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Abstract

The goal of the present study was to determine whether the habitat preference of collembolan species is more influenced by soil properties or by microclimate and whether the preference for a given soil matches the preference for the corresponding microclimate. To answer these questions, we set up a soil core transfer experiment between a forest and an adjacent pasture. We first eliminated the entire soil fauna from forest and pasture soil cores and inoculated them with a new community originated from forest or pasture. After enclosing them, in order to prevent exchanges of soil animals between treated soil and surrounding environment, soil cores were transplanted back to the field for four months and a half. The experimental design comprises every combination of three factors (community origin, soil nature and microclimate) for a total of 8 treatments. Twenty-two species were present in the experiment, 16 of which were present in more than 10 % of the experimental soil cores. We determined habitat preference for these 16 species using a large dataset comprised of field observations in the same region. Results showed that most forest species did not withstand pasture

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microclimate, although some of them preferred pasture soil. Likewise several pasture species were favoured by the forest microclimate, some of them also preferring forest soil. We concluded that forest species were absent (or less abundant) in pastures because they are not resistant enough to drought, while pasture species were absent (or less abundant) in forests because of food requirements, and/or soil physicochemical properties such as soil pH and organic carbon content, and/or were less competitive. Moreover, when selecting their habitat, some species are submitted to a trade-off between preferences for different habitat features.

1. Introduction

The search for unifying principles in community ecology led to the identification of three processes that interact to shape species assemblages: 1) habitat selection, 2) dispersal and 3) biotic interactions (Weiher and Keddy, 2001; Wardle, 2006; Mayfield et al., 2009). Understanding the factors that determine the preference of a species for a given habitat is thus essential to predict species distribution and local community composition. In most habitats, many different factors (biotic and abiotic) interact, creating environmental conditions that allow or impede species persistence and reproduction (Bull et al., 2007). Furthermore, different species show different levels of specialization for a given habitat, from specialists which are only found in a restricted array of environmental conditions to generalists which are found in a wide array of environmental conditions (Egas et al., 2004; Julliard et al., 2006). The extent to which a species is specialist of a given habitat probably depends on how much it is adapted to the different habitat features and the level of specialization is likely to differ between habitat features.

For invertebrate species inhabiting soil and litter layers, habitat is at least twofold. First, the nature of the soil and the humus form are very influential: (1) they determine the availability and quality of resources such as organic matter, which in turn determines the composition and activity of microbial communities, one of the main food sources of soil invertebrates (Ponge, 1991; Murray et al., 2009; Sabais et al., 2011); (2) soil and humus through several physicochemical properties, such as pH, moisture, structure, carbon content, etc., are critical parameters for collembolan survival (Ponge, 1993; Berg et al., 1998; Loranger et al., 2001). Second, the type of vegetation is also influential: (1) it

influences the quality and quantity of organic matter inputs; (2) it influences the local microclimate and interacts with soil and humus to determine temperature and moisture levels which prevail within the soil (Chen et al., 2008; Ponge, 2013). For example tree canopy cover in forests prevents most UV radiation from reaching the ground surface and creates lower soil temperatures in forests compared to pastures (Scott et al., 2006).

Collembolan communities have been shown to vary according to vegetation types, e.g. open vs closed vegetation (Ponge et al., 2003; Vanbergen et al., 2007). Forests (closed vegetation) benefit from high inputs of litter which create thick organic (and organic-mineral) layers. High soil carbon content induces both low pH and high soil moisture and creates conditions favouring overall collembolan abundance and diversity (Hopkin, 1997). In addition, high organic inputs in forests provide abundant trophic resources. In contrast, open vegetation (e.g. any habitat without trees such as pastures or meadows) is characterized by intense export through mowing, grazing, or harvesting, and more active decomposition, which induces lower organic contents and reduced or absent organic layers (Compton and Boone, 2000). Additionally, the absence of tree cover induces higher temperatures in summer and lower soil moisture than in forests (Batlle-Aguilar et al., 2011). Thus, in collembolan communities, specialists of a given habitat should be intolerant to at least one feature of non-preferred habitats (microclimate, resource quality and/or availability, physicochemical factors): for example, forest specialists should be intolerant either to soil properties or microclimate of open habitats. In contrast, generalist species should be generalist for both soil and microclimate.

In their experiment, Auclerc et al. (2009) determined habitat preference and dispersal ability of a large set of collembolan species. Using a soil transplant experiment between a forest and a meadow, they showed that several forest-preferring and forest-strict species actually colonized more efficiently meadow soil transferred to forest than non-transferred forest soil. They suggested that certain forest species, more abundant in the transplanted meadow soil, could not survive in the meadow because of its microclimate. However, in their study the effect of species ability to colonize both soil types through dispersal was difficult to distinguish from the effects of actual preferences for a given habitat. Moreover, Auclerc et al. (2009) only transplanted soil cores from one type of habitat to another but did not submit collembolan communities to a different microclimate. This did not allow a full

disentanglement of the effects of soil and humus nature from the effects of microclimate determined by plant cover.

The present experiment thus aimed at addressing the two following questions. Are forest or pasture species excluded from (or less abundant in) pastures and forests, respectively, because they do not withstand differences in temperature and related soil moisture (microclimate) in these habitats, or because they do not find appropriate trophic resources and suitable physicochemical conditions (soil nature)? Are generalist species tolerant to both soil and microclimate? We hypothesize that forest and pasture species are not primarily influenced by the same habitat features. Forest species would be absent (or less abundant) in pastures because of physiological requirements for forest microclimate (i.e. higher humidity and lower temperature) whereas pasture species would be absent (or less abundant) in forests because they do not find appropriate trophic resources in them.

Given our choice of a transfer experiment in which animals cannot freely move to find suitable conditions for their growth and reproduction, preferences will be only inferred from their ability to survive and multiply better under certain conditions than others. This is also the sense given to the word “affinity” in similar experiments (Huhta, 1996) but we here refer to the definition given by Pey et al. (2014) of “ecological preference” as “the optimum and/or the breadth of distribution of a trait on an environmental gradient”, considering “ecological preference” as the result of multiple interacting ecophysiological traits each species display and “habitat preference” as a subset of “ecological preference.

2. Material and methods

2.1. Study site

The study was set up in a forest and an adjacent pasture in the Morvan Regional Natural Park at the same location as the experiment reported in Auclerc et al. (2009). The Morvan Natural Park is located in the centre of France (Burgundy) and has a submontane-atlantic climate with continental influence (mean annual rainfall 1000 mm and mean temperature 9 C). The bedrock is granite and soils are moderately to strongly acidic (pH < 5). The forest canopy is comprised of deciduous trees (*Fagus sylvatica* and *Quercus petraea*) and has been in place over at least a century, according to stand

structure. The forest soil is an Acrisol and the humus form is a dysmoder sensu Brêthes et al. (1995). The nearby pasture used to be mowed every year in spring and then grazed by cattle in summer and autumn, but mowing had been abandoned for several years because of poor forage production due to several consecutive drought years. The pasture soil is a Cambisol and the humus form is an eumull. The transition between forest and pasture is sharp.

2.2. Experimental design and soil core manipulation

We designed a soil core transplantation experiment between forest and pasture (closed vs. open vegetation, respectively) coupled with a manipulation of invertebrate communities. Eight treatments (five replicates each) corresponded to all possible combinations of three factors: community origin, COM (forest vs. pasture), soil origin, S (forest vs. pasture) and microclimate, CLIM (forest vs. pasture) (Fig. 1, see also Fig. 2 for a global view of manipulation steps). The setup took place between March and June 2011 (fauna removal, inoculation and transplantation) and the experiment ended in the beginning of November 2011.

2.2.1. Fauna removal and re-inoculation

In order to control the communities present in both soils (forest and pasture), we first removed the fauna and re-inoculated it with a new community extracted from a fresh soil core. This allowed us to have a forest community in the pasture soil and conversely a pasture community in the forest soil. Thirty soil cores (20 cm diameter x 10 cm depth) were taken in both forest and pasture (60 soil cores in total, i. e. the soil, including the soil biota, was sampled by taking of soil samples) and brought back to the laboratory. Soil fauna was then eliminated by repeatedly freezing soil cores. Each soil core was dipped in liquid nitrogen for 45 min. This was repeated after a week interval, in order to eliminate possible resistant eggs that could have been stimulated to hatch by the first freezing. In between, soil cores were stored in a cold chamber at 15 °C.

We then inoculated each soil core with a new community. To do so, 48 soil cores (24 for each soil) of the same volume (20 cm diameter x 10 cm depth) were taken at the same site. These cores were split into four equal parts in the field, packed into semi waterproof bags (plastic bags with holes

allowing gas exchanges) and brought back to the lab within two days. They were immediately stored in a cold chamber at 15 °C before being used as a new community source for re-inoculation. Fourteen defaunated pasture soil cores were inoculated with a community originating from the pasture (4 of which were used as controls, see following section) and 10 pasture soil cores were inoculated with a community originating from the forest. Likewise, 14 defaunated forest soil cores were inoculated with a community originating from the forest (4 of which were used as controls, see following section) and 10 forest soil cores were inoculated with a community originating from the pasture. To re-inoculate communities, we used a Berlese dry-funnel extractor. We placed the fresh soil on the extractor sieve and the soil core which had been previously defaunated under it. This procedure allowed transferring the new community from the fresh to the defaunated soil core. Each quarter of the fresh cores was left one week on the extractor sieve. Re-inoculation thus lasted 4 weeks. Each week, one quarter of the soil cores used for re-inoculation was placed on the extractor sieve after the previous quarter was removed. Soil cores were watered every week with 100 mL distilled water. After fauna removal and before re-inoculation, we watered all soil cores with a soil suspension (10 g of soil sampled the same day per litre distilled water) sieved to 20 µm. Pasture and forest soil cores were watered with a soil suspension prepared with pasture and forest soils, respectively. This procedure was performed in order to re-establish the microbial community in soil cores after fauna removal (freezing).

2.2.2. Soil core enclosure and transplantation to the field

In order to prevent as much as possible exchanges of soil animals between treated soils and the surrounding environment, soil cores were enclosed in PVC pipes covered with a 350 µm mesh at their top and a 20 µm mesh at their bottom. We finally brought the 46 manipulated soil cores back to the field. Each soil-community treatment was transplanted both in the forest and in the pasture and was left in the field from June 15 to November 2, 2011 (four and a half months).

The experimental design thus comprised every combination of three factors (community origin, soil and microclimate) for a total of 8 treatments with 5 replicates each (Fig 1). Additionally, it included 3 types of manipulation controls and 2 types of natural references (3 to 5 replicates depending on the type of control, see next section).

2.2.3. Experimental controls and natural references

At each stage of the experimental setup, controls were implemented. This allowed us to assess the efficiency of: 1) fauna removal, 2) community re-inoculation, 3) exclosure, and allowed us to determine the composition of forest and pasture communities in a non-manipulated situation.

To check for the efficiency of fauna removal, we randomly selected 3 soil cores of each soil directly after fauna removal and we performed fauna extraction (fauna removal controls).

To check for the efficiency of community re-inoculation, 8 soil cores (4 forest and 4 pasture cores inoculated with their own community) were randomly selected directly after re-inoculation and placed in a Berlese dry-funnel extractor (inoculation controls).

To check for the efficiency of exclosure, 6 soil cores (3 for each soil) were randomly selected and directly enclosed after fauna removal (i. e. without inoculation with a fresh community) and brought back to the field for transplantation (exclosure controls).

In order to determine the composition of both communities in the undisturbed (i.e. non-manipulated) situation, 3 samples (5 cm diameter x 10 cm depth) were taken at the same time in each habitat (forest and pasture) when sampling for the soil material used to re-inoculate experimental soil cores (natural control t_0). They were brought back to the laboratory on the same day for fauna extraction. Likewise, 5 samples (5 cm diameter x 10 cm depth) were taken in each habitat (forest and pasture) at the end of the experiment and brought back to the laboratory within three days for fauna extraction (natural controls t_{end}).

All fauna extractions were performed using a Berlese dry-funnel apparatus and lasted 12 days.

2.3. Soil sample treatments

At the end of the experiment, we sampled each core according to three methods. First, a sample 6.3 x 6.3 x 10 (depth) cm was taken at the centre of each core for fauna extraction (fauna samples). Second, a 300-g sample was taken in each core, air dried and sieved (2 mm) for soil analysis (soil pH_{water}, total carbon, and total nitrogen content by gas chromatography). And third, another 300-g sample was taken in each core and immediately packed in waterproof bags for soil moisture measurements.

Fauna samples were brought back to the lab within three days and placed in a Berlese dry-funnel extractor for 12 days. Animals were collected and stored in 70 % ethyl alcohol until identification. Collembola were mounted, cleared in chloral-lactophenol and identified to species level under a light microscope (magnification x 400), according to Hopkin (2007), Potapov (2001), Thibaud et al. (2004) and Bretfeld (1999). Due to the very large number of individuals belonging to this species group, we pooled the two species *Folsomia quadrioculata* and *F. manolachei* together.

2.4. Calculation of species overall habitat preference

The two ecological traits describing the habitat preference (IndF and IndA, see below) of each species were calculated using the IndVal index (Dufrêne and Legendre, 1997) adapted to the measurement of preference for a given habitat type by Auclerc et al. (2009). For this calculation, we used the data set produced in Ponge et al. (2003), who worked in exactly the same region. One species present in our study (*Detriturus jubilarius*) was absent from the study by Ponge et al. (2003). The habitat preference of this species was assessed according to expert knowledge (Salmon, unpublished data).

The IndVal index combines the specificity of a species for a habitat type (maximized when the species is found only in a given habitat) and its fidelity to this habitat (maximized when the species is found in all samples of a given habitat):

$Ind_{ij} = A_{ij} * B_{ij} * 100$, where

A_{ij} = average abundance of species *i* in samples of habitat *j* divided by the average abundance of species *i* in all samples.

B_{ij} = number of samples of habitat *j* where the species is present divided by the total number of samples of habitat *j*.

Ind_{ij} ranges from 0, when species *i* is absent from habitat *j*, to 100 (its maximum value), when species *i* is present in all samples of habitat *j* and absent in all other habitat samples. We thus obtained two

IndVal values for each species, one for forest (IndF) and one for agricultural land (IndA). Classes of habitat preference were then determined using the IndVal values IndF and IndA for each species. Species present in both habitat types and having a ratio IndF/IndA (or the reverse) higher or equal to 0.25 were classified as “generalists”. Species having a ratio IndA/IndF lower than 0.25 were classified as “forest-preferring” and species having a ratio IndA/IndF = 0 were classified as “strict forest” species. Species having a ratio IndF/IndA lower than 0.25 were classified as “agricultural-preferring” and species having a ratio IndF/IndA = 0 were classified as “strict agricultural” species (sensu Auclerc et al., 2009).

2.5. Data analyses

2.5.1. Assessing the effect of experimental manipulation

In order to detect possible effects of soil manipulation, inoculation, and exclosure on species abundance, we implemented linear models testing the effect of control type (natural controls t_0 and t_{end}, inoculation control, exclosure control, and experimental control, i.e. treated soil cores transplanted in their own microclimate with their own community), habitat type (forest vs. pasture) and the interaction between these factors, on total abundance (type III sum of squares used for unbalanced design). As the soil volumes sampled for natural controls (t_0 and t_{end}) and experimental controls were different, we transformed the total abundance into areal density (number of individuals per m^2). To fulfil linear model assumptions, areal density was log-transformed. In order to compare community structure and composition of all types of controls (natural controls t_0 and t_{end}, inoculation control, exclosure control, and experimental control), we performed a principal component analysis using abundances of common species (i.e. present in at least 10 % of the experimental cores).

In order to detect the effects of experimental treatments on soil properties (total carbon and nitrogen content, soil pH and moisture) we implemented linear and generalized linear models (Gamma link function) testing the effect of soil nature (forest vs. pasture) and microclimate (forest vs. pasture) on soil properties. Data for total carbon and nitrogen content and for soil moisture were log-transformed to fulfil linear model assumptions.

2.5.2. Effect of experimental treatments on collembolan diversity and abundance

In order to detect the effects of experimental treatments on collembolan diversity and abundance, we tested the effect of the three experimental factors (origin of the community, soil nature and microclimate) and the interaction between these factors on species richness, Shannon diversity index, and total abundance using linear models. Abundances were log-transformed to fulfil linear model assumptions. Models were tested after a procedure of automatic model selection based on AIC criterion (stepwise procedure). Combinations of experimental treatments were compared using least square means and associated multiple comparisons of means (Tukey).

2.5.3. Effect of experimental treatments on collembolan community structure and species abundance

In order to detect the effect of experimental treatments on community structure, we implemented a between-group multivariate analysis (Baty et al., 2006) on abundances of common species in each treatment. Between-group analysis is a particular case of instrumental variables methods where a single qualitative variable is accounted for (Baty et al., 2006), providing the best linear combination of variables maximizing between-group variance. Between-group analysis was performed using a combination of the three experimental factors (origin of the community COM, soil nature S and microclimate CLIM, 8 combinations) as the explanatory variable. The significance of the composite factor COM/S/CLIM was tested using a Monte-Carlo permutation test (999 permutations).

The effects of experimental factors (COM, S, CLIM and all possible interactions) on the abundance of each common species (i.e. species present in at least 10 % of the experimental cores) were tested using generalized linear models (poisson link function) after a procedure of automatic model selection based on AIC criterion (stepwise procedure). Combinations of experimental treatments were compared using least square means and associated multiple comparisons of means (Tukey). Based on the results of these models, we classified species according to their response to experimental factors. Species being significantly more abundant in a given soil and/or microclimate were considered as preferring this soil and/or microclimate. Species showing similar preferences for soil nature and microclimate were grouped together.

All statistical analyses were performed using vegan, ade4, car, and lsmeans packages of R software (R Development Core Team, 2010).

3. Results

3.1. Experimental controls

In total, 28 species were found (controls included), of which 22 species were present in the experimental treatments (controls excluded). Among these 22 species, 6 were present in less than 10 % of the experimental soil cores (< 4 cores) and were thus excluded from the analysis for improving robustness of the conclusions. Among the 16 species kept for the analysis, 9 were also present in exclosure controls. Among these 9 species, four were present in both pasture and forest exclosure controls (*Lepidocyrtus lanuginosus*, *Mesaphorura macrochaeta*, *Parisotoma notabilis* and *Sphaeridia pumilis*), four were present in pasture exclosure controls only (*Brachystomella parvula*, *Isotoma viridis*, *Protaphorura armata* and *Sminthurides schoetti*) and one species was present in forest exclosure controls only (*Xenylla tullbergi*) (Table 1). Thirteen species were successfully inoculated in the experimental soil cores, among them four species were successfully inoculated in both forest and pasture soils, seven were inoculated in forest soil only and two were successfully inoculated in pasture soil only (Table 1). No Collembola were found in the fauna removal control either in pasture or forest soil.

The linear model testing the effect of treatments on collembolan density showed that the type of control (natural controls t_0 and t_{end}, inoculation control, exclosure control, and experimental control) and the interaction between control type and soil nature exerted an influence on collembolan density ($p<0.001$ and $p<0.01$, respectively). Collembolan density was significantly higher in inoculation controls and in experimental controls than in natural controls taken at the end of the experiment (t_{end}) (Fig. 3). Additionally, post-hoc tests (Tukey) showed that the natural control taken at the end of the experiment (t_{end}) in the pasture showed a lower collembolan density than both forest and pasture experimental controls. It also showed a lower density than the natural controls taken at the end of the experiment in the forest and than exclosure and inoculation controls in the pasture (Fig 3). The first two axes of principal component analysis (PCA) implemented on species abundances of controls (Fig.

289 4) extracted 34.5 % of the total variance (29.4 % and 15.1 %, respectively). PCA showed that
290 communities were distinguished according to community origin on axis 1, pasture communities
291 standing on the positive side and forest communities standing on the negative side of axis 1. However,
292 the exclosure control in the forest (TexF) displayed communities closer to the pasture on axis 1. The
293 community in the forest experimental control (FFF) lay close to the community of forest natural
294 reference both at the beginning and at the end of the experiment. In contrast, the community of the
295 pasture experimental control (PPP) lay close to the community of the pasture natural reference at the
296 end of the experiment but far from the one present at beginning of the experiment.

297 *3.2. Effects of experimental treatments on soil physicochemical properties*

298 Linear and generalized linear models (Table 2) testing the effect of soil nature (forest vs.
299 pasture) and microclimate (forest vs. pasture) on soil properties (total carbon and nitrogen content, soil
300 pH and moisture) showed that the total carbon content was higher in forest than in pasture soil. In
301 contrast, the total nitrogen content did not differ with soil nature or microclimate. Soil pH was higher
302 in pasture than in forest soil ($p<0.001$) and soil pH in pasture soil was higher under forest than under
303 pasture microclimate ($p<0.001$, Fig. 5a). Soil moisture was significantly affected both by soil nature
304 and microclimate ($p<0.001$, and $p<0.01$ respectively). Soil moisture was higher in forest than in
305 pasture soil and soil moisture in pasture soil was higher under forest than under pasture microclimate
306 (Fig. 5b).

307 *3.3. Effects of experimental treatments on collembolan diversity and abundance*

308 Linear models testing the effect of the three experimental factors (origin of the community,
309 soil nature and microclimate) on species richness, Shannon index, and total abundance (Table 3)
310 showed that the three factors (community origin, soil nature and microclimate) had an effect on total
311 abundance ($p<0.01$, $p<0.05$, and $p<0.001$, respectively). Collembola were more abundant in the
312 pasture than in the forest community (community origin), they were also more abundant in the pasture
313 than in the forest soil, but they were more abundant under forest than under pasture microclimate (Fig.
314 6a). Only the origin of the community exerted an effect on species richness ($p<0.001$). The community

originating from the forest displayed higher species richness than the community originating from the pasture, whatever the microclimate or the soil in which they were inoculated (Fig. 6b). Finally, these models showed that community origin, soil nature, and the interaction between community origin and microclimate had a significant effect on the Shannon index ($p<0.001$, $p<0.01$, and $p<0.01$ respectively). The Shannon index was higher in forest than in pasture community and was also higher in forest than in pasture soil. Post-hoc tests (Tukey) showed that the interaction between community origin and microclimate was due to the fact that the Shannon index was higher under forest than under pasture microclimate, but only for the community originating from the pasture (Fig. 6c).

3.4. Effects of experimental treatments on collembolan community structure and species abundance

The individual response to experimental treatments of the 16 most common species is shown in the Appendix. Between-group analysis (Fig. 7) performed on species abundances taking a combination of community origin, soil nature, and microclimate as the explanatory variable extracted 56 % of the total variance. Axes 1 and 2 accounted for 44 % and 23 % of the variance extracted, respectively. Nine species contributed to the formation of axis 1, four on the positive side (*Protaphorura armata*, *Parisotoma notabilis*, *Mesaphorura macrochaeta* and *Pseudosinella alba*) and five on the negative side (*Folsomia* spp., *Isotomiella minor*, *Detriturus jubilarius*, *Megalothorax minimus* and *Friesea truncata*). Axis 1 discriminated communities according to their origin, pasture on the positive side and forest on the negative side. Only three species mostly contributed to the formation of axis 2, all of them negatively (*Sminthurides schoetti*, *Isotoma viridis* and *Xenylla tullbergi*). Axis 2 discriminated forest communities according to the microclimate in which they were transplanted, forest microclimate on positive side and pasture microclimate on negative side. For the pasture community, treatments were much less discriminative on axis 2 than for the forest community. A Monte-Carlo permutation test showed that the composite factor COM/S/CLIM significantly affected the community ($p=0.001$).

339 *3.5. Species classification based on the effect of experimental treatments on species abundance*

340 Using generalized linear models testing the effect of the three factors COM, S, and CLIM on
341 species abundance, we classified species into six groups according to their response to the factors
342 (Table 1). Group A was comprised of three species (*Isotomiella minor*, *Megalothorax minimus*, and
343 *Pseudosinella mauli*) that were more abundant in forest community, soil and microclimate. They were
344 labeled "true forest species" (Fig 8a). Group B was comprised of three species (*Folsomi*a spp., *Friesea*
345 *truncata* and *Detriturus jubilarius*), that were more abundant in both forest community and
346 microclimate, but were more abundant in pasture soil (Fig. 8b). They were labeled "forest species
347 preferring pasture soil". Species of groups A and B were classified as forest species except *Folsomia*
348 spp. that were classified as generalists using the IndVal index calculated with the data set produced in
349 Ponge et al. (2003) (Table 1). Group C was comprised of two species (*Protaphorura armata* and
350 *Pseudosinella alba*) that were more abundant in the pasture community but more abundant in the
351 forest soil. Additionally, while *Protaphorura armata* was also more abundant in the forest
352 microclimate (Fig. 8c), microclimate did not exert an effect on the abundance of *Pseudosinella alba*.
353 Group C was labeled "pasture species preferring forest soil". Group D was comprised of two species
354 (*Mesaphorura macrochaeta* and *Parisotoma notabilis*) which were more abundant both in pasture
355 community and soil but were more abundant in forest microclimate (Fig 8d). They were labeled
356 "pasture species preferring forest microclimate". Group E was comprised of three species
357 (*Brachystomella parvula*, *Lepidocyrtus lanuginosus*, and *Sphaeridia pumilis*) that were more abundant
358 in pasture microclimate. However, in this group, all three species showed a preference for a different
359 component of the forest habitat, either for soil (*Lepidocyrtus lanuginosus*) or forest community, i.e.
360 were more abundant in cores inoculated with a forest community (*Sphaeridia pumilis*), or both
361 components (*Brachystomella parvula*). Group E was labeled "species preferring pasture
362 microclimate". And finally, group F was comprised of three species (*Xenylla tullbergi*, *Isotoma viridis*
363 and *Sminthurides schoetti*), that were more abundant in both pasture soil and microclimate. *Isotoma*
364 *viridis* (Fig. 8e) and *Sminthurides schoetti* were as abundant in cores inoculated with a pasture
365 community as in cores inoculated with a forest community whereas *Xenylla tullbergi* (Fig. 8f) was
366 more abundant in cores inoculated with a forest community. This group was labeled "pasture species".

Most species of groups C, D, E and F were classified as agricultural and generalist species except for *Xenylla tullbergi* that was classified as a forest species according to the IndVal index calculated with the data set produced in Ponge et al. (2003) (Table 1).

4. Discussion

4.1. Effect of soil nature and microclimate on collembolan total abundance and community structure

Our results show that collembolan abundance was higher in forest than in pasture microclimate for both forest and pasture communities. Transplantation decreased the moisture content of forest cores when transplanted in the pasture and it increased the soil moisture of pasture cores transplanted in the forest (Fig. 5b, Table 2). Collembola are known to be sensitive to drought (Vannier, 1987). We thus attribute to this physiological trait the overall abundance increase in forest microclimate and decrease in pasture microclimate. It means that forest species are likely to be absent (or less abundant) in pasture mainly because they survive poorly in pasture climate conditions. This may concern only some stages of collembolan life, such as the moisture-sensitive first stadium, stemming in the incapacity of some species to endure moisture and temperature fluctuations which characterize open environments as opposed to closed environments (Betsch and Vannier, 1977). Additionally, we showed that forest communities were different under pasture and forest microclimate whatever the nature of the soil. This means that microclimate conditions are the first driver shaping collembolan communities in the forest. We thus suggest that forest species display physiological traits (namely poor resistance to drought) that prevent them from surviving or growing larger populations in open habitats. The pasture community did not show such a trend, suggesting that microclimate change (pasture to forest) did not affect its species composition. Thus, microclimate conditions are not likely to be the most important constraint shaping the pasture community.

4.2. Species preferences for soil and microclimate

Our experimental design enabled us to unravel species responses to soil nature and microclimate. We showed that some species, classified as forest species according to field occurrence data, are more abundant in forest soil and microclimate and that these species are also more abundant

in the communities originating from the forest (Group A). These species can thus be regarded as “true forest species” because they need both forest microclimate (moisture, temperature) and soil (food resources and physicochemical properties) to fully develop, at least in the studied region. This is supported by previous experiments showing that *I. minor* and *M. minimus*, two out of the three “true forest species” (Group A), are particularly sensitive to drought (Makkonen et al., 2011). However, some other species, also classified as forest species using the large data set from Ponge et al. (2003), are shown to prefer the pasture soil when transplanted to the forest microclimate (Group B). Hence, for these species, preferences for soil and microclimate are not tuned. It means that although they prefer the forest microclimate (temperature and moisture) they prefer trophic resources or physicochemical properties of the pasture soil. Their confinement to forest habitats is thus the result of climate requirements overwhelming soil quality requirements, i.e. least-worst strategy (Berger et al., 2012).

Some authors have already underlined the strong influence of microclimate on Collembola (Lindberg and Bengtsson, 2005; Makkonen et al., 2011; Petersen, 2011). In their experiment, Krab et al. (2010) showed that most species found in a subarctic community tended to select microclimate over substrate quality. Here, we go further and show that some forest species survive better in pasture soil (of mull type) if they can find forest climate conditions. Such conditions (forest microclimate and pasture soil quality) are fulfilled in not or poorly acidic forest soils, as already shown on census basis (but not experimentally demonstrated) by Ponge (1993).

Likewise, we showed that some pasture and generalist species benefit from the forest microclimate (Group D plus *Protaphorura armata*) but that the abundance of some species decreases when they are transferred to the forest soil (Group D). These species are thus also favoured by higher soil moisture and lower temperature but probably do not find in forest habitat appropriate resources and/or physicochemical features, or are too poorly competitive to maintain populations as large as in the pasture soil. However, pasture species of Group C are more abundant in the forest soil indicating that this soil fulfils their trophic and/or physicochemical requirements. We can thus genuinely ask why these species are more abundant in pasture, given that they seem to be favoured by forest microclimate and soil. Since we eliminated environmental filters (microclimate, soil quality) and dispersal limitation

(eliminated in our experimental design) the answer probably relies in species interactions. Although suspected to explain cases of species richness deficit or species turnover at the local scale (Hågvar, 1990; Winkler and Kampichler, 2000), competition within soil communities is still a too scarcely investigated topic (Bardgett, 2002; Decaëns, 2010). Despite being primarily carried out in laboratory conditions and with a reduced number of species, the few studies trying to shed light on the importance of competition in structuring soil communities suggest that competition occurs and is an important mechanism (Christiansen, 1967; Christiansen et al., 1992; Theenhaus et al., 1999; Postma-Blaauw et al., 2005). Our experiment does not allow directly testing this hypothesis, but our results show that some pasture and generalist species would perfectly withstand and even benefit from forest climate conditions and/or soil quality. This suggests that they are prevented from developing larger populations in forests by forest collembolan species that might be more efficient in exploiting forest resources. To these effects of other members of the collembolan community must be added those of members of a much wider community, the complete trophic network in which Collembola are included, still imperfectly known up to present (Brose and Scheu, 2014). Biotic interactions in which Collembola are dynamically involved include negative interactions such as predation (Lawrence and Wise, 2000), but also positive interactions such as earthworm attraction (Salmon, 2001).

Finally, several species are more abundant under pasture microclimate (Groups E and F). They were all classified as agricultural or generalist species with a single exception: *Xenylla tullbergi* is the only forest species (present in the original forest community only) that is more abundant in pasture soil and under pasture microclimate. This result may be explained by the fact that *Xenylla tullbergi* is mostly found in corticolous habitats (Ponge, 1993). It is thus drought tolerant but found more abundantly in trees (absent from agricultural plots such as pasture). Its absence in the pasture community may also result from competition with pasture species. All other species of Groups E and F are agricultural or generalist species that prefer pasture microclimate (Group E) or pasture microclimate and soil (Group F). In Group E, two species were more abundant in the forest soil, which suggests that they either prefer resources found in forest soil or are favoured by higher soil moisture (or other physicochemical properties linked to forest soil) as we showed that under pasture microclimate, soil moisture was higher in the forest than in the pasture soil. We only found two

449 species classified as agricultural species that were actually more abundant in pasture soil and under
450 pasture microclimate as supported by previous observations in agricultural habitats (Fratello et al.,
451 1985; Dittmer and Schrader, 2000; Frampton et al., 2001). These two “pasture species” are thus likely
452 to be primarily influenced by microclimate, resources, and soil physicochemical properties rather than
453 by interspecific competition. However, conclusions about *Sminthurides schoetti* (one of the two
454 abovementioned species) must be drawn with caution. Indeed, this species is the only one that did not
455 succeed in re-inoculated samples but was present in the exclosure controls in the pasture. It is thus
456 present in the experimental soil cores as a pure “invader”. Therefore, the preference of this species for
457 pasture or forest microclimate could not be ascertained. However we can be fairly certain that this
458 species preferred the pasture soil as it was more abundant than in the forest soil independently of the
459 community that was present in the soil beforehand.

460 Our results show that all forest species are better represented under forest microclimate, but
461 that some of them prefer the pasture soil. It means that the most important factor constraining forest
462 species is actually the microclimate. This is probably explained by physiological intolerance of forest
463 species to summer drought. Thus, for some forest species (Group B) habitat preference seems to be the
464 result of a trade-off between physiological requirements and requirements for resources and/or the
465 physicochemical environment.

466 *4.3. Methodological limitations*

467 We were not able to fully prevent exchanges between experimental cores and their
468 surroundings. More than half of the species present in more than four experimental soil cores (i.e.
469 common species) invaded the mesocosms. All these species but one were agricultural or generalist
470 species. This means that agricultural and generalist species have a greater mobility than forest species,
471 as they had to climb or jump over the mesocosms in order to penetrate them. This is also partly why
472 forest communities transplanted to pasture microclimate largely differed from forest communities
473 transplanted to forest microclimate. The latter communities were not influenced by species invading
474 from the surrounding pasture. Additionally, soil moisture in pasture soil cores was higher under forest
475 than under pasture microclimate and we showed that total collembolan abundance was also higher in

476 pasture experimental control than in natural controls. Thus, microclimate conditions created in the
477 mesocosms seem to overall favour species abundance of the pasture community. Hence some of our
478 results must be interpreted cautiously. First we showed that species richness was not affected by any
479 experimental treatment. Species richness was only lower in the original pasture than in the original
480 forest community. However, the invasion of the forest community by pasture species in microcosms
481 transplanted to the pasture artificially increased species richness. Second, we cannot totally refute that
482 the decrease in the abundance of some forest species under pasture microclimate was due to
483 competitive exclusion from species invading from the surrounding pasture. Besides, we do not know
484 what effects experimental manipulations had on microbial communities. Nevertheless, we were able to
485 successfully re-inoculate most common species despite a long-lasting experimental procedure and to
486 provide responses about soil and microclimate preferences of several collembolan species. This is very
487 encouraging for future experiments dealing with Collembola as more studies are still needed to fully
488 understand mechanisms responsible for patterns of species distribution.

489 Changes in species composition are known to occur over the year in collembolan communities
490 (Chagnon et al., 2000). Thus in our transfer experiment starting in spring and ending in autumn
491 temporal variability accompanied the effects of microclimate and soil change, and thus could have
492 blurred these effects. This cannot avoided, because expected effects take necessarily some time to
493 appear at community level, through the combination of growth, reproduction, dispersal and species
494 interactions, adding their effects to immediate mortality. However, natural controls, sampled at the
495 beginning and at the end of our transfer experiment, allowed discerning changes in species
496 composition in the meadow while no discernible change occurred in the forest (Fig. 4). Data collected
497 on the same sites in the abovementioned experiment by Auclerc et al. (2009) can be used to support
498 this assessment. A sign-test done on the 16 more common species (unpublished data) showed that over
499 the six months of this experiment (from December to June) the species composition did not change in
500 the forest (exact P value = 0.454) while it significantly changed in the meadow (exact P value =
501 0.021). Thus temporal changes of collembolan populations are probably included in the observed
502 effects of transfer from forest to pasture but not in the reverse case, to the possible exception of species
503 with genetically coded cycles of egg diapause (Leinaas and Bleken, 1983).

5. Conclusion

We showed that habitat preference depends on responses to microclimate and soil quality and that environmental constraints have a different importance depending on the overall habitat preference of species. We conclude that an anthropogenic-induced stress, such as habitat conversion (deforestation or afforestation), modifies collembolan communities to a large extent, and that species show different levels of resistance to perturbations and respond to different constraints (e.g. microclimate, soil, interspecific competition). Generally, forest species seem to be primarily influenced by microclimate, whereas pasture species seem more influenced by trophic resources and competition. This suggests that trade-offs between several habitat constraints are at play and structure collembolan communities in open vs. closed vegetation. More insights into the importance of competition and predation in structuring collembolan communities are still needed at community level.

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654

Figure captions

Figure 1. Schematic representation of the experimental design. Soils cores are represented by squares (dark grey for the forest and light grey for the pasture). Letters on squares summarize the treatments: the first letter refers to the origin of the community ("F" for forest and "P" for pasture); the second letter refers to the origin of the soil ("F" for forest and "P" for pasture) and the third letter refers to the habitat (microclimate) in which the core has been transplanted ("F" for forest and "P" for pasture). For species codes see Table 1.

Figure 2. Summary of manipulation steps.

Figure 3. Mean collembolan density in 5 types of controls (experimental, inoculation, natural at the beginning (t_0) and at the end (t_{end}) of the experiment, exclosure) in forest (grey bars) and pasture (white bars) soils (see text for details). Letters indicate significant differences among means. Error bars represent standard errors.

Figure 4. Principal component analysis using abundances of common collembolan species (i.e. present in at least 10 % of the samples) in the 5 types of controls (3 manipulation controls e.g. inoculation, exclosure, and experimental controls and 2 natural references e.g. t_0 and t_{end} controls). Left: Projection of dataset variability plotted on a factorial map of the first two principal components. Labels on the gravity centers correspond to each treatment. TF0: natural reference in forest at beginning of the experiment, TFend: natural reference in forest at end of the experiment, FFF: control experiment for forest community, TeF: inoculation control for forest community in forest soil, TexF: fauna removal control for forest community, TP0: natural reference in pasture at beginning of the experiment, TPend: natural reference in pasture at end of the experiment, PPP: control experiment for pasture community, TeP: inoculation control for pasture community in pasture soil, TexP: fauna removal control for pasture community. Right: Correlation circle plot with species vectors (vector labels correspond to species codes in Table 1).

Figure 5. Mean soil pH (a) and mean soil moisture (b) in experimental forest (left) and pasture (right) soil cores, placed in forest (grey bars) and pasture (white bars) microclimates and in natural references (dashed bars). Letters indicate significant differences among means. Error bars represent standard errors.

683 **Figure 6:** Mean collembolan abundance (a), species richness (b) and Shannon index (c) in
684 experimental soil cores. From the left to right: forest community in forest soil, forest community in
685 pasture soil, pasture community in forest soil, and pasture community in pasture soil. Grey bars: forest
686 microclimate and white bars: pasture microclimate. Letters indicate significant differences among
687 means. Error bars represent standard errors.
688 **Figure 7:** Between-group analysis on the abundance of common species, with the composite factor
689 COM/S/CLIM as explanatory variable. Left: Projection of dataset variability plotted on a factorial map
690 of the first two discriminating axes according to a combination of COM, S and CLIM. Labels on the
691 gravity centers correspond to each treatment (treatment codes according to Fig. 1). Right: Correlation
692 circle plot with species vectors (vector labels correspond to species codes in Table 1). Eigen values
693 0.44, 0.24, 0.16 for axes 1 to 3, respectively; Randtest: simulated p-value: 0.001; Explained variance:
694 0.56.
695 **Figure 8:** Abundance of six species in the experimental treatments. (a) *Isotomiella minor* (Group A);
696 (b) *Detriturus jubilarius* (Group B); (c) *Protaphorura armata* (Group C); (d) *Mesaphorura*
697 *macrochaeta* (Group D); (e) *Isotoma viridis* (Group E); (f) *Xenylla tullbergi* (Group E); Upper right:
698 correlation circle of the between-group analysis (Fig. 7). For group codes see Table1. Letters on bars
699 indicate significant differences among means. Labels under bars correspond to each treatment (for
700 treatment codes see Fig. 1). Error bars represent standard errors.
701

Table 1. Presence/absence in inoculation and exclosure controls of the 16 species which were common in experimental soil cores (X = not present in controls; F = present in forest control only; P = present in pasture control only; FP = present in both forest and pasture controls). Results of generalized linear models testing the effect of three factors (community origin, soil nature and microclimate) on each species abundance (* = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$; / = not significant; F = species more abundant in forest community, soil or microclimate; P = species more abundant in pasture community, soil or microclimate). Habitat preference was calculated using IndVal index with the data set produced in Ponge et al. (2003): g = generalist species; f = strict-forest species; fp = forest-preferring species; a = strict agricultural species; ap = agricultural-preferring species. Response groups correspond to the six groups formed using species responses to the three factors community origin, soil, and microclimate. Group A = true forest species; Group B = forest species preferring pasture soil; Group C = pasture species preferring forest soil; Group D = pasture species preferring forest microclimate; Group E = species preferring pasture microclimate; Group F = pasture species.

	Species codes	Exclosure	Inoculation	Community	Soil	Microclimate	Habitat preference	Response group
Isotomiella minor	Iso.min	X	F	F ***	F ***	F ***	fp	A
Megalothorax minimus	Meg.min	X	F	F ***	F ***	F ***	fp	A
Pseudosinella mauli	Pse.mau	X	F	F ***	F ***	/	f	A
Folsomia quadrioculata/manolachei	Fol	X	FP	F ***	P ***	F ***	g	B
Friesea truncata	Fri.tru	X	F	F ***	P **	F **	fp	B
Detriturus jubilarius	Det.jub	X	F	F ***	P ***	F ***	f	B
Protaphorura armata	Pro.arm	P	P	P ***	F *	F ***	ap	C
Pseudosinella alba	Pse.alb	X	X	P ***	F ***	/	a	C
Mesaphorura macrochaeta	Mes.mac	FP	FP	P ***	P ***	F ***	g	D
Parisotoma notabilis	Par.not	FP	FP	P ***	P ***	F ***	ap	D
Brachystomella parvula	Bra.par	P	X	F ***	F **	P ***	ap	E
Lepidocyrtus lanuginosus	Lep.lan	FP	FP	/	F *	P *	g	E
Sphaeridia pumilis	Sph.Pum	FP	F	F *	/	P *	ap	E
Xenylla tullbergi	Xen.tul	F	F	F ***	P ***	P ***	f	F
Isotoma viridis	Iso.vir	P	P	/	P ***	P ***	ap	F
Sminthurides schoetti	Smi.sch	P	X	/	P ***	P **	ap	F

718 **Table 2.** Effect of soil nature and microclimate (and interaction between both factors) on total carbon
719 (Ctot) and nitrogen (Ntot) content, soil pH and soil moisture of experimental soil cores. Results of
720 linear and generalized linear models (F value/Chi square and degrees of freedom df). Significance
721 levels: ** = $p < 0.01$; *** = $p < 0.001$; NS = not significant.

722

		F values/Chi square			
	df	Ctot	pH	Moisture	Ntot
Soil (S)	1	48.7 ***	30.49 ***	105.2 ***	1.52 NS
Climate (Cli)	1	0.14 NS	20.35 ***	9.56 **	0.3 NS
S : Cli	1	0.07 NS	2.4 NS	0.03 NS	0.36 NS
model type		Normal	Gamma	Normal	Normal
transformation		$\log_{10}$	none	$\log_{10}$	$\log_{10}$

723

724

725

726 **Table 3.** Effect of community origin, soil nature and microclimate on total abundance, species
727 richness and Shannon index. Results of linear models (F values and degrees of freedom df) tested after
728 a procedure of automatic selection based on AIC criterion. NT = not tested. * = $p < 0.05$; ** = $p <$
729 0.01; *** = $p < 0.001$; NS = not significant.

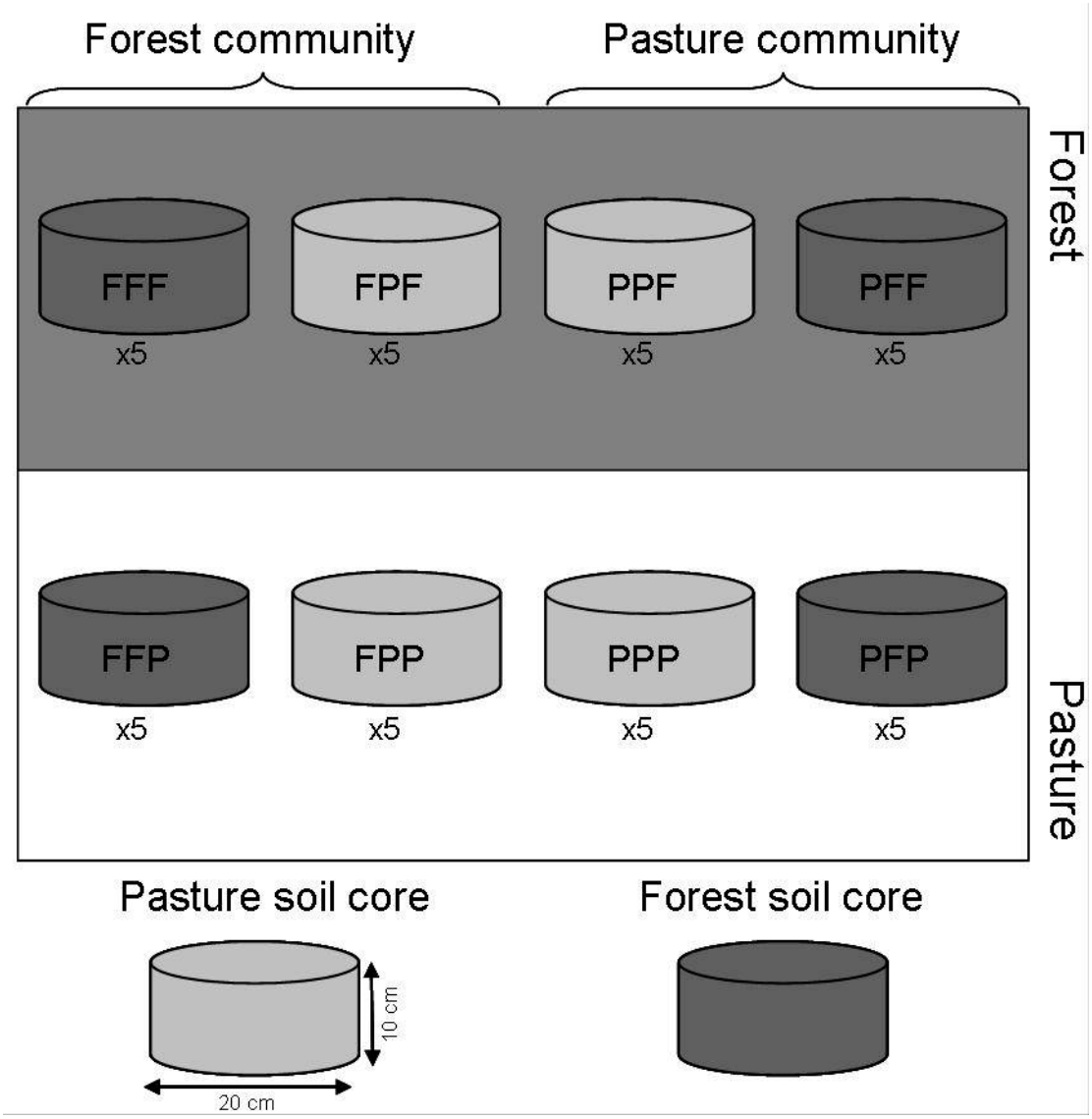
	F values							
	df	Abundance		df	Species richness		df	Shannon index	
Community (Co)	1	10.98	**	1	15.8	***	1	33.85	***
Soil (S)	1	5.29	*	1	1.9	NS	1	9.33	**
Climate (Cli)	1	50.02	***	1	0.06	NS	1	0.88	NS
Co : S	NT			1	0.8	NS	NT		
Co : Cli	NT			1	0.007	NS	1	11.04	**
S : Cli	NT			1	0.007	NS	NT		
Co : S : Cli	NT			1	0.16	NS	NT		
model type		Normal			Normal			Normal	
transformation		$\log_{10}$			none			none	

730

731

732

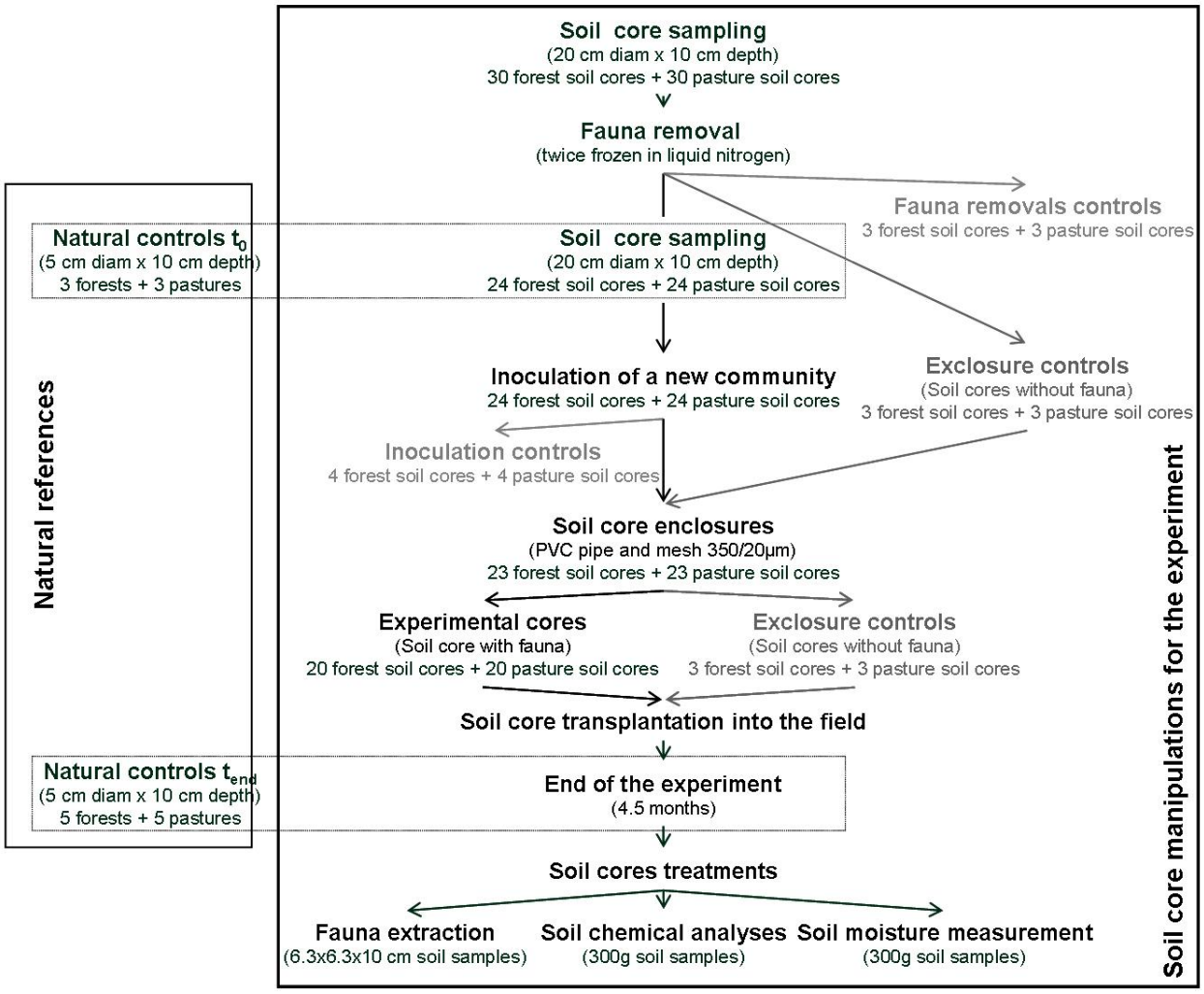
733



734

735 **Fig. 1**

736



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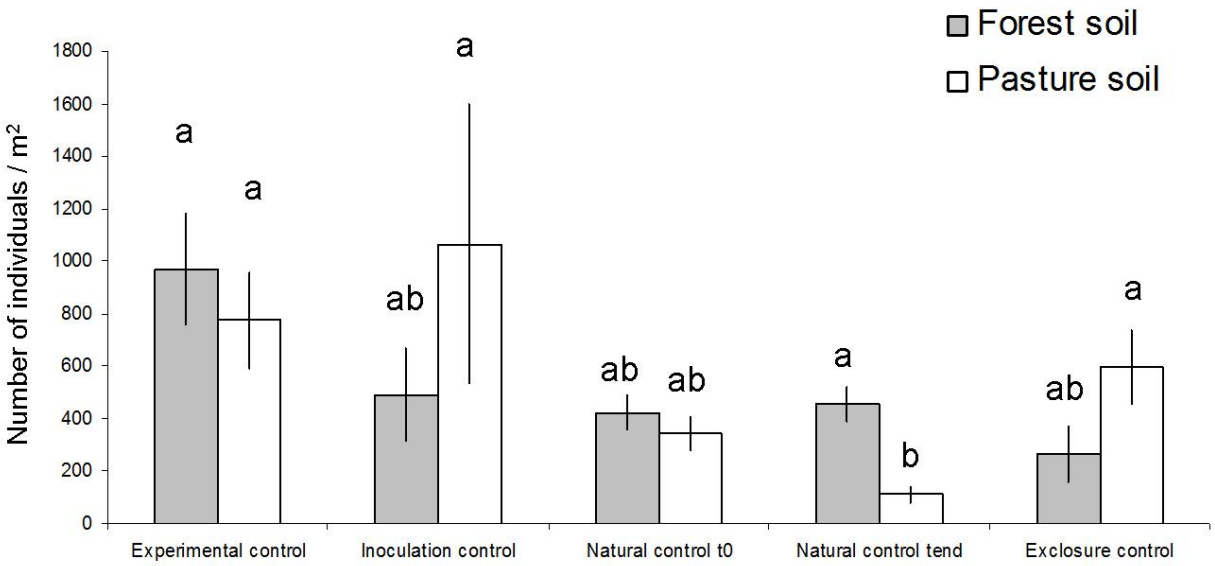
738 **Fig. 2**

739



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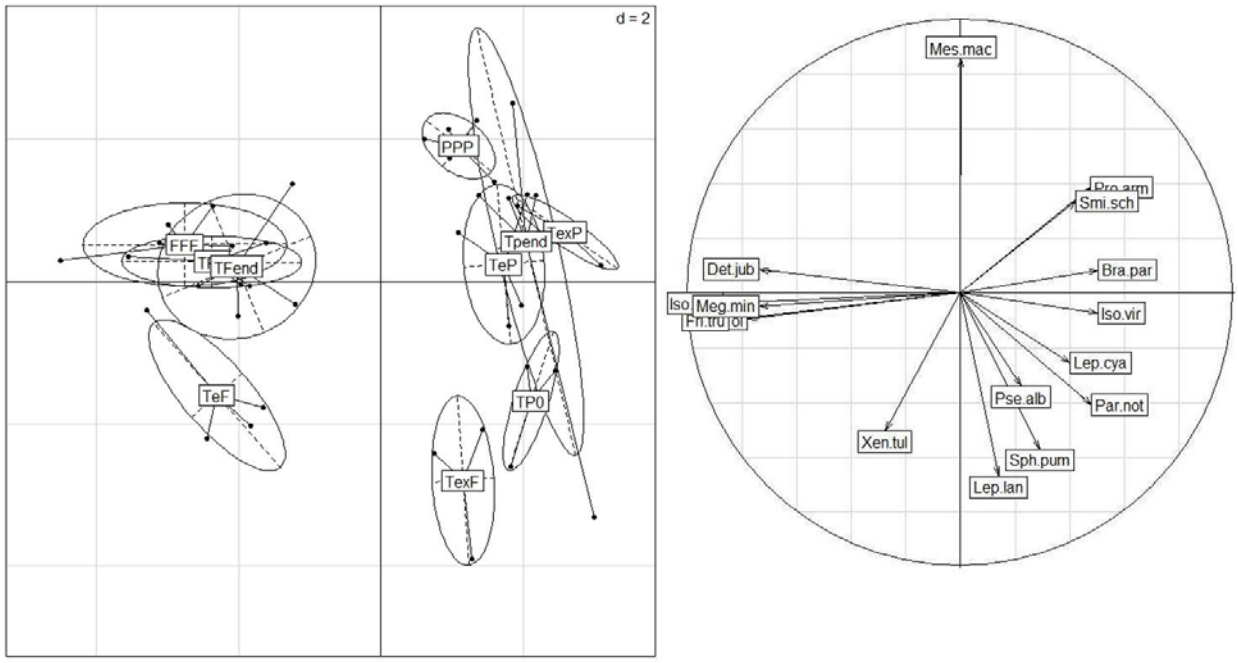
741 **Fig. 3**

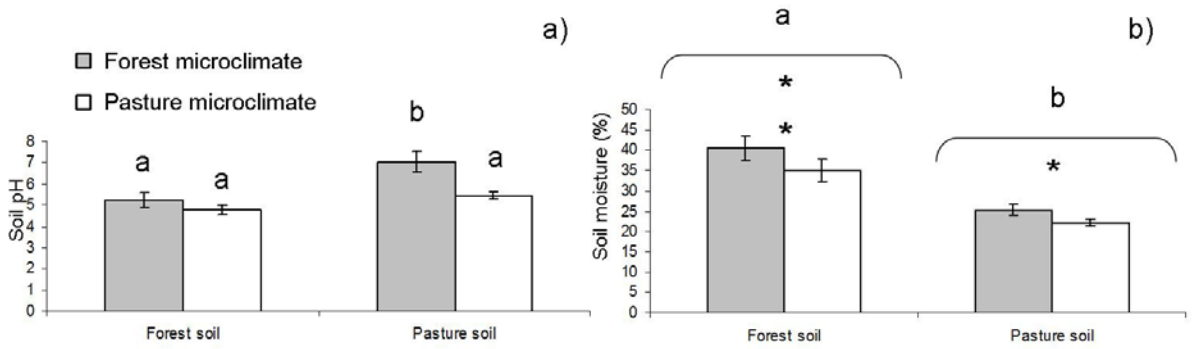
742



743

744 **Fig. 4**

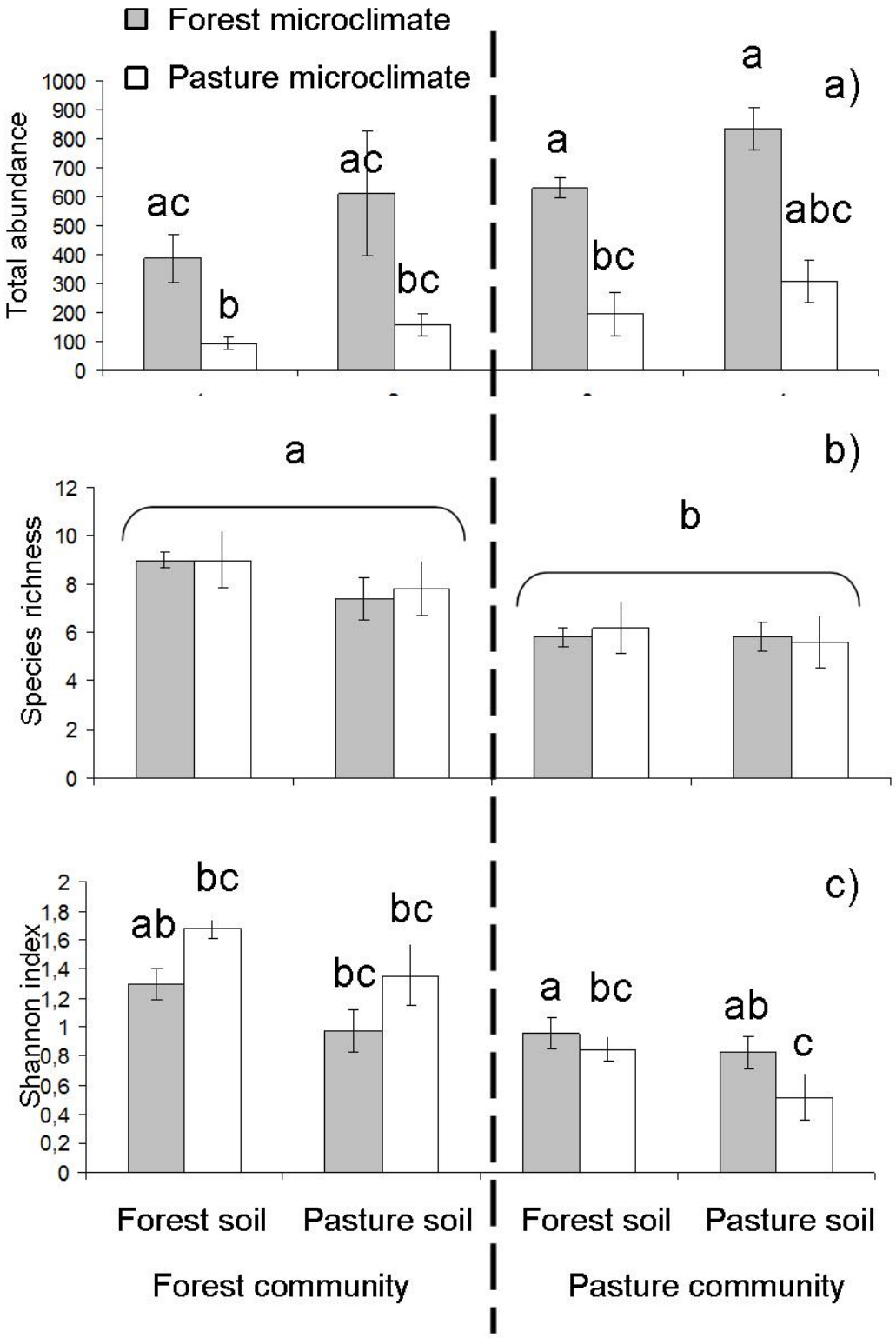
745



746

747 **Fig. 5**

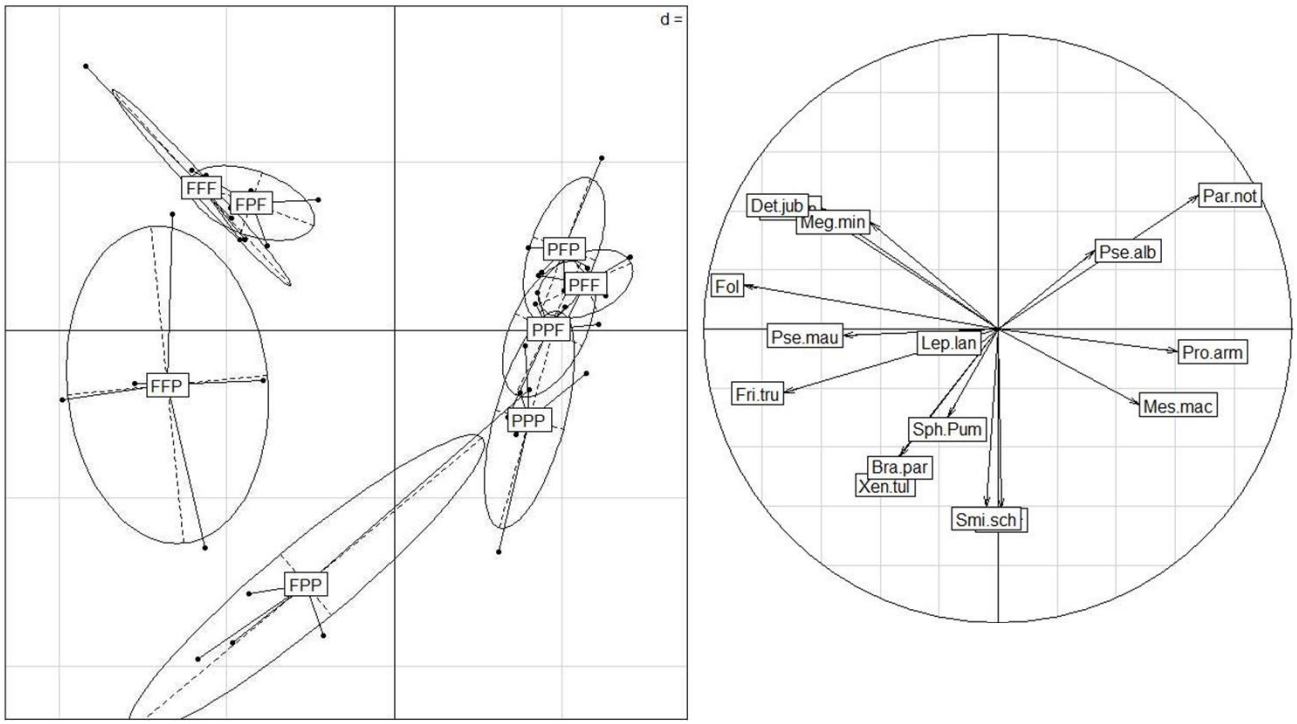
748



749

750 **Fig. 6**

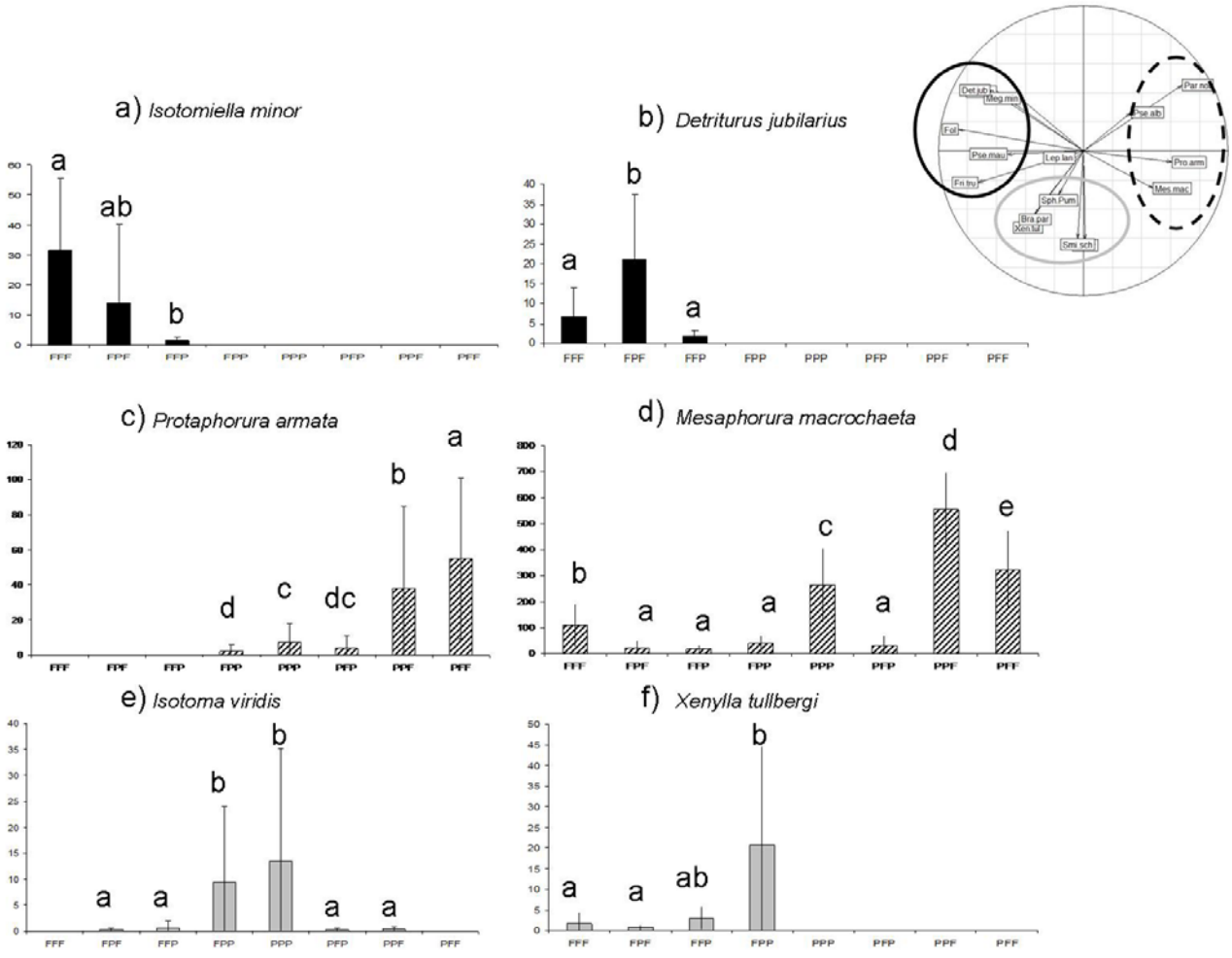
751



752

753 **Fig. 7**

754

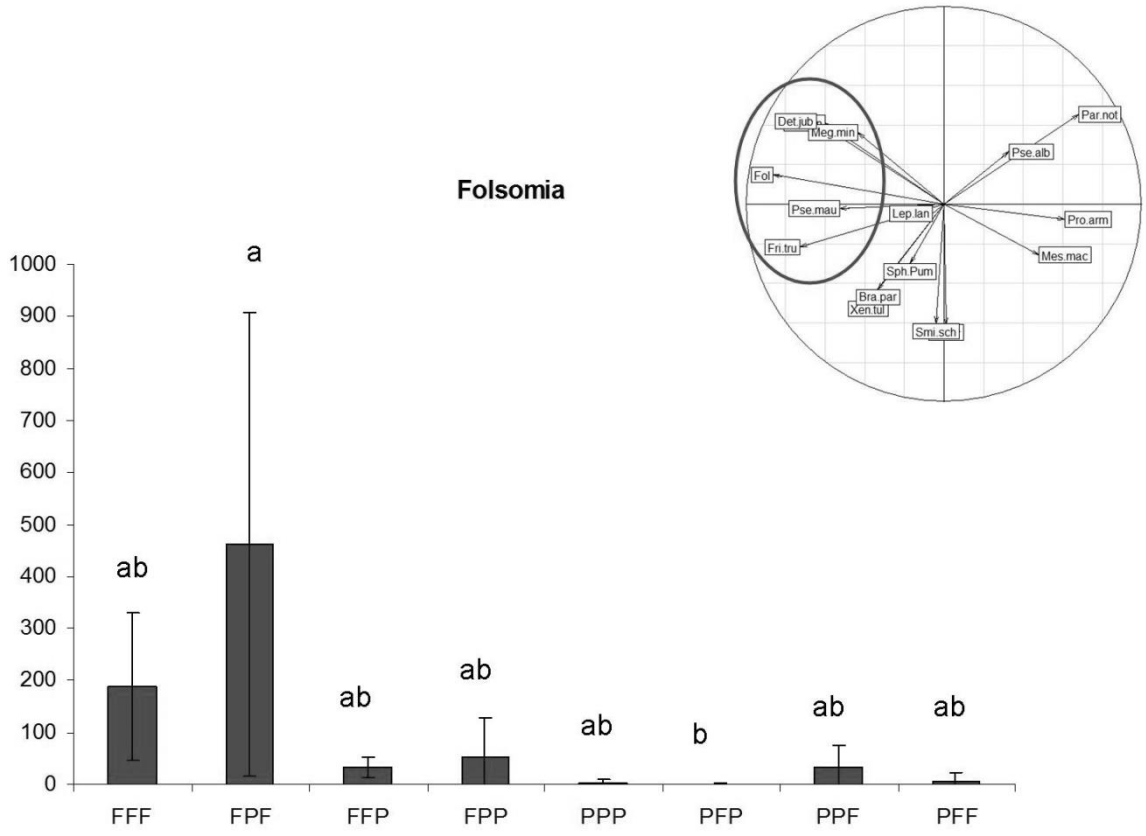


755

756 **Fig. 8**

757

758 **Appendix.** Abundances of the 16 common species in the eight experimental treatments together with
759 the correlation circle of between-group analysis performed on the abundances of the 16 common
760 species using a combination of community origin, soil, and microclimate as explanatory variable.
761 Letters on bars indicate significant differences. Labels under bars correspond to each treatment (codes
762 according to Figure 1).



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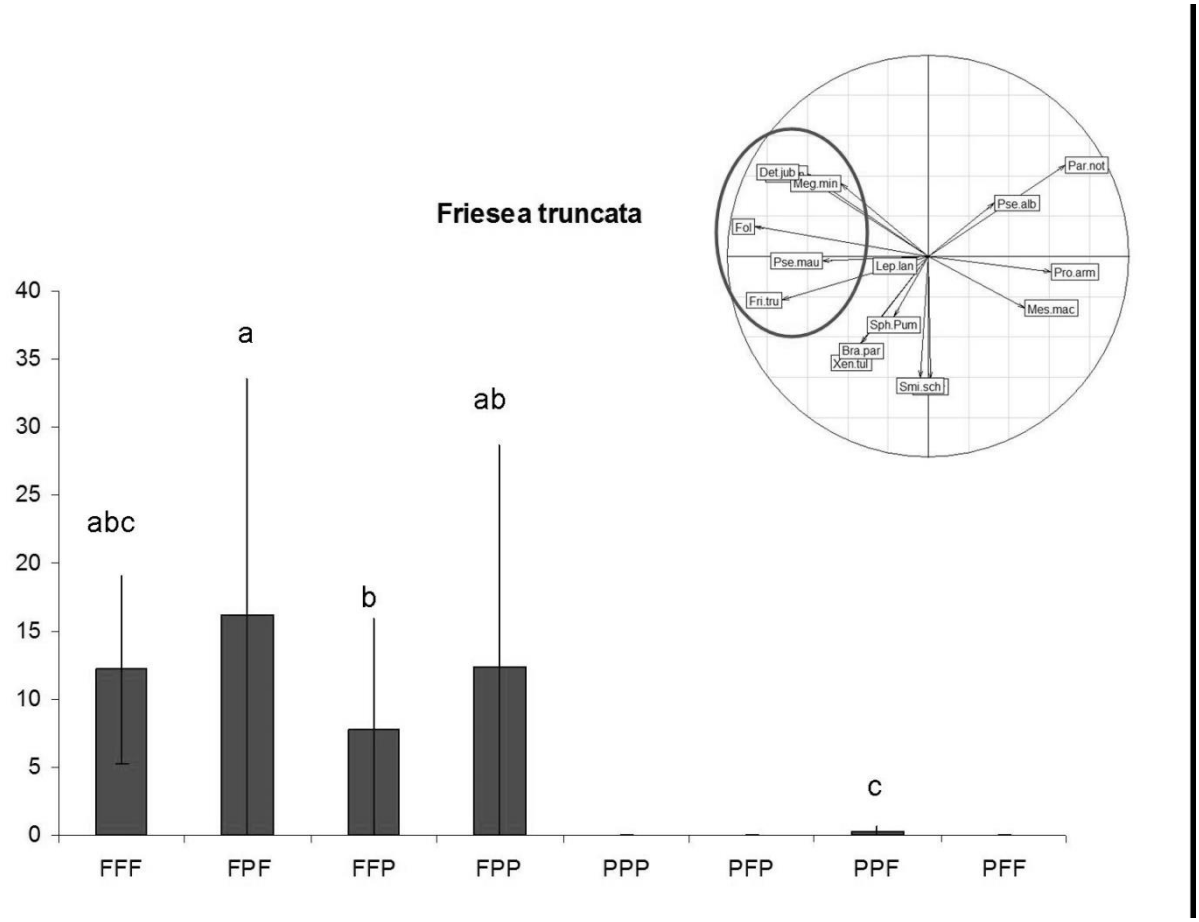
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Det.jub
Meg.min
Par.not
Pse.alb
Fol
Pse.mau
Lep.lan
Pro.arm
Fri.tru
Mes.mac
Sph.Pum
Bra.par
Xen.tul
Smi.sch
40
35
30
25
20
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c
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PFP
PPF
PFF

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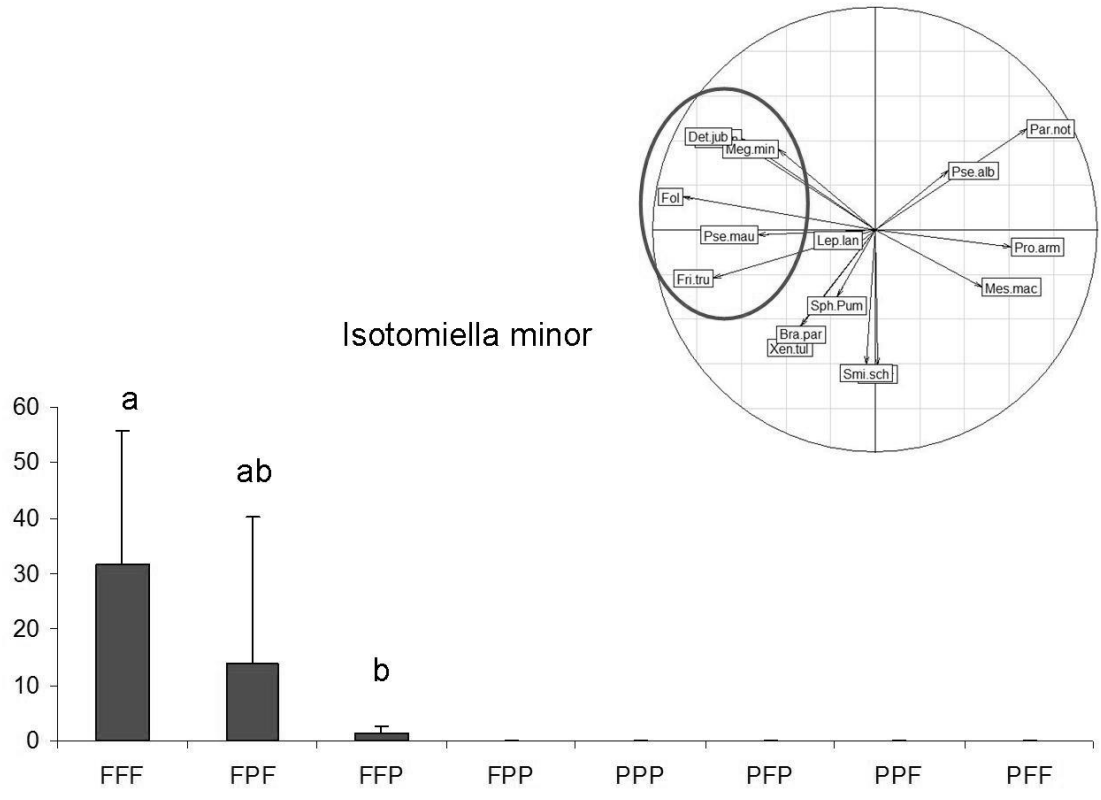
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Meg.min
Par.not
Pse.alb
Fol
Pse.mau
Lep.lan
Pro.arm
Fri.tru
Mes.mac
Sph.Pum
Bra.par
Xen.tul
Smi.sch
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PPF
PFF

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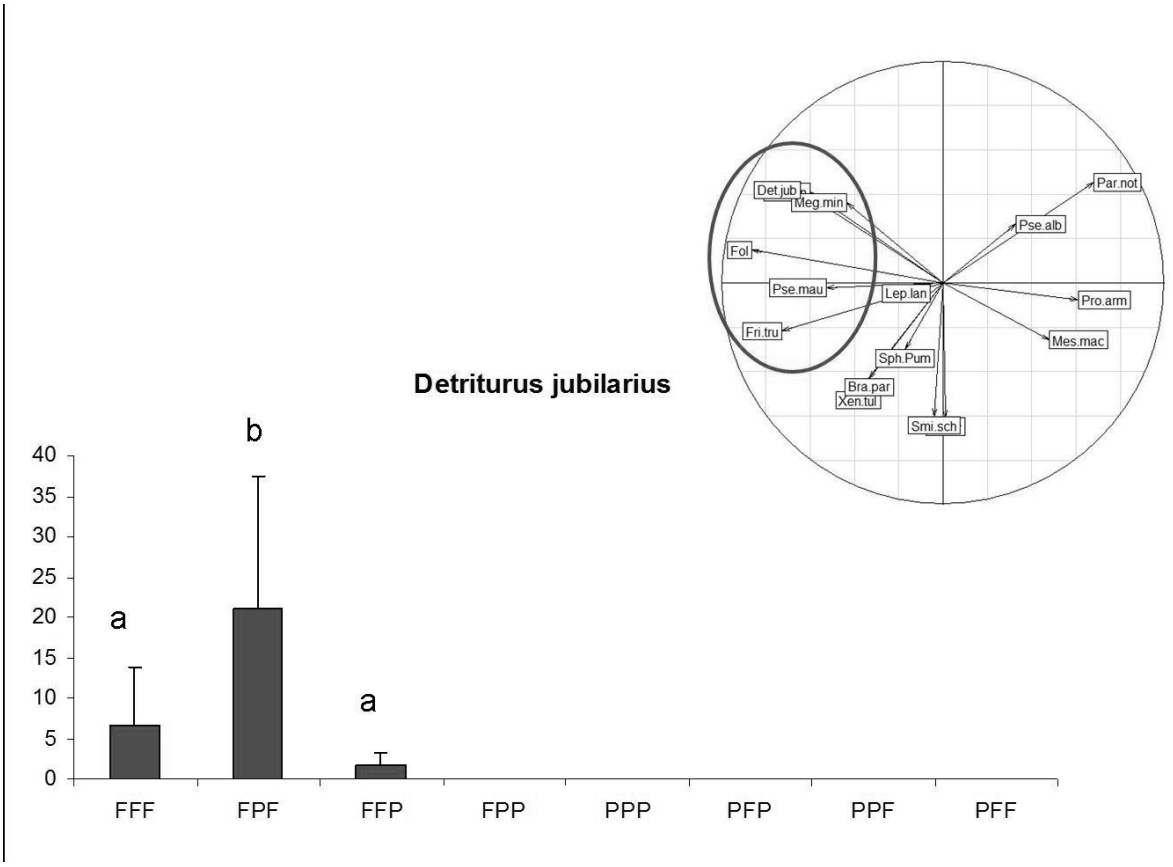
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Meg.min
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Pse.mau
Fri.tru
Bra.par
Xen.tul
Sph.Pum
Lep.lan
Smi.sch
Par.not
Pse.alb
Pro.arm
Mes.mac
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35
30
25
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PPF
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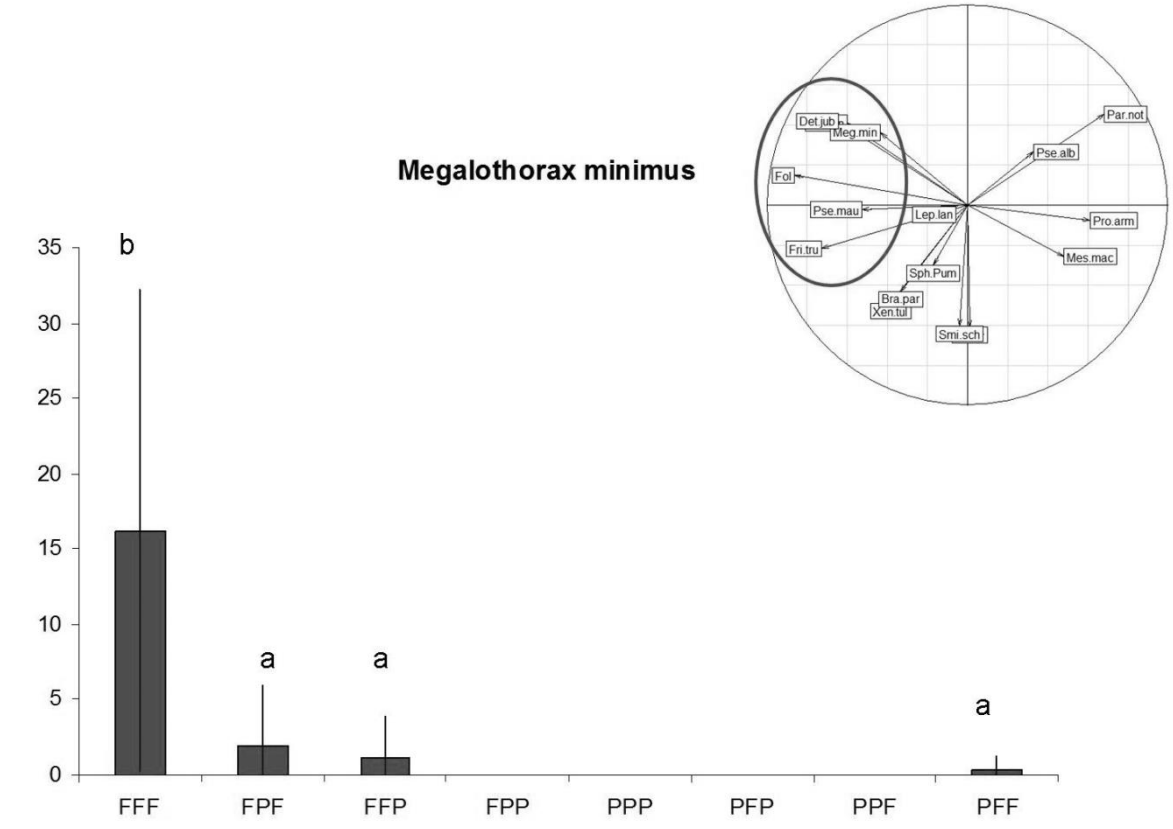
766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Meg.min
Fol
Pse.mau
Fri.tru
Bra.par
Xen.tul
Sph.Pum
Lep.lan
Smi.sch
Par.not
Pse.alb
Pro.arm
Mes.mac
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30
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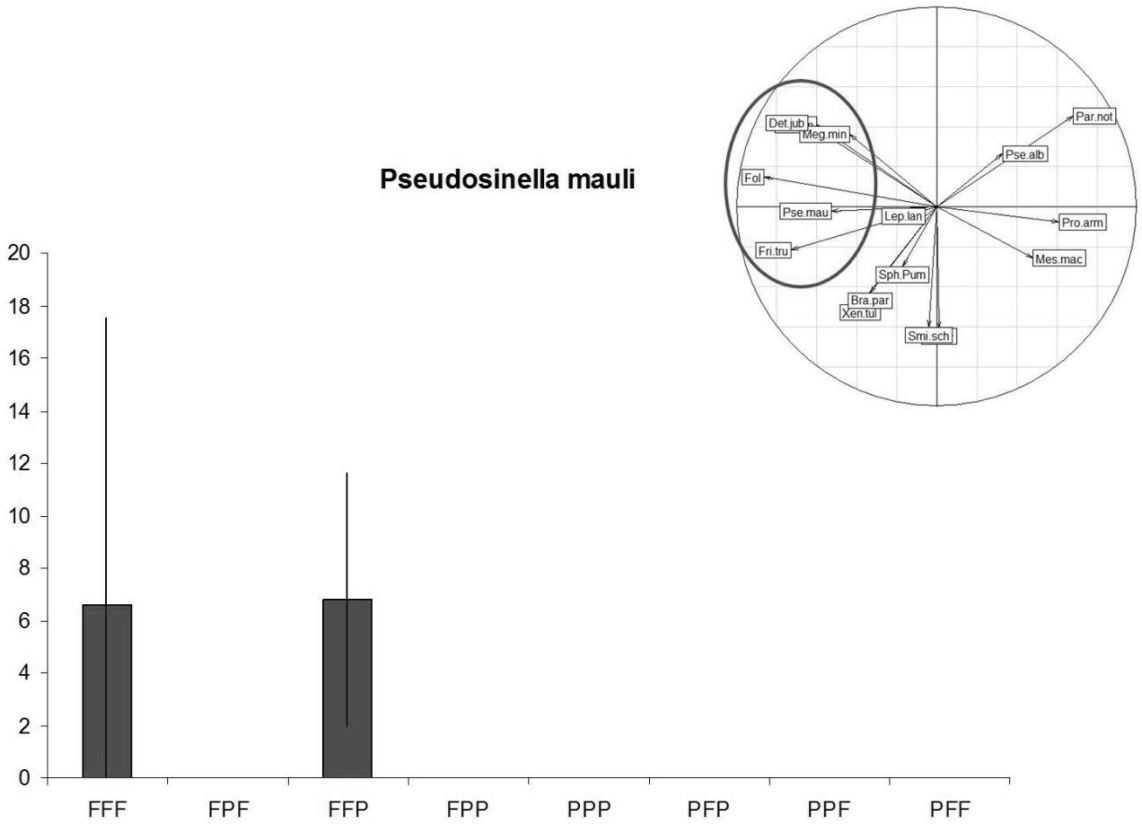
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Meg.min
Par.not
Pse.alb
Fol
Pse.mau
Lep.lan
Pro.arm
Fri.tru
Mes.mac
Sph.Pum
Bra.par
Xen.tul
Smi.sch
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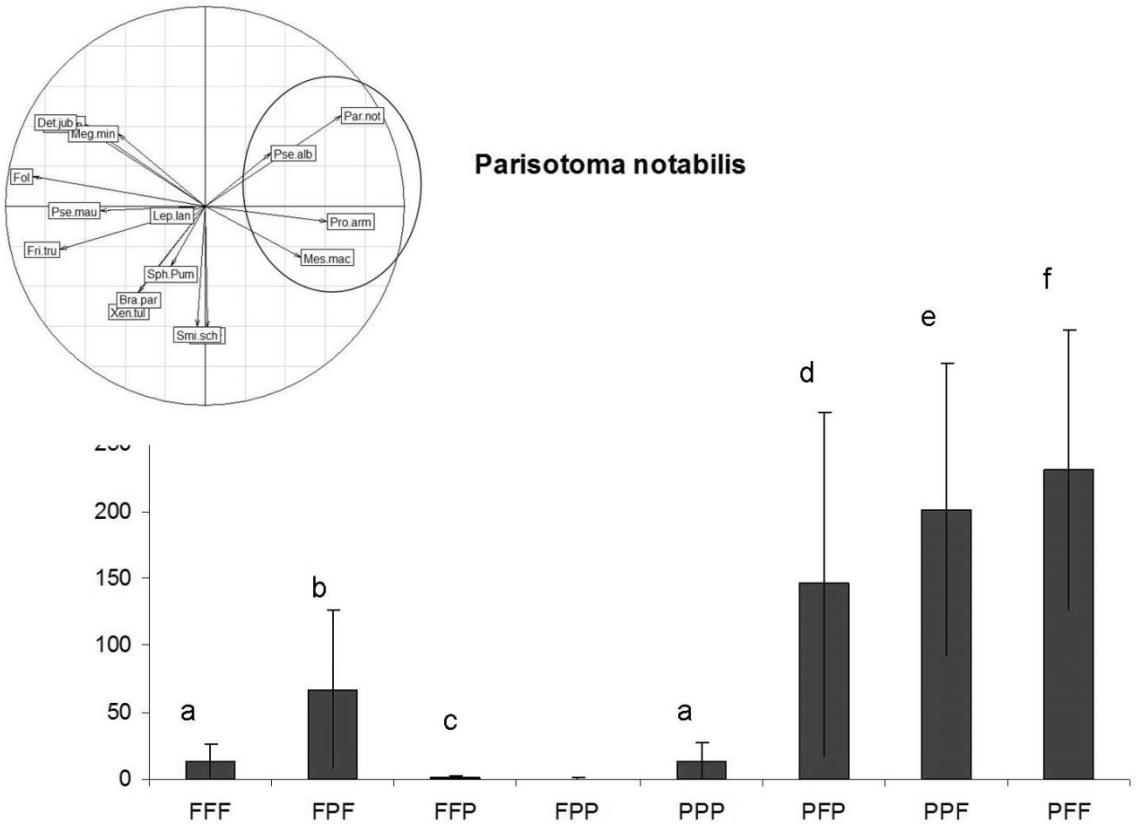
Parisotoma notabilis
Det.jub
Meg.min
Par.not
Pse.alb
Fol
Pse.mau
Lep.lan
Pro.arm
Fri.tru
Mes.mac
Sph.Pum
Bra.par
Xen.tul
Smi.sch
200
150
100
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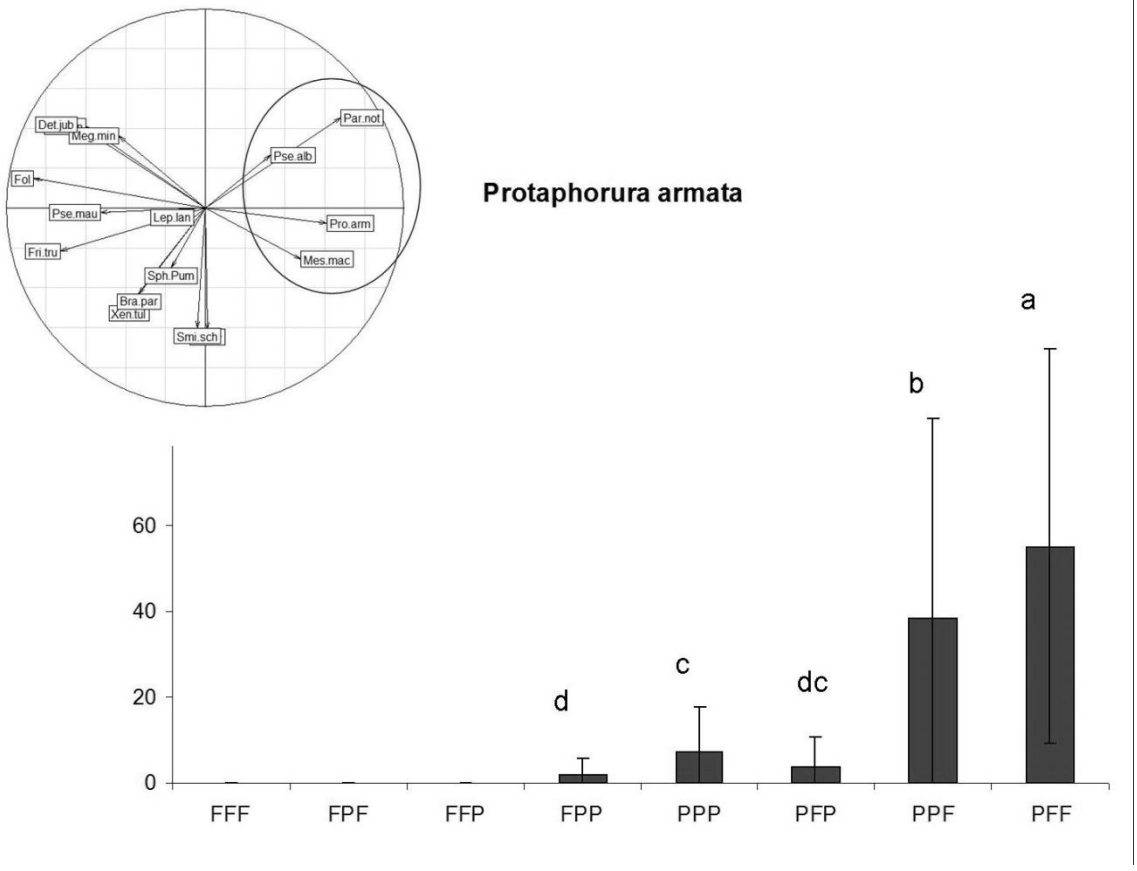
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Meg.min
Fol
Pse.mau
Lep.lan
Fri.tru
Sph.Pum
Bra.par
Xen.tul
Smi.sch
Par.not
Pse.alb
Pro.arm
Mes.mac
Protaphorura armata
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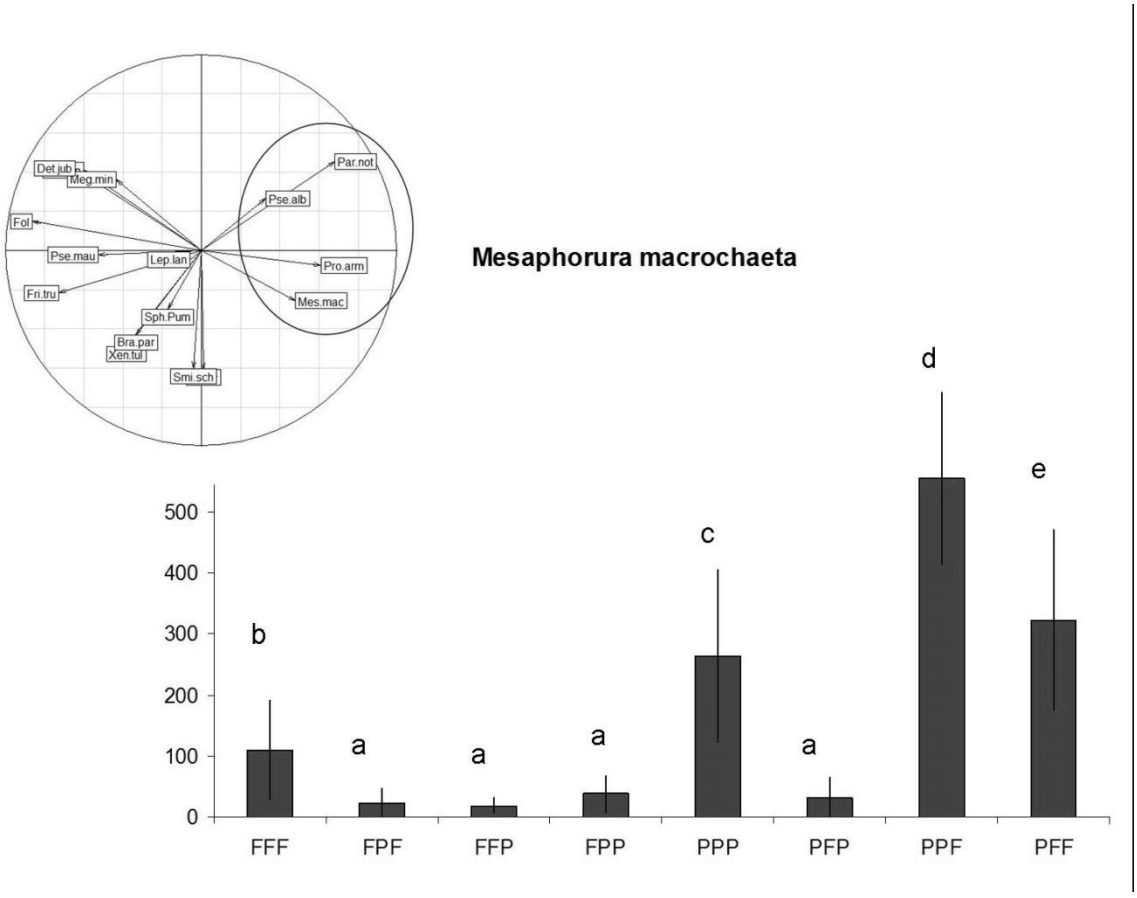
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Pse.alb
Pro.arm
Mes.mac
Mesaphorura macrochaeta
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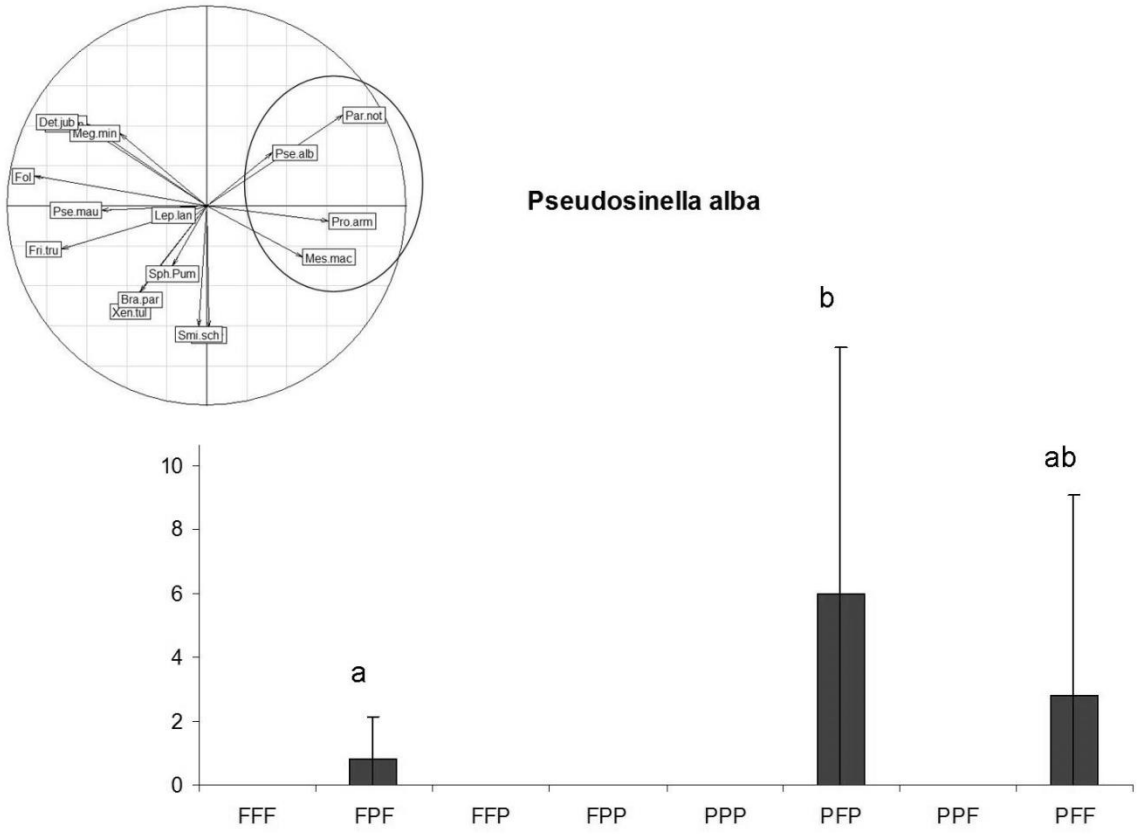
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Fol
Pse.mau
Lep.lan
Fri.tru
Sph.Pum
Bra.par
Xen.tul
Smi.sch
Par.not
Pse.alb
Pro.arm
Mes.mac
Pseudosinella alba
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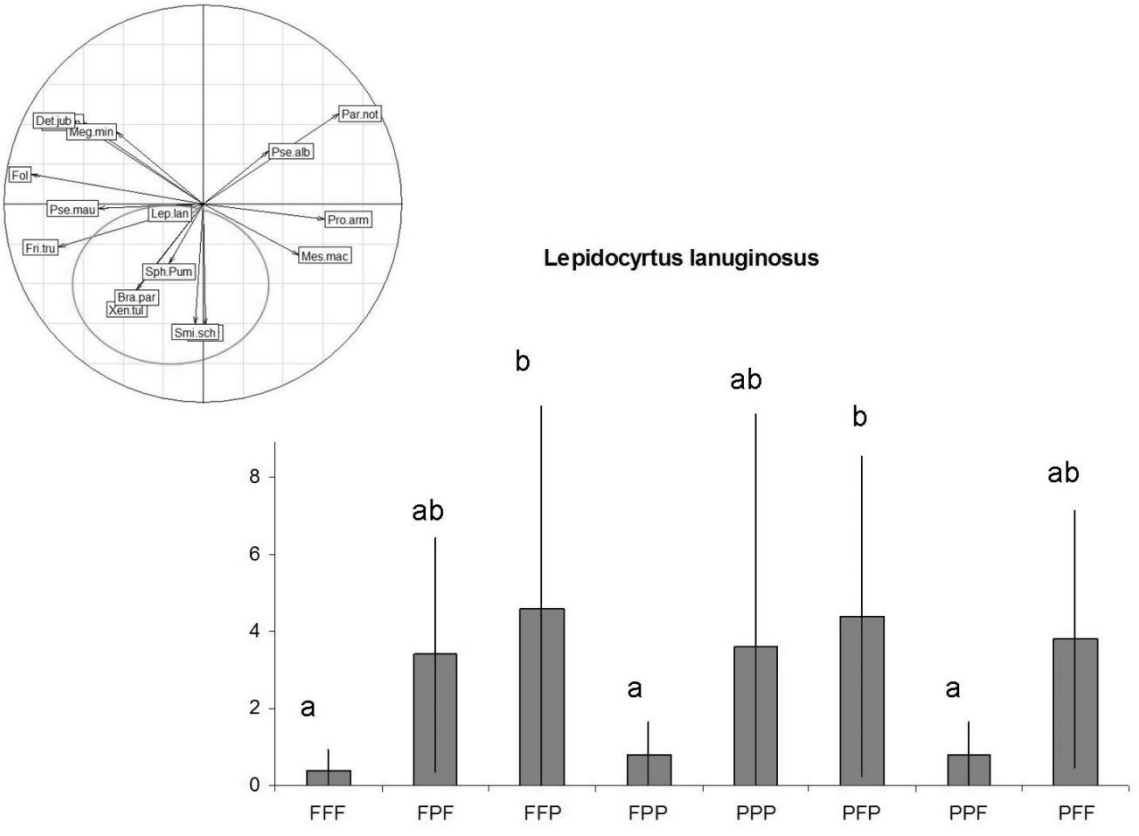
Det.jub
Meg.min
Fol
Pse.mau
Lep.lan
Fri.tru
Sph.Pum
Bra.par
Xen.tul
Smi.sch
Par.not
Pse.alb
Pro.arm
Mes.mac
Lepidocyrtus lanuginosus
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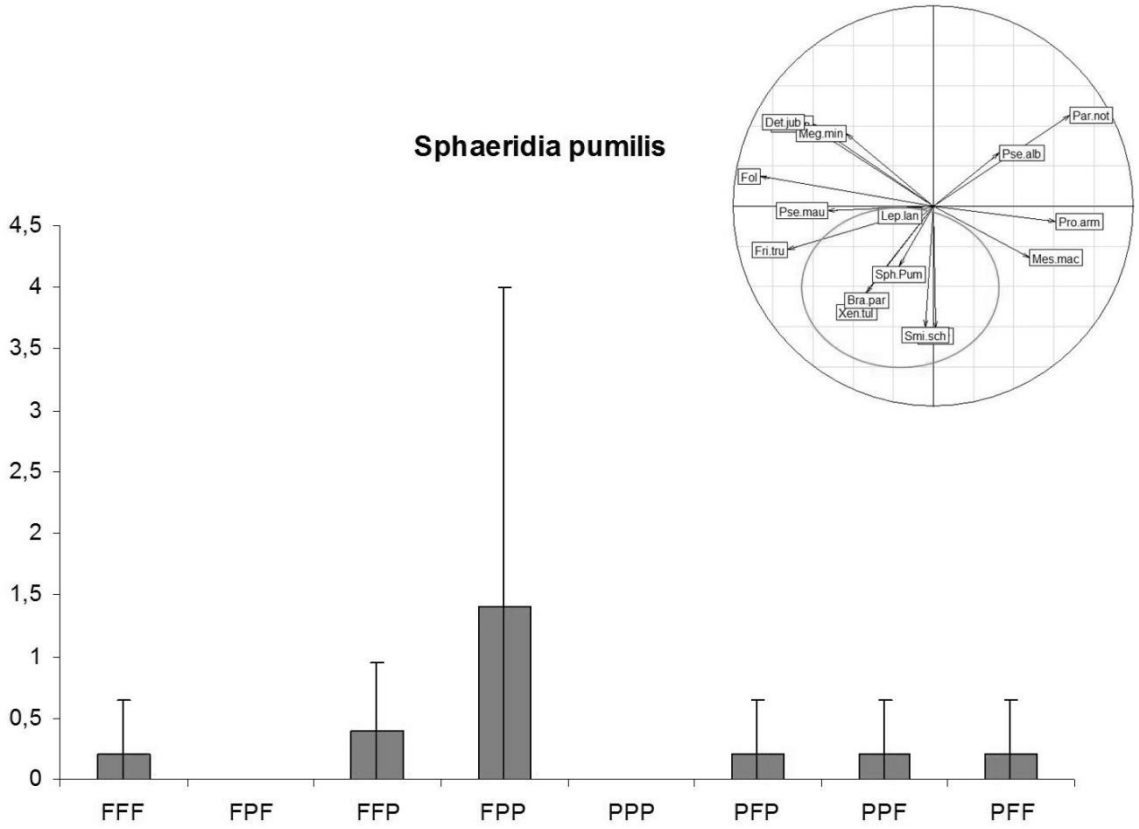
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Mes.mac
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Xen.tul
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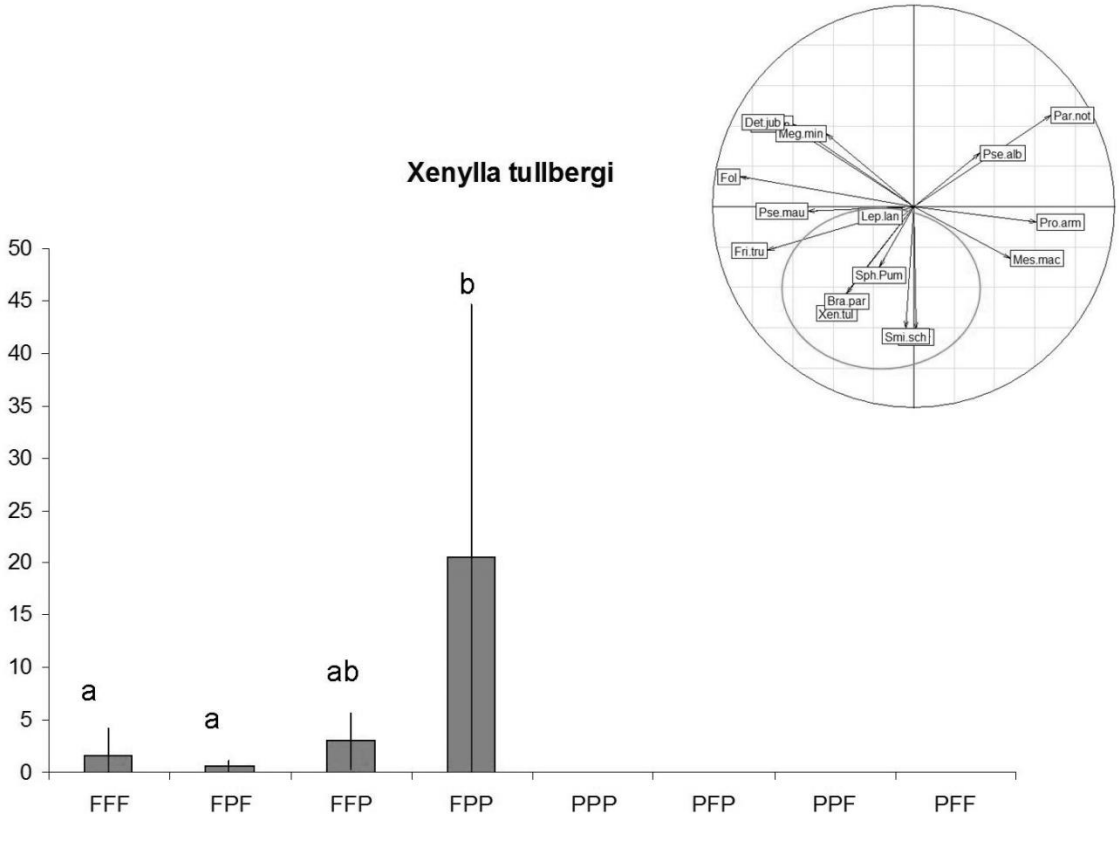
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Mes.mac
Sph.Pum
Bra.par
Xen.tul
Smi.sch
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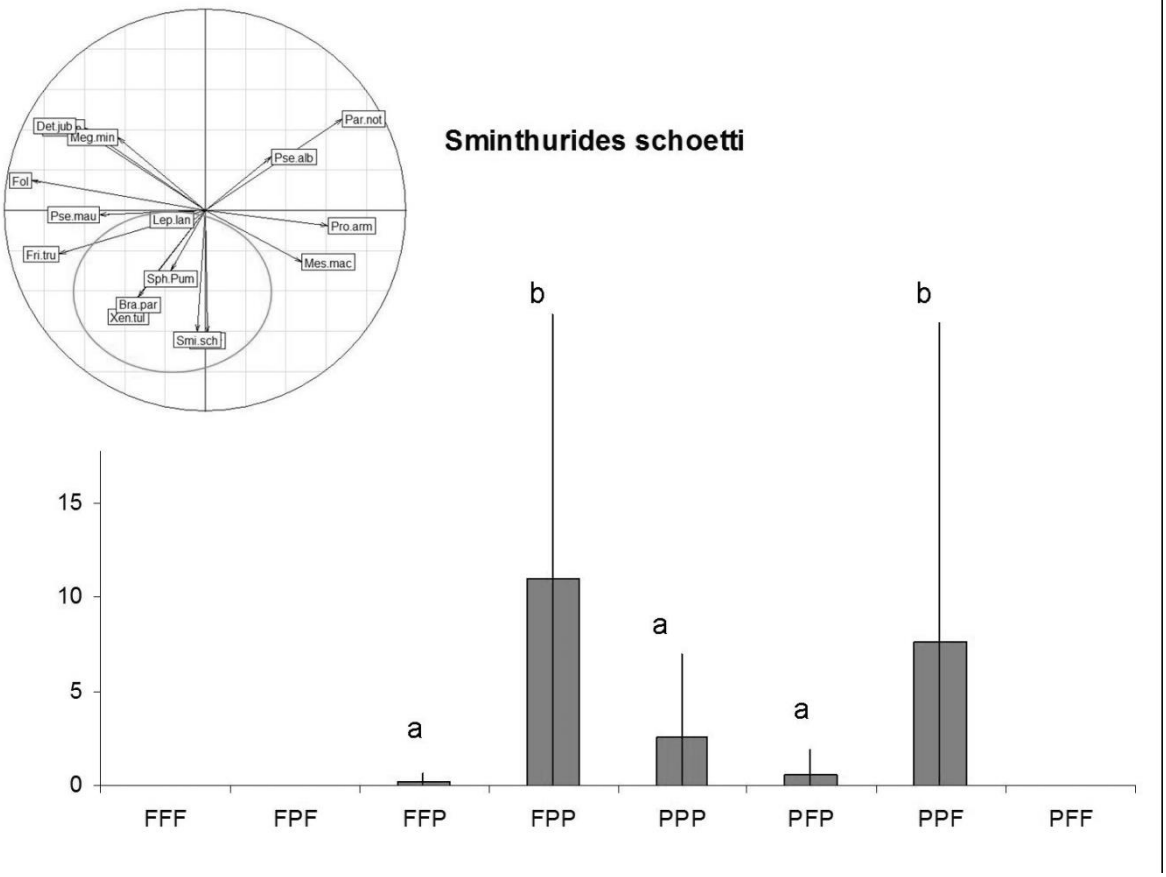
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Lep.lan
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Mes.mac
Sph.Pum
Bra.par
Xen.tul
Smi.sch
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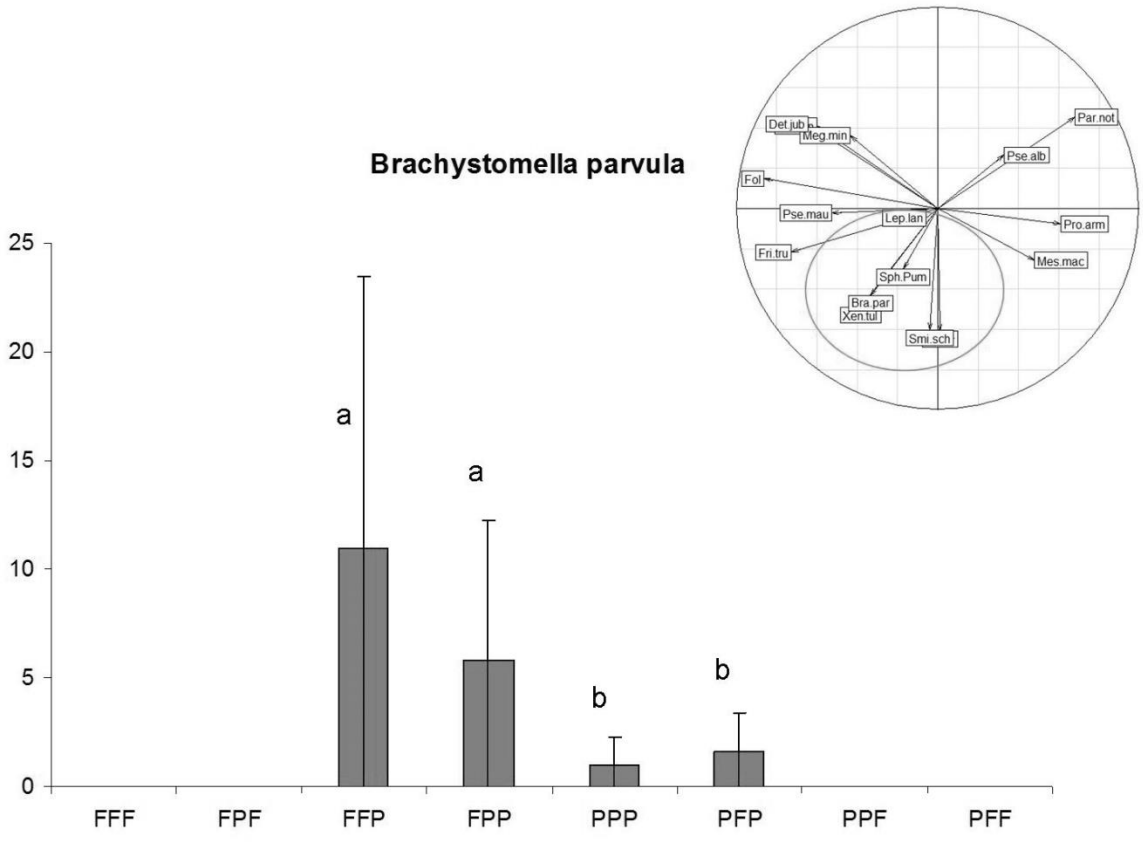
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Mes.mac
Sph.Pum
Bra.par
Xen.tul
Smi.sch
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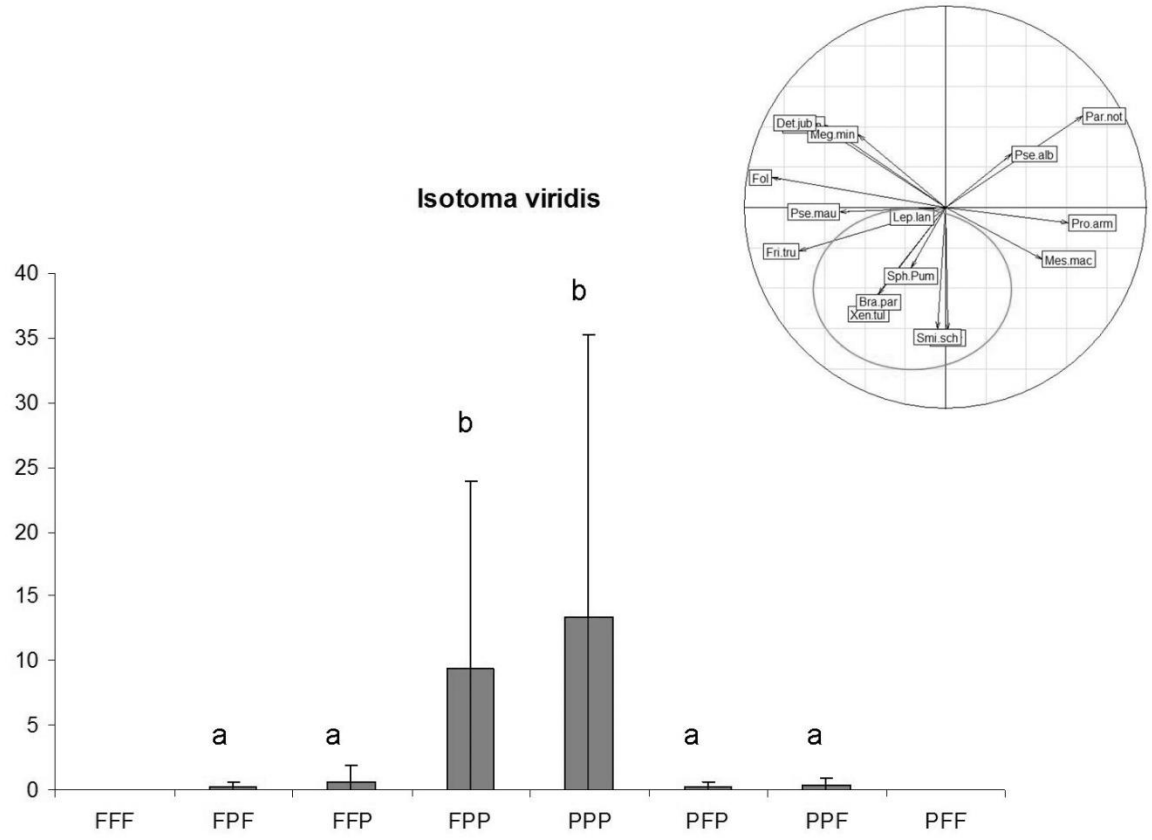
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Meg.min
Par.not
Pse.alb
Fol
Pse.mau
Lep.lan
Pro.arm
Fri.tru
Mes.mac
Sph.Pum
Bra.par
Xen.tül
Smi.sch
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778

779