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Distribution of *Heteromurus nitidus* (Hexapoda, Collembola) according to soil acidity: interactions with earthworms and predator pressure.

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Summary Culture (8 weeks, in sieved fresh humus) and choice (16 weeks in compartmented boxes containing fresh or defaunated humus, or 5 days on compacted humus) experiments at varying pH levels demonstrated that the soil-dwelling Collembolan *Heteromurus nitidus* (Entomobryomorpha) can live and even prefer humus with pH<5.0 , contrary to results of field studies. Choice experiments on moder (pH 7.8) and calcic mull (pH 3.9) showed that *H. nitidus* was significantly attracted by the earthworms *Allolobophora chlorotica* and *Aporrectodea giardi* whatever the humus form, except when moder was present on both sides. This attraction by earthworms may partly explain the field distribution of *H. nitidus*. A strong predator pressure was detected in some of the replicates, which seemed to have an impact on densities and distribution of *H. nitidus*, as well. Causes of the attraction by earthworms (food resources, pore size, moisture) are discussed. A trophic cause is particularly suspected.

INTRODUCTION

Soil fauna participate, directly or through their action on microflora, to the decomposition of litter and to the building of humus profiles (Ponge *et al.*, 1986). Therefore, the study of the distribution of soil animals is of importance in characterizing soil-forming processes (Ponge, 1983; Arpin *et al*., 1984). Among the large number of factors (e.g. moisture, temperature, light, depth, food resources), which determine the distribution of soil fauna, humus form (Brêthes et al. 1995) and soil pH have a marked influence on Collembolan communities (Hågvar and Abrahamsen, 1984; Ponge, 1993; Klironomos and Kendrick, 1995). Thus, a number of edaphic Collembolan species may be classified into acid-tolerant and acid-intolerant species. However, the effect of pH is difficult to identify, because this measurement is strongly related to humus form, C/N ratio, base saturation and ionic composition of the soil solution. Some relationships have been found previously between the abundance of some Collembolan species and base saturation (Ca, Mg, and Mn ; Hågvar and Abrahamsen, 1984). In fact, the effect of soil pH can be either direct or indirect. Hågvar (1984) suggested several hypotheses according to which soil acidity could act through ground vegetation, humus form, predator pressure, food resources and competition between species. On the other hand, some experimental studies showed that pH had a strong effect on activity, fecundity, longevity of adults, and absorption of solutions by the ventral tube (Mertens, 1975; Hutson, 1978; Jaegger and Eisenbeis, 1984).

According to field studies by Ponge (1983, 1993), *Heteromurus nitidus* (Templeton, 1835), an edaphic Collembola (Entomobryidae), was always found in mull humus at pH above 5. This species, which is readily cultured in the laboratory, was chosen in order to determine whether pH, directly or indirecly, explains *H.nitidus* field distribution.

In preliminary experiments we attempted to reproduce in experimental vessels the results obtained in the field, i.e. to determine whether *H. nitidus* can live and reproduce only in a humus at pH>5.0 or if this is a behavioural trait. Results suggested that earthworms could be implicated in the distribution of *H. nitidus*. This hypothesis was further tested by giving *H. nitidus* a choice between humus containing or not containing earthworms. The impact of predators was taken into account in the analysis of results, since it appeared to interact with the above mentioned factors.

MATERIALS AND METHODS

Preliminary field study

A preliminary study was carried out in the field to see whether *H. nitidus* was located only in soils at pH≥5.0 (Ponge, 1993), when a choice between soils at different pH levels was offered. The distribution of other Collembolan species present in the samples was also studied.

Sixty samples were taken in a plot located in the Senart forest near Paris (France). The soil was a silt-clay loam with a mull humus form under oak (*Quercus petraea*), with understory vegetation composed of lime (*Tilia cordata*), hornbeam

(*Carpinus betulus*) and bramble (*Rubus ulmifolius*). Varying conditions of soil acidity have been recorded on this plot, due to the presence of small limestone grains within a patch approximately 3m diam from which bramble was absent. Twenty samples of soil+litter were taken with a spade in the central zone without bramble, and forty samples were taken in the surrounding more acidic zone with bramble. Soil arthropods were extracted by the dry-funnel method, i.e. animals escape from the drying sample and are collected at the bottom of a funnel into which they fall. Determination of Collembola was made at the species level, using a dissecting microscope (x40) for larger individuals, and under a light microscope (x400) for smaller ones. Soil pH was measured in a soil/water mixture (1:2 w/w). Data (i.e. presence of species) were analysed by correspondence analysis (Greenacre, 1984). This multivariate method permits the simultaneous representation of samples and species (together with additional variables such as pH) into a plane formed by the first two factorial axes.

Preliminary culture experiments

The specimens of *H.nitidus* used in all the experiments arose from cultures on water-moistened Fontainebleau sand (pure fine quartz sand), fed with a mixture of terrestrial microalgae (*Pleurococcus*) and lichens taken from bark scrapings. All cultures, as well as boxes for choice experiments, were kept at 15°C, under a 10h:14h light:dark photoperiod.

Two culture experiments, each made of two series of five and three replicates (one replicate = one box), respectively, were performed using three different types of humus: a calcic eumull (pH 7.2-7.4), an oligomull (pH 4.0-4.6), and an eumoder (pH 4.0-4.3). Classification of humus forms follows Brethes *et al*. (1995). The eumoder and the oligomull came from the Senart forest and the calcic eumull came from the laboratory park (black rendzina under hornbeam). Sampling sites have been described by Arpin *et al*. (1984) and Bouché (1975). Fifteen adult or sub-adult *H. nitidus* (i.e. specimens 1.8-2.4mm in length according to Krool and Bauer, 1987) were introduced into circular plastic boxes (8 cm diam, 5 cm height) filled with fresh roughly sieved (10mm) humus. In one series the individuals were fed with lichens and microalgae, in the other no food was added. The purpose of this food/no food comparison was to detect a possible trophic effect on population densities. Cultures were kept at 15°C for 9 weeks, so that *H. nitidus* could reproduce several times (about 3 weeks for an egg-to-egg cycle). Animals were then extracted and counted and humus pH was measured as described above.

H. nitidus individuals were counted in all replicates. Within each experimental run, mean numbers of animals in the different substrates were compared by one-way ANOVA (Sokal and Rohlf, 1995). Data were log-transformed because the reproduction of animals is a non-linear phenomenon, the variance of abundances being proportional to their mean. When significant differences among humus forms were detected, then means were compared by the Newman-Keuls procedure (Sokal and Rohlf, 1995). The two distinct experimental series were treated separately because humus sampling was not made at the same time.

Another culture experiment, with three replicates, was performed on sphagnum moss from the Senart forest. Sphagnum moss is acid (pH 4.0) like eumoder (pH 4.0-4.3) but it is poorer in food resources for Collembola (i.e. absence of animal faeces and humified organic matter). Fifteen adult *H. nitidus* were placed on sphagnum moss, in the same boxes as above and were kept for 9 weeks at 15°C. The number of individuals was counted at the end of the experiment.

<u>Preliminary choice experiments</u>

Choice experiments were carried out in rectangular boxes (12cm x 18cm x 6.5cm) divided into three compartments by perforated plastic walls. Holes (2mm diam) allowed free movement by adult *H. nitidus*. The boxes were placed in a chamber maintained at 15°C with a 10h:14h day:night photoperiod.

In a first experiment, with three replicates, a fresh sample block of each humus form, (i.e. oligomull, eumoder or calcic eumull), was placed in each compartment, the position of the humus changing from a box to another. Eight sub-adult or adult animals were placed in each compartment, thus 24 individuals were present in each box. After 9 weeks fauna were extracted separately from each block of humus. No additional food was supplied. Abundances of *H. nitidus* in each compartment were log-transformed and means were compared between humus forms using two-way ANOVA with experimental boxes as blocks. Humus pH was measured at the end of the experiment. The same experiment was performed with air-dried (ambient temperature, 5 months) then remoistened (with deionized water) humus in order to reduce to a minimum pre-existing fauna without inducing deep changes in humus characteristics (e.g. pH, organic matter).

A third experiment was performed using the same boxes, but filled with sieved and compacted humus in such a way that *H. nitidus* could not sink in it. This allows continuous counting of surface located collembola. Seven sub-adults or adults were placed in each of the three humus blocks, thus 21 individuals were present in each box. The abundance of *H. nitidus* in each compartment was recorded 3 times a day (at 8h, 13h and 18h) for 5d. Between counting periods boxes were incubated at 15°C. Means of the fifteen countings for each humus form and each box were compared as described above. A fourth experiment was performed, using fresh humus blocks (six replicates), as in the first experiment. *H. nitidus* could only chose between the two humus forms which differ the most by their pH, i.e. eumoder and calcic eumull. Thirty adult or sub-adult *H. nitidus* were evenly distributed on both humus blocks within each of the six boxes. These were kept for 7d at 15°C, a period too short for the reproduction of animals, which facilitated counting and avoided log-transformation of the data. Animals were extracted separately from each block. Humus pH was measured as above. *H. nitidus* were counted as were potential predators of Collembola, i.e. Chilopoda, Pseudoscorpionida, Araneida, and Formicida (Vannier, 1971; Manley *et al*., 1976; Bachelier, 1978). The presence of other fauna (e.g. other collembola species, oribatid mites, Isopoda, Diplopoda) was noted. Ranked abundances of *H. nitidus* were compared by Kruskal-Wallis test (Sokal and Rohlf, 1995). Without reproduction, abundances were too small to allow variance analysis. Differences in predator numbers between eumoder and calcic eumull were tested by the same method.

Choice experiments with earthworms

The aim of these experiments was to discover if *H. nitidus* preferred humus blocks with and without earthworms, independantly of pH or humus form (eumoder or calcic eumull).

Experimental boxes were divided into two compartments by 1 mm-mesh wire net to minimize the possibility of earthworms moving from one compartment to the other. Compartments were filled with blocks of fresh, non sieved humus. Earthworms were collected in the calcic eumull by expelling them with 4‰ formalin. The lumbricid community was dominated by *Allolobophora chlorotica* (Savigny, 1826), a small (50mm), endogeic (soil-dwelling and feeding species) and *Aporrectodea giardi* (Savigny, 1826), a large (150 mm) anecic (soil-dwelling species feeding nightly on litter; Sims and Gerard, 1985). Both species are neutrophilic and live in soil with little organic matter, but *A. giardi* is more tolerant to acidity than *A. chlorotica* (Bouché, 1972). Because of their large size, we added only one adult *A. giardi* to one or both compartments. In one of the experiments, we used two adult *A. chloratica* together with one adult *A. giardi*. All earthworms which had been found by hand-sorting in humus blocks during field sampling were discarded before the experimental run. Combinations between humus forms and presence or absence of earthworms were tested with six replicates each. Thirty adult *H. nitidus* were added to each box at the same time earthworms were introduced. Collembola individuals were distributed in equal number in both compartments. After seven days at 15°C, animals were extracted in each compartment separately. The abundance of *H. nitidus* was estimated as well as that of total predators.

Differences between mean abundances of *H. nitidus* and predators with regard to presence or absence of earthworms and to humus form were tested by Kruskal-Wallis test.

RESULTS

Preliminary field study

Table 1 lists the 27 Collembolan species found during the field investigation. Results of correspondence analysis (Fig. 1) indicate that soil pH, although not involved as a main variable in the analysis, was strongly correlated with axis 1, with a highly significant coefficient of determination R^2 ($P<0.001$). Thus the Collembolan community reflects well the distribution of pH throughout the sampling area, ranging from 3.9 to 7.4. Axis 1 shows the distribution of several Collembolan species according to soil pH. Axis 2 has no ecological significance. *Sminthurinus signatus* was located in more acidic sites, while *H. nitidus, Pseudosinella decipiens, P. alba*, and *Folsomides parvulus* preferred higher pH soils. Only three *H. nitidus* individuals were found in all our samples, all at pH 6 or above. These results corroborated previous field studies (Ponge, 1993).

Culture experiments

Culture experiments without food supply revealed that *H. nitidus* reproduces and survives at pH≤5.0 and even better than at pH>5, i.e. in oligomull and eumoder (Table 2). The population in the eumoder (pH 4.0 to 4.2) was three to four times more abundant than in the calcic eumull (pH 7.2 to 7.4) after 9 weeks rearing. Abundances in the acid mull showed discrepancies between both experiments. However, the experiments were not run at the same time (the one with three replicates was in May, the other was in June) and some changes could have occurred in humus properties, for instance soil pH varied significantly in the oligomull (F test) between sampling dates. From these first culture experiments we concluded that any possible pH effect on the field distribution of *H. nitidus* was indirect. In laboratory cultures this species not only tolerates acid pH but this condition seems to be more favourable to its population dynamics than neutral pH, contrary to observations from field studies.

In cultures with a supply of lichens and microalgae, *H. nitidus* population levels largely exceed those obtained in cultures without any food supply, whatever the pH (Table 2). There were no significant differences between the three humus forms. However, in the experiment with three replicates, the highest abundance of *H. nitidus* was in the calcic eumull. Nevertheless, the residual error was so high and the degrees of freedom were so small that no difference was significant. The fact that the influence of humus form disappeared or changed when food was added may nevertheless suggest that, more important than humus form and acidity, trophic factors are involved in the distribution of *H. nitidus*.

In cultures on sphagnum, there were very few *H. nitidus* (3.7 ± 1.1 individuals per box) and only adult animals were recovered, indicating that, in addition to the high mortality rate, no reproduction was occurring. This may be explained by the absence of food available to Collembola, and confirms the involvement of a trophic factor in the distribution of *H. nitidus.*

Preliminary choice experiments

Nine weeks choice experiments did not reveal any preference of *H. nitidus* for a given humus form, both on fresh and defaunated substrates (Table 3). The abundance of *H. nitidus* was much higher (x5.5)on defaunated humus than on fresh humus, particularly in the oligomull, probably because of the increasing microflora following remoistening of the air-dried soil (Soulides and Allison, 1961; Scheu and Parkinson, 1994). Given the long duration of this experiment, considerable reproduction occurred, and overpopulation may have masked some choice behaviour. For this reason shorter-term experiments were also performed.

Short-term experiments, where *H. nitidus* were counted three times a day for five days on compacted humus, indicated that this species was found more frequently on eumoder, calcic eumull being the less-preferred humus form (Table 3). These results confirm the results of culture experiments.

Choice experiments on fresh blocks of eumoder and calcic eumull, where *H. nitidus* were counted after seven days, indicated that these animals were significantly more abundant ($P<0.05$) in moder (mean pH = 3.9) than in calcic eumull (mean pH = 7.8) which confirmed results from previous three-compartment choices and cultures (Table 4, "preliminary choice experiment"). In one out of six replicates, *H. nitidus* was more abundant in calcic eumull. This box was characterized by the presence of an earthworm.

Choice experiments with earthworms

When *H. nitidus* could choose between a block with earthworms and a block without earthworms, their numbers were significantly higher in the block with earthworms (Table 4). This choice was independent of the humus form (combinations 1, 2, 3), except in combinations where eumoder was present in both compartments (combinations 5, 6). Thus *H. nitidus* was attracted by earthworms or at least remained longer after random movement in compartments containing earthworms. When earthworms were present in compartments filled with calcic eumull and eumoder (combination 4), *H. nitidus* was not significantly more abundant in eumoder. Thus the preference for eumoder is real but less strong than the earthworm effect.

In some replicates we registered a negative relationship between predator and *H. nitidus* numbers. In one replicate of combination 3 (Table 4), there were a lot of ants (92) in the compartment with eumoder and *A. giardi*, and the abundance of *H. nitidus* decreased, contrary to what was found in other replicates (0 or 1 ant). Moreover, replicates of combination 6 showed a significant ($P<0.005$) negative correlation between numbers of *H. nitidus* and large centipedes (>4 mm) in eumoder (Fig.2). There was no significant interaction between centipede abundance and the presence of earthworms (ANOVA). When we compared the number of predators likely to prey on Collembola, i.e. Chilopoda, Pseudoscorpionida, Araneida and

Formicida, in eumoder and calcic eumull (Table 5), we noted that eumoder accommodated significantly more predators than calcic eumull. The abundance of predators did not seem to have any effect below a certain threshold which has not been reached in the calcic mull (Table 5). Therefore the high abundance of predators of collembola in eumoder (and perhaps in other acid humus forms) could be an additional reason for the absence of *H. nitidus* in soils with pH<5.0.

DISCUSSION

In contrast to our field results and those of Ponge (1983, 1993), our culture and choice experiments showed that *H. nitidus* prefers acid soils between pH 4 and 5 in which conditions, possibly food resources, are more favourable to its development than in neutral-alkaline soils. From this it follows that soil acidity (at least at pH 4), does not have a direct effect on *H. nitidus*. These results are inconsistent with those obtained by Kopeszki (1992) in a field experiment, which indicated that the abundance of *H. nitidus* decreased according to soil pH-KCl within the range of 4.5 to 3. However, comparison is difficult because experimental conditions as well as pH measurements were different and, above all, because in Kopeszki's experiments soil acidification was induced by acid rain, comprising other compounds such as SO_4^{2-} which probably had a greater influence than the pH (Sequeira, 1987). Hågvar (1984) showed that three microarthropod species (including a Collembola species) did not have the same reaction towards soil pH when they were cultured alone on defaunated soils compared with cultures in natural soils with complete fauna. Our results support the hypothesis that other organisms affect the distribution of *H. nitidus*.

The presence of *H. nitidus* in neutro-alkaline soils only may be determined by two types of factors: positive factors which attract it to neutro-alkaline and negative factors which prevent it living in acid soils. In our choice experiments we demonstrated that *H. nitidus* moved to compartments with earthworms, the distribution of which is influenced by soil pH and calcium content (Satchell, 1967; Piearce, 1972a and 1972b). Piearce (1972b) found earthworms were more important (in terms of species richness, population density and biomass) in soils > pH5.0 compared to more acidic soils. Moreover, *H. nitidus* was always found in soils > pH5.0, thus in mull humus forms. Mull humus forms are rich in earthworms, particularly earthworms belonging to the anecic ecological category (Jabiol *et al*., 1995), while the lumbricid fauna is poorly represented in moder (Bouché, 1975). Consequently, the distribution of *H. nitidus* in relation to soil pH is likely to be controlled by the presence of earthworms. However, this relationship is probably species-specific since a number of earthworms are acid-tolerant and inhabit oligomull humus forms at <pH5.0. *Aporrectodea giardi* and *Allolobophora chlorotica*, which attracted *H. nitidus* in our choice experiments, are considered neutrophilic and live in soils with little litter (Bouché, 1972). Therefore they will not be present in oligomull. There is little information about *Aporrectodea giardi* which occupies a very restricted geographic area, while *Allolobophora chlorotica* is an acid-intolerant species (Piearce, 1972a).

Earthworms have a great impact on the soil environment and therefore the attraction of *H. nitidus* to soils containing earthworms may be due to several causes. Some consider earthworm burrows as a favourable microhabitat for microarthropods, without distinguishing attractive factors (Bayoumi, 1978; Loksa, 1978). A major initial impact of burrowing is its effect on soil structure (Satchell, 1967). Soil-dwelling Collembola are sensitive to soil compaction, and any reduction in soil pore size produces a decrease in Collembola densities (Heisler and Keiser, 1995). Furthermore, larger Collembola are more abundant in zones with high earthworm densities than in zones without or with few earthworms (Marinissen and Bok, 1988; Loranger *et al*., 1998). Thus earthworm tunnels could allow *H. nitidus*, a large soil-dwelling Collembola, to move within the soil profile, either to search for food or to escape unfavourable conditions near the surface. This would be impossible in moder where mineral horizons are compact (Bernier, 1996). Some authors assigned the positive influence of earthworms upon microarthropod populations to improvement in water retention capacity (Hamilton and Sillman, 1989) or drainage (Loranger *et al*., 1998). However, *H. nitidus* has never been found in oligomull at <pH5, despite the presence of earthworm burrows.

Our results from culture and choice experiments give more support to a trophic cause for the attraction of *H. nitidus* by earthworms, since their gut contents were mostly made of ingested invertebrate faeces (Arpin *et al*., 1980; data not presented). Increase in food availability has been evoked often as an explanation for the observed impacts of earthworms upon soil fauna (Brown, 1995; Loranger *et al*., 1998). Several processes may explain this increase:

(1) Microorganisms. Some bacteria (including actinomycetes) are more abundant in fresh casts than in surrounding soil (Satchell, 1967; Martin and Marinissen, 1993), which implies that *H. nitidus* would have to live in close proximity to earthworms in order to benefit from fresh cast deposition.

(2) Mineral nutrients. Generally, earthworm casts are richer in total and exchangeable Ca^{2+}, exchangeable K^+ and Mg^{2+}, inorganic PO_4^{3-}, and NO_3^- (Lunt and Jacobson, 1944; Sharpley and Syers, 1976; Martin and Marinissen, 1993). Acid-intolerant species of earthworms secrete a greater quantity of calcium than others (Piearce, 1972b; Wiecek and Messenger, 1972).

(3) Organic compounds. Casts and burrow walls have generally a higher content in organic matter than surrounding soil, at least in deep horizons (Lunt and Jacobson, 1944; Kretzschmar, 1987). Earthworms excrete a number of organic compounds such as proteins and glycoproteins, urea, amino-acids, vitamins, osides. These are excreted not only in casts, but also directly in the environment through their nephridiae (El Duweini and Ghabbour, 1971), and as epidermal mucus which is considered as an important nitrogen source for soil microorganisms and plants (Needham, 1957; Dubash and Ganti, 1964; Atlavinyte and Daciulyte, 1969; Cortez and Bouché, 1987). These products may be different according to species and some of them, particularly nitrogenous compounds, are susceptible to rapid decomposition, which could necessit a rapid uptake by *H. nitidus*, if this species is capable of using them as food.

It is not known whether *H. nitidus* is attracted to earthworms by chemical signals or merely remains in a beneficial environment after random exploration of the soil. The latter process could be reinforced by aggregation pheromones which have been found in Collembola (Verhoef *et al.*, 1977), including *H. nitidus* (Krool and Bauer, 1987). It has been demonstrated that some Collembolan species are attracted by odours produced by fungal species on which they feed (Bengtson *et al.*, 1988), which may support the idea of chemoattraction if such odours are produced by earthworms. Furthermore, glycoproteins excreted by *Lumbricus terrestris* have been suspected to induce attack by its predators (Halpern *et al*., 1984).

The attraction of *H. nitidus* by earthworms may be a reason why this species is present only in soils at >pH5 but does not explain why it was not found in oligomull at <pH5 even though it can be cultured in the laboratory in moder at lower pH. As this research demonstrated, a strong predator pressure has a negative impact on the presence of *H. nitidus*. Furthermore, Vannier (1971) noted that ants capture *H. nitidus*, and spiders and centipedes are among the most important predators of Collembola (Manley et al., 1976). In our samples, all three of these predators were much more abundant in eumoder than in calcic eumull. Thus, predation could explain the absence of this species at pH<5.

Studying the spatial distribution of soil animals is difficult because several factors interact with each other (Ponge *et al*., 1997). In the case of *H. nitidus*, strong relationships with earthworms seem established but underlying mechanisms remain to be studied, as well as quantification of the impact of predators in the field.

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LEGENDS

Fig. 1 Correspondence analysis on 60 field samples from the Senart forest and 27 Collembolan species. Projection in the plane of axes 1 and 2. Collembolan species are coded by three letters. λ = soil with limestone grains, ○ = surrounding acid soil.

Fig. 2 Linear regression between densities of *H. nitidus* and big-size centipedes (>4 mm) in combination 6 of choice experiments with earthworms (see text).

Table 1. List of Collembolan species found in the field study and represented in the correspondence analysis (Fig. 1)

AFU	*Allacma fusca* (Linné, 1758)
ATE	*Arrhopalites terricola* (Gisin, 1958)
DMI	*Dicyrtomina minuta* (Fabricius, 1783)
EMU	*Entomobrya multifasciata* (Tüllberg,1871)
FMA	*Folsomia manolachei* (Bagnall, 1939*)*
FPA	*Folsomides parvulus* (Stach, 1922)
HMA	*Heteromurus major* (Moniez, 1889)
HNI	*Heteromurus nitidus* (Templeton, 1835)
IMI	*Isotomiella minor* (Schäffer, 1896)
LCU	*Lepidocyrtus curvicollis* (Bourlet, 1839)
LLA	*Lepidocyrtus lanuginosus* (Gmelin, 1788)
MMI	*Megalothorax minimus* (Willem, 1900)
MMA	*Mesaphorura macrochaeta* (Rusek, 1976)
NMU	*Neanura muscorum* (Templeton, 1835)
OIN	*Onychiurus insubrarius* (Gisin, 1952)
OCI	*Orchesella cincta* (Linné, 1758)
OVI	*Orchesella villosa* (Geoffroy, 1764)
PCA	*Paratullbergia callipygos* (Börner, 1902)
PNO	*Parisotoma notabilis* (Schäffer, 1896)
PAL	*Pseudosinella alba* (Packard, 1873)
PDE	*Pseudosinella decipiens* (Denis, 1924)
SSI	*Sminthurinus signatus* (Krausbauer, 1898)
SIN	Undetermined Symphypleona
TBO	*Tomocerus botanicus* (Cassagnau, 1962)
VAR	*Vertagopus arboreus* (Linné, 1758)
XGR	*Xenylla grisea* (Axelson, 1900)
XAR	*Xenyllodes armatus* (Axelson, 1903)

Table 2. Densities of *H.nitidus* in culture experiments on three humus forms at different pH values. CM: calcic eumull, AM: oligomull, MO: eumoder. SEM: standard error of the mean. ANOVA was performed on log-transformed data. A posteriori comparisons (Newman-Keuls test) were done at 0.05 level

Cultures	Number of Replicates	Densities of *H. nitidus* in each humus form (mean ± SEM)	F value (ANOVA)	Probability	Newman-Keuls test
Without food supply	3	CM (pH 7.39) : 7.3 ± 3.2 AM (pH 4.64) : 25.3 ± 2.9 MO (pH 4.00) : 21.7 ± 1.9	6.41	0.0328	MO=AM>CM
	5	CM (pH 7.24) : 12.6 ± 5.7 AM (pH 4.11) : 9.8 ± 2.6 MO (pH 4.23) : 28.0 ± 3.7	4.81	0.0290	MO>CM=AM
With food supply	3	CM (pH 7.40): 2374.3 ± 249.7 AM (pH 4.43) : 348.3 ± 116.0 MO (pH 4.04) : 504.3 ± 250.9	3.29	0.1079	
	5	CM (pH 7.27) : 2658.0 ± 621.9 AM (pH 4.05) : 1883.6 ± 249.7 MO (pH 4.27) : 2485.6 ± 255.4	0.48	0.6326	

Table 3. Densities of *H.nitidus* (mean of three replicates) in preliminary choice experiments using three humus forms at different pH values. CM: calcic eumull, AM: oligomull; MO: eumoder. SEM: standard error of the mean. A posteriori comparisons (Newman-Keuls test) were done at 0.05 level

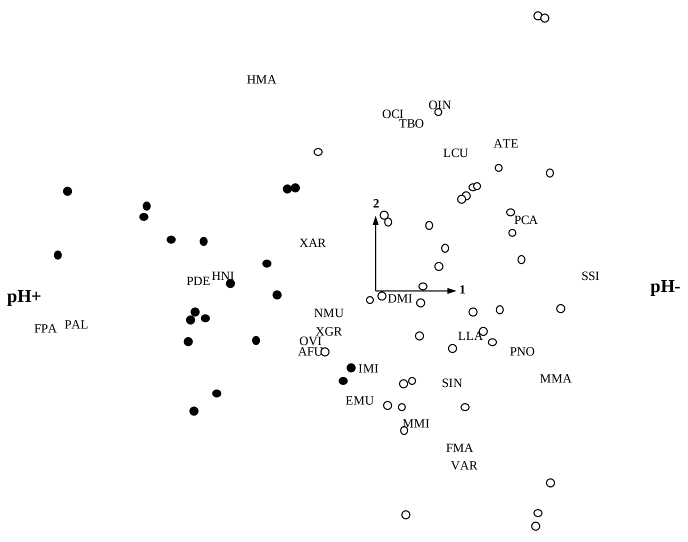
Choice Experiments		*H. nitidus* number in each humus type (mean ± SEM)		F value (ANOVA)	Probability	Newman-Keuls test
25 *H. nitidus* for 2 months	on fresh humus	CM (pH 7.51) : 54.7 ± 7.9 AM (pH 4.32) : 64.0 ± 22.2 MO (pH 3.87) : 40.7 ± 6.2		0.16 (log-transformed data)	0.8562	
	on dried and remoistened humus	CM (pH 7.42) : 185.3 ± 42.0 AM (pH 4.75) : 458.3 ± 99.7 MO (pH4.32) : 250.7 ± 10.1		5.29 (log-transformed data)	0.0763	
20 *H. nitidus* for 5 days on compacted humus		CM : 4.58 ± 0.5 AM : 5.96 ± 0.4 MO : 8.64 ± 0.4	(Mean of 15 countings)	26.35	0.000	MO>AM>CM

Table 4. Distribution of *H. nitidus* with regard to the presence of earthworms and to humus form. Each combination was run with 6 replicates and 30 adults. CM: calcic eumull, MO: eumoder, NS: not significant

Combination	Blocks	Densities of *H. nitidus* (mean of replicates/block)	X^2 test (Kruskal-Wallis)	Preferred block
Preliminary choice experiment	MO without earthworms	17	$P<0.05$ ($P<0.01$ without the replicate containing an earthworm in CM)	MO
	CM without earthworms except in one replicate	7		
1	CM + A. giardi	25	$P<0.005$	CM + A. giardi
	CM without earthworms	3		
2	CM + A. giardi	28	$P<0.005$	CM + A. giardi
	MO without earthworms	3		
3	CM without earthworms	7	$P<0.05$ ($P<0.001$ without the replicate containing 92 ants)	MO + A. giardi
	MO + A. giardi	19		
4	MO + A. giardi	15	NS	
	CM + A. giardi	9		
5	MO + A. giardi	14	NS	
	MO without earthworms	9		
6	MO + A. giardi + A. chloratica	17	NS	
	MO without earthworms	12		

Table 5. Densities of predators (Chilopoda, Pseudoscorpionida, Araneida and Formicida) in choice experiments with regard to humus form and presence of earthworms. Each combination was run with 6 replicates. CM: calcic eumull, MO: eumoder.

Combination	Blocks	Densities of predators (mean of replicates/block)	X^2 test (Kruskal-Wallis)	Humus with the highest predator number
Preliminary choice experiment	CM without earthworms except in one replicate	1.33	P<0.005	MO
	MO without earthworms	7.50		
2	CM + A. giardi	1.33	P<0.05	MO
	MO without earthworms	5.50		
3	CM without earthworms	0.83	P<0.005	MO
	MO + A. giardi	20.50		
4	CM + A. giardi	1.00	P<0.005	MO
	MO + A. giardi	9.00		


HMA
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MMI
FMA
VAR

Fig. 1

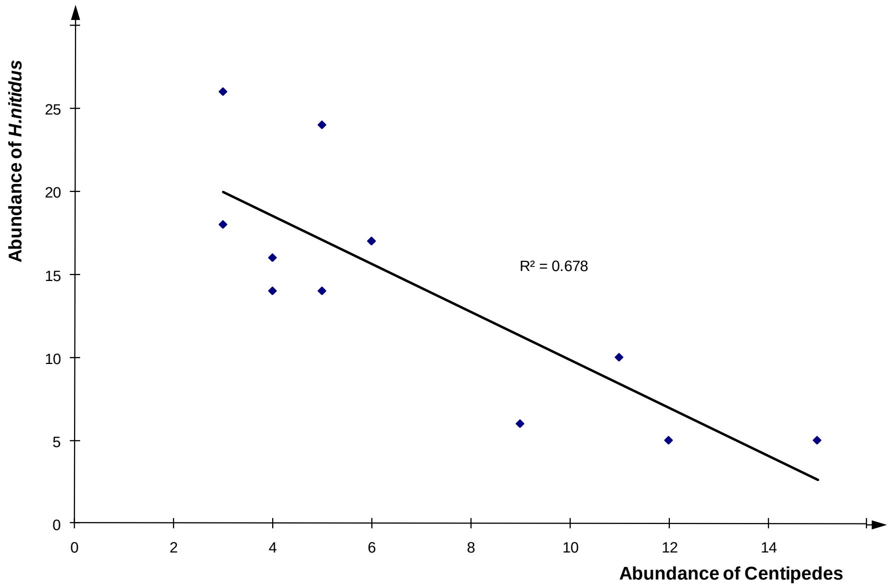
Abundance of *H.nitidus*
25
20
15
10
5
0
0
2
4
6
8
10
12
14
Abundance of Centipedes
$R^2 = 0.678$

Fig. 2