboratory. Sampling took place in June 2001. Extraction was
4 performed within ten days using the dry funnel method. Animals collected under the desiccating soil
5 were preserved in 95% ethyl alcohol before being sorted under a dissecting microscope. Collembola
6 were mounted in chloral-lactophenol (25 ml lactic acid, 50 g chloral hydrate, 25 ml phenol) and
7 identified to species under a phase contrast microscope at x400 magnification. Identification was done
8 using Gisin (1960), Zimdars and Dunger (1994), Jordana et al. (1997), Fjellberg (1998) and Bretfeld
9 (1999).

10
11 Humus forms (Table 1) were identified in the vicinity of core samples, after visual inspection of
12 trenched soil, using morphological criteria defined by Brêthes et al. (1995). Mor was separated from
13 Dysmoder using Ponge et al. (2000). The Humus Index was measured at each sampling plot after
14 scaling humus forms according to principles presented by Ponge et al. (2002).

15
16 Amphimoder was defined for the first time in order to classify humus forms presenting both
17 features of mull (crumby A horizon) and mor (litter with an OM horizon, without any visible signs of
18 animal activity). Agricultural Moder was also defined for the first time to classify an agricultural solum
19 with a spongy structure made of small enchytraeid faeces (Didden, 1990; Topoliantz et al., 2000), and
20 was given a Humus Index of 6 as for Eumoder. Other agricultural soils exhibited a crumby structure
21 made of faeces of earthworms or large enchytraeids. The Humus Index of these soils was assigned to
22 1 as for Eumull. Hydromorphic variants of humus forms such as Hydromull, Hydromoder and
23 Hydromor were given the same Humus Index as their aerial counterparts exhibiting similar
24 development of OL, OF, OH, and OM horizons.

25
26 Woody plant species growing in the vicinity of sampling plots were identified using Rameau et
27 al. (1989).

28 29 *2.3. Statistical analyses*

30

1 Densities of the different collembolan species were analysed by simple correspondence
2 analysis (CA), a multivariate method using the chi-square distance (Greenacre, 1984). Active (main)
3 variables were species, coded by the number of individuals. Contrary to canonical correspondence
4 analysis (Ter Braak, 1987) passive (additional) variables were projected as if they had been used in
5 the analysis but they did not influence to any extent the formation of the factorial axes. In the present
6 study, additional variables were land use units (each coded as 1 or 0), land use types (each coded as
7 1 or 0), species richness and total abundance of collembolan populations (counts), woody species
8 (each coded as 1 or 0) and the Humus Index (scoring from 1 to 9).

9
10 In order to give the same weight to all parameters, all variables (discrete as well as
11 continuous) were transformed into $X = (x-m)/s + 20$, where x is the original value, m is the mean of a
12 given variable, and s is its standard deviation. The addition to each standardized variable of a constant
13 factor of 20 allows all values to be positive, correspondence analysis dealing only with positive
14 numbers (commonly counts). Following this transformation, factorial coordinates of variables can be
15 interpreted directly in term of their contribution to the factorial axes. Variables were doubled in order to
16 allow for the dual nature of most parameters (the absence of a given species is as important as its
17 presence, low values are as important as high values for measurement data). To each variable X was
18 thus associated a twin X' varying in an opposite sense ($X' = 40 - X$). Such a doubling proved useful
19 when dealing with ecological gradients (Ponge et al., 1997; Loranger et al., 2001). The
20 transformations used here give to correspondence analysis most properties of the well-known
21 principal components analysis (Hotelling, 1933), while keeping the advantage of the simultaneous
22 projection of rows (variables) and columns (samples) onto the same factorial axes and the robustness
23 due to the principle of distributional equivalence.

24
25 In each LUU the variety of land use types was expressed by the Shannon Index, i.e. the
26 number of binary digits (bits) measuring the information given by a sample according to the formula \sum
27 $p_i \cdot \log(p_i)$, where p_i is the probability given to land use type i among the 16 samples taken in a LUU.

28
29 One-way analyses of variance (ANOVA) followed by SNK procedure for comparisons among
30 means were performed on some parameters (Glantz, 1997). Homogeneity of variances between the

1 different LUUs and normal distribution of residuals were tested prior to analysis. The absence of
2 spatial autocorrelation was checked by computing Spearman rank correlation coefficients between
3 adjacent rows and columns of each 16-pt sampling grid. None of these coefficients gave any
4 significant value at the 0.05 level, thus the distance between adjacent samples (200 m) was judged
5 enough to avoid autocorrelation. Given the absence of autocorrelation, the 16 samples taken in each
6 LUU were considered as replicates.

7

8 **3. Results**

9

10 Table 2 shows the distribution of land use types among the 16 samples taken in each LUU.
11 One of the 16 plots could not be sampled in LUU 4, due to waterlogging. The most widespread land
12 use types were deciduous forests, coniferous forests, and pastures.

13

14 Table 3 shows total numbers for springtail species found in every LUU. The most abundant
15 species were the isotomids *Folsomia quadrioculata* (1742 ind.), *Isotomiella minor* (1517 ind.) and
16 *Parisotoma notabilis* (1017 ind.).

17

18 *3.1. Analysis of collembolan communities*

19

20 The matrix analysed crossed 95 columns (samples) and 89 x 2 rows (species, doubled as
21 mentioned above), as main (active) variables. Additional variables (84) were added, in order to
22 facilitate interpretation of factorial axes. Only the first axis of correspondence analysis (6.5% of the
23 total variance) was interpretable in terms of ecological factors. The second axis (5.0% of the total
24 variance) was roughly a quadratic function of the first axis, i.e. when samples and variables were
25 projected in the plane of the first two axes their cloud formed a parabola, i.e. they exhibited a Guttman
26 or horsehoe effect (Greenacre, 1984). In this case, only the first axis (corresponding to the first eigen
27 value of the distance matrix) was used for projecting the cloud of data. For the sake of clarity only
28 main variables (collembolan species) and additional variables, but not individual samples, will be
29 further considered.

30

1 Collembolan species could be projected on factorial axes both as high (original data, with their
2 mean and standard deviation forced to 20 and 1, respectively) and low values (complement to 40), but
3 for the sake of clarity only high values will be shown and discussed (Fig. 1). Collembolan species were
4 continuously scaled along Axis 1, indicating that the first factorial axis expressed changes in
5 collembolan communities according to some gradient. Significance of this gradient was shown by the
6 projection of additional variables. The six LUUs were scaled in the order 2, 1, 3, 5, 4, 6, with a large
7 space between 3 and 5. This corresponded to an opposition between woodland (LUUs 1 to 3, positive
8 side of Axis 1) and grassland environments (LUUs 4 to 6, negative side of Axis 1), with a slight
9 departure from the original scaling of increasing intensity of land use (1 and 2 were inverted, 4 and 5
10 were inverted, too). The projection of land use types on Axis 1 reinforced the view that woodland
11 areas were opposed to agricultural areas along Axis 1. This interpretation was strengthened by the
12 fact that species typical of grassland environments (Ponge, 1980; Ponge, 1993), such as *Isotoma*
13 *viridis*, *Lepidocyrtus cyaneus*, *Deuterosminthurus sulphureus*, *Sminthurus nigromaculatus*,
14 *Brachystomella parvula*, *Sminthurus viridis* and *Isotoma tigrina*, were all on the negative side of Axis 1,
15 whereas species typical of woodland environments (Ponge, 1980; Ponge, 1993), such as
16 *Pseudisotoma sensibilis*, *Xenylla tullbergi*, *Entomobrya nivalis* and *Orchesella cincta* were all on the
17 positive side (Table 2). Hedgerows exhibited an intermediate position between grassland and
18 woodland environments. Coniferous woodlands did not exhibit profound changes in collembolan
19 communities when compared to deciduous woodlands, as well as clearcut areas, but forest influence
20 was at a maximum in deciduous forests, followed by coniferous forests then by clearcut areas. On the
21 negative side, pastures, hay meadows and agricultural fields did not exhibit differences in collembolan
22 communities, forming a homogeneous group on the negative side of Axis 1. Changes in total
23 abundance and species richness were also depicted by Axis 1, more species and more individuals per
24 unit surface being present in forested than in agricultural areas. The total abundance of Collembola
25 and the species richness of individual samples were linearly correlated with Axis 1 ($P < 0.001$ and $P <$
26 0.01 , respectively).

27

28 Collembolan communities of pastures and hay meadows did not change according to LUUs,
29 contrary to agricultural fields and woodlands (Fig. 2). In LUU 3 and LUU 4 collembolan communities
30 from agricultural fields were not very different from their coniferous woodland counterparts, as

1 exemplified by the projection of the corresponding passive variables at the same level of Axis 1. Far
2 from the origin on the positive side of Axis 1 (thus most typical for forest environments) were
3 deciduous woodlands from LUU 1 and LLU 3, and coniferous woodlands from LUU 2, other forested
4 sites being less different from open environments.

5
6 Discrepancies between forested sites were reflected in the projection of woody plant species
7 on Axis 1 (Fig. 3). Although *Quercus petraea*, *Fagus sylvatica* and *Abies alba* were far from the origin
8 on the positive side of Axis 1, other timber trees such as *Picea abies* and *Pseudotsuga menziesii* were
9 near the origin, not far from open environments. Thus collembolan communities from spruce and
10 Douglas fir plantations in agricultural landscapes (LUUs 3 to 6) differed less from agricultural fields
11 and pastures than they differed from old beech and oak forests or from silver fir plantations in forested
12 landscapes (LUUs 1 and 2). Trees typical of early stages of forest succession (abandoned fields) or of
13 woodland borders, such as *Prunus spinosa* L., *Crataegus monogyna* Lacq., *Malus sylvestris* Mill.,
14 *Pyrus pyraeaster* Burgsd., *Cytisus scoparius* (L.) Link, *Salix* spp., *Acer pseudoplatanus* L., *Prunus avium*
15 L., and *Sambucus racemosa* L., were nearly at the same position as planted spruce and Douglas fir,
16 indicating that collembolan communities of Douglas fir and Norway spruce plantations did not differ to
17 any great extent from early stages of forest succession (old fallows).

18
19 The projection of humus forms along Axis 1 revealed that forest samples exhibited thick
20 organic horizons (typically Dysmoder and Amphimull) as opposed to agricultural fields and meadows
21 which were characterized by Eumull (Fig. 4). The Humus Index exhibited a highly significant linear
22 correlation with Axis 1 ($P < 0.001$). Thus Axis 1 reflected also a decreasing trend of soil biological
23 activity from open to closed environments. This interpretation was reinforced by the position of all
24 species known to live only in raw humus (Mor, Dysmoder) and other acid humus forms, i.e.
25 *Sminthurinus signatus*, *Mesaphorura yosii*, *Willemia anophthalma*, *Proisotoma minima*, *Xenylla*
26 *tullbergi*, *Pseudosinella maui* and *Micraphorura absoloni* on the positive side of Axis 1, and the
27 projection of all species known to live only in Eumull, i.e. *Sminthurinus aureus*, *Pseudosinella alba*,
28 *Parisotoma notabilis*, *Onychiurus jubilarius*, *Heteromurus nitidus* and *Stenaphorura denisi*, on the
29 negative side of Axis 1. The position of Agricultural Moder is worthy of note, since it was projected not
30 far from the origin, thus far from samples typical of agricultural fields (Fig. 1). This indicated that its

1 species composition differed somewhat from Eumull, showing similarities with forest humus forms with
2 thick litter horizons, despite the total absence of litter. Examination of individual samples revealed that
3 acidophilic species such as *Sminthurinus signatus*, *Willemia anophthalma* and *Mesaphorura yosii*
4 were present in Agricultural Moder (4 samples, all but one in LUU 4), and not in agricultural soils with
5 Eumull (9 samples, all but one in LUU 6). On the contrary, the acido-intolerant species *Pseudosinella*
6 *alba* was present in agricultural soils with Eumull, not in Agricultural Moder. In both agricultural crop
7 environments, the open-habitat species *Isotoma viridis* and *Lepidocyrtus cyaneus* were present.

8
9 Waterlogging (and the associated humus forms Hydromull, Hydromoder and Hydromor) did
10 not influence species composition to a great extent. All corresponding samples were not far from the
11 origin (Fig. 4), and no other factorial axis was found to isolate these samples. It should be noticed that
12 hygrophilic species such as *Isotomurus palustris*, *Lepidocyrtus lignorum* and *Sminthurides schoetti*
13 were all far from the origin on the negative side of Axis 1, indicating that these species were present in
14 open environments, even when soils were not waterlogged.

15
16 3.3. Biodiversity and land use variety

17
18 The total species richness (cf. 40-50 species found in each LUU) showed little variation
19 between LUUs (Table 3), i.e. each contained around half the total number of species found in the
20 whole sample (89). In contrast, the individual species richness (the number of species found in a core
21 sample 5 cm diameter and 10 cm depth) varied markedly among the six LUUs (Fig. 5). Analysis of
22 variance (ANOVA) revealed a significant heterogeneity according to LUUs ($F = 2.7$, $P < 0.05$), most
23 difference (significant at 0.05 level) being between LUU 1 and LUU 4. The curve formed by the six
24 mean values was saddle-shaped, indicating a continuous decrease from LUU 1 to LUU 4 followed by
25 a continuous increase up to LUU 6, although the latter did not reach the level of species richness
26 exhibited by LUU 1.

27
28 The distribution of land use types (Table 2) can be used in each LUU to measure the variety of
29 the landscape. The Shannon Index (Shannon, 1948) allowed to compare the species richness of
30 individual samples with a quantitative landscape factor (Fig. 5). The curve of land use variety mirrored

1 that of local species richness, the latter increasing then decreasing in contrast to the former, which
2 was better exemplified by a correlation plot (Fig. 6). The least variation in land use occurred in a
3 square kilometer, the more species occurred together at the scale of the core sampler.

4
5 The hypothesis that negative effects of landscape variety on local species richness could be
6 due to changes in the dominant land use types was tested by examining individual trends followed by
7 the main land use types when crossing several LUUs. Given results from correspondence analysis,
8 coniferous and deciduous forests were pooled into an unique woodland category. Accordingly,
9 pastures, hay meadows and agricultural crops (cereals, rape) formed the grassland category. It
10 appeared that in grassland the species richness of individual samples exhibited only a slight increase
11 from LUU 3 to LUU 6 (no grassland occurred in LUU 1 and LUU 2), while strong variation according to
12 LUUs was observed in the woodland category (Table 4). The decrease observed from LUU 1 to LUU 4
13 when taking only woodland into account (approximating 50%) was more pronounced than when all
14 land use types were included in the calculation (Fig. 5). Thus the decrease in biodiversity observed
15 from LUU 1 to LUU 4 concerned only woodland.

16
17 Examination of individual data did not reveal any meaningful trend of extinction of species.
18 Rather, a collapse in the total population was observed in woodland samples taken in LUU 4 (Table
19 4), which could explain the observed fall in local species richness. Such changes in total abundance of
20 Collembola were never observed in grassland samples.

21

22 **4. Discussion**

23
24 In the Morvan Nature Regional Park, land use intensification caused changes in species
25 composition, total abundance and species richness of collembolan communities. The first axis of
26 correspondence analysis showed a global trend contrasting forest sites (closed, with accumulation of
27 organic matter at the ground surface) with agricultural sites (open, with rapid incorporation of organic
28 matter). The Humus Index (Ponge et al., 2002) showed an improvement of soil biological activity in
29 grassland, compared to woodland soils. This may result from a combination of factors, all of them
30 acting in the same direction: choice of the best soils for crop and cattle production (Braojos et al.,

1 1997), more heat and water in the soil (Jansson, 1987), use of organic manure or fertilizers to improve
2 primary production (Koerner et al., 1997). Changes in species composition followed changes in both
3 micro-climate and edaphic parameters, as revealed by the replacement of woodland species such as
4 *Pseudisotoma sensibilis* by grassland species such as *Isotoma viridis* (Szeptycki, 1967; Ponge, 1993),
5 and the replacement of acidophilic species, such as *Pseudosinella mauli* and *Sminthurinus signatus*,
6 by acido-intolerant species such as *Pseudosinella alba* and *Sminthurinus aureus* (Ponge 1993). This
7 could allow the species composition of collembolan communities to be used as an indicator of the
8 intensification of land use, provided underlying ecological factors are clearly identified. This is an
9 important point to be highlighted, given the fuzzy contour of the human factor. For instance, Hågvar
10 and Abrahamsen (1990), studying a transect through a naturally lead-contaminated site (an
11 abandoned mine), observed that the isotomid *Isotoma olivacea* (syn. *I. tigrina*, present in our sample)
12 was favoured by lead contamination, compared to all other species, because of its higher abundance
13 at the most polluted site. Examination of their site description allowed us to reinterpret the abundance
14 of this species at the most polluted site as resulting from the collapse of tree vegetation. In a similar
15 study on a zinc-polluted abandoned field Gillet and Ponge (2003) observed that typical grassland
16 species such as *Lepidocyrtus cyaneus* were abundant at the most polluted site, due to collapse of the
17 poplar plantation. Other instances concern atmospheric pollution, most effects of which on the soil are
18 due to acidification, as this has been repeatedly observed in northern and Central Europe (Tamm and
19 Hallbäcken, 1988; Hambuckers and Remacle, 1987; Falkengren-Grerup, 1987). In this latter case, the
20 effects of human activities are exactly opposed to those recorded in the present study, where most
21 acid soils are those least subject to human influence, i.e. soils from old deciduous forests.

22

23 The decrease in local species richness observed when the landscape becomes more
24 diversified, in the absence of any decrease in regional species richness, seems at first sight more
25 difficult to interpret. The independence between regional (γ) and local (α) diversity of collembolan
26 populations has been already observed in temperate grassland communities (Winkler and Kamplicher,
27 2000) but it conflicts with studies on macroarthropod (Halme and Niemelä, 1993; Duelli and Obrist,
28 1998; David et al., 1999) and plant communities (Tilman, 1999). Some explanation can be found in the
29 past history of the sites and in the scale at which these tiny soil animals are living. We have shown
30 that the shift from woodland to grassland (and associated changes in climate, soil and vegetation) was

1 the main factor explaining changes in soil collembolan communities. Other studies indicate the rates at
2 which collembolan communities may recover (or shift to another equilibrium stage) following changes
3 in vegetation cover. Cyclic changes in the species composition of collembolan communities have been
4 observed to occur at the scale of centuries in near-natural mountain spruce forests, following cyclic
5 changes in soil acidity in the course of vegetation dynamics (Loranger et al., 2001). In such forest
6 mosaics, the rate of change and the availability of refuges allow the progressive recovery of
7 communities as far as environmental conditions (micro-climate, soil chemistry, litter quality) return to
8 original conditions. On the contrary, it has been observed that sudden deforestation (Takeda, 1981;
9 Gers and Izarra, 1983; Mateos and Selga, 1991) as well as afforestation (Jordana et al., 1987) causes
10 a rapid collapse in total abundance and species richness of collembolan communities. Cassagnau
11 (1990) underlined that in both cases rarefaction of species typical of past land use was more rapid
12 than immigration of species typical of the new environment thus created, which could explain the
13 decrease in biodiversity observed in landscapes most subject to recent changes in land use,
14 compared to more stable landscapes. Along our gradient of intensification of land use (LUU 1 to LUU
15 6) both sides did not exhibit any profound changes over the last decades. For instance coniferous
16 plantations in LUU 2 (mostly silver fir) occurred in previous old deciduous forests, as ascertained by
17 the continuous presence of relict beech and oak. Thus no sharp transition occurred in the course of
18 time, despite clear-cut operations and shift from hardwood to softwood (remind that clear-cut areas did
19 not exhibit change in species composition, too). Most severe changes in land use occurred in zones
20 intermediate between wide forested areas (on the less fertile soils) and plain land devoted to cereal
21 crops for a long time (on the more fertile soils). The grassland past of present Norway spruce or
22 Douglas fir plantations (more especially in LUU 4) can be ascertained by the presence of certain
23 pasture plants still growing in the understory. Over the last ten decades the Morvan region has been
24 subject to severe changes in land use (Braojos et al., 1997), due to i) abandonment of fire wood
25 silviculture at the turn of the nineteenth century, ii) progressive abandonment of agriculture after the
26 second world war, iii) recent increase of Christmas-tree fields. Variegated landscapes (LUUs 3 to 5)
27 reflects best such recent shift in land use, afforestation of previous grassland occurring at a rate
28 probably too rapid for the development of adapted soil animal communities. We hypothesize that the
29 imbalance between immigration rates of new species and changes in land use will not occur for
30 colonizers that have better dispersal mechanisms such as most plants and winged insects. The

1 stability of regional biodiversity observed along our gradient of land use intensification can be ascribed
2 to a compensation between an increase in the number of species in more variegated landscapes
3 (through the addition of grassland to woodland communities) and the above mentioned loss of species
4 resulting from too rapid changes in land use.

5
6 It was surprising to see that cereal crops, which undergo heavy disturbance by deep
7 ploughing, pesticides and the absence of plant cover over a large part of the year, did not display any
8 significant reduction in total abundance and species richness when compared with hay meadows and
9 permanent pastures. Studies on agricultural soils showed a vertical redistribution of collembolan
10 populations following annual ploughing and burying of crop residues (Van Amelsvoort et al., 1988;
11 Petersen, 2000), which probably helps to maintain abundance of food at a depth where these tiny
12 animals are protected from winter frost and summer drought. This may compensate for the absence
13 of litter and plant cover during cold and dry seasons. Moreover the cyclicity of changes taking place in
14 agricultural soils may allow communities to adapt themselves to changing conditions, by synchronizing
15 their population dynamics with the cycle of change, as this has been demonstrated in forest soils
16 (Usher, 1970; Takeda, 1987; Gauer, 1997). In short, it can be said that cyclic disturbance is not
17 disturbance at all (Odum, 1969; Chernova and Kuznetsova, 2000). On the contrary, non-cyclic
18 changes may damage communities until new, better adapted communities, develop, mainly through
19 immigration of new species. Time is important in this respect (Burgess, 1960). Recovery of collembolan
20 populations may last decades or centuries, depending on dispersal capabilities of the species,
21 proximity of possible sources for the immigration of better adapted species, and absence of a new
22 shift in land use during the meantime (Bengtsson et al., 1994; Mebes and Filser, 1997; Ojala and
23 Huhta, 2001).

24
25 Another example of the effect of land use intensification on the structure and diversity of soil
26 animal communities can be found in a study of nematodes in tropical soils by Bloemers et al. (1997).
27 These authors did not detect any profound influence of slash-and-burn and heavy machinery
28 deforestation on the trophic structure of nematode communities, as expressed by the Maturity Index
29 (Bongers, 1990), but they observed a 40% decrease in species richness. This short-term depressive
30 effect can be considered as in line with our results on temperate Collembola. Here too, most

1 disturbance resulted from the abrupt passage from forest to open environments, the reverse
2 (plantation of trees on previous agricultural soils) being not considered.

3

4 The results of this study show that a critical assessment is required over the choice of
5 Collembola as bioindicators of land use intensification. On one hand we have seen that collembolan
6 communities differ clearly between low (forest) and high (crop) land use intensity and that they could
7 be used to some extent as bioindicators of this factor, in spite of a correlation with other ecological
8 factors (soil acidity) not directly related to human activities. On the other hand we have also shown
9 that it is necessary to take into account landscape dynamics. This second observation points to limits
10 for the use of Collembola, and more generally animal communities, for the bioindication of land use
11 intensity or land use type, since they do not adapt rapidly to changes in land use. The aim of
12 bioindication must be clearly expressed before this interesting tool could be used for monitoring or
13 predicting biodiversity.

14

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16

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21

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1 **Legends of figures**

2

3 **Fig. 1.** Correspondence analysis. Projection of collembolan species (three-letter codes according to
4 Table 3), population parameters (higher values in bold type, lower values in italic type), land
5 use units (numbers in boxes) and land use types (underlined) on Axis 1. Position of the origin
6 is indicated by an arrow. Positive and negative Axis 1 coordinates are on the lower and upper
7 side, respectively

8

9 **Fig. 2.** Correspondence analysis. Projection of collembolan species (three-letter codes according to
10 Table 3), land use units (numbers in boxes) and land use types separated by land use units on
11 Axis 1. Position of the origin is indicated by an arrow. Positive and negative Axis 1 coordinates
12 are on the lower and upper side, respectively

13

14 **Fig. 3.** Correspondence analysis. Projection of collembolan species (three-letter codes according to
15 Table 3), land use units (numbers in boxes) and woody plant species on Axis 1. Position of the
16 origin is indicated by an arrow. Positive and negative Axis 1 coordinates are on the lower and
17 upper side, respectively

18

19 **Fig. 4.** Correspondence analysis. Projection of collembolan species (three-letter codes according to
20 Table 3), Humus Index (higher values in bold type, lower values in italic type), waterlogging
21 (presence in bold type, absence in italic type) and humus forms on Axis 1. Position of the
22 origin is indicated by an arrow. Positive and negative Axis 1 coordinates are on the lower and
23 upper side, respectively

24

25 **Fig. 5.** Distribution of local species richness of collembolan communities and land use variety
26 (Shannon Index) over a gradient of land use intensity (LUUs 1 to 6). Vertical bars indicate
27 standard errors of the means

28

29 **Fig. 6.** Correlation plot crossing local species richness of collembolan communities and land use
30 variety (measured by the Shannon Index). Numbers in boxes represent the six land use units

31

Table 1. Humus Index and morphological criteria used for the separation of humus forms according to Brêthes et al. (1995) and Ponge et al. (2000, 2002)

Humus Index	Humus form	OL horizon	OM horizon	OF horizon	OH horizon	A horizon
1	Eumull	absent	absent	absent	absent	crumby
2	Mesomull	present	absent	absent	absent	crumby
3	Oligomull	present	absent	present but less than 1 cm	absent	crumby
4	Dysmull	present	absent	1 cm or more	absent	crumby
5	Amphimull	present	absent	present	present	crumby
5	Hemimoder	present	absent	present	absent	compact
6	Eumoder	present	absent	present	present but less than 1 cm	compact
7	Dysmoder	present	absent	present	1 cm or more	compact
8	Amphimoder	present	present	absent	absent	crumby
9	Mor	present	present	absent	absent	compact A or E horizon

1

2

Table 2. Distribution of land use types among the six land use units (LUUs). Sixteen samples were taken in each LUU according to a regular grid, except LUU 4 with fifteen samples only due to flooding

	LUU 1	LUU 2	LUU 3	LUU 4	LUU 5	LUU 6
Deciduous forest	16	1	8	0	3	0
Coniferous forest	0	14	2	3	2	0
Clearcut	0	1	0	1	0	0
Hedgerow	0	0	0	0	1	0
Hay meadow	0	0	4	4	4	0
Pasture	0	0	1	3	6	2
Fallow	0	0	0	1	0	5
Agricultural field	0	0	1	3	0	9
Not sampled	0	0	0	1	0	0

1

2

Table 3. Collembolan species and main features of collembolan populations in the six sampled land use units

	Axis 1	LUU 1 (n = 16)	LUU 2 (n = 16)	LUU 3 (n = 15)	LUU 4 (n = 16)	LUU 5 (n = 16)	LUU 6 (n = 16)	Total
AFU <i>Allacma fusca</i>	0.003	0	1	0	1	0	0	2
AGR <i>Anurida granaria</i>	-0.011	0	0	0	0	0	1	1
AUN <i>Anurida unifomis</i>	-0.011	0	0	0	0	0	2	2
ABI <i>Arrhopalites bifidus</i>	0.003	0	0	2	1	0	0	3
ASP <i>Arrhopalites sp.</i>	0.007	1	0	0	0	0	0	1
BPA <i>Brachystomella parvula</i>	-0.007	0	1	2	7	3	0	13
CAR <i>Ceratophysella armata</i>	0.004	26	2	0	0	0	0	28
CDE <i>Ceratophysella denticulata</i>	-0.012	0	2	1	15	0	0	18
CLU <i>Ceratophysella luteospina</i>	0.009	0	0	2	0	1	3	6
CAL <i>Cyphoderus albinus</i>	-0.007	0	0	1	0	0	0	1
DSU <i>Deuterominthurus sulphureus</i>	-0.012	1	0	3	1	1	6	12
DFU <i>Dicyrtoma fusca</i>	-0.005	0	0	0	1	1	0	2
DMI <i>Dicyrtomina minuta</i>	-0.006	3	0	1	5	0	4	13
DOR <i>Dicyrtomina ornata</i>	-0.002	0	0	0	0	1	0	1
EMU <i>Entomobrya multifasciata</i>	-0.006	1	0	0	1	0	3	5
ENI <i>Entomobrya nivalis</i>	0.005	0	1	0	1	0	0	2
FQS <i>Fasciosminthurus quinquefasciatus</i>	-0.002	0	0	0	0	0	3	3
FCA <i>Folsomia candida</i>	-0.006	0	0	0	4	0	0	4
FFI <i>Folsomia fimetaria</i>	-0.008	0	0	11	0	0	0	11
FQU <i>Folsomia quadrioculata</i>	0.025	446	502	378	221	156	39	1742
FCL <i>Friesea clavisetata</i>	0.001	0	7	0	0	1	4	12
FMI <i>Friesea mirabilis</i>	0.003	6	0	0	0	0	0	6
FTR <i>Friesea truncata</i>	0.029	46	163	83	2	29	46	369
HNI <i>Heteromurus nitidus</i>	-0.007	0	0	2	4	1	0	7
IAN <i>Isotoma antennalis</i>	-0.008	0	0	0	39	0	3	42
ITI <i>Isotoma tigrina</i>	-0.001	0	0	0	0	11	2	13
IVI <i>Isotoma viridis</i>	-0.019	1	0	128	46	61	176	412
IMI <i>Isotomiella minor</i>	0.024	502	291	359	87	136	142	1517
IPR <i>Isotomodes productus</i>	0.000	0	1	0	0	0	6	7
IPA <i>Isotomurus palustris</i>	-0.020	0	0	25	87	1	33	146
KBU <i>Kalaphorura burmeisteri</i>	0.000	0	0	0	0	2	0	2
LCY <i>Lepidocyrtus cyaneus</i>	-0.012	0	0	2	5	0	98	105
LLA <i>Lepidocyrtus lanuginosus</i>	0.002	36	49	53	32	99	33	302
LLI <i>Lepidocyrtus lignorum</i>	-0.018	2	2	38	43	50	23	158
LLU <i>Lipthrix lubbocki</i>	0.011	13	11	6	0	0	0	30
MMI <i>Megalothorax minimus</i>	0.025	48	107	77	14	54	30	330
MBE <i>Mesaphorura betschi</i>	0.009	0	1	0	0	0	0	1
MJE <i>Mesaphorura jevanica</i>	0.022	90	144	136	0	14	12	396
MLE <i>Mesaphorura leitzaensis</i>	0.011	1	19	0	0	0	0	20
MMA <i>Mesaphorura macrochaeta</i>	0.010	86	247	107	43	118	157	758
MYO <i>Mesaphorura yosii</i>	0.021	51	50	8	5	3	0	117
MPY <i>Micranurida pygmaea</i>	0.013	8	20	4	0	6	1	39
MSE <i>Micranurida sensillata</i>	0.004	1	9	0	0	0	0	10
MAB <i>Micraphorura absoloni</i>	0.015	0	2	6	0	0	0	8
NMU <i>Neanura muscorum</i>	0.014	2	6	4	1	1	0	14
NMI <i>Neelides minutus</i>	0.011	3	0	2	0	0	0	5
NRA <i>Neotullbergia ramicuspis</i>	-0.011	0	0	0	0	0	1	1
OCR <i>Oncopodura crassicornis</i>	0.016	0	0	1	0	0	0	1
OPS <i>Onychiurides pseudogranulosus</i>	0.008	24	1	0	2	0	0	27
OCE <i>Onychiurus cebennarius</i>	0.019	33	11	125	0	3	2	174
OJU <i>Onychiurus jubilaris</i>	-0.008	0	0	0	2	6	1	9
OCI <i>Orchesella cincta</i>	0.002	0	0	2	18	0	6	26
OQU <i>Orchesella quinquefasciata</i>	-0.008	0	0	0	0	0	1	1
OVI <i>Orchesella villosa</i>	-0.008	0	0	0	0	0	1	1
PCA <i>Paratullbergia callipygos</i>	0.010	54	1	26	14	47	8	150
PNO <i>Parisotoma notabilis</i>	-0.014	55	75	244	97	323	223	1017
PFL <i>Pogonognathellus flavescens</i>	0.008	14	5	11	0	4	0	34
PMI <i>Proisotoma minima</i>	0.018	0	5	0	0	1	1	7
PAR <i>Protaphorura armata</i>	-0.019	26	51	46	73	85	139	420
PME <i>Protaphorura meridiana</i>	-0.003	2	3	36	0	0	0	41
PPR <i>Protaphorura prolata</i>	0.000	3	0	2	3	0	0	8
PPA <i>Pseudachorutes parvulus</i>	0.013	9	5	0	0	5	1	20
PBI <i>Pseudanurophorus binocolatus</i>	0.000	1	0	0	0	0	0	1
PSE <i>Pseudisotoma sensibilibis</i>	0.027	3	138	10	0	6	0	157
PAL <i>Pseudosinella alba</i>	-0.015	0	0	1	3	21	36	61
PIL <i>Pseudosinella illiciens</i>	-0.008	0	0	0	0	0	5	5
PMA <i>Pseudosinella mauii</i>	0.015	3	7	1	0	6	0	17
SPA <i>Sminthurides parvulus</i>	-0.008	0	0	0	1	3	4	8
SSC <i>Sminthurides schoetti</i>	-0.015	3	1	5	14	3	6	32
SAU <i>Sminthurinus aureus</i>	-0.022	1	3	24	19	68	45	160
SNI <i>Sminthurinus niger</i>	-0.012	0	0	0	1	0	0	1
SSI <i>Sminthurinus signatus</i>	0.022	9	12	10	7	0	1	39
SNS <i>Sminthurus nigromaculatus</i>	-0.005	0	0	0	0	0	1	1
SVI <i>Sminthurus viridis</i>	-0.006	0	0	1	18	0	3	22
SPU <i>Sphaeridia pumilis</i>	-0.024	3	1	30	54	131	71	290
SED <i>Spinonychiurus edinensis</i>	-0.007	0	0	10	0	0	2	12
SVA <i>Stenacidia violacea</i>	-0.007	0	0	2	6	1	0	9
SDE <i>Stenaphorura denisi</i>	-0.005	0	0	0	1	0	0	1
SQU <i>Stenaphorura quadrispina</i>	-0.002	0	0	0	2	0	13	15
TMI <i>Tomocerus minor</i>	0.001	0	2	0	8	0	0	10
VAR <i>Vertagopus arboreus</i>	0.004	0	0	2	0	0	0	2
WAN <i>Willemia anophthalma</i>	0.018	5	56	2	0	2	3	68
WDE <i>Willemia denisi</i>	0.013	18	0	4	0	0	0	22
WIN <i>Willemia intermedia</i>	0.008	0	0	17	0	3	0	20
WNI <i>Willowsia nigromaculata</i>	-0.006	0	0	0	0	0	1	1
XGR <i>Xenylla grisea</i>	0.004	28	0	1	0	2	0	31
XTU <i>Xenylla tullbergi</i>	0.016	1	52	0	5	8	0	66
XAR <i>Xenyllodes armatus</i>	0.025	13	30	11	0	0	0	54
Total species richness		43	42	51	44	42	47	
Mean abundance (±S.E.)		105±11	131±25	129±27	68±13	92±16	88±16	
Mean species richness (±S.E.)		14±1	13±1	11±1	10±1	11±1	12±1	
Humus Index (±S.E.)		5.4±0.4	6.1±0.3	2.9±0.6	2.6±0.6	2.0±0.6	1.4±0.3	

Table 4. Total abundance and number of species of Collembola in individual core samples (5 cm diameter, 10 cm depth) according to main land use types in the six land use units investigated (mean followed by standard error)

	Abundance		Species richness	
	Woodland	Grassland	Woodland	Grassland
LUU 1	105±11		13.9±0.9	
LUU 2	122±24		12.7±1.0	
LUU 3	131±37	126±42	11.9±1.4	10.2±1.9
LUU 4	37±21	83±17	7.7±2.2	10.3±1.2
LUU 5	71±10	105±24	10.2±0.8	10.7±1.1
LUU 6		102±22		11.2±1.6

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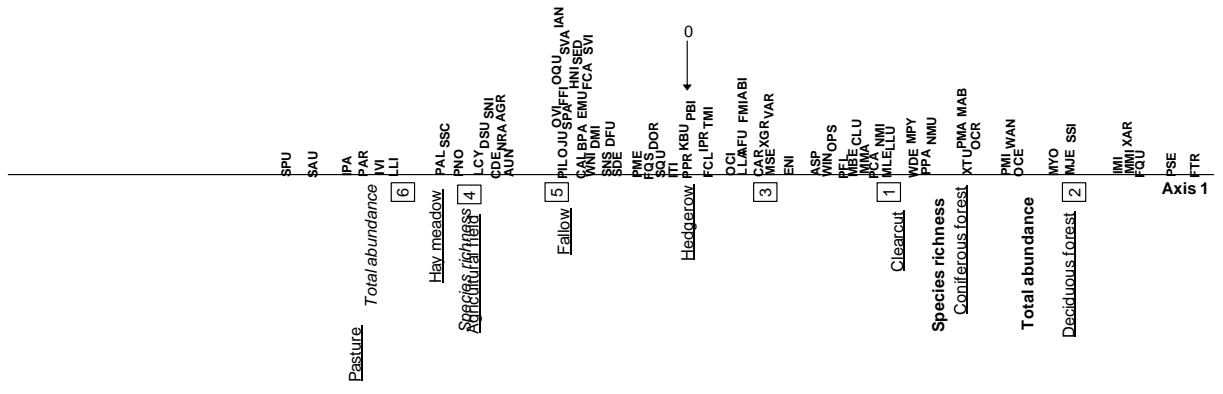


Fig. 1

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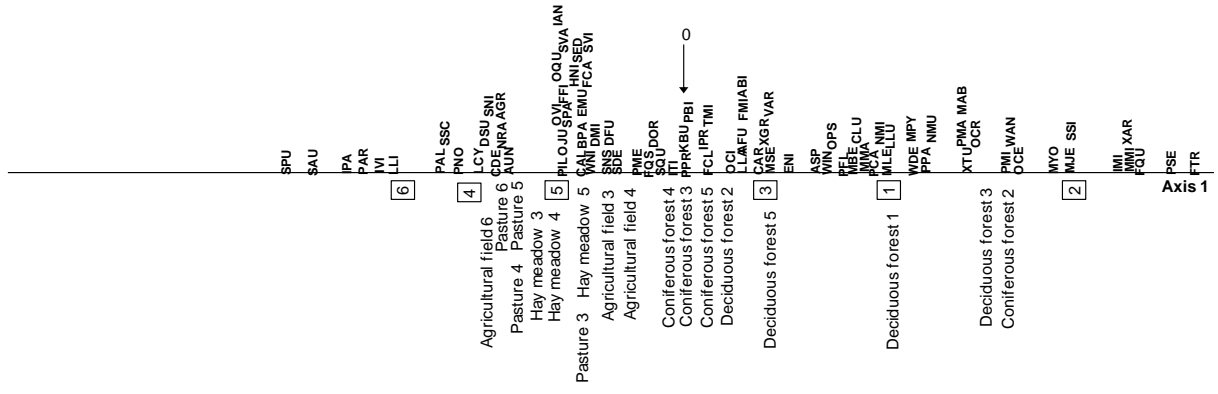


Fig. 2

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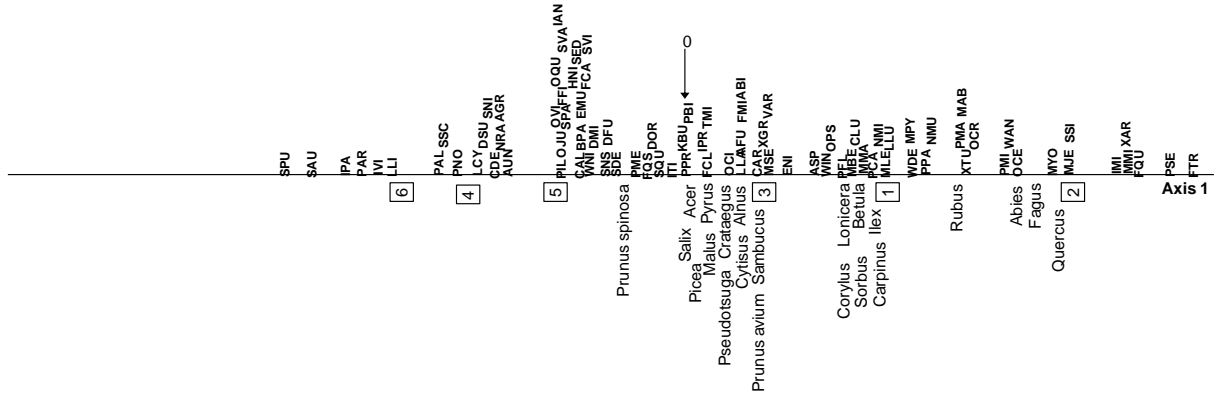
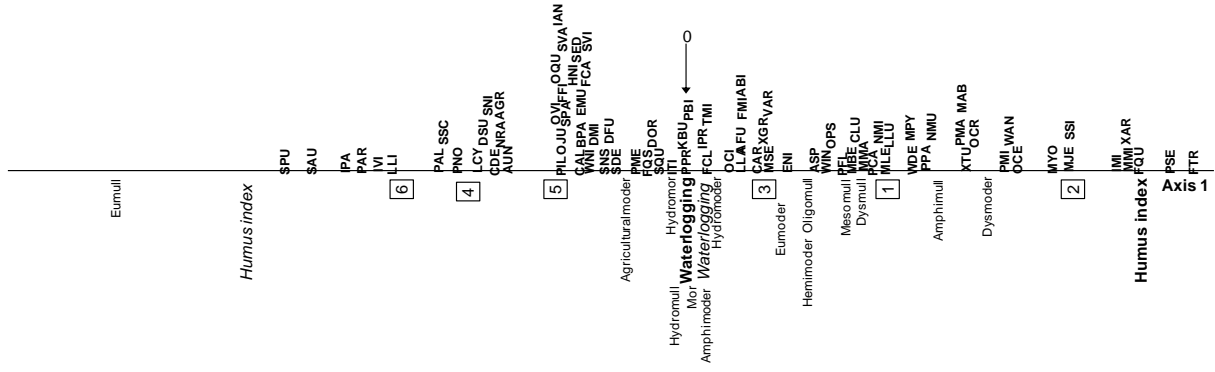
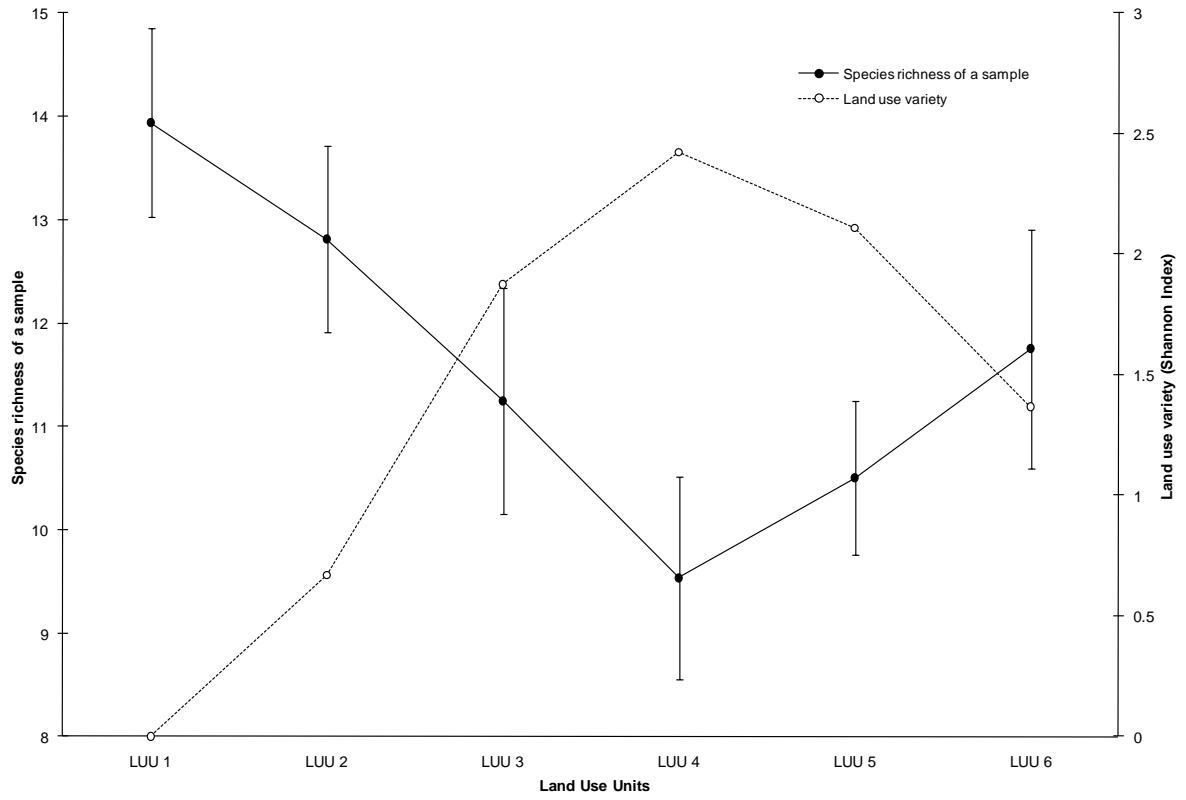


Fig. 3



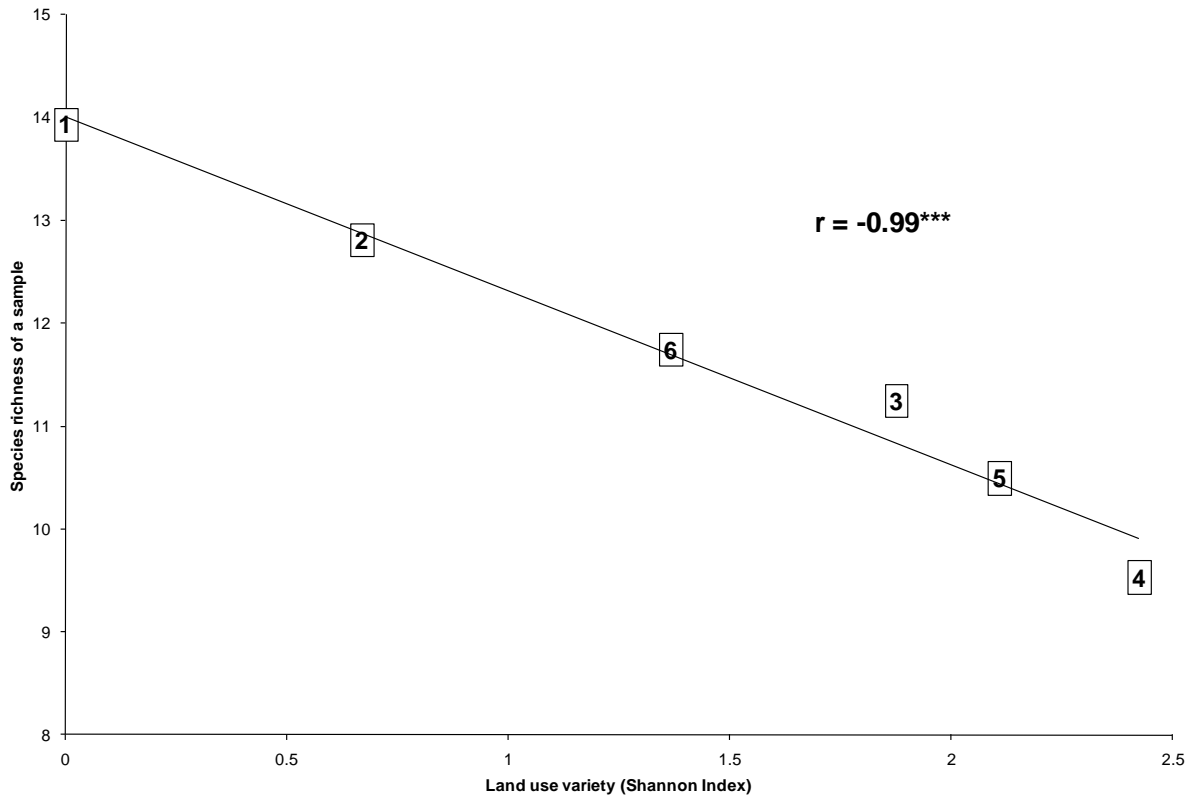
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2 Fig. 4
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2 Fig. 5

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2 Fig. 6