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Effects of Intra- and Interspecific Interactions in Earthworm Assemblages: A Comparative Study

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Abstract—Among the factors modifying the structure of associations and activity of earthworms, the influence of intra- and interspecific interactions has been studied insufficiently. In field experiments the relative importance of these interactions has been compared in lumbricid species that are trophic competitors: in the soil detritophages *Allolobophora chlorotica* and *Aporrectodea caliginosa* and in the leaf litter consumers *Lumbricus rubellus* and *L. terrestris*. For each species the relative significance of the intra- and interspecific interactions were evaluated by comparison of the state of lumbricid individuals in conditions of low (control) and high population densities in one- or two-species populations. The increase in population density (due to either conspecifics or species-competitor) usually negatively affected the important parameters of the current earthworm generation (growth, mortality, and fecundity), and also of the subsequent generation (numbers and size of the cocoons produced). For three species (except for *L. terrestris*), trends were revealed indicating the greater strength of intraspecific than interspecific interactions. The species reactions were determined by different factors: by the trophic competition for the litter-dwelling *L. rubellus*, whereas for the soil dwellers *Al. chlorotica* and *A. caliginosa* (in conditions of a surplus of food resources) they were presumably determined by competition for the space.

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INTRODUCTION

The importance of earthworms as a key group of organisms, the activity of which largely determines the soil profile structure, the nature of organic matter transformations and the nutrient turnover, as well as the functioning of detrital food webs and terrestrial ecosystems in general, is well known (Edwards and Bohlen 1996; Briones 2014; Filser et al., 2016). In temperate ecosystems, the diversity and numbers of earthworm associations are highly variable: from 1 to 10–15 species, from single individuals to thousands of specimens per square meter (Petersen and Luxton, 1982; Dymond et al., 1997; Uvarov, 2009). These fluctuations depend on the state of the environment: climate, habitat character, vegetation, soil type, litter quality, etc. It is assumed that the population and interspecific interactions also significantly modify the structure of the earthworm associations and the functioning of individual species in associations (Uvarov, 2009); however, this issue has been studied insufficiently.

The nature of the interspecific relationships of earthworms is determined by the species affiliation to one functional group or another (epigeic, endogeic, burrow: according to Bouché, 1977; Lee, 1985), life strategy (Satchell, 1980), as well as by the specific features of their biology and behavior. The large amount of resources and the variety of ways to divide soil niches suggest that synergistic relationships play a significant role in the development of soil communities (Anderson, 1975; Striganova, 2006; Wardle, 2006). However, among the wide range of interspecific reactions (from synergistic to antagonistic) described for earthworms, negative interactions prevail (Uvarov, 2009), which suggests that competitive relations are an important factor in structuring associations of lumbricids (Curry, 1998; Decaëns et al., 2008; Xia et al., 2011). Direct experimental evidence of interspecific competition has recently been presented by Chang et al. (Chang et al., 2016). Most studies of intraspecific relationships in lumbricids, regardless of the species functional group, support the presence of resource competition and density-dependent regulation of species populations: for example, with increasing density growth, maturation, and reproduction rates decrease, but mortality increases (Uvarov, 2009, 2017).

Theoretically, the degree of negative influence of intraspecific interactions in comparison with interspecific ones is assumed to be more significant (Lowe and Butt, 2002). However, the experimental data are inconsistent. For example, in *Octolasion lacteum*, the decrease in reproduction and growth rates with an increase in population density was more significant than with the presence of *Aporrectodea longa* and *Lumbricus terrestris*. On the contrary, the presence of *O. lacteum* and especially *L. terrestris* more strongly inhibited growth and reproduction rates in *A. longa* than an increase in its population density (Butt, 1998). In other experiments with *A. longa*, intraspecific relations had a greater influence on changes in the biomass than coexistence with *Aporrectodea caliginosa*; for the latter species, the reverse trend was observed in the presence of *A. longa* and *L. terrestris* (Dalby et al., 1998; Baker et al., 2002; Eriksen-Hamel and Whalen, 2007). For the species *Lumbricus rubellus* and *O. lacteum*, evaluations of the growth rate and survival of individuals did not allow us to draw definite conclusions about the ratio between the intraspecific and interspecific effects (Xia et al., 2011). There is an assumption that the relative influence of intra- and interspecific relations among earthworms is species-specific (Uvarov, 2009), but it is unclear to what extent this specificity is determined by the belonging of the species to a particular functional group. Generalization of the available data is also hampered by the variety of experimental conditions and usually increased (compared to the natural) density of lumbricids in experimental microcosms.

In this paper we evaluate the relative importance of intraspecific interactions (with an increase of the species density in its natural limits) and interspecific interactions (in two-species associations) in earthworms. The experiments were carried out under conditions close to natural ones: the lumbricids were kept in large volume soil systems exposed in the forest soil during the main part of the growing season. The species compared in paired experiments consume similar resources (leaf litter in *L. terrestris* and *L. rubellus*, soil detritus in *A. caliginosa* and *Allolobophora chlorotica*); i.e., they are active trophic competitors. Despite the latter circumstance, we expected that the negative effects of intraspecific interactions would still be stronger in comparison to interspecific ones. It was also expected that for the species from the same functional group, i.e., theoretically with sharper competitive contradictions (endogeic *A. caliginosa* and *Al. chlorotica*), the differences between intra- and interspecific effects would be less evident than in species belonging to different functional groups (anecic *L. terrestris* and epigeic *L. rubellus*).

MATERIALS AND METHODS

The litter and soil were sampled in a beech-oak forest (Mazury Landscape Park, northeastern Poland) at the beginning of June 2006. Linden, hazel, and maple were in the undergrowth, and grass cover was almost absent. The overwintered litter 2–4 cm thick was weakly stratified (horizons *L* and *F/H*) and consisted mainly of oak, beech, and linden leaves, which were markedly affected by the activity of the soil biota. A weakly structured sandy soil (haplic arenosol, FAO/UNESCO classification) was sampled from horizon *A* (to a depth of 15 cm, pH 5.5). The carbon content in litter and soil was 37.3 and 2.7%, and nitrogen content 1.6 and 0.17%, respectively.

The experiments were carried out in a beech–oak forest on the territory of the Mikolajki scientific station of the Polish Academy of Sciences. The microcosms were plastic cylinders with an inner diameter of 20 cm and a height of 60 cm, with an airtight lid; the lid had a 2-cm hole in diameter for air exchange. The hole and the bottom of the microcosms were covered with a gause cloth to prevent the escape of animals. In the microcosms (half dug into the soil), soil systems were modeled: 9.5 L of soil were covered with 100 g of *F/H* litter; the soil-litter boundary inside and outside the microcosm coincided. The amount of litter in the microcosms corresponded to ~2.1 kg dry weight/m^2; i.e., it was at the upper limit of litter supply typical for European deciduous forests (Basilevich, 1993). The soil was presieved (4 mm) for homogenization, and roots and representatives of macrofauna were removed; the litter (after removing earthworms and predatory mesofauna) was mixed. To compensate for the loss of microbiota during the litter preparation, 50 mL of an aqueous suspension prepared from the native litter were introduced into the microcosms. After a three-week stabilization of the soil systems in the natural field conditions, earthworms were settled in the microcosms, which meant the start of the experiment (July 10, 2006). The duration of the experiment was 130 days. Earthworms were collected in June and early July in the Piska and Kampinos forests and were kept in containers with soil and litter at 4°C before the start of the experiments.

The temperature regime in the microcosms was thermologger-measured at the level of the litter–soil boundary. The average monthly temperatures during the experiment were 17.9 (July), 16, 14.2, 10.5, and 5.2°C (November). The initial moisture content was 70% of the total capacity of the systems; during the experiments, the microcosms were regularly watered, maintaining a favorable moisture regime. The amount of water added corresponded to the amount of precipitation of the rainy summer–autumn of 2006.

The study design (Fig. 1) included four experiments with two pairs of earthworm species that are trophic competitors: soil detritophages *Al. chlorotica* (Savigny) and *A. caliginosa* (Savigny), and leaf litter consumers *Lumbricus rubellus* Hoffmeister and *L. terrestris* L.. All these species are common in European forests and are often found together in lumbricid associations. The experiment for each species was presented in three variants: single-species group with (A) a lower and (B) an increased population density; (C) two-species group with the density of each species as in variant A and the total biomass close to that in

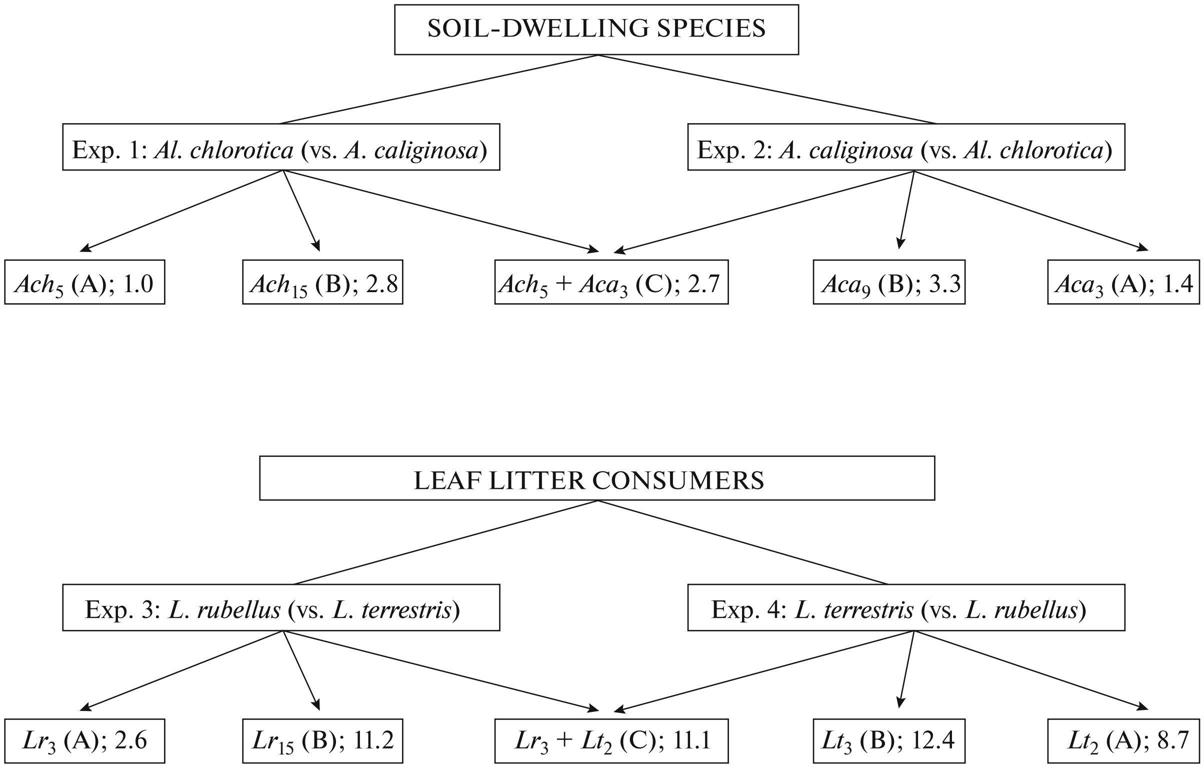

Fig. 1. Variants (A, B, and C) of four field experiments. Lumbricid species: *Ach*, *Allolobophora chlorotica*; *Aca*, *Aporrectodea caliginosa*; *Lr*, *Lumbricus rubellus*; *Lt*, *L. terrestris*. The subscript in the designations of species is the number of individuals of this species; the number is the average biomass (g) of lumbricids in the microcosm.

variant B. Such a structure of the variant C allowed a comparison of the measured parameters of the investigated species with those in the control and excluded the influence of variability of total lumbricid biomass when comparing variants B and C. The relative impact of intra- and interspecific interactions for each species was evaluated by comparison of the control variant A with variants B and C. The lumbricid densities in microcosms, as compared with natural ecosystems, ranged from moderate to high and were 5 and 15 specimens in variants A and B, respectively, for *Al. chlorotica* (150 and 450 sp./m^2), 3 and 9 specimens (90 and 270 sp./m^2) for *A. caliginosa*, 3 and 15 specimens (90 and 450 sp./m^2) for *L. rubellus*, and 2 and 3 specimens (60 and 90 sp./m^2) for *L. terrestris*. At the beginning of the experiments, the earthworms of the genus *Lumbricus* were represented by sexually mature individuals, earthworms of *A. caliginosa* by large juveniles, and the groups of *Al. chlorotica* contained 40% mature and 60% juvenile individuals. The live weight of gut-free individuals before and after the experiments was determined after keeping the worms on wet filter paper for 24 hours. At the end of the experiments, the number of dead individuals, the proportion of sexually mature worms (for *Al. chlorotica* and *A. caliginosa*), the production of offspring (the sum of cocoons and juvenile worms), and the individual mass of cocoons were determined. Counting of cocoons and small juveniles was carried out by careful hand-sorting of half of the collected litter and approximately 1 kg of mixed soil samples (taken from different depths of the soil layer of microcosms). The fecundity of the earthworms was expressed per individual or (in *Al. chlorotica* and *A. caliginosa*, due to the presence of immature worms in the initial group) per group of five or three individuals, respectively. The specific fecundity (mass of cocoons/1 g of the earthworm mass at the beginning of the experiment) was considered as a measure of the energy allocated into reproduction. In addition to the lumbricid sampling, other indicators of the state of the soil system and its biota were assessed: total community respiration and organic matter loss in microcosms, biomass and respiration of microorganisms, densities of nanofauna (nematodes and Bdelloidea rotifers) and microfauna (enchytraeids, springtails, oribatid and mesostigmatid mites). In this paper, we do not provide a detailed analysis of this information, but use it as supplementary data in explaining the results of our experiments.

For statistical processing of the data, one-way analysis of variance (ANOVA) was used followed by the Tukey test. The data, if necessary, were log-transformed, and the percentages (mortality, change in the mass of individuals, the proportion of mature individuals) were arcsin-transformed. To analyze the proportion of mature individuals, the nonparametric Kruskal—Wallis test was used. All the variants had four replicates. Calculations were made using the Statistica-6 software.

RESULTS AND DISCUSSION

Soil-Dwelling Species. Experiment 1: Al. chlorotica vs. A. caliginosa

In the control microcosms (variant *Ach*$_5$), all the juveniles reached maturity by the end of the experiment and there was no mortality of the worms. The situation in the other two variants was different: sporadic cases of earthworm death were observed there and not all the individuals reached maturity (Table 1). As compared with the control, a sharp decrease in the average earthworm mass, total and specific fecundity, and a decrease in the average mass of cocoons (Table 1) was observed in *Al. chlorotica* both with its density increase in the single-species assemblages and in the presence of *A. caliginosa*. In the dense single-species assemblages (*Ach*$_{15}$) compared with the two-species assemblages (*Ach*$_5$ + *Aca*$_3$), the decrease in the maturity achievement by *Al. chlorotica* juveniles individuals and a tendency to the total and specific fecundity decrease were noted; however, the average cocoon mass was lower in the presence of *A. caliginosa*.

Soil-Dwelling Species. Experiment 2: A. caliginosa vs. Al. chlorotica

In all the variants (Table 1), there was no mortality and the average mass of *A. caliginosa* individuals increased (in the control, *Aca*$_3$, this increase was noticeable, but not statistically significant). The total and specific fecundity was reduced in variants *Aca*$_9$ and (*Aca*$_3$ + *Ach*$_5$) in comparison with the control (significantly in the variant *Aca*$_9$). The mass of cocoons in both variants was significantly lower than in the control. In the *Aca*$_9$ variant, the degree of maturity by the end of the experiment was only 3/4 (versus 100% in other variants), and fecundity was two times lower than in the variant (*Aca*$_3$ + *Ach*$_5$) (Table 1).

Leaf Litter Consumers. Experiment 3: L. rubellus vs. L. terrestris

The mortality of *L. rubellus* was high in all variants (Table 1), but in the control (*Lr*$_3$) it was significantly lower; the difference between the control and the two other variants, taken together (*Lr*$_{15}$ and *Lr*$_3$ + *Lt*$_2$), was close to significant ($F_{1, 10} = 3.44$, $P = 0.09$). By the end of the experiment, the average mass of the surviving individuals in the control increased by 15%, but sharply decreased in other variants. The total and specific fecundity of *L. rubellus* in the *Lr*$_{15}$ and *Lr*$_3$ + *Lt*$_2$ variants, taken together, was lower (at $P < 0.1$) as compared with the control. Furthermore, the average mass of cocoons decreased significantly (Table 1). Comparison of the *Lr*$_{15}$ and *Lr*$_3$ + *Lt*$_2$ variants showed a clear tendency to deterioration of the state of *L. rubellus* in *Lr*$_{15}$: an increase (approximately double) in individual weight loss and a decrease (by 1.5—2 times) in their total and specific fecundity.

Leaf Litter Consumers. Experiment 4: L. terrestris vs. L. rubellus.

In the control variant (*Lt*$_2$), mortality of *L. terrestris* was absent, and in both other variants, one individual died. During the experiment, the average mass of an individual practically did not change. The values of the total and specific production of cocoons were by 1.5—2 times higher in the variant with three individuals (*Lt*$_3$) than in both variants with two individuals of *L. terrestris* in the microcosm (Table 1). The differences in the latter parameters between the variant *Lt*$_3$ and the *Lt*$_2$ and *Lt*$_2$ + *Lr*$_3$ variants, taken together, turned out to be significant (at $P < 0.05$). The average weight of cocoons was significantly decreased in the range of the *Lt*$_2$—*Lt*$_3$—*Lt*$_2$ + *Lr*$_3$ variants (Table 1).

The positive reaction of the fecundity of *L. terrestris* to its population density increase is very interesting and requires a special experimental confirmation. As a preliminary explanation of this result, we could point to the possibility of choosing a more optimal reproduction partner in groups of three individuals, as opposed to microcosms with only two individuals. The presence and ecological importance of choosing a partner for *L. terrestris*, a species with a complex social organization of populations, has been shown previously (Michiels et al., 2001).

Impact of Intra- and Interspecific Interactions

The results of our experiments revealed a variety of negative reactions to the density increase in the assemblages of the species studied, regardless of whether this increase was induced by conspecifics or a competing species. These reactions reflected both changes in the state of earthworms (the relative decrease in the mass of individuals and the increase in mortality, the slowing of sexual maturity, the decrease in the reproductive potential), and the consequences for the subsequent generation (reduction in the mass of cocoons). Some negative reactions to the density increase were observed in all species, regardless of the feeding type of the worms (consumption of soil detritus or leaf litter).

In the maternal generation of the three species, deterioration in the state of worms in dense single-species assemblages in comparison with the two-species groups was determined. These features were delayed maturation (*Al. chlorotica* and *A. caliginosa*) and more dramatic weight loss (*L. rubellus*). In all three species, there was also a tendency to a decrease of the total and specific fecundity in single-species compared with

Table 1. Intra- and interspecific interactions in lumbricids: reactions to the density increase of single-species assemblages and to the presence of a competing species

Parameter	Exp. 1: *Al. chlorotica* vs. *A. caliginosa*			Exp. 2: *A. caliginosa* vs. *Al. chlorotica*			Exp. 3: *L. rubellus* vs. *L. terrestris*			Exp. 4: *L. terrestris* vs. *L. rubellus*		
	Ach_5	Ach_{15}	$Ach_5 + Aca_3$	Aca_3	Aca_9	$Aca_3 + Ach_5$	Lr_3	Lr_{15}	$Lr_3 + Lt_2$	Lt_2	Lt_3	$Lt_2 + Lr_3$
Mortality, %	0	5	5	0	0	0	41.7	65	75	0	8.3	12.5
Changes in the average mass of the individual, %	49.1^a	17.2^b	14.3^b	58.2	44.9	1.3	15.2^a	-50.7^b	-23.9^b	6.4	2.5	5.9
	$F_{2,9} = 6.76, P = 0.016$			NS			$F_{2,7} = 81.6, P = 0.001$			NS		
Proportion of mature individuals, %	100^a	68.5^b	95.0^a	100^a	77.8^b	100^a	–	–	–	–	–	–
	$H_{2,12} = 9.41, P = 0.009$			$H_{2,12} = 10.5, P = 0.005$								
Number of cocoons, ind	43.3^a	14.7^b	23.6^{ab}	45.3^a	5.6^b	12.9^{ab}	27.5	9.5	17	13.2	20.2	8.7
	$F_{2,9} = 4.85, P = 0.037$			$F_{2,9} = 6.35, P = 0.019$			NS			NS		
Mass of 1 cocoon, mg	13.1^a	12.7^b	11.8^c	25.4^a	23.1^b	22.1^b	13.2^a	12^b	11.8^b	64^a	59.1^b	55.6^c
	$F_{2,171} = 27.7, P = 0.001$			$F_{2,76} = 17.2, P = 0.001$			$F_{2,268} = 30.8, P = 0.001$			$F_{2,101} = 15, P = 0.001$		
Mass of cocoons /W_i, mg/g	538.1^a	211.7^b	249.9^{ab}	774.4^a	121.9^b	210.9^{ab}	409.2	151.8	223.1	193.5	290.8	125.5
	$F_{2,9} = 4.36, P = 0.048$			$F_{2,9} = 4.84, P = 0.037$			NS			NS		

The numbers of cocoons in *Al. chlorotica* and *A. caliginosa* are calculated for a group of five and three individuals, respectively; in other species, for one individual. W_i is the mass of individuals of the given species in the microcosm at the beginning of the experiment. To compare the variants, one-factor ANOVA (F) or the nonparametric Kruskal–Wallis test (H) were used, the subscripts for F and H indices are the degrees of freedom. The significance of differences ($P < 0.05$) is marked by superscripts (different letters denote significant differences within each experiment); NS, the differences are not significant; (–), data absent. The designation of the variants is presented in Fig. 1.

two-species assemblages; the values of these parameters in the single-species groups of the soil-dwelling species were significantly lower than in the control. Consequently, for these species, the greater impact of negative intraspecific in comparison to the interspecific interactions (Lowe and Butt, 2002), i.e. the first hypothesis of this work, seems to be supported.

On the contrary, data on the state of *L. terrestris* individuals did not allow us to reach clear conclusions about the relative importance of intra- and interspecific interactions. An increase in the total and specific fecundity in denser single-species assemblages may indicate a positive value of the possibility of choosing a partner, which is not available in other variants. Therefore, the relative importance of intra- and interspecific interactions for *L. terrestris* should be evaluated in experiments taking into account the specific behavior of individuals and the territorial organization of populations, as well as, possibly, the duration of the life cycle of this species.

On the other hand, the reactions of the subsequent generation turned out to be similar in all four species: larger cocoons were noted in densely populated single-species than in two-species assemblages. Consequently, in the latter case, the initial conditions (supply of resources) for the growth of individuals of the subsequent generation or for overwintering of cocoons in all the species were less favorable. This result implies the necessity of considering the problem of intra- and interspecies interactions in a series of successive generations.

The comparison of the relative impact of intra- and interspecific interactions among lumbricids from different ecological groups showed contradicting results. Thus, the mass of cocoons in representatives of all ecological groups was 91–97% and 87–90% of control values in densely populated single-species and two-species assemblages, respectively. The total and specific production of cocoons in the anecic-species *L. terrestris* increased, whereas in the litter-dwelling species *L. rubellus* and in both soil-dwelling species, the value of these parameters decreased in the dense single-species in comparison to two-species assemblages. At this step of the research, we can only state that the influence of the functional group on the ratio between intra- and interspecific effects in lumbricids was not found; thus, our second hypothesis was not confirmed.

The characteristics of the functional parameters of the soil system and components of the soil community provide some explanations of the results obtained. Thus, total community respiration, loss of organic matter in the soil and litter, and the biomass and specific respiration coefficient of microorganisms were similar in the variants with soil-dwelling lumbricids (Ach_{15}, $Ach_5 + Aca_3$, and Aca_9); between these variants, no significant differences in the population density of the most important groups of the animal community (nanofauna, enchytraeids, and microarthropods) were found either. Consequently, the effects of worms on the soil systems in these variants with different population structures, but similar earthworm biomass values, were presumably similar. According to calculations (Uvarov, 2016, 2017), food consumption by soil lumbricids did not exceed 4 g of carbon over the entire time of the experiments. The total carbon costs of microbial respiration can be estimated as about 10 g. In total, carbon losses due to the activity of soil microorganisms and lumbricids make up only a small fraction of the initial organic matter reserves in the microcosm soil (~77 g only in the upper 10 cm). Thus, the above mentioned negative reactions of earthworms to the increase in population density are not associated, apparently, with the depletion of food resources, but could be explained by competition for living space rather than for available food. Hence, the differences in the intra- and interspecific effects in biomass-similar assemblages of *Al. chlorotica* (Ach_{15} and $Ach_5 + Aca_3$) and *A. caliginosa* (Aca_9 and $Ach_5 + Aca_3$) in the conditions of a surplus of food resources were probably not associated with trophic competition.

On the contrary, a comparison of the variants with the litter consumers (Lr_{15}, $Lr_3 + Lt_2$ and Lt_3) revealed a number of significant differences in the values of the functional parameters of the soil system and the fauna population densities. In particular, the differences affected the biomass of microorganisms, the intensity of organic matter decomposition, and the populations of trophic competitors of lumbricids, enchytraeids, and springtails. This indicates ambiguous rearrangements of soil systems in assemblages with similar worm biomass but different combinations of *L. rubellus* and *L. terrestris* species.

The consumption of leaf litter by *L. rubellus* reached 6–7 g of carbon (Uvarov, 2017). Together with microbial respiration, this suggests the loss of about half of the litter organic matter. Simultaneously, the quality of food material (an increase in the proportion of coarse residues), as well as the environmental conditions of the litter, decreased. Consequently, the reaction of *L. rubellus* to an increase in the population density could be driven by increased shortages in the food resources. The comparison of the assemblages Lr_{15} and $Lr_3 + Lt_2$ showed a combination of a worse state and a lower reproductive capacity of worms in the variant Lr_{15} (Table 1); in the microfauna population, we observed a replacement of enchytraeids that are important food competitors of litter-dwelling worms (Uvarov and Karaban, 2015), with springtails. This suggests that the trophic competition in the variant Lr_{15} was more significant than in the variant $Lr_3 + Lt_2$.

The maximum nutritional requirements of lumbricids in variants with *L. terrestris* were even higher, up to 9 g of carbon (Uvarov, 2017); there was almost no leaf litter on the soil surface of the microcosms by the end of the experiment (it was partially concentrated in the burrows of *L. terrestris*). However, there was no acute shortage of food resources for *L. terrestris*. Although in each of the variants Lt_3 and $Lt_2 + Lr_3$ one individual died, deterioration of the state of living *L. terrestris* specimens was not noted. Most likely it could be explained by a stimulation of the activity of litter microorganisms in the burrows of *L. terrestris* (Tiunov and Scheu, 1999; Tiunov et al., 2001; Aira et al., 2009), which results in intensification of the microbial biomass cycle and organic matter decomposition in the litter and soil, which in turn leads to the occurrence of additional nutritional resources for earthworms. In our experiment, an increase in the metabolic coefficient of microbial respiration (qO_2) and in the total respiration of microcosms indicated the activation of the microbial biomass in microcosms with *L. terrestris*.

CONCLUSIONS

In the gradients of the natural population density of earthworms, the population density increases (due to either conspecifics or species-competitors) influenced the state of both individuals and populations. Lumbricid reactions affected the most important indices of the current generation (growth, maturity, fecundity, and mortality), as well as the subsequent generation (the number and size of produced cocoons). Regardless of the functional group of the species, negative trends of the reactions to the density increase prevailed, which indicates a pronounced intra- and interspecific competition in the lumbricid species studied. For three lumbricid species studied, evidence of a stronger intraspecific (in comparison to interspecific) negative interactions were found. The reactions of the species were probably determined by various factors: trophic competition was essential for the litter-dweller *L. rubellus*, whereas for the soil-dwelling species *Al. chlorotica* and *A. caliginosa* competition for space turned out to be more important in conditions of a surplus of food resources. It was not possible to make definite conclusions about the relative importance of intra- and interspecific interactions in the anecic species *L. terrestris*; such an assessment requires a consideration of the territorial organization of its populations and the specific behavior of individuals of this species.

Our results show that intra- and interspecific competition can play an important role in regulating the structure and dynamics of associations of earthworms, which are one of the key links in the functioning of the soil system. It seems to be true that the relative strength of the influence of intra- and interspecific relations among earthworms is species-specific; however, this question needs further analysis.

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest. The authors declare that they have no conflict of interest.

Statement on the welfare of animals. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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