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1 **Short term responses of two collembolan communities after abrupt environmental
2 perturbation: a field experimental approach**

3

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5

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11

12 Running title: Collembolan communities after abrupt environmental perturbation

13

1 **Summary**

2

3 A soil transfer field experiment has been designed in order to study (i) whether and how
4 Collembolan communities are affected by a sudden perturbation (a shift from agricultural land
5 to heathland, and the reverse), and (ii) whether species do respond in the same direction and
6 to the same extent according to their habitat preference (ascertained by controls). The study
7 was conducted in the Parc Naturel Régional de la Brenne (Indre, France) in a private property
8 where the land is shared between heathland and pasture. We showed that heathland differed
9 from pasture in its species composition, which is not novel, but that both communities did not
10 evolve in the same manner when transferred in another environment. The heathland
11 community seemed more stable than the pasture community, although it was colonized by the
12 surrounding fauna within two months, while the the pasture community seemed less stable
13 when transferred to heathland.

14

15 **Keywords** Collembola; Heathland; Pasture; Habitat preference

16

1 **Introduction**

2

3 The sustainable management of secondary heathland is a central problem of nature
4 conservation following the abandonment of agriculture in the Atlantic domain of western
5 Europe (Pakeman et al., 2003; Bartolomé et al., 2005). A proper conservation of patrimonial
6 habitats should take into consideration all their communities, whether visible or invisible, and
7 should not privilege individual species (either keystone or not) over species assemblages
8 (Lin and Xie, 2005). It has been shown that following landuse changes, soil animal
9 communities did not recover at the same rate as plant communities, due to poorer dispersal
10 rates and to the absence of persistent diaspores (Kardol et al., 2005). Not all species are
11 concerned by this lag in recovery, depending on their habitat specialization and locomotory
12 activity (Dunger et al., 2002; Ponge et al., 2006).

13

14 The colonization of agricultural land by heathland species, in particular southern
15 arboreal species of the genus *Erica* such as *E. arborea* L. and *E. scoparia* L., involves a
16 change in micro-climate conditions as well as in litter amount and quality (Bartolomé et al.,
17 2005). Given the well-known contrast in species assemblages of Collembola (springtails)
18 between woodland and agricultural land (Kaczmarek, 1973; Pozo et al., 1986; Ponge et al.,
19 2003), we may expect that the establishment of woody vegetation, or the reverse when it has
20 been cut will cause changes in species assemblages of soil animals therefore modifying both
21 the community composition (number, type and abundance of species) and then ultimately the
22 biodiversity. Such responses will lie on the different life history traits of the involved species,
23 such as habitat preferences, dispersal rates, generation time. However, factors which
24 determine changes in community composition between woodland and agricultural land are

1 still poorly known. Betsch and Vannier (1977) showed that first stages of epigaeic springtail
2 species living in either sun or shade conditions exhibit different tolerance levels to air
3 dryness, pointing on the importance of climate in habitat preferences. Ponge et al. (1993)
4 showed that experimental variation in the amount of leaf litter caused severe changes in forest
5 collembolan communities, pointing on the importance of food resources and habitat structure.
6 Positive and negative interactions between species and random extinction can also shape
7 community dynamics at the local scale (Keddy, 1992; Bengtsson, 2002; Gonzalez and
8 Chaneton, 2002).

9

10 The aim of this study was (1) to compare the biodiversity and the composition of
11 springtail soil communities between two contrasted habitats (pasture and heathland) and (2) to
12 follow how this biodiversity and community composition respond in the short term to habitat
13 change. By transferring non-defaunated blocks of soil from pasture to heathland (and the
14 reverse) we intend to mimic at least partly (micro-climate, throughfall) the changes which
15 might occur after a shift from agricultural land to heathland, and when cutting heath
16 vegetation for conservation purposes, respectively. We hypothesize that Collembolan species
17 specialized for a habitat (either heathland or agricultural land) will be more affected than
18 ubiquitous species. Our study may also throw light on environmental filters which operate
19 between regional and local species pools, a central question of community and restoration
20 ecology (Rajaniemi et al., 2006).

21

22 To our knowledge, this is the first time such a transfer procedure is used to follow
23 short-term effects of abrupt perturbations on soil springtail communities. However, block
24 transfer has been already used to follow changes in soil structure which may occur under

1 forest to pasture conversion in Amazonia (Barros et al., 2001). A similar technique was
2 used to study the impact on soil animal communities of environmental factors such as
3 atmospheric deposition and altitude (Briones et al., 1997; Coûteaux et al., 1998).

4

5 **Material and methods**

6

7 Study site

8

9 The study was conducted in the Parc Naturel Régional de la Brenne (Indre), located in
10 the Centre of France, where sustainable development and nature conservation are aimed to be
11 kept at an equilibrium. The climate is oceanic, with a total annual rainfall averaging 770 mm
12 and a mean annual temperature averaging 11°C. Following transformation (shift from crop to
13 pasture) then progressive abandonment of agriculture after the Second World War, more land
14 has been colonized by spontaneous vegetation. The establishment of heathland (dominated by
15 *E. scoparia* in mesic conditions) follows the disappearance of permanent cattle grazing, as a
16 final or intermediate stage of successional development of the natural vegetation (Rallet,
17 1935). Given its patrimonial interest, the *E. scoparia* arboreal heath (local name ‘brande’) is
18 periodically renewed by cutting operations, or controlled by moderate cattle grazing.

19

20 The study was conducted in a private property where the land is shared between
21 pasture and nature conservation. We selected arbitrarily two pasture sites and two heathland
22 sites for crossed soil transfers. The two pasture plots exhibited a similar vegetation dominated
23 by tussocks of *Festuca ovina* L. and *Juncus* spp., while the two heathland plots were

1 dominated by *E. scoparia* (~3m height) overlying a near continuous carpet of the
2 moss *Scleropodium purum* (Hedw.) Limpr. Soils were acidic (pH 4.9 and 4.5 in pasture and
3 heathland, respectively), but pasture exhibited less organic matter (3.3% against 7.1%), a
4 lower C/N ratio (13.7 against 18.1) and more microbial activity (0.7 g against 0.3 g CO².h⁻¹
5 .kg⁻¹) than heathland (Benoist, unpublished memoir). The humus form was an eumull sensu
6 Brêthes et al. (1995) in pasture, with an earthworm-dominated saprophagous macrofauna with
7 *Dendrobaena octaedra* and *Lumbricus centralis* as dominant species, and an eumoder in
8 heathland, with a millipede-dominated saprophagous macrofauna with *Polyxenus lagurus* and
9 *Polydesmus inconstans* as dominant species (Benoist, unpublished memoir; Salmon,
10 unpublished data).

11

12 Experimental design, field sampling and laboratory procedure

13

14 On 14th February 2006 four soil blocks, 35 cm diameter and 10 cm depth, were
15 randomly selected in each site (P1, P2 for pastures and H1, H2 for heathland) then digged up
16 carefully to avoid any physical disruption of the continuous soil environment. For each site,
17 two blocks were transferred to another environment while the two others were replaced in
18 their original position (Fig. 1). Pasture blocks were transferred with their grassy vegetation
19 (only foliar bases at the time of study), while heathland blocks were transferred with their
20 moss cover, without any further pre-treatment. In addition to disturbed control blocks
21 (labelled C), two non-disturbed control blocks (undigged soil block, labelled N) were
22 randomly selected in each site (Fig. 1). We have done two types of control blocks (C and N)
23 in order to control for any effect of soil manipulation by itself such as root trenching for
24 instance.

1

2 At each site, each of the 6 blocks was core sampled just after the initial transfer (14th
3 February) and one and two months after (14th March, 14th April). Sampling took place by
4 forcing a 5 x 20 cm (diameter x depth, = 393 mL) cylindrical steel core into the soil within
5 each transferred or control block. The soil cores (samples) were immediately carried to the
6 laboratory to be extracted within 10 days in a Berlese-Tullgren apparatus at low light
7 incidence, according to the dry funnel method (Edwards and Fletcher, 1971). Springtails were
8 preserved into 95% (v/v) ethyl alcohol until identification. They were sorted under a
9 dissecting microscope then identified at the species level under a light microscope at 500 X
10 magnification using Gisin (1960), Zimdars & Dunger (1994), Jordana et al. (1997), Fjellberg
11 (1998), Bretfeld (1999), Hopkin (2000) and Potapov (2001).

12

13 Measurement of biodiversity

14

15 For each soil sample, we measured the number of individuals of each identified
16 species. Being primarily interested in monitoring changes in biodiversity through time of our
17 four treatments (pasture, heathland, pasture transferred to heathland and heathland
18 transferred), we explored several measures of biodiversity. First, the overall collembolan
19 density, measured as the sum over species of the number of individuals per unit area. Then the
20 species richness (number of different species) was measured for each soil sample. Because
21 overall density is likely to be dominated by the most common species and because species
22 richness does not take into account the relative abundance of the species we also used two
23 other indices of biodiversity, Simpson and Shannon indices. These indices take into account
24 not only the number of species but also the evenness of their abundances. We computed for

1 each sample the Simpson index as one minus the sum across species of the square of their
2 relative abundance. The Shannon index is computed as minus the sum across species of the
3 product of their relative abundance with the logarithm of their relative abundance. For all of
4 theses measurements high values indicate high diversity (Legendre and Legendre, 1998).

5

6 Characterisation of the two communities

7

8 In order to characterise pasture and heathland communities we conducted a
9 correspondence analysis (CA) on the untransferred control samples (N and C, Fig. 1). The
10 abundances (numbers of individuals) of each species in these soil samples were analysed by
11 this multivariate method which allows to discern most prominent trends in the data matrix
12 (Greenacre, 1984). Active (main) variables were the species, none being discarded.
13 Transferred samples (heath to pasture PH and pasture to heath HP, Fig. 1) were projected as
14 additional samples, the factorial axes being calculated only on the set of control samples. As
15 in previous studies on communities (Ponge et al., 2003; Féodoroff et al., 2005), each variable
16 was standardized (mean 20, standard deviation 1) and associated to a conjugate one ($x' = 40 -$
17 x) in the search for possible gradients of global abundance. The first axis of CA, which
18 separated heathland from pasture species (on the base of control samples), was later used as a
19 Community Index for the statistical testing of treatment influence on Collembolan
20 communities.

21

22 Characterisation of species' habitat preference

23

1 Species were classified into heathland or pasture species by using a generalised
2 linear mixed effect model to analyse the number of specimens (Poisson model) or the
3 presence/absence (binomial model) of each species per soil sample as a function of species
4 and habitat. We included a code for month and for each block as random effects. We used the
5 *glmmPQL* function of the *MASS* package from the software R to run these models. Being
6 interested here in the natural distribution of species between the two habitats, we only used in
7 this analysis data from control blocks. This analysis provided for each species an estimate
8 (and its confidence interval) for the mean density (Fig. 2) and the mean probability of
9 occurrence (not shown) in pasture and in heathland and some t-test (Table 1) that compares
10 for each species the two estimates. We used the results of these analyses to classify species as
11 heathland or pasture species if their density and /or their probability of occurrence significantly
12 differed between both habitats.

13

14 Statistical treatment of the data

15

16 We analysed separately samples from February and those collected in March and April
17 because the experimental transfer took place the same day than the first sampling. Therefore
18 February samples were used to compare the two habitats whereas March and April samples
19 were used to compare the treatments.

20

21 We first analysed the impact of soil core transfer on the different measurements of
22 biodiversity. This was done by comparing two control treatments: blocks of soil that were

1 digged up and replaced in their initial position and undisturbed blocks of soil (C
2 and N in Fig. 1).

3

4 The influence of treatments (land use types, months, transfers) was tested on the
5 observed variables (abundance, species richness, Simpson and Shannon indices and
6 Community Index derived from correspondence analysis) by mean of a General Linear Mixed
7 Model using the function *lme* (Linear Mixed Effects) of the R program (Ihaka and Gentleman,
8 1996). The validity of the model hypothesis was verified using methods proposed by Pinheiro
9 and Bates (Pinheiro and Bates, 2000). We included the code of each block of soil in pasture
10 and heathland habitats (H1, H2, P1, P2) as nested random effects. Three samples (H1C1,
11 H2C1, H1P1) were lacking in our April data set, due to some transferred blocks which were
12 put upside down by wild boars between March and April.

13

14 **Results**

15

16 Species data

17

18 A total of 4995 springtails were identified to species level, and 37 species were found
19 in this study (Table 1, Figs. 2 and 3).

20

21 The comparison of presence/absence and density of the 37 species between the two
22 habitats in control blocks enabled us to characterize the habitat preference of 8 species and to

1 foresee some trend in habitat differentiation for another 4 species (see Table 1 and Fig. 2).
 2 For the other species, some of them look really ubiquitous (*Mesaphorura macrochaeta* or
 3 *Sminthurides schoetti* for instance) whereas others such as *Brachystomella parvula* or *Isotoma*
 4 *viridis* are probably pasture species that cannot be classified by our conservative statistical
 5 approach due to lack of data.

6

7 The effect of soil manipulation

8

9 When comparing springtail abundance, species richness, Simpson and Shannon
 10 diversity between the two kinds of control soil samples that have (C) or not (N) been
 11 manipulated we did not find any difference between these samples on none of these variables
 12 ($\chi^2_1 < 2.26$, $P > 0.13$). Therefore, in the following analysis, the two types of control samples
 13 were grouped together and differences between treatments were attributed to the effect of
 14 habitat perturbation rather than to perturbation due to soil digging in itself.

15

16 Correspondence analysis

17

18 Axis 1 of CA explained 15% of the total variance in species abundance (Fig. 4). The
 19 first factor of CA was used as a Community Index, scores of which could be attributed to
 20 every sample as a numerical distance to an average species assemblage with nil value. As
 21 seen from the projection of control samples in the plane of the first two factorial axes
 22 (Fig. 4b) samples from pasture (Δ), to the exception of only one of them, were projected on
 23 the negative side of Axis 1 while samples from heathland (\circ), to the exception of two of

1 them, were projected on the positive side of this axis. Species typical of pastures were
 2 those far from the origin on the negative side of Axis 1 on Figure 4a: *Isotoma viridis* (IVI),
 3 *Sphaeridia pumilis* (SPU), *Parisotoma notabilis* (PNO), *Brachystomella parvula* (BPA),
 4 *Protaphorura subuliginata* (PSU), *Ceratophysella denticulata* (CDE), *Cryptopygus*
 5 *thermophilus* (CTH). Species typical of heathland were those far from the origin on the
 6 positive side of Axis 1 on Figure 4a: *Friesea truncata* (FTR), *Lepidocyrtus cyaneus* (LCY),
 7 *Sminthurides parvulus* (SPA), *Isotomiella minor* (IMI), *Arrhopalites* group *pygmaeus* (APY),
 8 *Isotomodes bisetosus* (IBI), *Megalothorax minimus* (MMI), *Pseudachorutes subcrassus*
 9 (PSS), *Micranurida pygmaea* (MMI), *Sminthurinus signatus* (SSI), *Paratullbergia callipygos*
 10 (PCA). *Folsomia quadrioculata* (FQU), which was the dominant species in heathland samples
 11 (Figs. 2 and 3), belonged also to this group, but it was projected nearer the origin due to its
 12 presence in lesser abundance in the two pastures. Axis 2 (10% of the total variance) separated
 13 mainly one sample (an April heathland control sample) from the rest of the samples. Thus
 14 only Axis 1 could be interpreted with accuracy.

15

16 While control heathland (\circ) and pasture (Δ) samples did not vary from month to
 17 month in their species composition, as seen from their projection on Axis 1 (Fig. 4b),
 18 transferred blocks exhibited shifts in species assemblages. Blocks transferred from pasture to
 19 heathland showed a shift in their species composition in March (Fig. 4b), even more
 20 pronounced in April (\blacktriangle Fig. 4b), as compared with control samples and February transfer
 21 samples (Fig. 4b). Blocks transferred from heathland to pasture remained within the bulk of
 22 variation of control heathland samples but they exhibited a clear departure from typical
 23 heathland samples in March and April (\bullet , Fig. 4b).

24

1 Linear Mixed Models

2

3 Total collembola abundance varied from 3 to 247 with a mean of 72 collembolans per
4 soil sample which corresponded to 1,530 to 125,800 with a mean of 36,900 collembola per
5 m². We found that the abundance varied across months ($\chi^2_1 = 18.3$, P < 0.001). Springtail
6 abundance decreased markedly in March (Fig. 5), probably due to frost before and at time of
7 sampling. We found on average no difference between the two habitats nor between
8 treatments ($\chi^2_1 < 0.63$, P > 0.42). Biodiversity followed the same pattern. Species richness
9 (Fig. 5), Simpon and Shannon indices (Fig. 5) varied across months ($\chi^2_1 > 16.4$, P < 0.001)
10 but, surprisingly, none of these measurements differed between habitats or were affected by
11 the transplantation ($\chi^2_1 < 1.23$, P > 0.26). Despite changes in total abundance and species
12 richness and diversity, months did not influence the Community Index ($\chi^2_1 = 2.57$, P = 0.27),
13 pointing on the stability of the community (recruitment equilibrating individual mortality).
14 When analysing the Community Index in February we did not find, as expected, any effect of
15 transplantation ($\chi^2_1 = 1.23$, P = 0.27) but a difference between control (untransferred)
16 communities according to soil origin ($\chi^2_1 = 13.2$, P < 0.001, cf. Figs. 5 and 4b): communities
17 from pasture had lower values than those from heathland. In March and April, the Community
18 Index did not differ on average between the two months ($\chi^2_1 = 0.12$, P = 0.72) and control
19 communities (untransferred) differed from each other in a similar manner than in February:
20 pasture communities had a smaller Community Index than heathland ones ($\chi^2_1 = 9.9$, P =
21 0.002). In March and April, the transplantation treatment had a strong effect through an
22 interaction with soil origin ($\chi^2_1 = 8.46$, P = 0.003): soil samples transplanted from pasture to
23 heathland had a higher Community Index than control pasture soil samples ($\chi^2_1 = 8.73$, P =
24 0.003) whereas heathland transplanted to pasture tended on average to have a lower
25 Community Index than control heathland samples ($\chi^2_1 = 3.19$, P = 0.074). Therefore, after

1 one month, both transplanted communities seemed to change in the direction of the
2 community into which they have been introduced thus pointing on surrounding species pool
3 influence on species assemblages of Collembolan communities (Fig. 5). However, it should
4 be noted that (i) *Folsomia quadrioculata*, which was dominant in heathland together with
5 *Mesaphorura macrochaeta*, and was subordinate in pasture samples, kept its dominance after
6 transplantation, even after two months, (ii) heathland samples did not became colonized by
7 *S. pumilis*, codominant in pasture, after transplantation (Fig. 3). Conversely, pasture samples
8 transferred to heathland showed a decrease in subdominant species such as *Protaphorura*
9 *subuliginata* and were heavily colonized by *F. quadrioculata*, which became codominant with
10 *S. pumilis* and *M. macrochaeta* (Fig. 3).

11

12 Discussion

13

14 We observed a distinct species composition between heathland and pasture. This
15 corresponded to the well-known discrimination between ‘open-environment’ opposed to
16 ‘closed-environment’ or ‘meadow’ to ‘forest’, which has been recorded times and again in
17 Collembolan communities (Szeptycki, 1967; Kaczmarek, 1973; Pozo et al., 1986; Ponge,
18 1993; Ponge et al., 2003). The distribution of species between heathland and pasture in our
19 study site was similar to that observed by Ponge et al. (2003) between forest (deciduous or
20 coniferous) and agricultural land (meadow, pastures or agricultural crops) in another Parc
21 Naturel Régional located in Central France. *Lepidocyrtus cyaneus* (here typical of heathland)
22 is an exception, since it is considered as a typical inhabitant of non-forested environments
23 (Kaczmarek, 1973; Ellis, 1974; Ponge, 1993; Shaw, 1997; Ponge et al., 2003). It can thus be
24 tentatively concluded that arboreal heath harbours a forest community but that some species

1 of non-forested environments can be present, too. To the light of poor existing literature on
2 Collembola living in ericaceous heath (Delany, 1956; Petersen, 1995; Shaw, 1997) it appears
3 that some typical ‘sun’ species such as *Brachystomella parvula* or *Isotoma anglicana* are
4 absent from mature heath but can be found after clearance of the heath by cutting operations
5 or fire and that species living in mature heath such as *Entomobrya nicoleti* do not colonize or
6 colonize only the border of areas from which heather [*Calluna vulgaris* (L.)] has been
7 excluded.

8

9 The introduction of blocks of heathland soil, with their original fauna and litter, in
10 agricultural land (pasture) showed that the Collembolan community evolved after two months
11 in the direction of the pasture community, while keeping the dominance of *Folsomia*
12 *quadrioculata* and most of its original population (Fig. 3). Shaw (1997) observed that the
13 disappearance of heath following severe disturbances such as deep-burning fire or soil
14 scraping depauperated Collembolan populations while less severe disturbances such as
15 superficial fire and charring kept for its main part the original population. We may tentatively
16 conclude that the presence of the original litter allowed litter-dwelling dominants of the
17 heathland community to be maintained at least over several months, while immigration from
18 the surrounding soil, rather from subordinate species than from dominants, occurred in the
19 same time. This result may be important for the long-term maintenance of the heathland soil
20 animal community. If ericaceous species are allowed to regrow rapidly after they have been
21 cut, and if the soil is kept undisturbed (by scraping or mowing), then no dramatic change can
22 be expected at the community level. Accordingly, Huhta and Mikkonen (1982) and Ponge et
23 al. (2003) observed that areas temporarily clearcut (and not burned) for the need of forest
24 renewal did not exhibit any pronounced change in species assemblages, i.e. they did not lose

1 their original forest character. On the contrary, recovery of forest communities is
2 very difficult following afforestation of agricultural land, except for generalist species or
3 forest species with a high dispersal rate (Bonnet et al., 1977; Deharveng, 1996; Ojala and
4 Huhta, 2001; Ponge et al., 2006; Huhta and Ojala, 2006). The importance of litter for the
5 maintenance of forest soil Collembolan communities has been verified experimentally (Ponge
6 et al., 1993). When litter is absent, as it is the case in tropical rain forests, even temporary and
7 surface-restricted cutting operations cause a collapse in Collembolan communities (Takeda,
8 1981, Oliveira and Deharveng, 1995).

9

10 The transfer of soil from pasture to heathland seemed to cause severe damages to the
11 Collembolan community, the transferred blocks being rapidly colonized by dominant species
12 of the heathland community. Lack of a litter habitat in agricultural soils may explain at least
13 partly this phenomenon. The maintenance of the living root system of grasses and sedges (and
14 their associated microbial partners), like litter in forest and heath ecosystems, may be
15 expected to be a crucial point for Collembolan communities living in pastures and meadows
16 (Klironomos and Hart, 2001). It has already been observed that the bulk of species from the
17 original agricultural soil is severely affected by afforestation (Bonnet et al., 1977; Ponge et
18 al., 2006). Although our experiment cannot mimic what happens when agricultural land turns
19 to heathland, which needs several decades to be achieved, it shows that the initial collapse of
20 typical agricultural populations may be very rapid after the abandonment of agriculture and
21 that a considerable lapse of time is necessary before a complete forest or heathland
22 community could be reconstructed, as suggested by Bengtsson (2002). The study by Ponge et
23 al. (2006) showed that in a variegated landscape, although ancient woodlots were distant by

1 less than 100 m, more than 50 years were necessary for the recovery of a complete
2 forest community when agricultural land has been afforested.

3

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13

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Table 1. Collembolan species names with their code and habitat preference. P values correspond to t-tests that compared the density (quasipoisson model) or the presence/absence (quasibinomial model) of each species between the two habitats. Habitat preference is put into brackets when the models only show a trend in habitat differentiation.

Code	Species names	Difference between habitats, P-value		Habitat preference
		Count quasipoisson	Presence quasibinomial	
APY	<i>Arrhopalites pygmaeus</i> group	0.497	0.206	
BPA	<i>Brachystomella parvula</i>	0.999	0.999	
CAL	<i>Cyphoderus albinus</i>	0.999	0.999	
CDE	<i>Ceratophysella denticulata</i>	0.066	0.872	
CTH	<i>Cryptopygus thermophilus</i>	0.999	0.999	
DFU	<i>Dicyrtoma fusca</i>	0.999	0.999	
DPA	<i>Deuterostimnthus pallipes</i>	1	1	
EMU	<i>Entomobrya multifasciata</i>	0.942	0.872	
FCA	<i>Folsomia candida</i>	0.825	0.908	
FQU	<i>Folsomia quadrioculata</i>	0.000	0.0002	Heathland
FTR	<i>Friesea truncata</i>	0.0004	0.000	Heathland
IBI	<i>Isotomodes bisetosus</i>	0.999	0.999	
IFU	<i>Isotomurus fuciculus</i>	0.013	0.897	(Pasture)
IMI	<i>Isotomiella minor</i>	0.0018	0.0003	Heathland
IVI	<i>Isotoma viridis</i>	0.999	0.999	
LCY	<i>Lepidocyrtus cyaneus</i>	0.009	0.059	Heathland
LLA	<i>Lepidocyrtus lanuginosus</i>	0.999	0.999	
LLI	<i>Lepidocyrtus lignorum</i>	0.937	0.708	
MJE	<i>Mesaphorura jevanica</i>	0.044	0.335	(Heathland)
MMA	<i>Mesaphorura macrochaeta</i>	0.381	0.999	
MMI	<i>Megalothorax minimus</i>	0.120	0.064	
MPY	<i>Micranurida pygmaea</i>	0.234	0.031	(Heathland)
OCI	<i>Orchesella cincta</i>	0.999	0.999	
PCA	<i>Paratullbergia callipygos</i>	0.708	0.521	
PIM	<i>Pseudosinella immaculata</i>	0.999	0.999	
PMI	<i>Proisotoma minima</i>	0.955	0.846	
PNO	<i>Parisotoma notabilis</i>	0.000	0.017	Pasture
PSS	<i>Pseudachorutes subcrassus</i>	0.083	0.0003	Heathland
PSU	<i>Protaphorura subuliginata</i>	0.999	0.999	
SAU	<i>Sminthurinus aureus</i>	0.999	0.999	
SEL	<i>Sminthurinus elegans</i>	0.999	0.999	
SPA	<i>Sminthurides parvulus</i>	0.027	0.151	(Heathland)
SPU	<i>Sphaeridia pumilis</i>	0.000	0.001	Pasture
SSC	<i>Sminthurides schoetti</i>	0.168	0.404	
SSI	<i>Sminthurinus signatus</i>	0.004	0.013	Heathland
SVI	<i>Sminthurus viridis</i>	0.122	0.206	
XTU	<i>Xenylla tullbergi</i>	0.091	0.206	

1 **Figure legends**

2

Figure 1. Design of the field experiment. Soil blocks came from four parcels, two heathland (H1 & H2, grey) and two pastures (P1 & P2, white). Blocks were either kept intact (HN & PN), digged up and replaced in the same position (HC & PC) or transferred to an other habitat (PH, heathland transferred into pasture; HP, pasture transferred into heathland).

3

Figure 2. Mean density of Collembola in the two habitats (estimated from control treatments over three months, expressed in number of individuals per m² or per liter) for each species and corresponding 95% confidence interval (see text for details). Note that for some species ('DPA' or 'IVI' in heathland for instance), the model failed to estimate the 95% confidence intervals. * indicates species for which the two estimated densities clearly differ (see Table 1 for detailed statistical results and species' code).

Figure 3. Changes in the abundance of Collembolan species according to months and treatments.

4

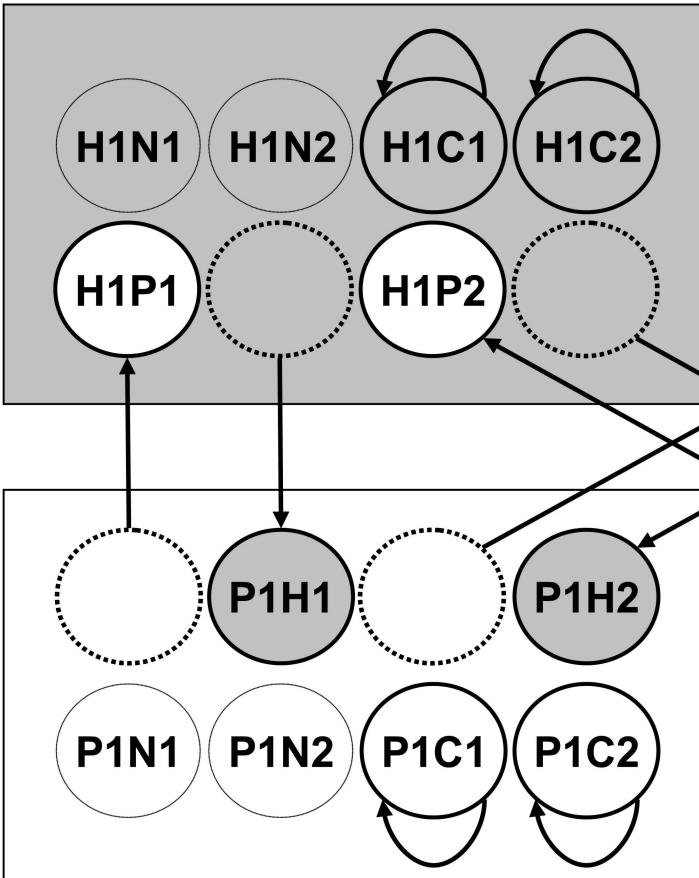
5 **Figure 4.** Correspondence analysis. Projection of species (left) and samples (right) in the
6 plane of the first two factorial axes. The arrow indicates the direction of a sample the
7 projection of which cannot be charted, being too far from the origin.

8

Figure 5. Mean and 95% confidence interval of collembola density, species richness, Shannon index and Community Index (Axis 1 of CA) for the three months of the experiment

and for the four treatments (untransplanted pasture and heathland and pasture transferred to heathland and heathland transferred to pasture).

Heathland 1 (H1)



Heathland 2 (H2)

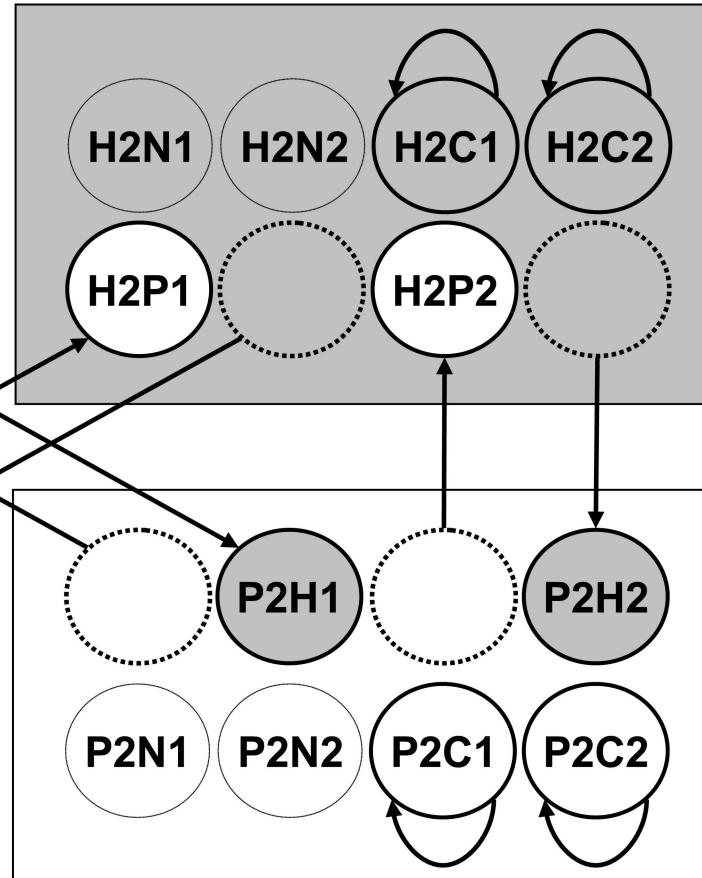
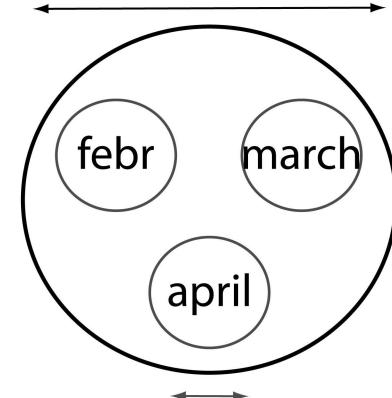


Figure 1

Transferred block
diam = 35cm

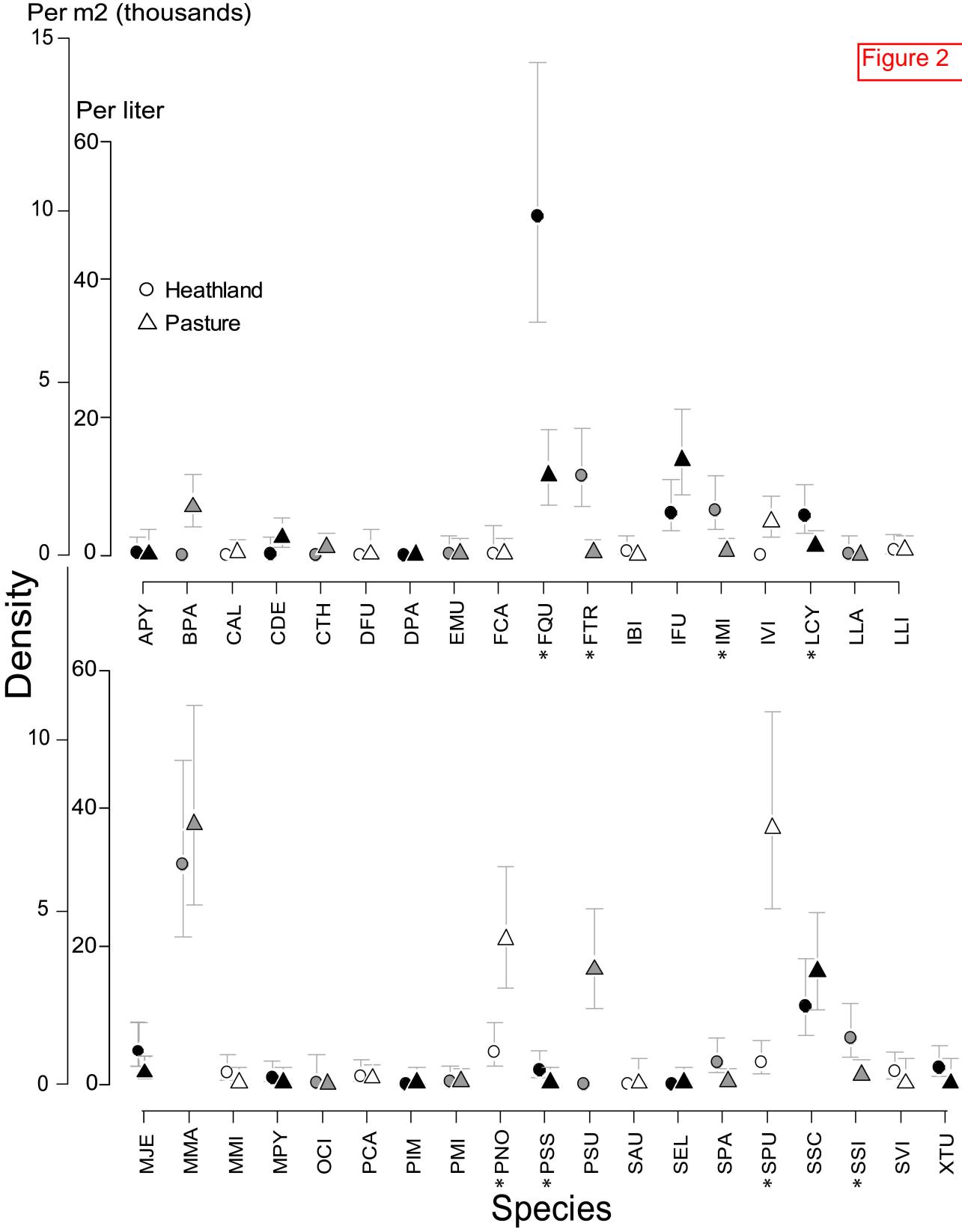


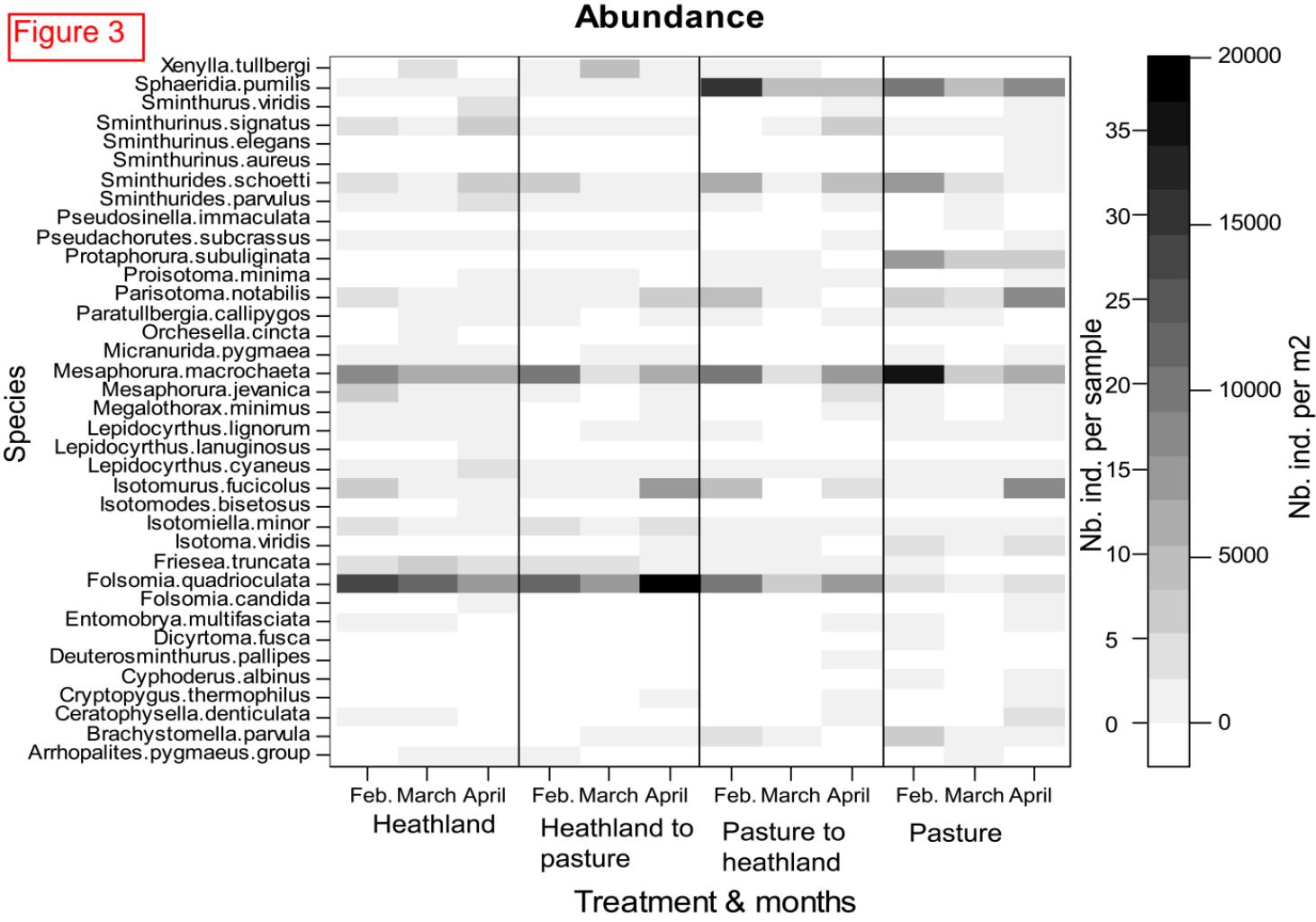
Core sample
diam = 5cm

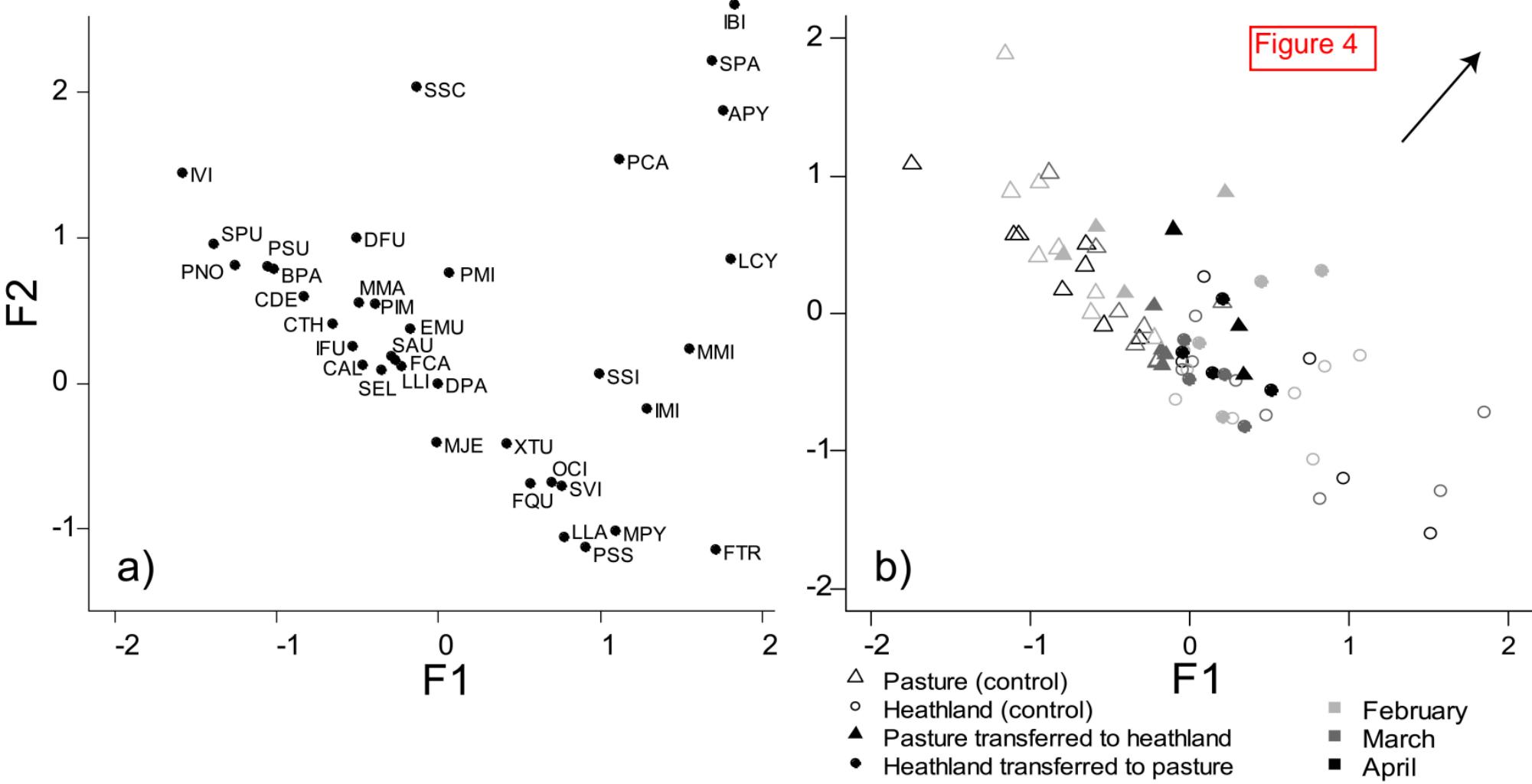
Pasture 1 (P1)

Pasture 2 (P2)

Figure 2







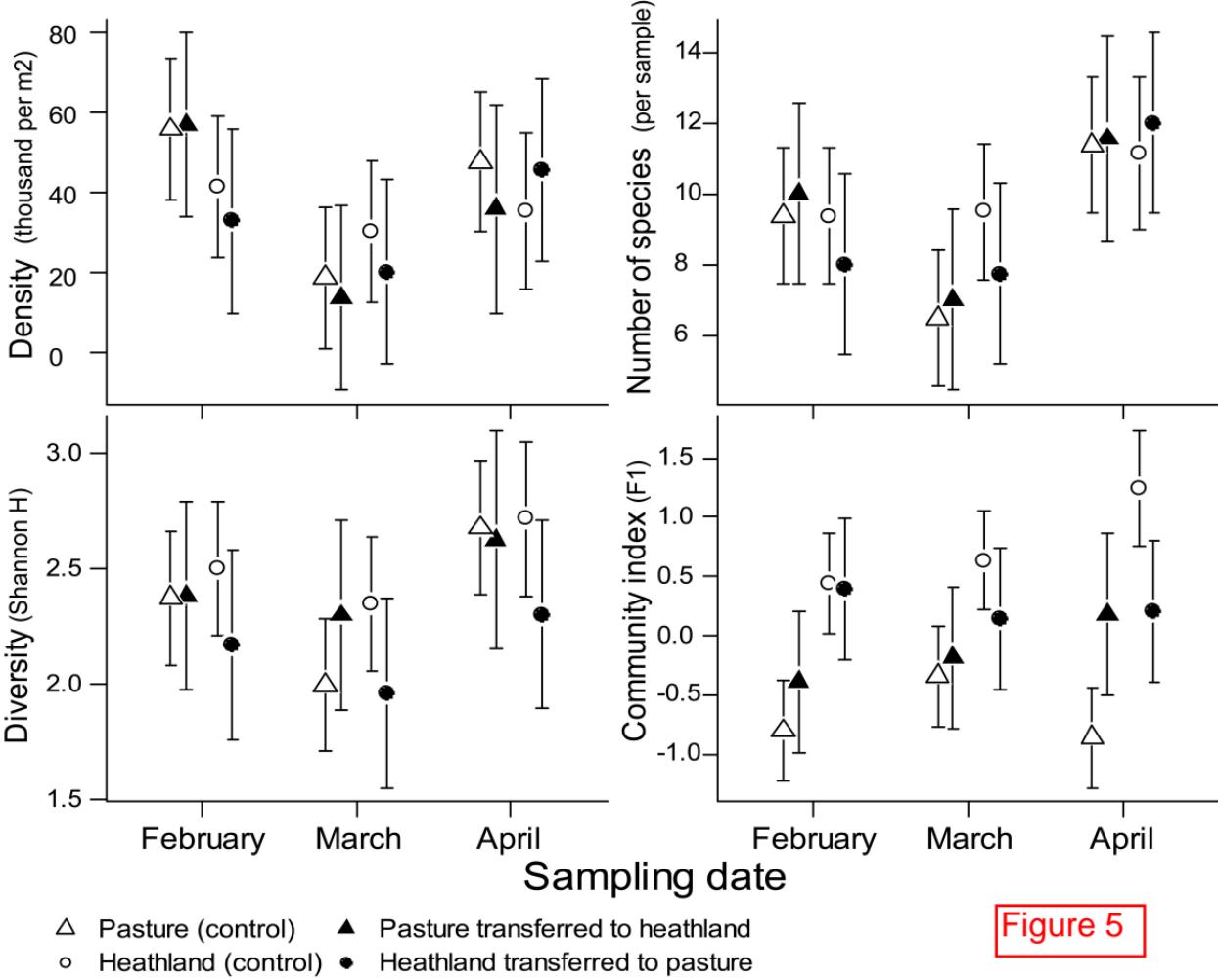


Figure 5