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EFFECTS OF THE EXOTIC CRUSTACEAN, *ARMADILLIDIUM VULGARE* (ISOPODA), AND OTHER MACROFAUNA ON ORGANIC MATTER DYNAMICS IN SOIL MICROCOSMS IN A HARDWOOD FOREST IN CENTRAL FLORIDA

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Soil biota play an important role in the transformation of soil organic matter (SOM), affecting its distribution in the soil profile, plus directly or indirectly affecting a large set of other soil parameters, such as water holding capacity and nutrient availability (Lavelle et al. 1997; Ponge 2003). Some microflora play a primary role in the decomposition and chemical transformation of SOM, whereas soil macrofauna contribute little to the mineralization of SOM, but can significantly affect distribution of SOM in the soil profile by litter fragmentation and its mixing with mineral soil, and thus indirectly affecting soil microflora (Anderson & Ineson 1984; Lavelle et al. 1997). The effects of soil macrofauna on organic matter removal from the litter layer have been the subject of many studies (e.g., Irmer 1995; Carcamo et al. 2001). However, relatively less attention has been paid to the quantification of the effects of soil fauna on organic matter stabilization and accumulation in mineral soil (Wolters 2000). Species replacement or displacement during succession may cause substantial changes in the transformation of SOM and formation of the upper soil layer (Dunger 1991; Rusek 1978; Frouz et al. 2001). Invasion by exotic species may produce changes, as exemplified by the extensive studies of Scheu & Parkinson (1994) and Boehlen et al. (2004) of an earthworm introduced into north temperate forests. However, fewer data are available on the ecological significance of invasion by other exotic soil invertebrates. *Armadillidium vulgare* (Latreille) is a common European terrestrial isopod that has been introduced into many locations in the USA (Ellis et al. 2000; Stoyenoff 2001), with reports of prevailing densities as high as 10,000 individuals per m^2 (Frouz et al. 2004). Terrestrial isopods are important macrosaprophagous organisms that may consume significant amounts of litter (Zimmer 2002).

The objective of this microcosm study was to elucidate the effects of soil macrofauna on SOM decomposition and accumulation in the mineral layer in a central Florida hardwood forest with specific reference to the role of *A. vulgare* in these processes. Field-placed microcosms facilitated the use of different treatments and the replication of treatments and controls.

The study was conducted in a hydric hardwood forest on sandy soil along the shore of Lake Apopka (28°38'18.54"N, 81°33'04.50"W), near the Mid-Florida Research and Education Center of the University of Florida at Apopka, Florida. In this area, *Celtis laevigata* Willd. was the major overstory tree with a scattering (~10%) of *Carya glabra* (Mill.). The major understory trees were *Prunus caroliniana* Aiton (70%), and small *Celtis laevigata* and *Sabal palmetto* (Walter) Lodd. ex Schult. & Schult. f. (20%).

The microcosms used in this study were similar in construction to those used previously by Frouz et al. (2006). Each microcosm consisted of a clear plastic box (18 × 25 × 5 cm) with twelve nylon net (0.3 mm) covered openings (1-cm diameter) on the top and bottom surfaces. Each box contained 100 g dry weight (DW) mineral sand and 10 g DW autochthonous litter in a 2-mm mesh litter bag with eight 1-cm diameter openings. Litter was collected from the study site forest floor at the planned exposure location of each microcosm, hand sorted, cut into about 1- × 3-cm pieces and mixed. Sand was collected from deeper soil layers (20-30 cm deep) at the same locations, sieved to remove roots, and washed several times in water. Both litter and sand were air dried before use. Separate samples were taken from each microcosm to determine dry weight and carbon content. Three treatments with 4 replicates each of different access for soil macrofauna to the microcosms were established. In the macrofauna accessible (MA) units, 6 horizontal openings (4 × 30 mm) were located in each box along lateral side. No openings were made in the macrofauna non-accessible (MN) boxes, or in the *A. vulgare*-colonized (AC) boxes to which 5 mature specimens of *A. vulgare* were added. This represented a density of ca.100 individuals per m^2, which was the mean density of *A. vulgare* in forest litter layer at the place and time of exposure of experimental boxes. This density was established by taking five 18- × 25- cm area samples of litter, and hand sorting the samples for *A. vulgare* which were introduced in equal numbers into the individ-

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TABLE 1. MEAN ± SD VALUES* OF CARBON CONTENT AND DRY MASS IN LEAF LITTER AND MINERAL SOIL LAYERS OF EXPERIMENTAL MICROCOSMS (MACROFAUNA NON-ACCESSIBLE; MACROFAUNA ACCESSIBLE; AND *ARMADILLIDIUM VULGARE*-COLONIZED) AT THE BEGINNING (INITIAL) AND AT THE END (FINAL) OF 3 MONTHS EXPOSURE (JUL 15 TO OCT 15, 2006) IN A CENTRAL FLORIDA HARDWOOD FOREST.

Carbon content/Dry mass	Mineral layer	Litter layer
Initial C content (%):	0.15 ± 0.02 a	30.73 ± 0.11 b
Final C content (%):		
Macrofauna non-accessible	0.14 ± 10.54 a	19.19 ± 10.49 a
Macrofauna accessible	1.45 ± 0.63 b	17.24 ± 5.78 a
Armadillidium vulgare-colonized	0.63 ± 0.28 a	24.70 ± 2.91 b
Initial dry mass (g)	100.00 ± 0.0 a	10.00 ± 0.0 c
Final dry mass (g)		
Macrofauna non-accessible	91.60 ± 6.6 a	4.90 ± 1.3 b
Macrofauna accessible	100.70 ± 1.6 a	1.00 ± 0.6 a
Armadillidium vulgare-colonized	100.90 ± 12.9 a	2.10 ± 1.2 a

*Mean values of the same parameter followed by the same letter are not significantly different (ANOVA, LSD test, $P < 0.05$): Mineral layer C content: $F_{3,15} = 9.75$, $P = 0.002$; Litter layer C content: $F_{3,15} = 5.32$, $P = 0.0145$; Mineral layer dry mass: $F_{3,15} = 1.19$, $P = 0.354$; Litter layer dry mass: $F_{3,15} = 62.97$, $P = < 0.0001$.

ual boxes. Boxes were exposed in the field for 3 months, from Jul 15 to Oct 15, 2006. This period covers warmest and wettest months of the year where decomposition is likely to be the fastest. After exposure, the litter bags were removed from the boxes and the litter bag contents, as well as the mineral layer, were air dried and weighed. From both layers of each box, 2 samples were taken for measurement of dry weight and carbon (C) content. Dry weight was determined gravimetrically; litter was dried to constant dry mass at 90°C and mineral samples at 105°C. The lower temperature was used for litter drying to avoid weight loss by possible volatilization of aromatic compound. Carbon content was established as oxidizable carbon content (C_{ox}), determined by the wet acidified dichromate oxidation method of Jackson (1958). Carbon stock in an individual soil layer was calculated as the layer DW multiplied by the corresponding C concentration. Carbon removal from litter bag contents was calculated as the difference between C stock in the litter bag at the beginning and at the end of the experiment. Incorporation of C into the mineral layer was calculated as the difference between the mineral layer C stock at the end of experiment and the start of experiment. Total loss of carbon from the box was calculated as difference between C stock in both layers at the start and end of exposure period.

Available P, K, and NO_3- ions as well as soil pH were measured in the mineral layer at the end of exposure period. Soil pH was measured in KCl solution (ISO 1992); K was measured by ion selective electrodes (type 20-19) in citric acid solution, NO_3- by ion selective electrodes (type 20-31) in KCl (Frant 1994); in all cases 1:5 sample solvent ratio was used. The electrodes were manufactured by Electrochemical Detectors, Turnov, Czech Republic. Available P was detected by ion exchange resin, which is assumed to approximate P available for plants (Machaček 1986).

Values of dry mass as well as C stock (mass × content) in litter bag contents had decreased significantly at the end of the experiment compared to the initial values, indicating significant losses of C from litter bag contents in all treatments (Table 1, Fig. 1). In agreement with other litter bag studies which indicate that the presence of mac-

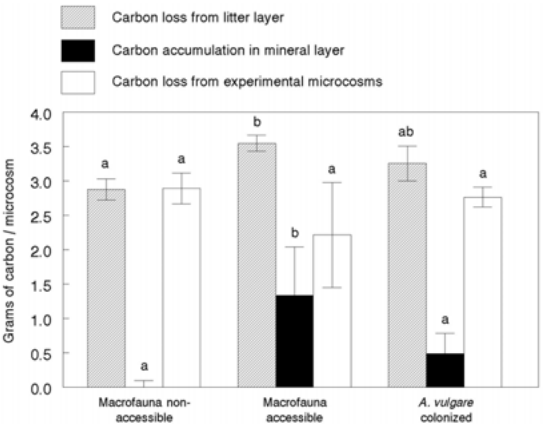


Fig. 1. Mean ± SD values of carbon loss from litter layer, carbon incorporated into mineral layer, and carbon total loss from experimental microcosms after 3 months exposure (Jul 15 to Oct 15, 2006) in a central Florida hardwood forest. Microcosms were either accessible to forest macrofauna, non-accessible to forest macrofauna, or non-accessible to forest macrofauna and colonized with *Armadillidium vulgare*. Values of same parameter labeled by different letter are statistically different (ANOVA, LSD test, $P < 0.05$.).

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TABLE 2. MEAN ± SD VALUES* OF PH (KCL), AVAILABLE P, K, AND NO_3- IN THE MINERAL LAYER OF EXPERIMENTAL MICROCOSMS AT THE END OF 3 MONTHS EXPOSURE (JUL 15 TO OCT 15, 2006) IN A CENTRAL FLORIDA HARDWOOD FOREST.

Microcosms	pH	P (mg/kg)	K (mg/kg)	NO_3 (mg/kg)
Macrofauna non-accessible	6.56 ± 0.15 a	9.7 ± 0.9 a	11 ± 3 a	64 ± 4 a
Macrofauna accessible	7.27 ± 0.02 b	38.8 ± 13.4 b	33 ± 8 b	211 ± 91 ab
Armadillidium vulgare-colonized	7.33 ± 0.10 b	29.5 ± 6.7 b	56 ± 41 b	261 ± 71 b

*Mean values under various chemical parameters in a column followed by the same letter are not significantly different (ANOVA, LSD test, $P < 0.05$): pH: $F_{2,11} = 44$, $P = < 0.001$; P: $F_{2,11} = 6.5$, $P = 0.020$; K: $F_{2,11} = 6.5$, $P = 0.021$; NO_3: $F_{2,11} = 4.8$, $P = 0.040$.

rofauna increases litter decomposition rates by 5-40% (Irmer 1995), macrofaunal accessibility to the microcosms in this study significantly increased dry mass and C removal from litter bag contents (Table 1).

Dry mass of the mineral layer did not differ significantly among treatments, although in MN-treated microcosms, the mean mass of the mineral layer was lower than the other treatments. We suspect that this was caused by rain, washing small particles from the mineral layer as happened in all treatments. However, in the MA and AC microcosms, this loss of mineral content was compensated by the incorporation of organic matter from the litter bag. This idea is supported by the significantly higher C content in MA treatment than in the MN treatment. (Table 1). In addition, incorporation of C in the mineral layer was significantly higher in the MA treatment than in the other 2 treatments (Fig. 1). The MA-treated microcosms tended towards the lowest overall system loss of C, although the differences were not statistically significant (Fig. 1). In agreement with previous experiments with similar enclosures (Frouz 2002; Frouz et al. 2006), we can conclude that access by soil macrofauna increased removal of C from the litter layer but not the overall mineralization, as most of the C which is removed from litter was stored in the mineral layer. Similar conclusions were made by Wachendorf et al. (1997) after comparing total mass loss with the mass loss caused by microbial and animal respiration in litter bags. Soils in the MA treatment also had significantly higher pH and content of available P and K than the MN treatment (Table 2). This is in agreement with other studies indicating that incorporation of organic matter into mineral soil by macrofauna in the MA treatment may substantially alter other soil properties, such as pH and water holding capacity (Frouz et al. 2006).

By comparing microcosms occupied by *A. vulgare* with those accessible to all macrofauna, we can see that *A. vulgare* plays an important role in the overall macrofaunal effect. This is more pronounced in C removal from the litter than in C incorporation into the mineral layer. *Armadillidium vulgare* activity had a strong effect on the chemistry of the mineral layer as indicated by increased pH level and content of available P, K, and NO_3- content This suggests a significant role of *A. vulgare* in the transformation of the topsoil layer, and this effect may be more pronounced at higher densities of *A. vulgare*. In some other locations in Florida, densities of *A. vulgare* were several orders of magnitude higher (up to 10,000 individuals per m^2)(Frouz et al. 2004), than in the present study. Thus, in some cases, *A. vulgare* invasion may significantly alter soil conditions and this poses a new question: How much does the effect(s) of *A. vulgare* activity influence the performance of other plant or animal species co-existing with this isopod?

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SUMMARY

In a study of the effects of the non-native Isopod *Armadillidium vulgare* on soil organic matter decomposition and incorporation into the mineral soil of field microcosm in a central Florida hydric hardwood forest, that species was found to have an important effect on the transformation of the topsoil layer. This was evidenced by increased pH, P, K and NO_3- in the mineral layer and increased removal of C from leaf litter layer.

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