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Ecological Analysis and Biodiversity of the Helminth Community of the Pool Frog *Pelophylax lessonae* (Amphibia: Anura) from Floodplain and Forest Water Bodies

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Abstract: This work presents an ecological analysis of the community and biodiversity of helminths of the Pool Frog *Pelophylax lessonae* (Camerano, 1882) from floodplain and forest reservoirs of the European part of Russia. The material for the work was personal collections of helminths made from 2018–2021 in the National Park “Smolny” (Republic of Mordovia). Two hundred and thirty-five amphibian specimens were examined from nine reservoirs and three types of hydrobiocoenoses: (1) floodplains of a medium-sized river (in terms of catchment area); (2) floodplains of a small river; (3) a number of isolated forest reservoirs. Twenty-four species of helminths have been registered: Trematoda (20) and Chromadorea (4). Similar features (common species of trematodes and nematodes) were determined as well as differences in the composition and structure of the helminth fauna, the level of infestation by individual species and groups of helminths, diversity, and community structure. Amphibians of the river floodplain have a richer helminth fauna, they are more infected with a large number of helminths, and their community is more complex. Amphibians of isolated forest ponds, on the contrary, have fewer helminths, they are generally less infected, and their community is simplified (reduced). Having intermediate indicators of composition, structure, and degree of infestation, frogs from the forest floodplain of the small river—differ in the most diverse and maximally evenness community of helminths. The results of the study demonstrate the influence of biotopic factors on the formation of an amphibian helminth community.

Keywords: trematodes; nematodes; helminth community; biodiversity; *Pelophylax lessonae*; hydrobiocoenosis; National Park “Smolny”; Central European Russia

1. Introduction

Green frogs (genus *Pelophylax*) are a common group of coastal hydrobionts in fresh-water bodies of the Western Palearctic [1,2]. In water, they undergo larval development and metamorphosis, feeding of individuals of all ages, mating and territorial behavior, egg laying, and winter hibernation [3]. Amphibians of this genus play a significant role in aquatic and terrestrial biocoenoses. On the one hand, they are a massive consumer of aquatic and coastal invertebrates and small vertebrates [4,5]; on the other hand, they serve as prey for a number of predators [3]. Helminths of different systematic groups, including pathogens, circulate through trophic links [6].

Trematodes are a large group of helminths of green frogs [6–10]. They have a complex life cycle with a change of hosts that requires an aquatic environment [11]. In reservoirs, there are different processes such as egg laying, hatching, dispersal, and infection of hosts of different ranks and resting [12]. Another group of helminths of green frogs—nematodes—is represented by a smaller number of species [13]. Some of them have an obligate association with the aquatic environment as a conduit of amphibian infestation by their larvae [14].

The helminth community of green frogs is formed under the influence of a set of abiotic and biotic factors characterizing a particular water body [15–18]. Trematodes indicate the presence of a particular set of invertebrate and vertebrate species in the biotope [19–21] and their trophic relationships [22]. In this aspect, amphibian trematodes are conveniently used as bioindicators (markers) for habitat characterization, environmental changes [23], and environmental stress [24–27]. The nematode community does not provide an adequate assessment due to the dominant influence of abiotic factors on their occurrence in the host.

One of the most common species of green frog in Europe is the Pool Frog *Pelophylax lessonae* (Camerano, 1882) [28]. This species inhabits a wide range of forest and floodplain reservoirs with standing water: lakes, ponds, old trees, swamps; can be rarely found in shallow waters of rivers and streams, in flood meadows. Along the floodplains of rivers, it penetrates into the forest-steppe and steppe zone [29–31], which sometimes causes the transfer of genetic material [32,33].

The helminth fauna of *Pelophylax lessonae* is characterized by species richness and diversity [6,9,13]. An active semi-aquatic lifestyle with the ability of terrestrial migration, a wide range of habitats, food and predators, and the absence of a “mating fasting”: all these factors contribute to host infestation by parasites of different systematic groups, developmental types, and modes of infestation. Inhabiting ponds of various types, in each of them, *Pelophylax lessonae* has its own individual helminth community with a unique, characteristic only for the given habitat, set of features. The study of changes in the helminth community of amphibians on the border of forest and floodplain is of interest in terms of ideas about helminth fauna transformation during biocenosis change (succession, eutrophication). *Pelophylax lessonae* is a very suitable model object in this respect. Examples of such studies are unknown to us; in the works of modern authors, it is reduced to the study of the helminth fauna of *Pelophylax lessonae* in the framework of a hybrid complex of green frogs (*Pelophylax esculentus* complex) [7,8,18,34].

The aim of the work is to find and characterize the differences of helminth communities of *Pelophylax lessonae* in natural hydrobiocoenoses of different types. The objectives of the study include: an ecological analysis of qualitative and quantitative composition of helminths, their community structure, and biodiversity, as well as indicators of their infestation of the host in floodplain and forest hydrobiocoenoses.

2. Materials and Methods

2.1. Study Area

The material for the study was collected from 2018–2021 from nine reservoirs of the National Park “Smolny” and its surroundings (the Republic of Mordovia, the center of the European part of Russia). The research in the protected areas was carried out in accordance with agreements on scientific cooperation between the Institute of Volga Basin Ecology of the Russian Academy of Sciences, a branch of the Samara Federal Research Centre of the Russian Academy of Sciences, and the Joint Directorate of the Mordovia State Nature Reserve and “Smolny” National Park.

All of them belong to three types of hydrobiocoenoses: (1) floodplain of a medium-sized river (in terms of catchment area); (2) floodplain of a small river; (3) isolated forest reservoirs. Each hydrobiocoenosis has an individual set of parameters: geographical location, size and extent, number of reservoirs and their hydrology (depth, water transparency), composition of near-water and aquatic flora and fauna, degree of isolation, and anthropogenic impact.

Plot 1. Floodplain of a medium-sized river.

The Alatyr River has a length of 130 km and a catchment area of 7880 km². It is a tributary of the 2nd order of the Volga River. In the study area, it has a channel width of 25–50 m, a depth of 2–3 m, and an extensive floodplain of a number of large reservoirs between the northern shore and the southern border of the forest in the National Park “Smolny”. It includes the lakes Dubovoye (No. 1), Mitryashka (No. 2), and Polunzerka (No. 3), lying at a distance of 750–850 m from each other near the squares 113, 108, and

109 of the Barakhmanovsky forestry. The reservoirs are 300–900 m long and 30–50 m wide and are surrounded by alder forest around the perimeter. The banks are marshy. From the north, oak and pine forest; to the south, willow thickets and floodplain meadows with various grasses and cereals. The coastal and aquatic flora is represented by a wealth of plant species: air-water tall grasses, rooted in the ground, floating in the water column, and on the water surface. The water surface in the central part of the lakes is open; the water level is stable. It is the habitat for *Pelophylax lessonae*, *P. esculentus* (?); and a spawning place for *Rana arvalis*, *Bufo bufo*, and *Pelobates vespertinus*. The anthropogenic load is insignificant and is of a recreational nature.

Plot 2. Floodplain of a small river.

The Tesovka River is short (17 km) and has a small catchment area located in the National Park “Smolny”. It is a tributary of the 3rd order of the Alatyr River and the 5th order of the Volga River. In the research area, it flows through a forest area in the vicinity of the village of Semenovka (No. 4) and the village of Obrezki (No. 5) in squares 62 and 63 of the Lviv forestry. It has a narrow floodplain with isolated small pools 7–15 m long, 3–10 m wide, and up to 1.5 m deep. Along the banks, willow thickets and isolated trees of other species. Floodplain meadows are occupied by various grasses herbs and cereals. In coastal shallow water, sedges grow, while air-water tall grasses are less common. The water surface is partially or completely covered by duckweed. The water level depends on that in the Tesovka river; during a drought, ponds are prone to shallowing and drying out. It is the habitat for *Pelophylax lessonae* and *P. esculentus* (?) and a spawning place for *Rana arvalis* and *R. temporaria*, *Bufo bufo*, *Pelobates vespertinus*, *Lissotriton vulgaris*, and *Triturus cristatus*. The settlements are uninhabited, so the anthropogenic load is negligible.

Plot 3. Isolated forest reservoirs.

Plot 3.1. Kuznal Pond. It is a large, isolated reservoir (No. 6) on the Kuznal creek in sq. 98 of the Barakhmanovsky forestry. It is the former worked-out lowland peat bog, 100 m long and 50 m wide, dammed by beavers. A pine and birch forest surrounds the reservoir. The banks are low and marshy with single living trees, littered with deadwood. Along the shore and in shallow water, sedges and air-water tall grasses grow. Water surface with fallen birch inversions and isolated islands with willow shrubs; no water surface. A family of beavers maintains a relatively constant water level and clogging of the reservoir. It is the habitat for *Pelophylax lessonae*, *P. esculentus* (?) and *P. ridibundus* (?), and a spawning site for *Rana arvalis* and *R. temporaria*, *Bufo bufo*, *Lissotriton vulgaris* (?), and *Triturus cristatus* (?). The area is experiencing a transport and recreational load.

Plot 3.2. Orlovo gnezdo Pond. It is a small, isolated reservoir (No. 7) in the vicinity of the village Kalysha in sq. 39 of the Alexandrovsky forestry. According to the landform, it has an artificial origin. It has a length of 20 m, width of 7 m, and depth of 1.3 m. The eastern shore adjoins a deciduous forest; the western shore is overgrown with meadow various grasses, weed, synanthropic vegetation and cereals. The banks are steep and densely overgrown with willow, which shades and prevents riparian vegetation from growing. In open shallow water, air-water tall grasses grow; in deeper water, species rooted in the ground and floating in the water column grow. The water surface is partly hidden by duckweed and littered with deadwood. It is the habitat for *Pelophylax lessonae* and a spawning place for *Rana arvalis*, *Lissotriton vulgaris*, and *Triturus cristatus*. The area carries a recreational load; the pond is littered by people.

Plot 3.3. Ponds in the Lesnoy village. It is artificially formed by the construction of several dams in the surrounding ravine, many of them were subsequently eroded. The upper pond (No. 8), more than 200 m long and 25–30 m wide, was inhabited and divided by beavers into several parts with different water levels; it becomes very shallow during drought. Surrounded by deciduous forest; steep banks with thickets of willow, bushes, and sedges. Aquatic vegetation is represented by mono-species communities of ground-rooted and floating species in the water column. The water surface is covered with a thick layer of duckweed; in places, there is no water surface. The lower pond (No. 9), 160 m long and up to 60 m wide, is located on the territory of the village surrounded by country

roads. Along the shore, there are solitary deciduous trees; at the water's edge, there are thickets of air-water tall grasses and sedges. Shallow waters are occupied by flora rooting in the ground, floating in the water column and on the water surface; the water surface is partially hidden by duckweed. All reservoirs serve as a habitat for *Pelophylax lessonae* and *P. esculentus*; and as a spawning site for *Rana temporaria*, *R. arvalis*, *Bufo bufo*, *Lissotriton vulgaris*, and *Triturus cristatus*. Unlike the upper beaver pond, which is not subject to anthropogenic impact, the lower one is influenced by recreation and transport load.

2.2. Helminth Examination

The material for the study was the own collections of helminths from 235 specimens of *Pelophylax lessonae*. Weakened and dead amphibians after hibernation, spawning, and drying up of water bodies, mating, and migratory periods were studied in the first place. Decomposed, crushed, mummified, and fragmented carcasses as well as females during the spawning season were not examined.

According to the Directive of the European Parliament and of the Council of 22 September 2010 on the protection of animals used for scientific purposes (EU Directive 2010/63/EU), all applicable institutional, national, and international guidelines for the care and use of animals were complied with. Sedation of amphibians was carried out with a solution of diethyl ether (ethoxyethane).

Adult amphibians were examined by the method of complete helminthological dissection [35]. Standard parasitological methods were used to collect, fix, and treat helminths [36]. Trematodes were fixed in 70° ethanol, stained with alum carmine, and, after clarification in a solution of dimethylphthalic acid, were enclosed in Canadian balsam. Nematodes were straightened by heating, fixed with 70° ethanol, clarified in lactic acid, and enclosed in glycerol-gelatine. Total preparations of helminths are stored in the Parasitological Collection of the Institute of Ecology of the Volga River Basin of the Russian Academy of Sciences, Samara Federal Research Centre of the Russian Academy of Sciences, Togliatti, Russia. Helminth species have been identified by K.M. Ryzhikov et al. [37] and V.E. Sudarikov et al. [38]. The validity of taxonomic names for compliance with the International Code of Zoological Nomenclature has been verified according to the "Fauna Europaea" website (<http://www.fauna-eu.org>; 14 January 2022) [39]. The study takes into account modern ideas on the taxonomy of trematodes [40–44] and nematodes [45].

2.3. Data Analysis

The following indicators were used to assess quantitative helminth descriptors: prevalence (extensity of infection), or the percentage of a host infested with parasites of one species (P, %); intensity (of infection), or the minimum (min) and maximum (max) number of parasites of one species (R, specimens); abundance (A, specimens), or the average number of parasites of one species [46]. The degree of dominance was determined by the percentage of each type of parasite in the community structure: dominant (30% or more of the total number of specimens), subdominant (10–30%), common (1–10%), rare (0.1–1%), and single (0.01–0.1%) [47]. Parasites of the first two categories are background species of the helminth community; parasites of the last three categories are adominant [48]. The Shannon index (H') was used to determine species diversity; the Simpson index (1-D) was used to assess evenness [49]. The natural logarithm (ln) was used to calculate the Shannon index (H'). At the same time, only the adult stages of helminths were taken into account, since the larval stages have the property of accumulating in the host body for a number of years. Evenness of abundance distribution between individual species in the helminth community was assessed using Pielou's evenness index (E) [49]. The similarity of the species compositions of helminths was determined by cluster analysis based on the calculation of the Jacquard coefficient (C_J) [49]. An overall comparison of the infestation of amphibians from different hydrobiocoenoses and the significance of differences was assessed using the Kruskal–Wallis test (H). The Mann–Whitney (U) test was used for pairwise comparison of the significance of differences. The total number of specimens of all helminth species per

individual host, or total intensity, was used as a descriptor. Differences were considered significant at $p < 0.05$. Statistical data processing was carried out using Statistica 6.1 and Microsoft Excel 2016 programs.

3. Results

In our studies, 24 helminth species from 19 genera, 11 families, 6 orders, and 2 classes were registered in *Pelophylax lessonae*: Trematoda (20) and Chromadorea (4). Below is a list of full species names of helminths and a table of their host infestation in different biocoenoses, indicating the values of infestation indicators and the proportion of the species in the community structure (Table 1).

TREMATODA: *Gorgoderia cygnoides* (Zeder, 1800), *G. microovata* Fuhrmann, 1924, *G. asiatica* Pigulevsky, 1945, *Gorgoderina vitelliloba* (Olsson, 1876), *Haematoloechus variegatus* (Rudolphi, 1819), *H. asper* (Looss, 1899), *Skrjabinoeces similis* (Looss, 1899), *Opisthioglyphe ranae* (Froehlich, 1791), *Brandesia turgida* (Brandes, 1888), *Pleurogenes claviger* (Rudolphi, 1819), *Pleurogenoides medians* (Olsson, 1876), *Prosotocus confusus* (Looss, 1894), *Diplodiscus subclavatus* (Pallas, 1760), *Paralepoderma cloacicola* (Luehe, 1909), larvae, *Strigea strigis* (Schränk, 1788), larvae, *S. sphaerula* (Rudolphi, 1803), larvae, *S. falconis* Szidat, 1928, larvae, *Neodiplostomum spathoides* Dubois, 1937, larvae, *Tylodelphys excavata* (Rudolphi, 1803), larvae, *Alaria alata* (Goeze, 1782), larvae.

CHROMADOREA: *Oswaldocruzia filiformis* (Goeze, 1782), *Cosmocerca ornata* (Dujardin, 1845), *Oxysomatium brevicaudatum* (Zeder, 1800), *Icosiella neglecta* (Diesing, 1851).

Fifteen species of helminths parasitize at the adult stage of development and seven species occur exclusively at the larval stage. For adult helminths, amphibians are the definitive hosts; for larval stages, frogs are intercalary (mesocercarial), additional (metacercarial), and/or reservoir (metacercarial) hosts. Two more species of trematodes (*Gorgoderina vitelliloba* and *Opisthioglyphe ranae*) combine different stages of development in the body of amphibians and use them as amphixenic host (Table 2).

Nineteen helminths species were found in Plot 1: Trematoda (16) and Chromadorea (3). Five trematode species were found at the larval stage of development. The total prevalence is 95.62%; the total abundance is significant—63.99 specimens. The trematodes *Opisthioglyphe ranae* ($P = 62.32\%$) and *Alaria alata*, larvae ($P = 49.28\%$) have the highest intensity of infestation. Trematodes *Pleurogenoides medians* ($A = 35.58$ specimens), *Prosotocus confusus* ($A = 9.22$ specimens) and *Opisthioglyphe ranae* ($A = 8.41$ specimens) had the largest numbers. The first species is the only dominant (55.61%) parasite in the structure of the helminth community; the latter are two subdominant (14.41% and 13.14%, respectively). The helminth community is complex and also includes common (4 species), rare (3), and single (9) categories of parasites according to the degree of dominance. There are three background parasite species and 16 adominant ones (Tables 1 and 3).

Fifteen helminths species were found in Plot 3.1: Trematoda (12) and Chromadorea (3). Among them, there are 4 trematode species at the larval stage of development. The total prevalence and the total abundance are even lower than the previous one—75.68% and 4.92 specimens, respectively. The nematode *Icosiella neglecta* still has the highest rates of Invasion ($P = 37.84\%$; $A = 1.89$ specimens). The same species is the dominant (38.46%) parasite in the structure of the helminth community. Trematodes *Pneumonoeces variegatus* ($P = 16.22\%$) and *Prosotocus confusus* ($P = 13.51\%$) have the greatest intensity of infestation; the highest abundance is registered in *Alaria alata*, larvae ($A = 1.05$ specimens). *Alaria alata*, larvae (21.43%) and *Pleurogenoides medians* (15.93%) belong to subdominant parasites in the structure of the helminth community. In addition, there are also common (7 species) and rare (5) categories of parasites according to the degree of dominance. There are 3 species of background parasites and 12 adominant ones (Tables 1 and 3).

Table 1. Helminths of *Pelophylax lessonae* in different water bodies.

Helminths Species	Floodplain Water Bodies		Plot 3.1	Forest Water Bodies	
	Plot 1	Plot 2		Plot 3.2	Plot 3.3
<i>Gorgodera cygnoides</i>	4.35 ± 2.45 (1–1) 0.04 ± 0.02	6.67 ± 3.22 (1–1) 0.07 ± 0.03			
<i>Gorgodera microovata</i>	1.45 ± 1.44 (1) 0.01 ± 0.01	6.67 ± 3.22 (2–6) 0.22 ± 0.12	2.70 ± 2.51 (2) 0.05 ± 0.05	5.00 ± 4.88 (2) 0.10 ± 0.10	12.25 ± 4.68 (1–5) 0.27 ± 0.13
<i>Gorgodera asiatica</i>			2.70 ± 2.51 (1) 0.03 ± 0.03		
<i>Gorgoderina vitelliloba</i>	1.45 ± 1.44 (1) 0.01 ± 0.01				
<i>Haematoloechus variegatus</i>	5.80 ± 2.81 (1–2) 0.10 ± 0.05	8.33 ± 3.57 (1–3) 0.17 ± 0.08	16.22 ± 6.06 (1–4) 0.24 ± 0.12	15.00 ± 7.99 (1–2) 0.20 ± 0.12	6.12 ± 3.42 (1–2) 0.10 ± 0.07
<i>Haematoloechus asper</i>	2.90 ± 2.02 (1–2) 0.04 ± 0.03				
<i>Skrjabinoeces similis</i>	4.35 ± 2.45 (1–1) 0.04 ± 0.02	1.67 ± 1.65 (5) 0.08 ± 0.08			4.08 ± 2.83 (1–1) 0.04 ± 0.03
<i>Opisthioglyphe ranae</i>	62.32 ± 5.83 (1–126) 8.41 ± 2.12	5.00 ± 2.81 (1–7) 0.18 ± 0.12	5.41 ± 3.72 (1–2) 0.08 ± 0.06	10.00 ± 6.71 (2–4) 0.30 ± 0.22	6.12 ± 3.42 (1–1) 0.06 ± 0.03
<i>Brandesia turgida</i>				5.00 ± 4.88 (2) 0.10 ± 0.10	
<i>Pleurogenes claviger</i>	1.45 ± 1.44 (1) 0.01 ± 0.01	5.00 ± 2.81 (1–4) 0.10 ± 0.07	2.70 ± 2.51 (1) 0.03 ± 0.03		
<i>Pleurogenoides medians</i>	44.93 ± 5.99 (1–540) 35.58 ± 11.21	18.33 ± 4.99 (1–36) 1.00 ± 0.62	8.11 ± 4.49 (1–27) 0.78 ± 0.73	25.00 ± 9.69 (1–3) 0.50 ± 0.22	2.04 ± 2.03 (7) 0.14 ± 0.14
<i>Prosotocus confusus</i>	39.13 ± 5.87 (1–137) 9.22 ± 2.77	6.67 ± 3.22 (1–6) 0.18 ± 0.11	13.51 ± 5.62 (1–4) 0.24 ± 0.12	10.00 ± 6.71 (1–1) 0.10 ± 0.07	
<i>Diplodiscus subclavatus</i>	18.84 ± 4.71 (1–8) 0.42 ± 0.14	20.00 ± 5.16 (1–4) 0.47 ± 0.13	2.70 ± 2.51 (1) 0.03 ± 0.03	10.00 ± 6.71 (1–1) 0.10 ± 0.07	
<i>Paralepoderma cloacicola</i> , larvae	42.03 ± 5.94 (1–35) 4.33 ± 0.99	1.67 ± 1.65 (12) 0.20 ± 0.20		10.00 ± 6.71 (4–7) 0.55 ± 0.39	
<i>Strigea strigis</i> , larvae	2.90 ± 2.02 (1–3) 0.06 ± 0.05	3.33 ± 2.32 (4–20) 0.40 ± 0.34	2.70 ± 2.51 (5) 0.14 ± 0.14	10.00 ± 6.71 (1–5) 0.30 ± 0.25	4.08 ± 2.83 (1–3) 0.08 ± 0.06
<i>Strigea sphaerula</i> , larvae	2.90 ± 2.02 (1–3) 0.06 ± 0.05	5.00 ± 2.81 (1–7) 0.17 ± 0.12	2.70 ± 2.51 (1) 0.03 ± 0.03		
<i>Strigea falconis</i> , larvae			2.70 ± 2.51 (1) 0.03 ± 0.03		
<i>Neodiplostomum spathoides</i> , larvae		1.67 ± 1.65 (15) 0.25 ± 0.25			
<i>Tylodelphys excavata</i> , larvae	1.45 ± 1.44 (3) 0.04 ± 0.04				
<i>Alaria alata</i> , larvae	49.28 ± 6.02 (1–37) 3.65 ± 0.79	1.67 ± 1.65 (99) 1.65 ± 1.65	8.11 ± 4.49 (1–35) 1.05 ± 0.95	10.00 ± 6.71 (9–26) 1.75 ± 1.35	
<i>Oswaldocruzia filiformis</i>	21.74 ± 4.96 (1–20) 0.65 ± 0.31	8.33 ± 3.57 (1–1) 0.08 ± 0.04	5.41 ± 3.72 (1–1) 0.05 ± 0.04	25.00 ± 9.69 (1–2) 0.40 ± 0.17	16.33 ± 5.28 (1–3) 0.20 ± 0.08
<i>Cosmocerca ornata</i>	11.59 ± 3.85 (1–2) 0.16 ± 0.06			5.00 ± 4.88 (1) 0.05 ± 0.05	6.12 ± 3.42 (1–7) 0.18 ± 0.14
<i>Oxysomatium brevicaudatum</i>		8.33 ± 3.57 (1–4) 0.13 ± 0.07	8.11 ± 4.49 (1–7) 0.24 ± 0.19	30.00 ± 10.25 (1–2) 0.40 ± 0.15	2.04 ± 2.03 (2) 0.04 ± 0.04
<i>Icosiella neglecta</i>	27.54 ± 5.38 (1–21) 1.13 ± 0.39	66.67 ± 6.08 (1–20) 3.78 ± 0.61	37.84 ± 7.98 (1–18) 1.89 ± 0.60	95.00 ± 4.88 (2–22) 8.45 ± 1.26	59.18 ± 7.02 (1–10) 2.35 ± 0.42
Total species	19/5	17/5	15/4	14/3	10/1
Trematoda	16/5	14/5	12/4	10/3	6/1
Chromadorea	3	3	3	4	4
Shannon diversity index, <i>H'</i>	1.09	1.51	1.45	0.93	1.21
Pielou's evenness index, <i>E</i>	0.37	0.53	0.54	0.35	0.53
Simpson index, 1-D	0.46	0.38	0.34	0.64	0.49
Total examined, specimens	69	60	37	20	49

Notes: prevalence (P, %) is in front of round brackets; intensity range (R, specimens) is in round brackets; abundance (A, specimens) is behind the round brackets. Prevalence and abundance values are accompanied by standard error values (±). Before the slash, the total number of helminth species; after the slash, the number of helminth species in the larval stage.

Table 2. Life cycles of *Pelophylax lessonae* helminths.

Helminths Species	Life Cycle	Citation
<i>Gorgodera cygnoides</i>	Sphaeriidae ¹ –Corduliidae ³ –Ranidae ⁵	[50]
<i>Gorgodera microovata</i>	unknown	none
<i>Gorgodera asiatica</i>	Sphaeriidae ¹ –Calopterygidae, Corduliidae, Limnephilidae ³ –Ranidae ⁵	[50]
<i>Gorgoderina vitelliloba</i>	Sphaeriidae ¹ –Ranidae (larvae), Sialidae ³ –Anura ⁵	[51–53]
<i>Haematoloechus variegatus</i>	Planorbidae ¹ –Culicidae, Calopterygidae, Libellulidae ³ –Anura ⁵	[54,55]
<i>Haematoloechus asper</i>	Planorbidae ¹ –Calopterygidae, Lestidae ³ –Anura ⁵	[56]
<i>Skrjabinoeces similis</i>	Planorbidae ¹ –Aeshnidae, Calopterygidae, Coenagrionidae, Corduliidae, Lestidae, Libellulidae ³ –Ranidae ⁵	[57]
<i>Opisthioglyphe ranae</i>	Lymnaeidae) ¹ –Lymnaeidae, Anura (larvae) ³ –Anura ⁵	[58,59]
<i>Brandesia turgida</i>	unknown	none
<i>Pleurogenes claviger</i>	Bithyniidae ¹ –Odonata, Coleoptera, Ephemeroptera, Trichoptera, Sialidae, Gammaridae, Asellidae ³ –Anura ⁵	[60,61]
<i>Pleurogenoides medians</i>	Bithyniidae ¹ –Odonata, Coleoptera, Ephemeroptera, Trichoptera, Sialidae, Chironomidae, Gammaridae, Asellidae ³ –Anura ⁵	[60,62]
<i>Prosotocus confusus</i>	Bithyniidae ¹ –Odonata, Coleoptera, Trichoptera, Sialidae, Gammaridae ³ –Anura ⁵	[60,63]
<i>Diplodiscus subclavatus</i>	Planorbidae ¹ –water–Amphibia ⁵	[64,65]
<i>Paralepoderma cloacicola</i> , larvae	Planorbidae ¹ –Anura ³ –Colubridae ⁵	[66,67]
<i>Strigea strigis</i> , larvae	Planorbidae ¹ –Anura (larvae) ² –Anura ^{3,4} –Colubridae, Insectivora, Mustelidae, Canidae ⁴ –Strigidae ⁵	[68–71]
<i>Strigea sphaerula</i> , larvae	Planorbidae ¹ –Anura (larvae) ² –Anura ^{3,4} –Colubridae ⁴ –Corvidae ⁵	[68,69,71,72]
<i>Strigea falconis</i> , larvae	Planorbidae ¹ –Anura (larvae) ² –Anura ^{3,4} –Colubridae, Insectivora, Mustelidae, Canidae ⁴ –Accipitridae ⁵	[68,71]
<i>Neodiplostomum spathoides</i> , larvae	Planorbidae ¹ –Anura ³ –Colubridae, Corvidae, Laridae, Anatidae ⁴ –Accipitridae ⁵	[73–75]
<i>Tylodelphys excavata</i> , larvae	Planorbidae ¹ –Anura ³ –Ardeidae ⁵	[73]
<i>Alaria alata</i> , larvae	Planorbidae ¹ –Anura ² –Ranidae, Colubridae, Viperidae, Corvidae, Laridae, Anatidae, Strigidae, Accipitridae, Rodentia, Insectivora, Carnivora ⁴ –Canidae ⁵	[76–78]
<i>Oswaldocruzia filiformis</i>	soil–Amphibia ⁵	[79–81]
<i>Cosmocerca ornata</i>	water–Anura ⁵	[14]
<i>Oxysomatium brevicaudatum</i>	soil–Anura ⁵	[80,82]
<i>Icosiella neglecta</i>	Ceratopogonidae ¹ –Ranidae ⁵	[83,84]

Note: ¹—intermediate host; ²—intercalary host; ³—additional host; ⁴—paratenic host; ⁵—definitive host.

Table 3. Degree of dominance (%) in the helminth community structure.

	Plot 1	Plot 2	Plot 3.1	Plot 3.2	Plot 3.3
<i>Gorgoderia cygnoides</i>	0.07	0.73	—	—	—
<i>Gorgoderia microovata</i>	0.02	2.37	1.10	0.76	7.65
<i>Gorgoderia asiatica</i>	—	—	0.55	—	—
<i>Gorgoderina vitelliloba</i>	0.02	—	—	—	—
<i>Haematoloechus variegatus</i>	0.16	1.83	4.95	1.51	2.94
<i>Haematoloechus asper</i>	0.07	—	—	—	—
<i>Skrjabinoeces similis</i>	0.07	0.91	—	—	1.18
<i>Opisthioglyphe ranae</i>	13.14	2.01	1.65	2.26	1.77
<i>Brandesia turgida</i>	—	—	—	0.38	—
<i>Pleurogenes claviger</i>	0.02	1.10	0.55	—	—
<i>Pleurogenoides medians</i>	55.61	10.95	15.93	3.77	4.12
<i>Prosotocus confusus</i>	14.41	2.01	4.95	0.76	—
<i>Diplodiscus subclavatus</i>	0.66	5.11	0.55	0.76	—
<i>Paralepoderma cloacicola</i> , larvae	6.77	2.19	—	4.15	—
<i>Strigea strigis</i> , larvae	0.09	4.38	2.75	2.26	2.35
<i>Strigea sphaerula</i> , larvae	0.09	1.83	0.55	—	—
<i>Strigea falconis</i> , larvae	—	—	0.55	—	—
<i>Neodiplostomum spathoides</i> , larvae	—	2.74	—	—	—
<i>Tylodelphys excavata</i> , larvae	0.07	—	—	—	—
<i>Alaria alata</i> , larvae	5.71	18.07	21.43	13.21	—
<i>Oswaldocruzia filiformis</i>	1.02	0.91	1.10	3.02	5.88
<i>Cosmocerca ornata</i>	0.25	—	—	0.38	5.29
<i>Oxysomatium brevicaudatum</i>	—	1.46	4.95	3.02	1.18
<i>Icosiella neglecta</i>	1.77	41.42	38.46	63.77	67.65

Fourteen helminths species were found in Plot 3.2: Trematoda (10) and Chromadorea (4). There are 3 trematode species at the larval stage of development. The total prevalence is maximum (100%); the total abundance has an average value of 13.25 specimens. The nematode *Icosiella neglecta* had the greatest indicators of infestation extensity ($P = 95.00\%$) and abundance ($A = 8.45$ specimens). This species is the only dominant parasite in the structure of the helminth community (56.51%). Among trematodes, the most common species are *Pleurogenoides medians* ($P = 25.00\%$) and *Pneumonoeces variegatus* ($P = 15.00\%$). The trematode *Alaria alata*, larvae had the largest number ($A = 1.75$ specimens); it is also the only subdominant (13.21%) parasite in the structure of the helminth community. The remaining species are common (7 species) and rare (5) according to the degree of dominance. There are two background species and 12 adominant ones (Tables 1 and 3).

Ten helminths species were found in Plot 3.3: Trematoda (10) and Chromadorea (4). There is only one trematode species at the larval stage of development. The total prevalence and the total abundance are minimal—73.47% and 3.47 specimens, respectively. The most frequent and massive helminth is the nematode *Icosiella neglecta* ($P = 59.18\%$; $A = 2.35$ specimens), which is also the only dominant (63.77%) parasite in the structure of the helminth community. The remaining species (9) are among the common parasites of this host. Trematodes *Gorgoderia microovata* has the highest level of infestation ($P = 12.25\%$; $A = 0.27$ specimens). The structure of the helminth community is maximally simplified due to the absence of categories of subdominant, rare and single parasites according to the degree of dominance. The number of background species is minimal and equal to one; and there are 9 adominant species (Tables 1 and 3).

The number of helminth species varies in different plots and decreases in the following row: Plot 1 (19 species)—Plot 2 (17)—Plot 3.1 (15)—Plot 3.2 (14)—Plot 3.3 (10). According to the adult stages (maritas) of trematodes, there is a decrease in the number of species from a maximum in Plot 1 (16 species) to a minimum in Plot 3.3 (6). In parallel, in the same row, the change in larval stages of trematodes correlates: from five species in Plot 1 and 2 to one in Plot 3.3. The opposite trend is obtained in nematodes: their number increases from three species in Plot 1, 2, and 3.1 to four in Plot 3.2 and 3.3. This is primarily due to

an increase from 2 to 3 species of nematodes with a direct developmental cycle. The only nematode-biohelminth species, i.e., developing with changing hosts, is stably present in all the studied reservoirs.

The qualitative composition of helminths also varied greatly in *Pelophylax lessonae*. Out of 24 helminth species, only 7 (29.17%) were recorded in all reservoirs: trematodes *Gorgoderina microovata*, *Haematoloechus variegatus*, *Opisthioglyphe ranae*, *Pleurogenoides medians*, *Strigea strigis*, larvae, nematodes *Oswaldocruzia filiformis*, and *Icosiella neglecta*. These species represent the “core” of the helminth fauna of this host in the study area. Another 4 species (*Prosotocus confusus*, *Diplodiscus subclavatus*, *Alaria alata*, larvae, *Oxysomatium brevicaudatum*) were found only in four hydrobiocoenoses, and the other 5 species (*Skrjabinoeces similis*, *Pleurogenes claviger*, *Paralepoderma cloacicola*, larvae, *Strigea sphaerula*, larvae, *Cosmocerca ornata*) were found in only three hydrobiocoenoses. Trematode *Gorgoderina cygnoides* was found exclusively in two samples. The remaining species have a strict local confinement.

Cluster analysis based on the Jacquard similarity coefficient (C_J) demonstrated the degree of kinship of the helminth compositions of *Pelophylax lessonae* from different plots (Figure 1). It showed two groups of clades with a certain similarity between them. The first group is the clades Plot 1 and 2, representing floodplain ecosystems, which have the most similar compositions of helminths ($C_J = 0.71$). The second group with a lesser degree of similarity ($C_J = 0.61$) is the clades of Plot 3.1 and 3.2 belonging to forest ecosystems. The species diversity of helminths has a maximum similarity within groups and a minimum among groups. On the other hand, the most distant from all was the Plot 3.3 clade, which shows that the forest hydrobiocoenosis has an artificial origin (Figure 1).

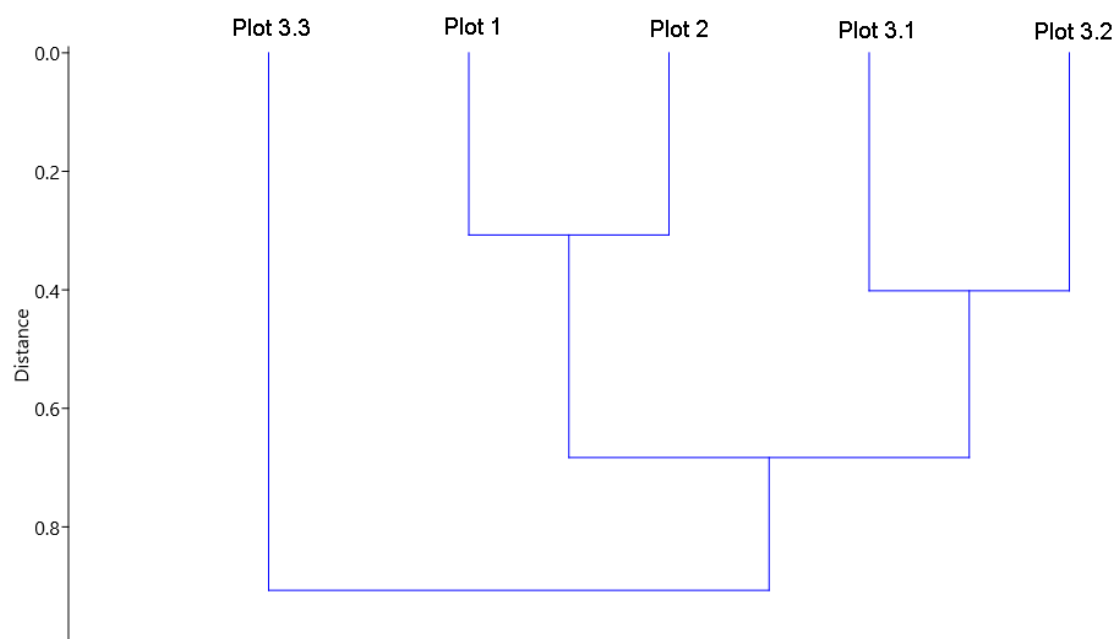


Figure 1. Dendrogram of helminth composition similarity according to Jaccard similarity index (C_J). Cophenetic Correlation Coefficient: $r = 0.780$.

Amphibians from Plot 1 were the most extensively infested. They were more or less heavily infested with 10 species of trematodes and nematodes: *Gorgoderina vitelliloba*, *Haematoloechus asper*, *Skrjabinoeces similis*, *Opisthioglyphe ranae*, *Pleurogenoides medians*, *Prosotocus confusus*, *Paralepoderma cloacicola*, larvae, *Tylodelphys excavata*, larvae, *Alaria alata*, larvae, and *Cosmocerca ornata*. Plot 2 is characterized by the highest infestation of only 5 species of trematodes: *Gorgoderina cygnoides*, *Pleurogenes claviger*, *Diplodiscus subclavatus*, *Strigea sphaerula*, larvae, and *Neodiplostomum spathoides*, larvae. An equal number, 5 helminth species with a higher degree of infestation, were recorded in Plot 3.2: *Brandesia turgida*, *Strigea strigis*, larvae, *Oswaldocruzia filiformis*, *Oxysomatium brevicaudatum*, and *Icosiella neglecta*.

Even fewer in Plot 3.1—only 3 species of trematodes: *Gorgoderia asiatica*, *Haematoloechus variegatus*, and *Strigea falconis*, larvae. Moreover, only one species of trematode, *Gorgoderia microovata*, is more heavily infested from reservoirs in Plot 3.3 (Table 1). Comparison of trematode infestation in *Pelophylax lessonae* using the Kruskal–Wallis test (H) revealed significant differences in amphibian infestation from different hydrobiocenoses ($H = 73.93$; $p < 0.0001$).

A Mann–Whitney test (U) comparison of infestation showed significant differences in *Pelophylax lessonae* helminth infestation between Plot 1 and 2, 3.1, 3.3, between Plot 2 and 3.1, 3.2, 3.3, between Plot 3.1 and 3.2, and between Plot 3.2 and 3.3. On the brink of credibility differences between Plot 1 and 3.2. Differences in frog infestation between Plots 3.1 and 3.3 are not statistically significant. Data with low values are grouped at the top and with high values at the bottom, respectively, there are differences in the samples considered (Table 4).

Table 4. Significance of differences (U (p)) in helminth infestation of *Pelophylax lessonae*.

	Plot 1	Plot 2	Plot 3.1	Plot 3.2	Plot 3.3
Plot 1		857.0 (<0.0001)	371.0 (<0.0001)	406.5 (0.0054)	475.0 (<0.0001)
Plot 2	857.0 (<0.0001)		842.5 (0.0459)	367.0 (0.0096)	1095.0 (0.0213)
Plot 3.1	371.0 (<0.0001)	842.5 (0.0459)		139.0 (0.0001)	890.0 (0.8877)
Plot 3.2	406.5 (0.0054)	367.0 (0.0096)	139.0 (0.0001)		162.5 (<0.0001)
Plot 3.3	475.0 (<0.0001)	1095.0 (0.0213)	890.0 (0.8877)	162.5 (<0.0001)	

All categories of parasite species are represented in the studied samples: dominant, subdominant, common, rare, and single. The proportion of individual helminth species varies in each biocoenosis; the number and composition of categories varies as well. Helminths from the category of single species are present only in Plot 1. Rare parasites are evenly represented in four samples: 3 species are noted in Plot 1 and 2; 5 species in Plots 3.1 and 3.2. Ordinary parasites, on the contrary, differ significantly in the number of species and are noted in all biocoenoses: from a minimum in Plot 1 (4) to a maximum in Plot 2 (11). Subdominant species are present in four biocoenoses with the exception of Plot 3.3: 2 species in Plots 1, 2, 3.1, and 1 species in Plot 3.2. Dominant species are present in all habitats, but by single species. The number of background parasite species decreases in a row: Plots 1, 2, and 3.1 (3 species)—Plot 3.2 (2)—Plot 3.3 (1). In the same sequence, the number of adominant species changes similarly: 16–14–12–12–9 (Table 1).

Pelophylax lessonae had the greatest species diversity in the helminth community in Plot 2 and Plot 3.1 (Table 1). The maximum values of the Shannon index ($H' = 1.51$ and 1.45 , respectively) prove this. In each of the hydrobiocoenoses, the numbers of helminth species differ little from each other, which indicates the evenness of their community. The minimum values of the Simpson index ($1-D = 0.38$ and 0.34 , respectively) confirm this. On the contrary, there was the least diverse and less equalized community of helminths in Plot 3.2 ($H' = 0.93$; $1-D = 0.64$). That implies that individual helminth species such as nematode *Icosiella neglecta* dominate over others in terms of number. The average values of the Shannon and Simpson indices from Plot 1 ($H' = 1.09$; $1-D = 0.46$) and Plot 3.3 ($H' = 1.21$; $1-D = 0.49$) show an intermediate degree of helminth community biodiversity (Table 1). It should be noted that the compositions of helminths in these hydrobiocoenoses are extreme (maximum and minimum) in terms of species richness.

Assessment by Pielou's evenness index generally confirms the results obtained. Its highest values in Plot 3.1 ($E = 0.54$) indicate a more even distribution of the relative abundance of helminth species in this community. The amphibian helminth communities from Plots 2 and 3.3 are similar in this indicator. In contrast, the lowest values of the Pielou index in Plot 3.2 ($E = 0.35$) indicate an imbalance in the helminth community, i.e., the presence of species that differ sharply in abundance. The values of the helminth community of frogs from Plot 1 are close to this (Table 1).

4. Discussion

The structure of helminth fauna of *Pelophylax lessonae* “adult stages of trematodes–larval stages of trematodes–nematodes with a direct developmental cycle–nematodes–biohelminths” remains unchanged in all hydrobiocoenoses. Only their quantitative component varies. This indicates that there is a reserve of stability in parasitic systems of trematodes and nematodes in green frogs within the study area.

The highest number of helminth species was found in frogs in water bodies of the middle river floodplain (Table 1). On the contrary, frogs of isolated forest ponds had the poorest composition of helminths. Amphibians from the reservoirs of the floodplain of the small river occupy an intermediate position in terms of the number of helminth species. Probably, there is a dependence of the composition of helminths on the degree of diversity or uniformity of amphibian habitat conditions in a particular hydrobiocoenosis [17,20,85,86].

The findings of local helminth species can characterize the habitat conditions of floodplain or forest hydrobiocoenoses. Thus, the species *Gorgoderina vitelliloba*, *Haematoloechus asper*, and *Tylodelphys excavata*, larvae were found only in frogs in Plot 1. The intermediate hosts of *Gorgoderina vitelliloba* are bivalves of the genera *Sphaerium*, *Pisidium*, and *Musculium* [51,52]. They live in riverbeds and floodplains with a weak watercourse, muddy bottom and clear water, well warmed and overgrown with algae, coastal and floating flora [87–89]. Such hydrobiocoenoses are also inhabited by larvae of *Calopteryx virgo* and *Coenagrion pulchellum* that are additional hosts for *Haematoloechus asper* [56]. In addition, river floodplains serve as a habitat for near-water birds of the family Ardeidae—the definitive hosts of the trematode *Tylodelphys excavata* [73].

Metacercariae *Neodiplostomum spathoides* were found only in Plot 2. This hydrobiocoenosis is located in a forest area, which is reliably inhabited by 16 species of birds of prey of the Accipitridae family [90]. Some of their species (*Aquila clanga*, *Milvus migrans*, *Circus aeruginosus*) serve as definitive hosts for this trematode species [73–75]. The *Gorgoderina asiatica* and *Strigea falconis*, larvae trematodes distinguish the *Pelophylax lessonae* helminth community from Plot 3.1. For Plot 2, the determining factor is the presence of additional hosts in the hydrobiocoenosis: probably some insect species of the orders Odonata and Trichoptera (the life cycle of the parasite is poorly known) [50]; for Plot 3.1, the determining factor is the presence of definitive hosts: birds of prey of the families Accipitridae and Strigidae [71]. The only finding of two specimens of the *Brandesia turgida* trematode was made in *Pelophylax lessonae* from Plot 3.2. It is difficult to explain this fact as the life cycle of the parasite is unknown [91]. By analogy with other trematodes species of the family Lecithodendridae (*Pleurogenes claviger*, *Pleurogenoides medians*, *Prosotocus confusus*), it can be assumed that some species of freshwater insects and/or crustaceans are involved in the infection of amphibians.

Moreover, certain helminth species can be considered as bioindicators of various types of hydrobiocoenoses. For example, trematodes *Gorgoderina cygnoides*, *Neodiplostomum spathoides*, larvae, and *Tylodelphys excavata*, larvae are found in frogs of floodplain reservoirs; nematode *Oxyomatium brevicaudatum* is found exclusively in forest biocoenoses.

The level of infestation of *Pelophylax lessonae* with individual species and groups of helminth species varies to different degrees in floodplain and forest hydrobiocoenoses. Thus, infestation with trematodes parasitizing in the bladder and lungs of amphibians does not reveal any pattern, since it varies slightly in individual host populations. The reason for this is probably easier prey than dragonfly larvae and imago, which serve as additional hosts for most species of this group of trematodes. The exception is the species *Haematoloechus variegatus*, with which *Pelophylax lessonae* is twice as infected in Plot 3.1 and 3.2 than in floodplain reservoirs. Additional hosts of the trematodes are larvae and imago mosquitoes of the family Culicidae [54,55], which prefer small standing shallow waters instead of extensive, deep river floodplain [92,93].

Infestation with intestinal trematodes, with the exception of rare species *Brandesia turgida* and *Pleurogenes claviger*, on the contrary, varies greatly in different biocoenoses. It is proven according to the dominant indicators of the extensity of infestation and the abundance of *Opisthioglyphe ranae*, *Pleurogenoides medians*, and *Prosotocus confusus* in Plot 1.

Diplodiscus subclavatus is close to them, the infestation with it is several times higher in Plots 1 and 2 than in Plot 3.3. This is explained by the peculiarities of the ecology of intermediate hosts of trematodes—gastropods. For *Opisthioglyphe ranae*, these are the species of the family Lymnaeidae [58,59]; for *Pleurogenoides medians* and *Prosotocus confusus*—family Bithyniidae [60–63]; for *Diplodiscus subclavatus*—family Planorbidae [64,65]. All of them prefer well-warmed floodplain reservoirs with stagnant and clear water, silted soil, and macrophyte thickets [89,94–96]. This contributes to the intensive circulation of trematodes, the infestation with them can increase dramatically in such conditions [97–99].

Among the larval trematode species, there is clearly a multiple excess of infestation with metacercariae *Paralepoderma cloacicola* and mesocercariae *Alaria alata* in Plot 1. This is probably due to the presence and high number of their definitive hosts in this biocoenosis that are species of the family Colubridae [66,67] and Canidae [76–78], respectively. The findings of metacercariae of other trematode species are sporadic in different hydrobiocoenoses.

We also note that there were low levels of infestation with nematodes with a direct developmental cycle in different biocoenoses. *Oswaldocruzia filiformis* demonstrates a spread of values, reaching the highest values in Plot 3.2. The maximum number of the nematode *Oxysomatium brevicaudatum* was also registered in the same reservoir. Infestation with *Cosmocerca ornata*, on the contrary, is slightly higher in Plot 1. This situation is explained due to the semi-aquatic lifestyle of the host, which favors contact with *Cosmocerca ornata* larvae in water [10] but prevents infestation with *Oswaldocruzia filiformis* and *Oxysomatium brevicaudatum* larvae on land [79,80,82]. The presence of the last two species indicates that frogs visit land for migration or foraging; and this happens more often in small isolated reservoirs, as indicated by the shift in their direction of the maxima of infestation of the mentioned nematode species.

Unlike nematodes with a direct developmental cycle, the species *Icosiella neglecta* is the most stable in all hydrobiocoenoses. Infestation with it varies significantly from the minimum values in Plot 1 to the maximum in Plot 3.2. This pattern is understandable due to the specifics of the parasite's life cycle. The nematode is a biohelminth; the intermediate host is woodlice of the family Ceratopogonidae, which prefer small shallow reservoirs rather than extensive deep river floodplains [83,84].

The reason for the changes in the structure of the helminth community and the number of their categories according to the degree of dominance is the varying degree of infestation in a particular hydrobiocoenosis. The high level of infestation with intestinal trematodes *Pleurogenoides medians*, *Prosotocus confusus*, and *Opisthioglyphe ranae* determines the complex structure of their community in floodplain reservoirs. Conversely, the simplified structure of the *Pelophylax lessonae* helminth community in isolated forest reservoirs is a consequence of low infestation with most helminth species, and primarily with trematodes. On the other hand, the abundance or numbers of individual helminth species is important within the community. The more obvious the dominance of any species, the less leveling and biodiversity of their community, as in *Pelophylax lessonae* in river floodplain and isolated forest ponds. The less the number of helminth species varies among amphibians of the same hydrobiocoenosis, the more uniform and diverse their community is. This is the case, for example, for frogs in the floodplain of a small forest river.

The characteristics of the helminth communities of *Pelophylax lessonae* in hydrobiocoenoses of different types are as follows. Amphibians from the middle river floodplain have a richer helminth community in terms of trematode composition, including larval stages. Among them, there are parasites of near-water birds. The overall infestation level is high due to intestinal trematodes. The structure of the community is complex. Biodiversity indicators are average. Background parasites are mass species of intestinal trematodes.

Frogs in the floodplain of the small river in the helminth community have a decrease in the number of species due to a decrease in the richness of trematodes, but while maintaining the number of larval stages. Parasites of near-water birds are replaced by those of forest predatory birds. The overall infestation is reduced due to a drop in the level of infestation by intestinal trematode species. As a result, single parasites fall out, and the structure of the

helminth community is simplified. The parameters of biodiversity are maximum. The role of the dominant parasite passes from trematodes to nematodes. The number of background species remains, but their partial replacement with nematodes-biohelminths and larval stages of trematodes occurs.

In amphibians in isolated forest reservoirs, the helminth community is impoverished to varying degrees in terms of the number of species due to a decrease in the richness of trematodes. The number of larval stage species is decreasing; parasites of diurnal predatory birds are the most vulnerable. The number of species of nematodes with a direct developmental cycle is increasing. The level of infestation with trematodes is falling; the overall infestation is reduced to a minimum. There are signs of degradation in the helminth community since rare and subdominant species fall out. The community structure is reduced. Biodiversity indicators vary from average to minimal. The role of the dominant parasite is performed by a nematode-biohelminth. The number of background species is reduced to one.

The differences in the degree of isolation and, as a consequence, the diversity of living conditions in a particular hydrobiocoenosis are due to stability and resistance to external changes. Each of them has an individual, historically formed, complex of abiotic and biotic factors that influence individual species and groups of hydrobionts in different ways. The openness of the river floodplain determines the diversity of habitat conditions, which has a positive effect on the development, abundance, and infestation of not only invertebrates and vertebrate hosts, but also amphibians themselves. As a result, the helminth community is in one extreme state—in progress. Isolation of forest ponds implies limited or even poor living conditions, lack of stability, and sometimes instability to external changes. Often the species diversity of such reservoirs is small, and the number of inhabitants is low. As a result, amphibians have a low diversity of helminths, up to the absence of individual species or groups of species. As a result, the reduction can be seen in the helminth community to another extreme state—to degradation. In the study area, the floodplain of the small river, by its nature, is transitional, intermediate (border) type of hydrobiocoenosis, i.e., ecotone. As it is known, the ecotone has a high level of biodiversity (marginal effect), as it is formed by ecologically different species from adjacent biocoenoses [100].

5. Conclusions

The study of the helminth fauna of *Pelophylax lessonae* in natural populations of the European part of Russia revealed a complex of biotopic differences between helminth communities in the openness floodplain and isolated forest hydrobiocoenoses. In the presence of similar features (common species of trematodes and nematodes), there are differences in the composition and structure of the helminth fauna, the level of infestation by individual species, and groups of helminths, diversity, and community structure. Amphibians of the river floodplain have a richer helminth fauna, are more infected with a large number of helminths, and their community is more complexly organized. Amphibians of isolated forest ponds, on the contrary, have fewer helminths, are generally less infected, and their community is simplified (reduced). Frogs from the border hydrobiocoenoses—the forest floodplain of the small river—with intermediate indicators of composition, structure, and degree of infestation, differ in the most diverse and maximally aligned community of helminths. The results of the work demonstrate the influence of biotopic factors on the amphibian helminth community. The obtained data make a certain contribution to the knowledge of the formation patterns in helminthofauna of lower terrestrial vertebrates under the influence of environmental factors [101] and may be of interest while studying succession and eutrophication [102] of reservoirs.

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