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Article

First Short-term Study of the Relationship between Native and Invasive Earthworms in the Zone of Soil Freezing in Western Siberia – Experiments in Mesocosms

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Abstract: Earthworm invasions often reduce biodiversity and affect the ability of ecosystems to perform ecosystem functions. Over the past few decades, European lumbricide species have spread widely in natural habitats in Western Siberia, without completely displacing the native species. The aim of the present experiment is to study the survival, reproductive potential, vertical distribution, abundance, and biomass of *Aporrectodea caliginosa* and *Lumbricus rubellus* invasive for the region and the native species *Eisenia nordenskioldi* and their influence on each other. For this purpose, winter and vegetation experiments were conducted in mesocosms simulating the real situation of invasions in the same communities on the same types of soils with the same amount and composition of litter. The authors found that the native species was significantly inferior to *A. caliginosa* in reproduction rate, number of offspring, and final biomass, but had an advantage over *L. rubellus*. The native species was positively influenced by the presence of *A. caliginosa*. In the experiment, there was a significant rejuvenation of the populations of the studied species, an increase in abundance and relative mass under interaction conditions compared to mono variants. The native species had advantages over the invasive species in terms of winter survival. The natural volume of litter used in the experiment was insufficient for *L. rubellus*. According to the results of the experiment, it can be assumed that the spread of *L. rubellus* will continue to be limited to non-freezing biotopes rich in organic matter. *A. caliginosa* will spread in natural communities and agrocenoses of Western Siberia.

Keywords: invasions; exotic species; inter- and intraspecific interactions; *Eisenia nordenskioldi; Aporrectodea caliginosa*; *Lumbricus rubellus*

1. Introduction

Species invasions are the cause of threats to the well-being of the biosphere and society [1]. Changes in the species composition of ecosystem engineers, which include earthworms [2], are of particular importance. Earthworm invasions can lead to cascading changes in ecosystems [3] and their ability to perform ecosystem functions [4]. The distribution of alien species of earthworms covers all continents [5]. In most areas, native species of earthworms are encountered except for regions where this group was originally absent due to Holocene glaciation. As a result of such a collision, native species can either be displaced or coexist [6–9]. Alien species of earthworms, once in the same habitat as the native ones, can have a variety of effects on each other: positive, neutral, or/and negative [10–11]. The more species involved in the interaction, the higher the number of negative effects [10]. Ecosystems where species introductions are relatively recent and where native and alien species interact are of great interest to researchers. Such an area is the West Siberian plain of Eurasia, where predominantly one native species, *Eisenia nordenskioldi* (Eisen, 1873), and several invasive species occupying the leading role in the communities are distributed [12]. According to genetic studies, *Aporrectodea caliginosa* (Savigny, 1826) (endogeic) appeared in the south of Western Siberia about 100–200 years ago [13] and by now

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has occupied most natural biotopes of the forest-steppe zone of Western Siberia [12, 14–15]. Until 2003, *Lumbricus rubellus* Hoffmeister, 1843 (epi-endogeic), which has spread widely recently, mainly in river valleys, vegetable gardens, and plantations, was not noted by researchers [16–17].

The goal of the present experiment is to study the characteristics of invasive and native species in separate and shared habitats, which would allow for predicting the possibility of further distribution of invasive species, and their impact on the native species and ecosystems. The main questions this study is designed to answer are as follows:

1. What is the reproductive potential of the invasive species *A. caliginosa* and *L. rubellus* compared to the native *E. nordenskioldi*?
2. Do species interactions affect each other's reproductive performance, survival and vertical distribution?
3. Are the quantity and quality of litter characteristics of natural habitats a limitation for invasive species?
4. Can invasive species tolerate the freezing soils in the absence of additional heat sources in the form of accumulations of organic matter?

Answers to these questions can be obtained under the conditions of experiments conducted in winter and vegetation periods, simulating the real situation of invasions in the same communities on the same types of soils with the same amount and composition of litter.

2. Materials and Methods

2.1. Experimental site

The simulation experiment was conducted in natural herb-grass meadows on common Vorony-Calcic Chernozems surrounded by birch groves (54°58'50.8 "N 73°18'10.1 "E). In this habitat type, as well as in its transformed variant, all three studied species occur: native – *E. nordenskioldi nordenskioldi* (epi-endogeic), invasive: *A. caliginosa caliginosa* (endogeic), *L. rubellus* (epi-endogeic).

The soils were characterised by a small amount of organic matter 5.2±0.5-6.3±0.6%, neutral reaction of the medium – 6.86±0.3, the proportion of valuable size fraction (1 to 5 mm) 50±7% in the soil structure, significant content of clay (44.1%) relative to sand (18.8%). In terms of anionic composition, the studied soils belonged to non-saline soils. Calcium (47.8±1.6 g/kg), potassium (17.2±0.9), and magnesium (8.63±0.27) dominated among the cations. Nitrate ions (104.6±15.6) dominated the anionic composition.

2.2. Preparation of soils, litter, and worms

Soils were selected layer by layer from pits in which mesocosms were placed, sieved through soil sieves with 5 mm holes to separate roots and soil macrofauna, and mixed. The dried litter was manually analysed to extract twigs and soil macrofauna.

The worms of each species in separate containers were sprinkled with water and incubated on moist filter paper to release the intestinal contents and weighed. Only sexually mature individuals were used for the experiment. The worms were placed in vessels. The total number of worms in the vessel, regardless of the variant, was 12 mature individuals.

2.3. Mesocosms

Plastic tubes were used as mesocosms with a diameter of 31 cm (0.075 m^2) in the vegetation experiment and 25 cm (0.049 m^2) in the winter experiment and of different lengths to allow vertical movement of the worms to the specified maximum depth. Silk bolting cloth No. 76 was attached at the bottom and top of the pipes. The cloth was secured to limit the entry of worms from outside and the exit of lumbricides from the mesocosms. Sieved soil was placed in the vessels in layers, repeating the natural soil profile, and dry litter of 100 g/vessel was placed on top. The soil in the vessels was moistened with tap water. Mesocosms were incubated without worms for 5 days.

2.4. *Experiment design during the vegetation period*

Mesocosms 40 cm deep were used for the experiment. There were 8 variants in the study during the growing season: mono-species, two-species, three-species, and control. The experiment was created in a fully randomised block design with five repetitions. There were 40 mesocosms in total. The experiment lasted four months, from June to October. Soil moisture in mesocosms was maintained at 60% during the growing season.

2.5. *Experiment design during the winter period*

In the winter experiment, there were 4 variants of the experiment, which differed in the depth of mesocosms (50, 100, 150, 200 cm). Loggers (iButton DS1922L-F5) were placed at the soil surface, as well as at a depth of 2, 50, 100, 150, and 200 cm. The winter experiment was set up in October and removed in May and lasted 7.5 months. Three species of earthworms were placed in mesocosms. The density of each species was 83 individuals/m^2.

2.6. *Statistical analysis*

Data normality was checked by the Shapiro-Wilk test at a critical level of significance p=0.05, and the homogeneity of samples – by the Levene test at a critical level of significance p=0.05 (Statistica 13.3).

In the case of normal distribution and homogeneity of the samples, the results were processed using descriptive statistics, one-factor, two-factor, and three-factor analysis of variance, as well as multiple regression analysis. The post-hoc Tukey's test for equal samples was used for the following pairwise comparison of significant results of the analysis of variance. To analyse the effect of experiment variation on the amount of litter, the authors used a sample of 8 variants and a three-factor analysis of variance, where each species was considered as a factor. To analyse the effect of the presence of earthworm species on each, the research team considered one of the species as control and used variants where this species is combined with others. In this case, a two-factor analysis was used. To test the hypothesis of equality of mean values corresponding to different variants of the experiments, the authors applied a one-factor analysis of variance and used data from the monovariants and data without controls.

If the sample did not meet the criteria of parametric tests, the Kruskal-Wallis analysis followed by a comparison of the mean ranks for all groups and the Spearman rank correlation were used.

3.Results

3.1. *Vegetation experiment*

3.1.1. Survival and reproductive potential of species in a monospecies experiment

The native species *E. nordenskioldi* had a better survival rate of sexually mature individuals placed in mesocosms (p=0.03). The percentage of surviving individuals in *E. nordenskioldi* was 24% higher than in *L. rubellus* and 5% higher than in *A. caliginosa*, but the Tukey test showed no significant difference (Figure 1A). The number of cocoons laid per sexually mature worm did not differ significantly among the studied species (Figure 1B), but the number of juvenile individuals was different (p=0.02). The maximum number of juvenile worms was found in *A. caliginosa* (1.9±0.5 individuals per sexually mature worm), which was 4.2 times higher than in the native species (p=0.03) and 3.8 times higher than in *L. rubellus* (p=0.04).

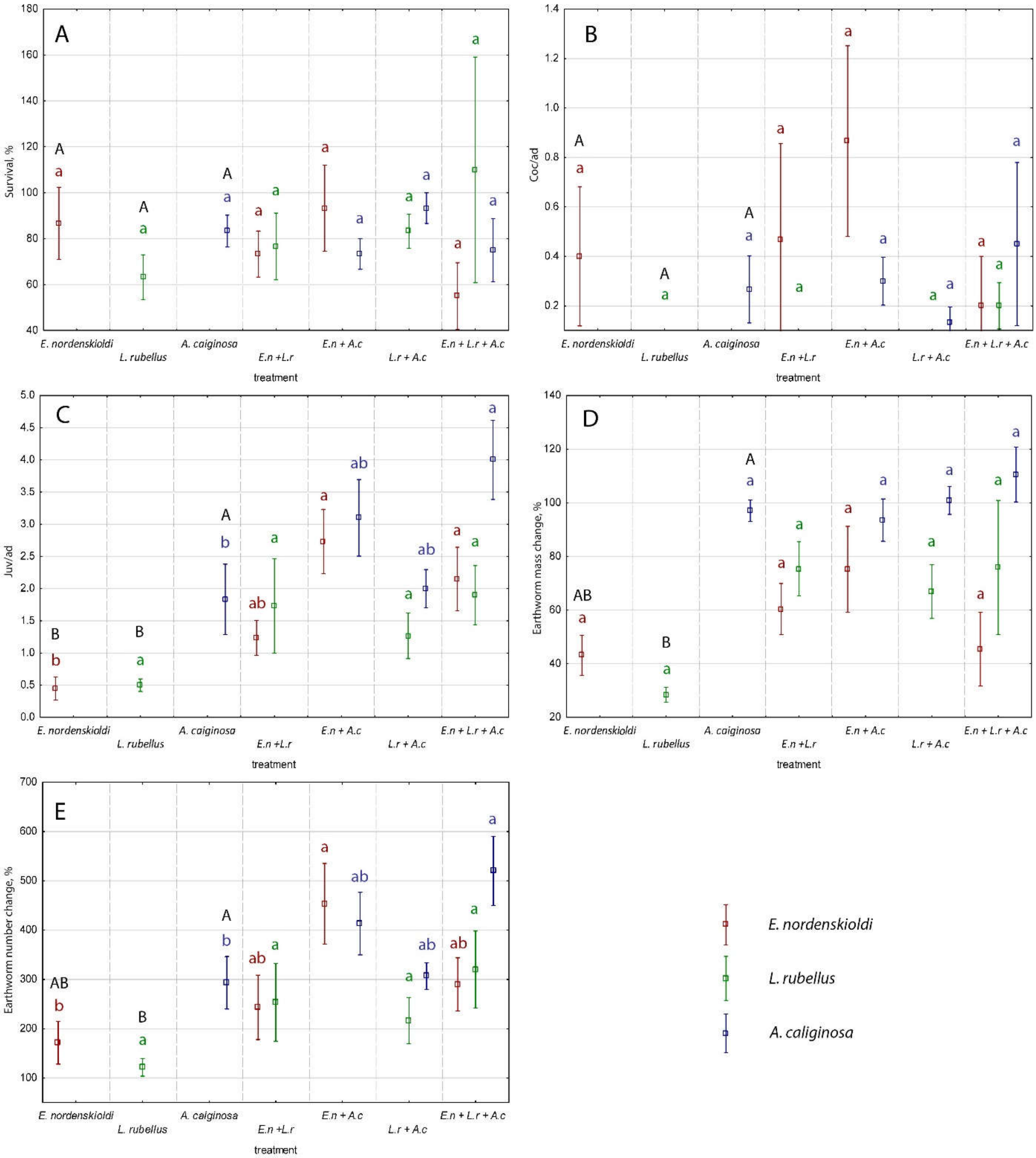

Figure 1. Indicators of earthworm population in different variants of the vegetation experiment in mesocosms (Mean±SE). A: survival rate of sexually mature animals, % of the initial number, B: productivity, number of cocoons/number of sexually mature individuals, C: тumber of immature/number of sexually mature, D: % of the starting biomass, E: % of the initial number. Variants with different letters show significant differences (α= 0.05 Tukey HSD). Capital letters show differences between species; small letters - between the treatments.

The invasive endogeic, *A. caliginosa*, also had the advantage in terms of total abundance (taking into account all age states) in the monospecies variants of the experiment (Figure 2A). Its total abundance was 2.4 times that of *L. rubellus* (p=0.03) and 1.6 times that of the native species (not significantly, p=0.13).

In monovariants, the total mass decreased in the series *A. caliginosa*, *E. nordenskioldi*, *L. rubellus* (Figure 2B).

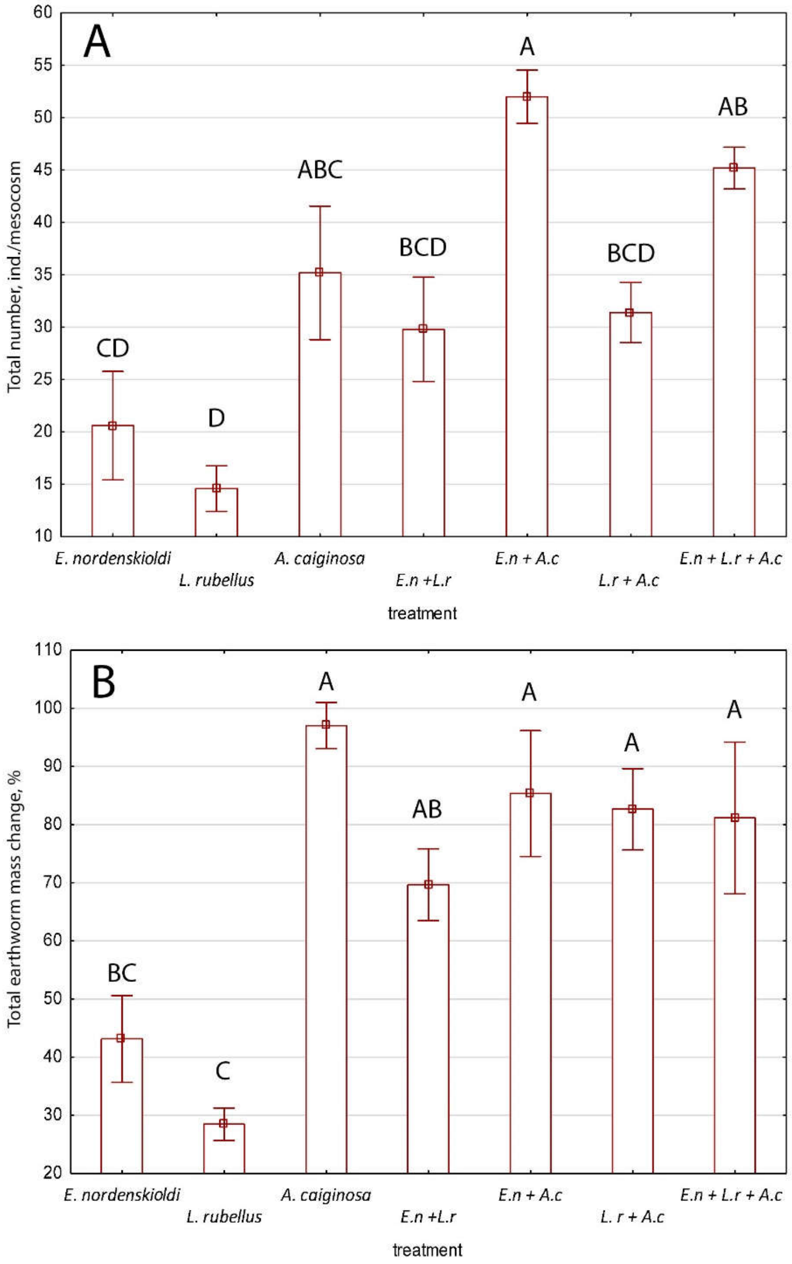

Figure 2. Total number and biomass of earthworms in different variants of the vegetation experiment in mesocosms (Mean±SE), A: numbers, individuals/vessel, B: biomass, % of starting values.Variants with different letters show significant differences (α= 0.05 Tukey HSD).

3.1.2. Interaction of species

There was no significant effect of invasive species on the number of sexually mature individuals of *E. nordenskioldi* (the percentage of the initial number was analysed). This parameter did not depend on the starting number of individuals of each species: 4, 6, or 12, the initial biomass, and the productivity of individuals (the ratio of the number of cocoons to the number of sexually mature individuals).

Also, invasive species had no significant effect on native species' productivity and biomass change. The effect of *A. caliginosa* on the number of juvenile and total abundance (all age states) of *E. nordenskioldi* was significant (p=0.02). The percentage of total abundance from the initial number of individuals of the native species in the variant with *A. caliginosa* exceeded this indicator in the monovariant by 2.6 times (p=0.03).

The influence of the species was reciprocal. The authors noted a significant effect of *E. nordenskioldi* on the relative number of immature individuals (p=0.007) and the total number of *A. caliginosa* (p=0.009). The relative abundance of juvenile *A. caliginosa* in the variant increased 1.7-fold (p=0.05) compared to the monovariant; the total abundance of the species increased 1.4-fold (p=0.05).

Survival of sexually mature individuals, productivity, the number of immature, and the number and weight of *L. rubellus* were independent of the presence of other species (Figure 1A-E).

3.1.3. Vertical distribution

In monovariants, the native species was found to a depth of 20 cm, *L. rubellus* to 15 cm, and *A. caliginosa* to 25 cm (Figure 3). *A. caliginosa* was influenced by cohabitation with *E. nordenskioldi*. The species became distributed across horizons close to the native species. The proportion of *A. caliginosa* individuals found in the -21–25 cm soil layer decreased 3-fold (p=0.04), in the 16–20 cm layer 3.5-fold (p=0.03) and the proportion of worms in the upper layers increased. The combination with *L. rubellus* in the variant did not cause a significant change in the vertical distribution of *A. caliginosa*. In the presence with *E. nordenskioldi*, the proportion of *L. rubellus* in the 0–5 cm layer increased from 68±9 to 93±12% (p=0.05). In the three-species experiment, species were active in all soil layers up to 25 cm deep.

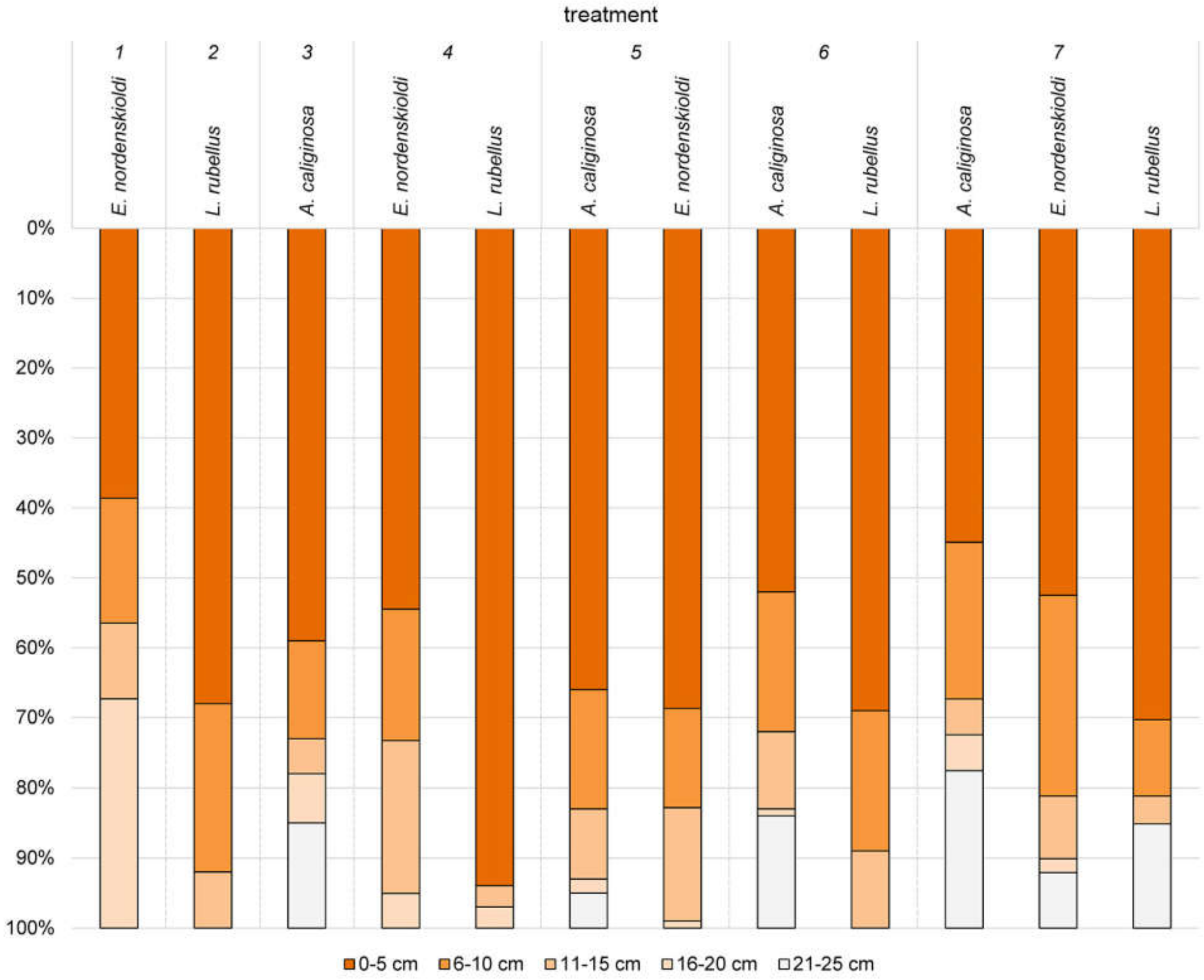

Figure 3. Vertical distribution of earthworms in a vegetation experiment.

3.1.4. Litter consumption

Among the species studied, the maximum litter consumption was noted for *L. rubellus*, the minimum for *A. caliginosa*.

Litter biomass depended only on the presence of *L. rubellus* (p=0.02) and its initial abundance (p=0.04).

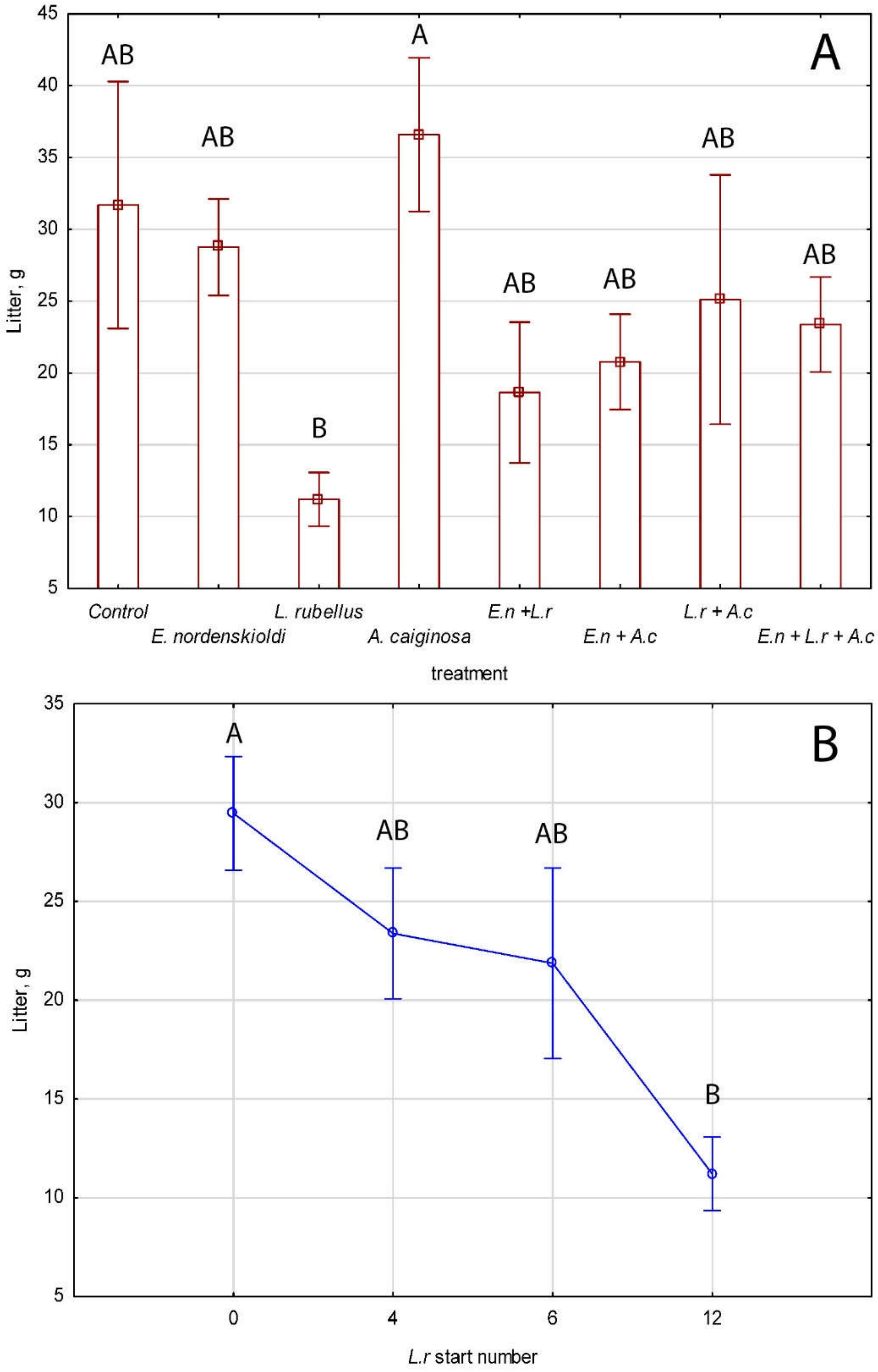

Figure 4. Amount of litter at the end of the vegetation experiment. A: in the variants of experiments, mean±error of mean, B: depending on the initial number of *L. rubellus*. Variants with different letters show significant differences (α= 0.05 Tukey HSD).

3.2. Winter experiment

The studies found that winter temperatures were limiting factors for *L. rubellus*, especially when limiting vertical migrations (p=0.05). For *A. caliginosa*, the limiting factor was the depth of mesocosms in winter (p=0.05), but starting from a vessel depth of 1 m, 100% survival was noted for the species. The native species had a winter survival advantage. Thus, small negative temperatures established in February at a depth of 50 cm

(Table) contributed to the decrease in *L. rubellus* survival to 8% with a range of data from 0 to 25% and to the decrease in *A. caliginosa* survival *to* 75±17%.

Table 1. Soil temperature at different depths of mesocosms during the winter experiment.

Soil layer		October	November	December	January	Febuary	Mart	April
0-5 cm	max t	3,4	-0,1	0,0	-0,9	-1,0	0,2	10,7
	min t	-1,8	-5,6	-2,9	-2,5	-2,5	-1,7	0,1
50 cm	max t	5,8	3,2	0,8	0,2	-0,1	0,1	7,3
	min t	3,2	0,8	0,2	-0,1	-0,4	-0,3	0,1
100 cm	max t	8,3	5,4	3,0	2,0	1,1	1,1	4,8
	min t	5,4	3,0	2,0	1,5	1,5	0,9	0,8
150 cm	max t	8,6	6,2	4,6	3,4	2,7	2,2	3,9
	min t	2,0	4,6	3,4	2,7	2,2	2,0	1,7
200 cm	max t	9,5	7,8	5,6	4,1	3,4	2,8	3,5
	min t	7,8	5,6	4,2	3,4	2,8	2,5	2,2

4. Discussion

4.1. Survival and reproductive potential of native and invasive species

The native species survived better than the invasive species, but it was significantly inferior to *A. caliginosa* in reproduction rate, the number of offspring, and final biomass, but had an advantage over *L. rubellus*. In this experiment, our research team grew a soil-litter form of *E. nordenskioldi nordenskioldi*, the most widely distributed in the south of Western Siberia and inhabiting together with the invasive species used in the experiment. It is known that, for nutrition, this species prefers the decay of soft-leaved tree species [18], which was used in the study and feeding on the soil surface, dwelling mainly in the accumulative humus horizon of soils. *L. rubellus* is active on the surface and in the upper 15 cm [19]. It is versatile in its preferences and absorbs both soil and all types of litter [20], but absorbs predominantly carbon from plant residues [21] and is even classified by Bottinelli *et al*. [22] as epigeic. It was this species that the authors of this study considered a possible competitor to the native species. According to the results of the present studies, it was inferior to *E. nordenskioldi* in all the studied indicators. According to isotopic analysis [21, 23] and X-ray tomography [19], the ecological niches of *L. rubellus* and *A. caliginosa* practically do not overlap. *A. saliginosa* has uniform swarming activity at least to a depth of 50 cm [19], and rare entries into deeper soil layers [24]. This species is also versatile in its preferences and ingests various types of litter as often as soil [20]. *A. caliginosa* uses plant litter as a source of carbon and nitrogen to a lesser extent than *L. rubellus*, and also actively eats bacteria [21]. Bottinelli *et al*. [22] classify it as an endogeic. Thus, the ecological niche of endogeic *A. caliginosa* is much wider than that of the two species inhabiting the upper 15 cm and feeding on litter. The species was not limited by either food or space resources in the experiment, which allowed it to leave the maximum number of offspring and increase the population biomass. The good reproductive potential of the species probably allowed it to spread widely in the south of Western Siberia, both in agrocenoses devoid of litter and in natural habitats [12, 14].

4.2. Interaction of species

In the experiment, there was a significant rejuvenation of the populations of the studied species, an increase in abundance and relative mass under interaction conditions compared to monovariants. This effect cannot be explained by the weakening of intraspecific competition, as the correlation analysis showed. The initial population density of earthworms in all experimental variants was 159 individuals/m^2, which is significantly lower than the density resulting in a decrease in the size and number of cocoons deposited [11, 25, 28]. For *L. rubellus*, it is 300 or more individuals/m^2 [11, 25, 28]. For *A. caliginosa*, it is 450 individuals/m^2 [11].

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By the end of the experiment, the maximum density of earthworms was observed in the bivariant of *E. nordenskioldi* with *A. caliginosa*. The total number of two species was 600 individuals/m^2, that of *E. nordenskioldi* – 293, and *A. caliginosa* – 307 individuals/m^2. These values were also not limiting for the species in the present experiment.

The increase in the number of non-mature individuals in species interactions can be explained by the possible positive influence of species on each other directly or indirectly through environmental changes [28–30]. In a meta-analysis of earthworm species interactions, Uvarov [10] showed that *A. caliginosa* often experienced positive effects from the presence of many species. This was manifested, for example, in the laying of cocoons in the presence of *L. rubellus* [31]. In the present three-month experiment for *A. caliginosa*, the presence of both species was most beneficial, but not paired with *L. rubellus.* For *E. nordenskioldi*, cohabitation with *A. caliginosa* was most beneficial. The relative abundance of juvenile *L. rubellus* in the monovariant was lower than in the bi- and trivariant experiments, but not significantly. Since *E. nordenskioldi* and *L. rubellus* belong to the same ecological group – soil-litter [18], but have different effects on *A. caliginosa*, it is not a matter of mutually beneficial interaction between endogenous and epi-endogenous worms. The positive effect of the presence of *E. nordenskioldi* can be explained by the probable eating of *E. nordenskioldi* coprolites by *A. caliginosa.* Coprolites are known to be more enriched with microorganisms and available nutrients than soil [32]. The content of ions in coprolites is species-specific [33]. Thus, coprolites of *E. nordenskioldi* on chernozem contained more nitrates compared to *L. rubellus* and *A. caliginosa* [34]. The hypothesis of *A. caliginosa* eating coprolites is confirmed by the shift of the species to the upper layers of soils in the bivariant. Also, the eating of coprolites can explain the significant assimilation of bacterial carbon and nitrogen by *A. caliginosa* according to the results of isotope analysis [21].

"Rejuvenation" of populations of various organisms: lichens, plants, rodents, woodlice, and millipedes in areas exposed to chemical and physical factors has been noted in ecotoxicological studies. It is a nonspecific response to stress, reflecting the processes of ontogenesis, and allows for maintaining abundance in ecosystems [35]. Such stress can be interspecific competition occurring in di- and tri-species variants. In such a case, the increase in young individuals, number, and weight in species interactions may be an attempt to leave more offspring in interspecific competition.

The increase in the total abundance (of all age states of the species) in the di- and trivariants was directly related to the increase in the number of immature individuals. Since juvenile individuals are much lighter than sexually mature ones, their numbers did not affect the mass of *A. caliginosa* and *E. nordenskioldi*, but the sum of all three species led to a significant difference between monovariants and a combination of species. An increase in the mass of *L. rubellus* in the divisional variant compared to the monospecific variant was noted in Hoeffner *et al*. [36].

The very modification of reproductive performance during species interactions has been noted in many studies. Changes in the number and size of cocoons deposited [11], the number of juvenile worms that hatch from cocoons [26], the survival rate of immature [37], maturation rate [38], and changes in numbers [11] and mass [38] have been recorded.

4.3. Vertical distribution

The vertical distribution of species in monovariants is consistent with the literature data on their ecological groups [18] and swarming activity [19, 24]. The influence of species interactions on changes in the vertical distribution of earthworms is confirmed by the study of Felten *et al*. [19]. In this work, the burrowing activity of *A. caliginosa* shifted from uniform to a depth of 50 cm in the monovariant to the upper 15 cm in the three-species variant with *L. rubellus* and *L. terrestris*. The authors attribute the change in the swarming activity of endogeic species to commensalism – the benefit of eating the organic-rich coprolites of detritophagous worms and saving energy in the secondary use of burrows. There is also evidence of the benefit of endogeic species when cohabitating with anecic species in experiments by Lowe and Butt [26–27].

4.4. Litter consumption

As the results of the present experiment showed, in the monovariants with *L. rubellus*, the litter was eaten completely, except for the leaf petioles, by the end of the study. In the bivariants and the trivariants, where 50% and 30% of the abundance was *L. rubellus*, respectively, the highest litter consumption was noted in the presence of two soil-litter species. The effect of *L. rubellus* on the degree of litter decomposition was described in Suarez *et al*. [39]. On sites with communities of invasive earthworms, the maximum decomposition of litter was observed in variants with the presence of *L. rubellus*. Also, the studies of Uvarov *et al*. [11] in experiments with litter-consuming species found that the trophic resource played a leading role in the interaction of these species. *L. rubellus* is an active consumer of litter [40]. Apparently, the natural level of litter in Western Siberia is insufficient and is a limiting factor for the active European invader. Perhaps that is why the species does not go beyond vegetable gardens with a large application of organic matter and floodplain meadows [12, 16]. It is known that the high availability of resources was a condition for the spread of the invasive species *Aporrectodea trapezoides* Duges, 1828 in the grasslands of California [7].

4.5. Soil freezing

Low negative temperatures contributing to the freezing of soils to a depth of 50 cm in February (Table) apparently contributed to the freezing of a significant part of the *L. rubellus* population in mesocosms 50 cm deep. This species is known not to tolerate negative temperatures as an adult [42]. When it is possible to migrate to the lower soil layers – below the freezing point, the populations of invasive species are preserved in full (Figure). Apparently, before 1985, when the soil frost level was more than 1 m, *L. rubellus* had no opportunity to establish itself in the soils of Western Siberia. All finds of the species in the Urals and Siberia [17, 41, 43, 44] refer to the period of low soil freezing according to the All-Russian Research Institute of Hydrometeorological Information [45]. In *A. caliginosa*, despite the ability of sexually mature individuals to tolerate negative temperatures down to -5 °C [42], the survival rate also decreased when vertical migrations were restricted. Nuutinen and Butt [46] found that immature individuals could hibernate in the freezing zone of soils, while mature individuals were active at +1 °C and made deep vertical migrations, up to 1 m deep.

5. Conclusion

Thus, the present study found that there were no limiting factors for *A. caliginosa* in Western Siberia. The species experienced the positive effects of the presence of a native species.

The distribution of *L. rubellus* may depend on the amount of litter and the depth of ground freezing. The natural volume of litter used in the experiment was insufficient for the species.

The native species is positively influenced by the presence of *A. caliginosa*. The species has advantages over the invasive in terms of winter survival.

According to the results of the experiment, one can assume that the spread of *L. rubellus* will continue to be limited to non-freezing biotopes rich in organic matter. *A. caliginosa* will continue to spread in natural communities and agrocenoses of Western Siberia.

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G.E.V.; writing—review and editing, K.K. All authors have read and agreed to the published version of the manuscript.

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