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2 **EARTHWORMS AND COLLEMBOLA RELATIONSHIPS: EFFECTS**  
3 **OF PREDATORY CENTIPEDES AND HUMUS FORMS**

4  
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26

## 1 **Abstract**

2

3 Relationships between anecic earthworms (*Lumbricus terrestris* and *Aporrectodea*  
4 *giardi*) and the collembolan species *Heteromurus nitidus* (Templeton, 1835), which is known  
5 to be attracted to earthworms, were investigated in an 8-week laboratory experiment. Our  
6 aims were (1) to assess whether earthworms influence the population dynamics of *H. nitidus*,  
7 and (2) to study pathways of influence and how earthworm effects are modified by humus  
8 forms and predators. Using microcosms with three defaunated humus forms, then provided  
9 with earthworms and predators, we intended to demonstrate that, amongst possible favourable  
10 effects of earthworms on springtail populations, earthworm activity may provide greater  
11 access and more pathways for springtails to explore soil and avoid predation. We expected  
12 that the effects of predators (centipedes) on the abundance of *H. nitidus* would increase from  
13 less (calcic mull) to more (moder) compact soil, and we hypothesized that earthworms would  
14 reduce predation pressure on *H. nitidus* by providing escape routes through increased  
15 macroporosity. Humus forms and earthworms only affected the population size of *H. nitidus*  
16 under high predation pressure. When collembolan numbers were higher in calcic mull than in  
17 moder, and were increased by the presence of earthworms. These results corroborate the  
18 hypothesis that earthworms, by increasing soil macroporosity, improve the escape routes for  
19 Collembola and thus evade predators. In moder humus earthworms increased the density of  
20 *H. nitidus* whether predators were present or not, so we cannot exclude that earthworms were  
21 also directly beneficial to *H. nitidus*. However, the hypothesis of a functional relationship  
22 mediated by soil macroporosity seems relevant since it was supported by differences observed  
23 when considering body size. When two size classes were distinguished within populations of  
24 *H. nitidus* (1) the positive effect of earthworms in moder was observed only on larger  
25 Collembola (> 1 mm), (2) the density of the larger Collembola was decreased by predation  
26 only in moder and not in mull, (3) the effects of predators on the smaller individuals were not  
27 influenced by the presence of earthworms whatever the humus form, and was not decreased  
28 by the presence of earthworms. Nevertheless, factors other than macroporosity may operate as  
29 the presence of earthworms in acidic mull led to an unexplained decrease in the abundance of  
30 small-sized *H. nitidus*.

31

32 *Keywords* Collembola ; Chilopoda ; Lumbricidae ; Predation ; Soil structure ; Interactions

33

## 34 **1. Introduction**

1  
2 Species may interact with each other according to four main pathways: competition,  
3 predation, parasitism and mutualism. Studies on between-species interactions, that affect  
4 population dynamics and species composition of communities, are usually focused on  
5 competition for food or upon predator-prey relationships (Begon et al., 1996). This is  
6 particularly true of interactions between soil invertebrates (Funke et al., 1995; Theenhaus et  
7 al., 1999; Chen and Wise, 1999). Conversely the positive influence of some soil invertebrates  
8 on other species is more rarely taken into account. Earthworms, called “ecosystem engineers”  
9 because of their strong influence on soil properties and functional processes (Jones et al.,  
10 1994), have been proposed to create favourable habitats for many other invertebrate species.  
11 Density and variety of microarthropods often increased in soils with high earthworm  
12 populations (Hamilton and Sillman, 1989; Loranger et al. 1998). Among microarthropods  
13 some collembolan species were found to be more abundant in earthworm burrows or middens  
14 than in the surrounding soil (Maraun et al. 1999; Tiunov and Kuznetsova, 2000). However, it  
15 seems that the work of Wickenbrock and Heisler (1997) is the only investigation to explain  
16 the direct positive effects of earthworms on the surrounding soil fauna. Their work showed  
17 that the collembolan *Folsomia candida* was attracted to an improved soil porosity due to  
18 earthworms. Thus, although foodweb studies are needed to understand the structure of biota  
19 in the soil-litter system (Schaefer, 1995), between-species relationships may also occur at a  
20 non-trophic level, i.e. the habitat *sensu stricto*.

21 Investigators have shown that the collembolan *Heteromurus nitidus* (Templeton, 1835)  
22 was attracted to earthworms, particularly to their excretions of mucus and ammonium  
23 (Salmon and Ponge, 1999, 2001; Salmon, 2001). This species, is restricted to mull humus  
24 forms at pH > 5 (Ponge, 1990, 1993; Salmon and Ponge, 1999) and its distribution, can be  
25 determined by the abundance of earthworms (Salmon, 2001). However the causes of this  
26 attraction remain unknown. Earthworms may provide *H. nitidus* with additional food  
27 resources, since this species feeds on faeces (Arpin et al, 1980; Salmon, 2004) and was shown  
28 to ingest the mixture of mucus and urine excreted by earthworms (Salmon and Ponge, 2001).  
29 However, *H. nitidus* may also benefit from the space created by anecic earthworms in soil  
30 through their burrowing activity. To test this hypothesis, we studied the influence of  
31 earthworms on the population dynamics of *H. nitidus* in soils of varying pore size. Results of  
32 preliminary experiments (Salmon, 2004) using fresh soil cores with their original fauna  
33 revealed that the activity of anecic earthworms in some cases affected the predation on *H.*  
34 *nitidus*. Cultures of *H. nitidus* in two distinct humus forms, a moder and a calcic mull, led to a

1 higher density of *H. nitidus* in the calcic mull than in the moder. This result was attributed to a  
2 higher abundance of predators in moder humus, but it might also be due to a difference in the  
3 structure of the two humus forms. Actually, calcic mulls are highly worked by anecic and  
4 endogeic earthworms, contrary to moders from which soil-dwelling earthworms are absent  
5 (Salmon, 2001). Considering the strong effects of these earthworms on the soil structure we  
6 may assume that an increased number of interconnected macropores in the calcic mull (Lee,  
7 1985; Lavelle, 1988; Edwards and Bohlen, 1996), allows *H. nitidus* to better avoid predation.

8 We investigated relationships between “ecosystem engineers” (Lumbricidae),  
9 detritivore microarthropods (Collembola) and predators (Chilopoda). We focused particularly  
10 on pathways by which the former favourably influence the second. We (1) investigated  
11 whether earthworms influence the population dynamics of *H. nitidus* in microcosms filled  
12 with different humus forms and (2) determined whether their influence might be because of a  
13 change in the physical habitat of Collembola, allowing them to avoid predation. To do this  
14 cultures of *H. nitidus* were established, in the presence or absence of an anecic earthworm, in  
15 three humus forms, a calcic mull (highly worked by earthworms), an acidic mull (slightly  
16 worked by earthworms) and a compact moder humus (not worked by anecic and endogeic  
17 earthworms). Humus profiles were used as defaunated blocks, with their original structure  
18 preserved. In half of the microcosms a controlled predation pressure was applied, which was  
19 identical in all humus forms. If earthworms, through their burrows, favour access of *H. nitidus*  
20 to the soil volume, then their activity should lead to a higher density of Collembola in the  
21 presence of predators and should have no effect in their absence. Earthworms should also  
22 influence preferentially the abundance of large-sized individuals (sub-adult and adult) *H.*  
23 *nitidus*, which hardly move in the compact moder, than immature individuals of smaller size.  
24 Differences according to humus forms were also expected.

25

## 26 **2. Material and methods**

27

### 28 *2.1. Experimental setup*

29

30 Microcosms were made of right-angle plastic boxes (L: 9.2 cm x l: 8.3cm x h:14.7 cm)  
31 filled with blocks of defaunated humus. Three different humus forms were used: a moder  
32 humus and an acidic mull, originating from the Senart Forest (leached acidic soil under sessile  
33 oak (*Quercus petraea*)) near Paris (France), and a calcic mull from the park of the laboratory  
34 (black rendzina under hornbeam (*Carpinus betulus*)), near the Senart Forest. Sampling sites

1 and soils have been described by Arpin et al. (1984) and Bouché (1975). Cores of humus, the  
2 structure of which was preserved, were defaunated by drying at 25°C for 14 d, followed by  
3 freezing at -20°C for 12 d. After thawing at ambient temperature (20°C), humus cores were  
4 remoistened to field capacity at d 0, and microcosms were weighed at once.

5 Four treatments were applied to each humus form: (1) addition of Collembola only,  
6 (2) addition of Collembola + predators, (3) addition of Collembola + earthworms, (4) addition  
7 of Collembola + predators + earthworms. Each treatment comprised five replicates.

8 Collembola came from a batch culture on water-moistened fine quartz sand, they were  
9 fed with a mixture of terrestrial microalgae (*Desmococcus* spp.) and lichens taken from bark  
10 scrapings. The batch culture started 5 months before the experiment from several individuals,  
11 which were extracted from the calcic mull.

12 Earthworms were extracted from the calcic mull with 4 ml formalin l<sup>-1</sup>. Two species,  
13 belonging to the anecic ecological category (Bouché, 1975) were used, i.e. *Aporrectodea*  
14 *giardi* (Savigny, 1826) and *Lumbricus terrestris* (Linnaeus, 1758).

15 Centipedes, as predators of Collembola, were extracted by the dry funnel method from  
16 soil taken from the acidic mull and from a heap of composted hornbeam leaves on the calcic  
17 mull. Predators were kept alive on plaster of Paris mixed with Prolabo<sup>®</sup> flame black covered  
18 with hornbeam leaf fragments for several weeks, the time needed to obtain the density  
19 required for all treatments. Animals were provided with prey (varying species of Collembola)  
20 and water once a week.

21 One adult *A. giardi* or *L. terrestris* was introduced into each of 30 microcosms, 24 h  
22 after humus had been moistened (D+1). All treatments with earthworms contained three  
23 replicates with *L. terrestris* and two replicates with *A. giardi*. Twenty seven adult *H. nitidus*  
24 were introduced into all boxes, 24 h after earthworm introduction (D+2). The addition of  
25 predators (14 per box) was made 5 d after Collembola were introduced (D+7), in 30  
26 microcosms, which then included each 7 adult Chilopoda Scolopendromorpha, 3 immature  
27 Chilopoda Scolopendromorpha, 2 Chilopoda Geophilomorpha, and 2 Chilopoda  
28 Lithobiomorpha. The density of predators chosen for the experiment (10 centipedes.dm<sup>-2</sup>) was  
29 defined on the basis of field investigations which were performed 3 months before in the three  
30 humus forms, and corresponded to the highest density found, i.e. that of the acidic mull.  
31 Chilopoda were determined at the species level at the end of the experiment according to  
32 Geoffroy (2000) and Jeekel (1999), on ethanol-preserved specimens.

33 To force Collembola to move downwards into the soil vertical gradients of moisture  
34 and light were created by covering boxes with a firmly-attached nylon gauze allowing water

1 evaporation. Microcosms were held under periodic 12:12 light at 15°C for 8 weeks. The  
2 moisture content was kept constant with deionized water after weighing boxes every 2 weeks.

3 At the end of the experiment, worms were removed by hand then humus blocks were  
4 placed on Berlese-Tullgren extractors (3 mm mesh) to collect Collembola and predators.  
5 Earthworms were rinsed in water and dried quickly on filter paper before being weighed.  
6 Specimens of *H. nitidus* were harvested in 90% ethanol, then counted under a dissecting  
7 microscope and classified into two size classes ( $< 1$  mm and  $\geq 1$  mm). Soil pH was measured  
8 on dried soil mixed with deionized water (soil:water 1:5 v/v) for 5 min, after decantation for  
9 4h (Anonymous, 1999).

## 11 2.2. Statistical analysis

13 The effect of three factors (humus, predators and earthworms) on the total abundance  
14 and large-sized individuals was first analysed by a three way ANOVA, after log-  
15 transformation of the data.

16 One replicate from the treatment acidic mull + earthworms + predators was excluded  
17 from analyses because of an abnormally low Collembolan density, due to anomalous dryness  
18 and compaction. The three-way ANOVA, performed on the total abundance of *H. nitidus*,  
19 revealed significant interactions between humus form and predators on one part, and between  
20 humus form and earthworms on the other part. Main effects of these factors were thus further  
21 analyzed by separate two-way ANOVAs. Separated analyses was further justified by the fact  
22 that the earthworm effect was not the same in moder and acidic mull, and also because three-  
23 way ANOVA was not possible on small-sized individuals even after transformation of the  
24 data.

25 Five two-way ANOVAs (earthworms and predators or earthworms and humus as  
26 treatments) were performed within each humus form and within treatments "with predators"  
27 and "without predators", respectively. ANOVAs were performed on total abundance as well  
28 as on abundance of two size classes, after square root-transformation of the data to  
29 homogenize variances. *A posteriori* multiple comparisons were done by the Newman-Keuls  
30 procedure using Statbox®. The effect of humus form on the total abundance of *H. nitidus* was  
31 also analyzed by one-way ANOVA in the treatment excluding both predators and  
32 earthworms.

33 Changes in earthworm body weight according to time and humus form were analyzed  
34 by two-way ANOVA for repeated-measures with time as repeat factor and humus as

1 treatment factor. Mean predator numbers recovered at the end of the experiment in the 30  
2 microcosms into which they had been introduced were analyzed by two-way ANOVAs to  
3 ensure that neither humus form, nor the presence of earthworms influenced their abundance.  
4 Mean pH values of the three humus forms were compared by one-way ANOVA. Within each  
5 humus form, pH variation due to treatments "earthworms" and "predators" were compared by  
6 two-way ANOVAs.

### 7 8 **3. Results**

#### 9 10 *3.1. Soil pH*

11  
12 Mean soil pH values differed significantly ( $P < 0.001$  for all comparisons) in calcic  
13 mull ( $7.70 \pm 0.02$ ), acidic mull ( $4.52 \pm 0.04$ ) and moder ( $4.31 \pm 0.04$ ), but it did not vary  
14 according to the presence or absence of earthworms and predators ( $P > 0.05$  for all  
15 comparisons).

#### 16 17 *3.2. H. nitidus : whole population*

18  
19 The three-way ANOVA revealed a strong negative influence of predators on the total  
20 abundance of *H. nitidus* ( $P < 0.0001$ ). The humus form, although at a low probability level ( $P$   
21 = 0.0575) was not significant, but two interactions were detected: humus form x earthworms  
22 ( $P = 0.0489$ ) and humus form x predators ( $P = 0.0368$ ). These factors were thus analysed  
23 separately by two-way ANOVAs (Table 1). The three-way ANOVA also revealed that the  
24 humus form significantly affected large-sized Collembola ( $P = 0.0003$ ) which were more  
25 abundant in calcic mull than moder and acidic mull.

26 The humus form and the presence of *A. giardi* or *L. terrestris* affected the abundance  
27 of *H. nitidus* but only when this species was subject to predation (Table 1). In the presence of  
28 predators the abundance of Collembola (1) was higher in the calcic mull than in the moder ( $P$   
29 = 0.015), densities in the acidic mull being intermediate ( $P > 0.05$ ), and (2) was higher in the  
30 presence of earthworms (Fig.1A). Without predators and earthworms, densities of Collembola  
31 were similarly high ( $P > 0.05$ ) in the three humus forms (Fig.1A).

32 In the three humus forms, centipede predatory activity reduced the total number of *H.*  
33 *nitidus*. Moder showed the most dramatic decrease, by a factor of three (Fig.1A). When the

1 three humus forms were analyzed separately (Table 1), the effects of anecic earthworms were  
2 significant only in moder, resulting in an increase in the number of *H. nitidus* (Fig. 1A).

### 3 4 3.3. *H. nitidus*: individuals larger than 1 mm

5  
6 When treatments with and without predators were analyzed separately, only the  
7 abundance of large individuals (adults and sub-adults) subject to predation differed according  
8 to the humus form (Table 2). It was higher in the calcic mull than in acidic mull ( $P < 0.001$ )  
9 and in the moder ( $P = 0.002$ ) (Fig.1B), the two latter humus forms being not significantly  
10 different the one from the other ( $P > 0.05$ ).

11 When the influence of predators was analyzed separately in each humus form, it was  
12 significant only in moder humus (Table 2), where a decrease in the density of large specimens  
13 was observed in the presence of predators (Fig. 1B). As for the whole population, the effects  
14 of earthworms was significant only in moder, where they led to an increase in the abundance  
15 of adults and sub-adults when treatments with and without predators were pooled (Fig.1B).

16 As a consequence, adults and sub-adults were more abundant in the calcic mull,  
17 compared to the two acidic humus forms, but this effect was revealed only in the presence of  
18 predators. However, negative as well as positive effects of predators and earthworms were  
19 found only in moder, not in acidic mull.

### 20 21 3.4. *H. nitidus* : individuals smaller than 1 mm

22  
23 The humus form did not affect populations of small-sized Collembola, whether  
24 predators were present or not (Table 3). On the other hand, predator activity resulted in a  
25 strong decrease in densities of small-sized individuals in the three humus forms (Fig.1C). No  
26 positive effect of earthworms was detected whatever the humus form. In the acidic mull, an  
27 interaction between earthworms and predators was observed. Without predators, the presence  
28 of *A. giardi* or *L. terrestris* decreased the number of small-sized Collembola, ( $P = 0.015$ ),  
29 which reached a value comparable to that resulting from predator activity. This decrease was  
30 not observed in the presence of predators and, conversely, the effects of predators were visible  
31 only without earthworms ( $P = 0.001$ ). As a consequence, only predators influenced  
32 populations of small-sized individuals except in the acidic mull, where earthworms decreased  
33 densities of immature individuals in the absence of predation.

34

### 3.5. Earthworms

At the end of the 8-week experiment, 10 *A. giardi* out of 12 and 14 *L. terrestris* out of 18 (three worms died in moder) were still alive. The two big-sized earthworm species thus adjusted to experimental conditions, despite the very shallow soil available in the microcosms. However, earthworms lost weight during the experiment ( $P = 0.008$ ), whatever the humus form ( $P = 0.945$ ).

The two anecic species dug galleries in the three humus forms. In several boxes, these biogenic structures were visible through the transparent walls. After 4 weeks, the inner part of some galleries was visible because at this time they had not been completely covered with cast material. We were then able to observe *H. nitidus* moving in the lumen of the earthworm galleries.

### 3.6. Predators

Only one predatory mite larger than 1 mm was found at the end of the experiment in two microcosms without predators added. The presence of scarce non-predatory mites (Acaridida) as well as a small number (1 to 4 per microcosms) of Collembola other than the introduced animals, were also noted. Thus, even though humus blocks were not fully defaunated, the small number of individuals which resisted defaunation did not probably bias the results.

Only 5.3 predators on average out of the 15 introduced into each of the 30 microcosms were recovered at the end of the experiment. This low rate of recovery was probably not completely due to mortality, but it may also result from the difficulty for the larger animals to pass through the 3 mm mesh sieve in the Berlese funnels. The mean abundance of recovered predators (Table 4) did not vary according to either humus forms ( $P = 0.218$ ) or the presence or absence of earthworms ( $P = 0.654$ ). Seven species of centipedes of variable size were found (Table 5), but most of individuals belonged to *Cryptops hortensis* (Scolopendromorpha, mean length: 20 mm, width : 2mm), *Necrophloeophagus flavus* (Geophilomorpha, mean length: 40 mm, width : 3 mm) and *Lithobius microps* (Lithobiomorpha, mean length: 6 mm, width 1 mm).

## 4. Discussion

#### 1 4.1. Comparison between calcic mull and moder

2

3 All treatments showed strong negative effects of Chilopoda on total populations of *H.*  
4 *nitidus* whatever the humus form. This result supports the high predation pressure by  
5 centipedes on Collembola observed by Poser (1988). However, the effect of predation varied  
6 according to the humus form, since for the same number of predators (at the beginning and at  
7 the end of the experiment), densities of Collembola were higher in the calcic mull than in the  
8 moder. The influence of humus form was only evident when Collembola were subject to  
9 predation pressure. These results support the hypothesis, evolved from preliminary  
10 experiments (Salmon, 2004), that the humus form influences the abundance of *H. nitidus*  
11 through its structural characteristics. Indeed, movements of Collembola, and thus their  
12 success of escape from predators probably varied according to soil pore size.

13 The anecic earthworms *A. giardi* and *L. terrestris* affected the population size of *H.*  
14 *nitidus* only when these animals were subject to predation. Earthworms did not interact  
15 directly with predators, but reduced the mortality rate of Collembola due to predation. These  
16 two earthworm species, through their action on the soil structure, thus reduce predation  
17 efficiency. This may occur through the burrowing of galleries that could facilitate movements  
18 of *H. nitidus* but also through the deposition of faecal material (aggregates) that offer refuges  
19 for subterranean collembolans. Indeed, the introduction of anecic earthworms in soils from  
20 which they were absent (like moder, in our case) is followed by the appearance of a network  
21 of galleries and an increase in pore size (Springett, 1985; Lighthart and Peek, 1997). This  
22 earthworm effect was particularly apparent in microcosms containing moder humus that was  
23 very compact at the beginning of the experiment because it never accommodated anecic or  
24 endogeic earthworms in the field, contrary to acidic and calcic mull (Salmon, 2001). Scheu et  
25 al. (1999) observed that the presence of earthworms increased the abundance of *H. nitidus* in  
26 deeper horizons, which corroborates the hypothesis that *H. nitidus* used inter-connected  
27 macropores created by anecic earthworms. The increase in the traffic of Collembola due to  
28 networks of earthworm galleries supports the hypotheses of Marinissen and Bok (1988),  
29 Wickenbrock and Heisler (1997) and Loranger et al. (1998).

30 The abundance of *H. nitidus* on the whole humus forms, unaffected by earthworms  
31 when predators were absent, indicates that the action of earthworms on the soil structure,  
32 resulting in improved access for *H. nitidus* to the total soil volume, is a key factor for the  
33 distribution of this acid-intolerant species. The hypothesis of a relationship between soil

1 structure and movements of *H. nitidus* was confirmed by differences observed between two  
2 size classes. The positive action of earthworms we observed in moder applied only to larger  
3 individuals, which were not preyed upon in mull, where they moved with ease in earthworm  
4 galleries. The effect of predation upon the smaller individuals did not vary with the humus  
5 form, and it was not affected by earthworms. Indeed, immature *H. nitidus* can move more  
6 easily than adults in small pores. Their success when escaping predators should consequently  
7 be the same in different humus forms. However they are more preyed upon than adults,  
8 because (1) they do not produce aggregation pheromones that decrease locomotory activity  
9 (Joosse and Verhoef, 1974; Verhoef et al. 1977a, 1977b; Krool and Bauer, 1987) and (2) their  
10 smaller size makes them easier for centipedes to catch.

11 Although this aspect was not considered here, because most earthworms were still  
12 alive at the end of our experiment, we cannot totally exclude that, in the field, part of the  
13 predation effort by centipedes is diverted to earthworms. Indeed, some Chilopoda (among  
14 which *Necrophloeophagus flavus* and *Haplophilus subterraneus* were used in our  
15 experiment), are known to be active predators of earthworms (Weil, 1958; Blandin et al.,  
16 1980; Lewis, 1981; Poser, 1988).

17 Even though their effects on the soil structure were prominent, the introduction of  
18 earthworms in moder increased the population size of *H. nitidus* whether predators were  
19 present or not. Thus we cannot exclude that, besides their effect on soil macroporosity,  
20 earthworms were also beneficial to *H. nitidus* at a trophic level. Their galleries are lined with  
21 mucus and casts (Kretschmar, 1987), onto which *H. nitidus* may feed (Arpin et al, 1980;  
22 Salmon and Ponge, 2001). Earthworms may have provided *H. nitidus* with organo-mineral  
23 faeces which are poorly abundant in moder humus, unlike mull (Delecour, 1983; Bernier and  
24 Ponge, 1994; Ponge, 1999).

25

#### 26 4.2. Case of the acidic mull

27

28 Without predators or earthworms, the abundance of *H. nitidus* remained high and  
29 comparable in the three humus forms. Thus the variation in the abundance of this species  
30 according to the humus form we observed in other treatments cannot be attributed to  
31 differences in food resources. Under predation pressure, the population size of *H. nitidus* in  
32 the acidic mull was intermediate between those recorded in the calcic mull and in the moder.  
33 Unlike moder, the acidic mull contained macropores at the start of the experiment, that had  
34 been created by anecic and endogeic earthworms, but these were less numerous than those in

1 the calcic mull where earthworm densities were higher (Salmon, 2001). Furthermore, unlike  
2 anecic species, the galleries of which are vertical and wide and remain devoid of excrement,  
3 endogeic species form a network of horizontal galleries close to the surface, most of which  
4 are partly filled with cast material (Springett, 1983; Edwards and Bohlen, 1996; Jégou et al.  
5 1998; Capowiez et al., 2001). We may thus consider that the mobility of *H. nitidus* in the  
6 topsoil is favoured in calcic mull, where large numbers of anecic earthworms occur, than in  
7 the acidic mull, which is rather dominated by endogeic and epigeic earthworms.

8 The hypothesis of a causal relationship between the structure of the topsoil and  
9 densities of *H. nitidus* is also supported by the fact that the abundance of larger individuals,  
10 contrary to the whole population, was higher in calcic than in acidic mull.

11 However, other factors than macroporosity can also explain the intermediate position  
12 of the acidic mull. Contrary to expectation, (1) the introduction of *A. giardi* or *L. terrestris* in  
13 the defaunated acidic mull did not benefit *H. nitidus*, (2) earthworms were even unfavourable  
14 to small-sized individuals. The fact that the effects of predators on the whole population were  
15 less pronounced in the acidic mull than in the moder can explain that the effect of the  
16 introduction of earthworms was less visible in the acidic mull (already containing  
17 macropores). Furthermore, densities of predators used in the present experiment were lower  
18 than those recorded in blocks of non-defaunated acidic mull (Salmon, unpub data). A stronger  
19 predation pressure could thus contribute to the absence of *H. nitidus* from acidic mull , as  
20 observed in the field.

21 The decreased density of small-sized *H. nitidus* in the acidic mull without predators  
22 but with earthworms is more difficult to explain. According to Brown (1995), activities of  
23 earthworms could result in a decrease in the abundance and species diversity of  
24 microarthropods, which Brown attributed to a lesser competitive ability of microarthropods  
25 for litter consumption. Such a competition for food is totally excluded in our case since *H.*  
26 *nitidus* does not feed on litter but only on faeces (Arpin et al, 1980; Salmon, 2004). McLean  
27 and Parkinson (2000) also showed that, in the long term, a high biomass of epigeic  
28 earthworms introduced in a forest soil was correlated with a low abundance of Arthropleona  
29 Collembola and oribatid mites, which they attributed to a modification of the structure of  
30 organic horizons resulting from earthworm feeding activities. However the introduced species  
31 was epigeic, thus without any pronounced effects on soil structure, contrary to anecic worms.

#### 32 33 4.3. Conclusions 34

1 To conclude, centipedes used in this experiment preyed efficiently on *H. nitidus*,  
2 particularly on immature individuals in all three humus forms. Variations in the abundance of  
3 *H. nitidus* according to humus form were mainly due to differences in soil structure,  
4 especially macroporosity due to earthworm burrows. The general effect of anecic earthworms,  
5 which resulted from their burrowing activity, allowed an increase of the population size of *H.*  
6 *nitidus*. The creation of earthworm burrows probably allowed *H. nitidus* to escape from  
7 predators more easily by improving its access to a larger volume of soil. Our results support  
8 the “Nested Biodiversity Hypothesis” according to which soil ecosystem engineers  
9 (earthworms) may determine the abundance and diversity of other soil organisms (Lavelle,  
10 1996). They contribute to clarify the role of earthworms in the soil ecosystem and to explain  
11 their interaction with some microarthropods, although an earthworm-induced decrease in the  
12 number of immature *H. nitidus* in the acidic mull remains unexplained. Further long-term  
13 laboratory experiments comparing the effects of earthworm burrows and artificial pores are  
14 needed to fully distinguish the effect of earthworms on soil structure from that of food  
15 resource addition.

16

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18

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20

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- 5

1 **Table 1.** Results (probabilities) from five two-way ANOVAs on the total abundance of *H.*  
 2 *nitidus* within each humus form, and within each of the two treatments "with  
 3 predators" and "without predators". Differences are significant at  $P < 0.05$  (shown in  
 4 bold). No interaction between tested factors was significant. Data were square-root  
 5 transformed prior to analyses.

	Calcic mull	Acidic mull	Moder	With predators	Without predators
Humus forms	-	-	-	<b>0.019</b>	0.152
Earthworms	0.591	0.178	<b>0.048</b>	<b>0.045</b>	0.873
Predators	<b>0.016</b>	<b>0.020</b>	<b>&lt; 0.001</b>	-	-

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**Table 2.** Results (probabilities) from five two-way ANOVAs on the abundance of *H. nitidus* > 1 mm within each humus form, and within each of the two treatments "with predators" and "without predators". Differences are significant at  $P < 0.05$  (shown in bold). No interaction between tested factors was significant. Data were squareroot transformed prior to analyses.

	Calcic mull	Acidic mull	Moder	With predators	Without predators
Humus forms	-	-	-	<b>&lt; 0.001</b>	0.075
Earthworms	0.612	0.629	<b>0.045</b>	0.111	0.710
Predators	0.934	0.850	<b>0.043</b>	-	-

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2 **Table 3.** Results (probabilities) from five two-way ANOVAs on the abundance of *H. nitidus*  
 3 < 1 mm within each humus form, and within each of the two treatments "with predators" and  
 4 "without predators". Differences are significant at  $P < 0.05$  (shown in bold). Data were  
 5 squareroot transformed prior to analyses.

	Calcic mull	Acidic mull	Moder	With predators	Without predators
Humus forms	-	-	-	0.277	0.201
Earthworms	0.617	0.121	0.083	0.067	0.724
Predators	<b>&lt; 0.001</b>	<b>0.004</b>	<b>&lt; 0.001</b>	-	-
Earthworms x Predators		0.050			

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2 **Table 4.** Abundance of predators recovered in treatments "with predators" at the end of the  
3 experiment (mean of 5 replicates  $\pm$  standard error), in the three humus forms, in the presence  
4 and in the absence of earthworms.

	Calcic mull	Acidic mull	Moder
With earthworms	4.4 $\pm$ 0.5	5.6 $\pm$ 1.2	5.4 $\pm$ 0.9
Without earthworms	6.2 $\pm$ 0.7	6.6 $\pm$ 0.7	3.6 $\pm$ 1.2

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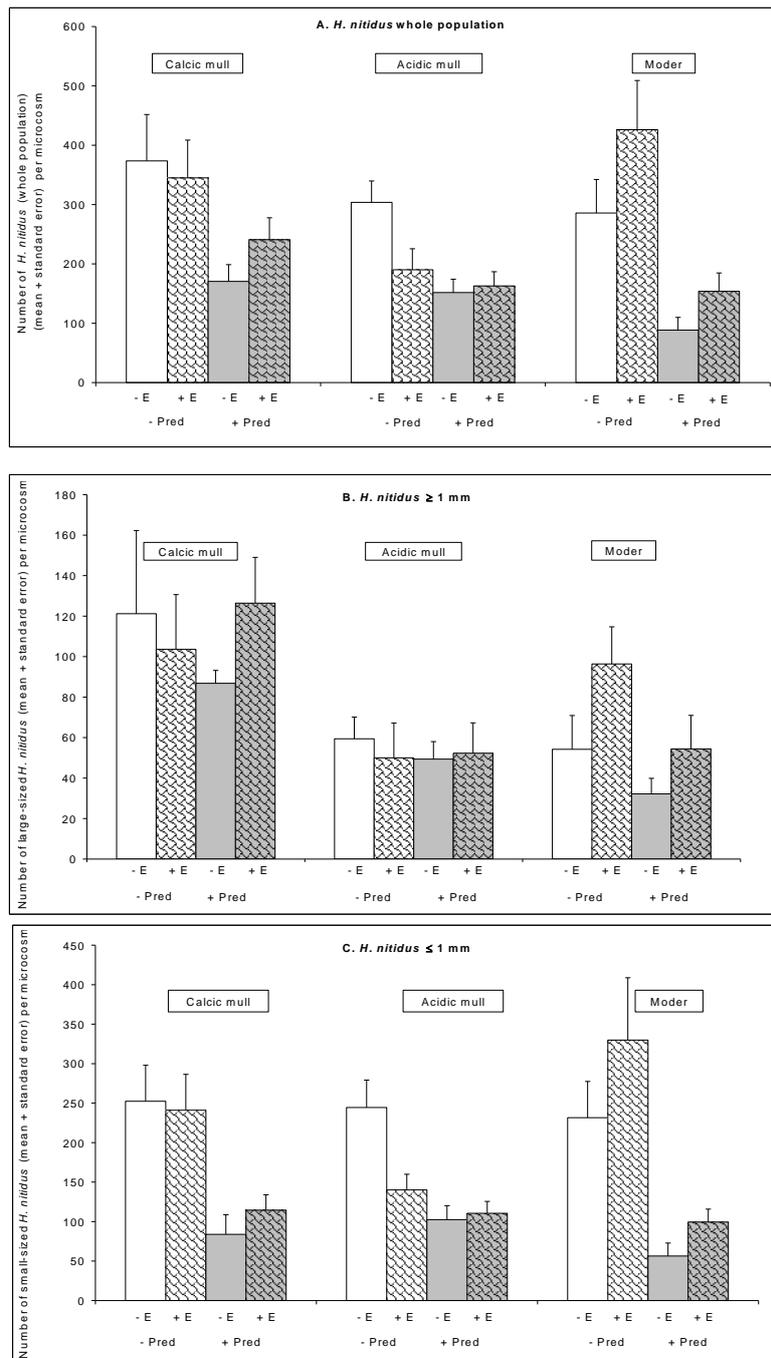
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1 **Table 5.** Species names and lengths of Chilopoda introduced into treatments "with predators".

<b>Order</b>	<b>Species</b>	<b>Length of adults</b>
Lithobiomorpha	<i>Lithobius microps</i> Meinert, 1868	5-8 mm
Scolopendromorpha	<i>Cryptops hortensis</i> Donovan, 1810	15-30 mm
	<i>C. parisi</i> Brolemann, 1920	15-40 mm
Geophilomorpha	<i>Henia vesuviana</i> (Newport, 1844)	70-95 mm
	<i>Necrophloeophagus flavus</i> (De Geer, 1778)	30-45 mm
	<i>Haplophilus subterraneus</i> (Shaw, 1789)	70-95 mm
	<i>Schendyla nemorensis</i> (C.L. Koch, 1837)	10-25 mm

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**Fig. 1** Effect of earthworms (E), predators (P) and humus forms (calcic mull, acidic mull, moder) on the abundance of (A) *H. nitidus* (whole population), (B) *H. nitidus* ≥ 1 mm and (C) *H. nitidus* < 1 mm (mean ± SE).