Dispersal of earthworms from the Rudny Altai (Kazakhstan) into Western Siberia

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Abstract
The aim of our study was to determine the current distribution, habitats, ecology, and possible dispersal routes of three species of the Rudny Altai (East Kazakhstan): Eisenia tracta, E. nana, and E. ventripapillata. We found that these species dispersed far beyond their original distribution into the flatland part of western Siberia (Russia) up to the central forest steppe of the Omsk oblast. E. tracta, E. nana, and E. ventripapillata were found in both floodplains and interfluvials. Hydrochory was the most plausible way of northward dispersal, while on interfluvials, they were probably introduced by humans. The studied species showed no preference for a particular habitat or river bank. The habitats were diverse and significantly different from the original ones in Rudny Altai. The factors that allowed E. tracta, E. nana, and E. ventripapillata to colonize western Siberia were probably their wide tolerance range to soil pH, temperature, density, and humidity, along with the decrease of winter soil freezing in recent decades. This is the first information about the occurrence of these species of earthworms in Siberia.

Key words: Lumbricidae, exotic species, Eisenia tracta, E. nana, E. ventripapillata.

Introduction
Regional faunas change over time (Bohlen et al. 2004a; Berg et al. 2010; Eisenhauer et al. 2014; Singh et al. 2019). Recently, rapid ongoing changes in species composition have been attributed to global warming (Bates et al. 2008; Bardgett & van der Putten 2014; Singh et al. 2019). The climate of western Siberia has become significantly warmer over the last decades (Frey & Smith 2003; Sada et al. 2019), which has resulted in the arrival of certain species from the south. Among those species are darkling beetles (Mordkovich et al. 2020), ground beetles (Stolbov et al. 2018; Mordkovich et al. 2020), myriapods (Farzalieva 2006; Nefediev et al. 2017; Dyachkov 2019), and mollusks (Vinarski et al. 2015; Kondakov et al. 2020). The soil is also

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getting hotter (Lembrechts et al. 2020); increased soil temperatures were reported in Canada (Qian et al. 2011), Ireland (Garcia-Suarez & Butler 2006), China (Chen & Zhou 2013; Zhan & Zhou 2019), and Russia (Zhang et al. 2001; Kalyuzhny & Lavrov 2016).

Increased soil temperatures allowed northward expansion of earthworm ranges (Bohlen et al. 2004a; Bohlen et al. 2004b; Tiunov et al. 2006; Hendrix et al. 2008; Berg et al. 2010; Eisenhauer et al. 2014). However, human-mediated dispersal is believed to be the main mechanism of earthworm long-range dispersal (Hale et al. 2005a; Cameron et al. 2007; Hendrix et al. 2008). Other mechanisms, such as hydrochory (Terhivuo & Saura 2006; Costello et al. 2010) and zoochory (Meijer 1972; Terhivuo & Saura 1988; Cameron et al. 2007), also contribute to this process.

Changes in earthworm community composition can impact many aspects of soils: the diversity and abundance of soil microbes (Eisenhauer et al. 2007; Eisenhauer et al. 2011; Uvarov et al. 2019), carbon and nitrogen cycles (Hale et al. 2005b; Huang 2015; Lubbers et al. 2015), availability of macro- and micronutrients (Lavelle et al. 2004, Bohlen et al. 2004b, Hendrix et al. 2006, Migge-Kleian et al. 2006), pH (Hopfensperger et al. 2011; Eisenhauer et al. 2007), soil structure, and water characteristics (Coleman et al. 2004; Hallam & Hodson 2020). Studying earthworm dispersal associated with the current climate changes is thus of interest not only to zoologists but also to ecologists.

E. tracta Perel 1985, E. nana Perel 1985, and E. ventripapillata Perel 1985 were previously considered endemic species of the Rudny Altai in eastern Kazakhstan. These species were reported by Perel (1985) for only three locations in Kazakhstan: Kalendarka (600 m above sea level), Gornaya Ulbinka (700 m), and Feklistovka (900 m) (Fig. 1). In Russia, E. tracta was found in a single location, on the left bank of the river Sema, a tributary of Katun, near the town Ulus-Cherga (Altai Republic) (Perel 1985; Vsevolodova-Perel 1997), and the other two species were never reported. We studied a sample of earthworms from the Omsk oblast from 2005–2006 and discovered two more locations for the abovementioned species on the plains of western Siberia.

The aim of our study was to detect the source of dispersal, habitat preferences, and ecological characteristics as well as putative dispersal mechanisms for the abovementioned earthworm species. We attempted to obtain answers to the following questions:

- Are there morphological differences between the populations from western Siberia and the Rudny Altai?
- How far northwards did these species disperse?
- What habitats do they prefer?
- Do soil conditions in the new habitats differ from the original ones?

Materials and methods

Field studies were performed from May to July 2018; sampling was initiated in the south just after the onset of the vegetation period and continued northwards. We investigated different habitats in the basin of the Irysh River, from the Zaysan Lake (East Kazakhstan oblast, Kazakhstan, 48°15' N, 83°03' E) to the Ust-Ishim village (Omsk oblast, Russia, 57°44' N, 71°10' E) (Figure 1). The distance between the furthestmost points was 1,329 km. We collected a total of 245 individuals of E. nana; 277 E. ventripapillata, and 323 E. tracta.

In each location, sampling was performed on both banks of the river in all major habitats: shoreline; floodplain forests and meadows; and forests, meadows, and fallow land on river terraces and interfluvials. Five sampling sites were taken for each habitat in all zones and subzones. Quantitative samples were taken according to International Organization for Standardization- Tropical Soil Biology and Fertility (ISO-TSBF) method (Anderson & Ingram 1993). For each habitat, we took at least six 25 x 25 cm samples. Each sample was divided into layers: litter, 0–10, 10–20, and 20–50 cm. Earthworms were fixed in 70% ethanol. Identification was performed according to the key of Vsevolodova-Perel (1997) and her paper on the Rudny Altai (Perel 1985).

For each sampling site, we documented soil properties in five replicates for soil density (Hand penetrometer; Eijkelkamp, Giesbeek, the Netherlands), pH (HI 99121; Hanna Instruments Inc., Smithfield, RI, USA), electric conductivity (HI 98331; Hanna Instruments), temperature (HI 99121 и HI 98331; Hanna Instruments Inc.), and humidity (by the thermostated weight method). We also determined precise geographical coordinates (Garmin 64st; Garmin, Olathe, KS, USA) and made vegetation descriptions.
Figure 1. Area of the field studies. Green triangle, *E. nana*; yellow square, *E. tracta*; red circle, *E. ventripapillata*; grey figures, the findings of Perel (1985); star stand for locations where none of these three species were detected; Arabic numerals refer to Table 1. Shading marks the Rudny Altai mountains. Roman numerals denote biomes: I, steppe; II, southern subzone of forest steppe; III, middle subzone of forest steppe; IV, northern subzone of forest steppe; V, subtaiga; VI, mixed forest; VII, boreal forest.

Morphological description and morphometry of earthworms were performed in the laboratory. We documented body length and its width at the 25th segment. We also studied all the main morphological features of the external and internal structure and measured the mass of fixed adult worms.

Normality of the data was assessed using the Shapiro–Wilk test at the $p = 0.05$ level. Statistical processing of the results was performed using descriptive statistics and single and multifactor analysis of variance. Pairwise comparison of soil parameters in different habitats was done using Tukey’s range test. The calculations were performed using Statistica 13 (StatSoft Inc., Tulsa, OK, USA). We also conducted a Principal Component Analysis (PCA) to reveal differences in soil parameters for different habitats, soil layers, and earthworm species using R (package “FactoMinerR”) (Lê et al. 2008).
Table 1. Earthworm density in different habitats in East Kazakhstan and the south of West Siberia (Omsk oblast). The location are arranged from the south to the north along the Irtysh river. V., village; d., district; c., city.

| №  | Location                                    | Latitude, N       | Longitude, E       | Altitude m | Habitat                                                                 | Soil layer, cm | Density, ind./m² | Distance to location | Distance to roads | Distance to river |
|----|---------------------------------------------|-------------------|--------------------|-------------|--------------------------------------------------------------------------|----------------|------------------|---------------------|-------------------|------------------|
| 1  | Karatobe aul, Zharma d.                      | 49°14'34.3800"    | 81°50'29.1600"     | 481         | Ravine with a stream, on a slope                                        | 0-10           | 9.00             | 2.93 km             | 152 m             | 230 m           |
|    |                                             |                   |                    |             |                                                                          | 10-20          | 1.00             |                     |                   |                  |
| 2  | Zhana-Ulga v., Katon-Karagai d.              | 49°11'57.1800"    | 85°46'36.9600"     | 864         | Floodplain meadow on a slope, motley tall-grass with Poaceae, sources of the Bukhtarma river | 10-20          | 1.00             | 1.6 km              | 35.4 m            | 820 m           |
|    |                                             |                   |                    |             |                                                                          | 20-20          | 2.00             |                     |                   |                  |
| 3  | Novaya Bukhtarma v., Altai d.                | 49°37'15.5400"    | 83°31'38.3400"     | 403         | Dead soil maple forest on the bank of the Bukhtarma Reservoir          | 0-10           | 2.00             | 0 m                 | 25 m              | 20 m            |
| 4  | Feklistovka v., Altai d.                    | 49°55'50.1600"    | 83°01'37.3200"     | 755         | Tall-grass aspen forest                                                | 0-10           | 9.00             | 3.6 km              | 25 m              | 8 km             |
|    |                                             |                   |                    |             |                                                                          | 10-20          | 1.00             |                     |                   |                  |
|    |                                             |                   |                    |             |                                                                          | 20-20          | 0.00             |                     |                   |                  |
| 5  | Gornaya Ulbinka v., Glubokoye d.             | 49°58'51.7522"    | 82°55'33.2944"     | 447         | Tall-grass aspen forest                                                | 0-10           | 13.00            | 461 m               | 190 m             | 200 m           |
|    |                                             |                   |                    |             |                                                                          | 10-20          | 4.00             |                     |                   |                  |
|    |                                             |                   |                    |             |                                                                          | 20-20          | 7.00             |                     |                   |                  |
| 6  | Bulak v., near Semey c.                      | 50°21'50.1000"    | 80°20'00.0600"     | 193         | Dead soil maple forest in the floodplain of Irtysh river              | 10-20          | 7.00             | 1 km                | 580 m             | 1 km             |
| 7  | Proletarka v., Bulan d.                      | 50°24'08.9400"    | 80°36'31.5000"     | 203         | Tall-grass aspen forest in the floodplain of Irtysh river            | 0-10           | 5.00             | 100 m               | 150 m             | 258 m           |

**Kazakhstan, East Kazakhstan oblast**

**Russian Federation, Omsk oblast**

| 8  | Tatarka v., Cherlak d.                       | 53°58'03.1800"    | 75°02'55.2600"     | 87          | Poplar and willow tall-grass forest                                    | 0-10           | 4.00             | 132 m               | 709 m             | 50 m             |
|    |                                             |                   |                    |             |                                                                          | 10-20          | 15.2             |                     |                   |                  |
|    |                                             |                   |                    |             |                                                                          | 20-20          | 3.20             |                     |                   |                  |
|    |                                             |                   |                    |             |                                                                          | 30-30          | 6.40             |                     |                   |                  |
| 9  | Rusanova v., Novovarshavka d.               | 54°05'35.8800"    | 74°35'43.9800"     | 95          | Steppe meadow, motley grass with feather grass                         | 0-10           | 4.00             | 4.8 km              | 124 m             | 9.7 km           |
|    |                                             |                   |                    |             |                                                                          | 10-20          | 4.00             |                     |                   |                  |
|    |                                             |                   |                    |             |                                                                          | 20-20          | 12.00            |                     |                   |                  |
| 10 | Lenin’s Path v., Cherlak d.                 | 54°13'55.2000"    | 74°53'32.8800"     | 120         | Fallow land, motley grass with feather grass                           | 0-10           | 4.00             | 5.6 km              | 790 m             | 10.6 km          |
|    |                                             |                   |                    |             |                                                                          | 10-20          | 2.00             |                     |                   |                  |
| 11 | Lenin’s Path v., Cherlak d.                 | 54°13'55.2000"    | 74°53'32.8800"     | 120         | Aspen and birch forest, stone bramble and motley grass                | 0              | 4.00             | 5.6 km              | 790 m             | 10.6 km          |
|    |                                             |                   |                    |             |                                                                          | 0-10           | 18.00            |                     |                   |                  |

..continued on the next page
### TABLE 1.

| No | Location                      | Coordinates                      | Area | Description                                             | 0-10 | 10-20 | 20-50 | 313 m | 80 m | 450 m |
|----|-------------------------------|-----------------------------------|------|---------------------------------------------------------|------|-------|-------|-------|------|-------|
|    |                               |                                   |      | Aspen and birch tall-grass forest                       |      |       |       |       |      |       |
| 12 | Achair v., Omsk d.            | 54°38'48",4200" - 73°54'23,6400" | 94   |                                                          |      |       |       |       |      |       |
| 13 | Ust-Zaostrovka v., Omsk d.    | 54°46'31,6800" - 73°38'40,2600"  | 112  | Sedge and fescue steppe meadow                          |      |       |       | 1.4 km| 2.2 km| 3 km |
| 14 | Omsk c.                       | 54°59'00,0000" - 73°30'21,3600"  | 120  | Mesophitic birch forest with motley grass                |      |       |       | 0     | 16 m | 8.3 km|
| 15 | Omsk c.                       | 54°59'00,0000" - 73°30'21,3600"  | 118  | Planted *Tilia* and low grass                           |      |       |       | 0     | 80 m | 8.2 km|
| 16 | Lyubinsky v., Lyubinsky d.    | 55°07'55,0200" - 72°48'10,3200"  | 115  | Mesophitic birch forest with motley grass                |      |       |       | 4.5 km| 120 m| 14 km|
| 17 | Politotdel v., Lyubinsky d.   | 55°12'26,3500" - 73°10'57,9972"  | 71   | Fallow land, motley grass with feather grass             |      |       |       | 890 m | 980 m| 303 m |
| 18 | Chernoluchie v., Omsk d.      | 55°16'37,4349" - 73°02'49,3040"  | 90   | Mesophitic birch and maple forest with motley grass      |      |       |       | 881 m | 2 km | 90    |
| 19 | Chernoluchie v., Omsk d.      | 55°16'54,7573" - 73°01'24,4457"  | 87   | Maple forest with low grass                              |      |       |       | 0     | 40 m | 650 m |
| 20 | Krasnoyarka v., Omsk d.       | N55°12'26,3500" - E73°10'57,997"  | 67   | Horsetail and high-grass birch forest                    | 10-20| 0.50  |       | 1.3 km| 840 m| 1.1 km|
| 21 | Bazhenovo v., Sargatskoye d.  | 55°37'42,1200" - 73°09'13,5000"  | 100  | Mesophitic meadow, motley grass with feather grass       | 0-10 | 2.00  |       | 3.06 km| 40 m | 21.8 km|
| 22 | Serebryanoye v., Gorkovskoye d.| 55°41'47,5200" - 74°24'44,6400" | 98   | Aspen and birch forest, bracken and motley grass        | 0    | 6.68  |       | 4.9 km| 900 m| 4.8 km|
Results

**Morphological analysis**

Morphometric differences were detected only among the populations of *E. tracta*. Individuals from the mountain populations of Kazakhstan were much bigger than those from the flatlands of Kazakhstan and Siberia (Fig. 2A and B) on average, 2.7 times longer and 2.4 times wider and 3.5 times the mass (n=27, \( p < 0.01 \)). The populations did not differ by morphological characteristics (prostomium, location of the girdle and location and shape of tubercle, location of male genital openings, etc.)

![Earthworm morphology](image)

**Fig. 2.** Earthworm morphology. A, *Eisenia tracta* (Omsk region); B, *Eisenia tracta* (East-Kazakstan region); C, *Eisenia ventripapillata*; D, *Eisenia nana*. Side view. Symbol: tb, tubercle; cl, clitellum. Scale bar = 5.0 mm.

**Distribution**

In Kazakhstan, we found five new locations for the studied species (Table 1). The investigated species were found in wet forests and tall-grass meadows of nemoral refugia as well as on floodplains and on ravine slopes. *E. tracta* was confined to lower soil layers; *E. ventripapillata*, to the depth of 10–20 cm; *E. nana*, to the upper 0–10 cm layer (\( p < 0.05 \)). We detected no significant association of any species with the river bank (left vs. right) or habitat type.

In western Siberia, we found 13 new locations (Table 1), both on floodplains and interfluvials. We detected no significant differences among the right (high) bank vs. left (low with a broad floodplain). The northernmost findings were in the central forest steppe (Fig. 1).

**Soil characteristics**

We used PCA to detect differences among the locations of the studied species from Russia and Kazakhstan, adjusted for layer.

The analyzed data contained 259 items, with five quantitative and two alternative characters in each. The first two dimensions accounted for 61.88% of the total inertia of our dataset (40.10% for the first axis and 21.78% for the second one). This was significantly higher than the reference value of 47.16% (the 0.95 quantile of the inertia percentage distribution obtained via the simulation of 1,444 data entries based on normal distribution).

Axis 1 was positively correlated with humidity (W), pH, and electric conductivity (G) and negatively correlated with temperature (T) and soil density (\( \rho \)). This axis delimited the Omsk oblast (Russia) and the
eastern Kazakhstan oblast (Kazakhstan). The locations from eastern Kazakhstan had higher soil humidity and pH, but lower density and temperatures compared with the Omsk oblast. Axis 2 reflected the differences among soil layers. This axis was positively correlated with soil temperature, pH, and electric conductivity.

*E. nana* was detected in habitats with weakly acidic and neutral pH and highly variable levels of soil electric conductivity, temperature, density, and humidity (Table 2). In western Siberia, the soil in *E. nana* habitats had significantly higher density and lower humidity compared with eastern Kazakhstan.

*E. tracta* was found in a variety of pH, from acidic to weakly basic, with a wide range of soil temperatures, density, and humidity; all habitats were characterized by low electric conductivity (Table 2). Its habitats in Omsk oblast had lower soil pH and humidity and higher density compared with Kazakhstan.

*E. ventripapillata* was found in weakly acidic, neutral, and weakly alkaline soils. Its habitats were characterized by wide ranges of temperature, density (from very friable to dense), and humidity (from almost dry to moderately humid), but invariably with low electric conductivity. Western Siberian habitats demonstrated certain differences in pH, temperature, density, and humidity.

Electric conductivity was the only soil characteristic that demonstrated no significant differences in western Siberian habitats compared with Kazakhstan.

**Figure 3.** The PCA factorial plane the corresponding correlation circle of earthworm distribution relative to soil layers and habitats. The vector show direction of correlation and its length indicate the strength of the variable. W, soil humidity; G, electric conductivity; T, temperature; ρ, density. OmEna, Omsk populations of *E. nana*; KazEna, Kazakhstan populations of *E. nana*; OmEve, Omsk populations of *E. ventripapillata*; KazEve, Kazakhstan populations of *E. ventripapillata*; OmEtr, Omsk populations of *E. tracta*, KazEtr, Kazakhstan populations of *E. tracta*.

**Discussion**

**Morphological analysis**

Differences between mountain and flatland populations of *E. tracta* might be caused by food (Bohlen et al. 1999; Butt 2011), biotic interactions with local pedobionts (Butt 1998; Uvarov 2009), and environmental factors (Mathieu 2018). Such effects were found, for example, for *Octolasion tyrtaeum* (Shekhovtsov et al. 2020). All mountain populations under study live in nemoral tall-grass aspen forests (Table 1) with a high humus content in the upper soil horizon, which could affect the increase in the mass and size of individuals.
Table 2. Habitat soil characteristics of the studied earthworms.

| Soil parameter       | Statistical indicators | Statistical indicators | Statistical indicators | Statistical indicators | Statistical indicators |
|----------------------|------------------------|------------------------|------------------------|------------------------|------------------------|
|                      | Eisenia nana (Kazakhstan) | E. tracta (Russia, West Siberia) | E. ventripapillata (Kazakhstan) |                      | E. ventripapillata (Russia, West Siberia) |
| pH                   | Mean±SE                | 7.1±0.09***            | 6.1±0.1**              | 7.0±0.13***            | 6.0±0.1***              | 6.6±0.11***            | 6.1±0.1***              |
|                      | Min–max                | 6.1–7.9                | 5.7–6.4                | 5.9–7.8                | 5.3–6.7                | 6.1–7.4                | 5.3–6.8                |
| Electric conductivity, mS/cm | Mean±SE                | 0.24±0.03              | 0.06±0.02              | 0.27±0.04              | 0.17±0.04              | 0.17±0.02              | 0.13±0.02              |
|                      | Min–max                | 0.04–0.74              | 0.01–0.12              | 0.06–0.83              | 0.02–0.59              | 0.06–0.25              | 0.03–0.44              |
| Temperature, °C      | Mean±SE                | 15.7±0.2               | 17.4±0.3               | 14.6±0.5               | 15.0±0.5               | 13.5±0.4***            | 16.7±0.5***            |
|                      | Min–max                | 12.7–18.2              | 16.7–18.2              | 11.8–18.0              | 13.1–20.0              | 12.2–17.1              | 14.2–21.1              |
| Density, N/cm²       | Mean±SE                | 67±7**                 | 246±20**               | 135±13**               | 244±26**               | 89±8***                | 262±33***              |
|                      | Min–max                | 10–110                 | 180–297                | 57–250                 | 124–460                | 42–153                 | 78–690                 |
| Humidity, %          | Mean±SE                | 43±1.8***              | 11±1.5***              | 37±0.8***              | 23±3.8***              | 37±0.9***              | 14±1.4***              |
|                      | Min–max                | 32–60                  | 6–15                   | 32–44                  | 8–65                   | 32–45                  | 7–21                   |

Note: *, significance level of pairwise comparison using the Tukey’s test for unequal samples; SE, standard error.

Earthworm body size might be determined by ploidy, but *E. tracta* is diploid (Viktorov 1993), and ploidy often does not correlate with body size (Vsevolodova-Perel & Bulatova 2008).

Species distribution
In 1983, three new endemic species were found in the dark taiga of the Rudny (western) Altai at an altitude of 600–900 m (Perel 1985). These altitudes belong to the acryogenic belt which is characterized by the absence of soil freezing (Gorbunov & Seversky, 2007). Such conditions are much more favorable for earthworms compared with the foothills and flatlands (Klevenskaya et al. 1968; Naplekova 1968), which freeze as deep as 180–200 cm (SNIP II-A.6-72 Climatology and Geophysics for Construction, SNIP 2.01.01-82 Climatology and Geophysics for Construction). In this study, we found that these three species have dispersed far beyond their original range.

Since the beginning of the twentieth century, average winter soil temperatures have increased in Siberia and adjacent regions (Anisimov & Zhiltsova 2012). This was probably the factor that allowed earthworms to disperse into the foothills of Altai and river valleys in eastern Kazakhstan, particularly along the valley of the Irtysch. Currently, the average freezing depth in eastern Kazakhstan is 99 cm, according to the SP RK 2.04-01-2017 Construction Climatology.

Further dispersal of the Altai endemics onto the flatlands of western Siberia was probably also facilitated by climate warming (Frey & Smith 2003; Anisimov & Zhiltsova 2012; Sada et al. 2019) and the decrease in soil freezing depth (Zhang et al. 2001; Kalyuzhny & Lavrov 2016). According to the All-Russian Research Institute of Hydrometeorological Information (http://www.meteo.ru/climate), soil freezing in weather stations in Omsk oblast decreased from 120–160 cm in the period from 1963–1978 to 40–80 cm in 2011 (Fig. 4).

Dispersal of southern animals into northern Kazakhstan and western Siberia in the last 30 years was also reported for the species that are associated with soil at some point in the life cycle. Those include darkling beetles (Mordkovich et al. 2020), ground beetles (Stolbov et al. 2018; Mordkovich et al. 2020), and myriapods (Farzalieva 2006; Nefediev et al. 2017; Dyachkov 2019).
The observed long-range colonization since 1983 obviously could not occur by means of natural active dispersal. Natural dispersal is estimated at 10–15 m/year (Hoogerkamp et al. 1983; Gilyarov & Perel 1984; Dymond et al. 1997; Hale et al. 2005a), while the distance between the most proximate locations in Kazakhstan and the Omsk oblast is about 600 km, so it would take about 40,000 years. The most obvious explanation for the observed colonization is hydrochory. Such cases were described in North America (Costello et al. 2011), where invasive earthworms drifted downstream with timber rafts and colonized the shores. Similar processes were also observed in Fennoscandia (Wackett et al. 2018). Populations from floodplains can be drawn into the water during floods or landslides (Zorn et al. 2005; Davids et al. 2006) and drift downstream (Cameron et al. 2007; Costello et al. 2011; Wackett et al. 2018). Earthworms and their cocoons remain viable in water (Roots 1956; Turner 2000; Zorn et al. 2008), so they can disperse for long distances along rivers.

Another factor affecting earthworm dispersal was probably the resettlement of the western Siberia by Russians from the eastern Kazakhstan region, which started in the 1990s following the collapse of the Soviet Union (Atantaeva & Kamalzhanova 2014). Due to the absence of direct railway and air traffic, this relocation was conducted using vehicles and boats (Atantaeva & Kamalzhanova 2014) and involved, among other things, seedlings and soil that could contain earthworms and their cocoons.

Further colonization of interfluvials was probably human-mediated. This could have included the transfer of earthworms and their cocoons attached to tire treads (Marinissen & van den Bosch 1992; Dymond et al. 1997; Cameron et al. 2007), soil relocation (Casson et al. 2002; Gundale et al. 2005; Cameron et al. 2007), and amateur fishing which involves the transport of bait (Reynolds 1977; Cameron et al. 2007).

**Habitat characteristics**

Colonization of new regions depends on the availability of suitable habitats. We found that the characteristics of the new habitats in Omsk oblast (Russia) were significantly different from the initial ones.
in eastern Kazakhstan, except for electric conductivity (Table 2). Electric conductivity may reflect overall soil salinity (Castellanos et al. 2000). Most of the habitats had low salinity (<1 mS/cm). Other soil parameters varied in a wide range, which will probably allow the studied species to colonize the most common soil types of western Siberia.

Conclusions

Our research demonstrates the invasion of new species of earthworms in Siberia. These are the latest reports, after research from North America, about the movement of the earthworm population to the northernmost areas. We found that *E. tracta*, *E. ventripapillata*, and *E. nana* dispersed far from the nemoral refugia where they were initially described, and they were detected both on floodplains and interfluvials. Our results indicate that species of earthworms considered endemic have a much wider tolerance than previously thought. Further research into the biology and ecology of these species is necessary. The northern border of the present distribution of these species is currently at the boundary of the central and northern forest steppe. The most probable way of northward dispersal is hydrochory, with subsequent anthropogenic transport to the interfluvials. In western Siberia, we found no reliable association of the studied species with particular soil layers, habitats, and the left or right bank of the Irtys. Soil environments in western Siberia are diverse and significantly different from those of the Rudny Altai. The only stable soil characteristic was its electric conductivity, which might indicate that these species prefer low salinity. The relatively high tolerance of these species toward pH, temperature, soil density, and humidity may be the factor favoring their dispersal into western Siberia, along with the decrease of soil freezing depth. The changes in the fauna of earthworms described in our work allow us to assume that, in the coming years in Siberia, there may be changes in the functioning of the soil and, thus, changes in the fauna and flora of ecosystems.

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