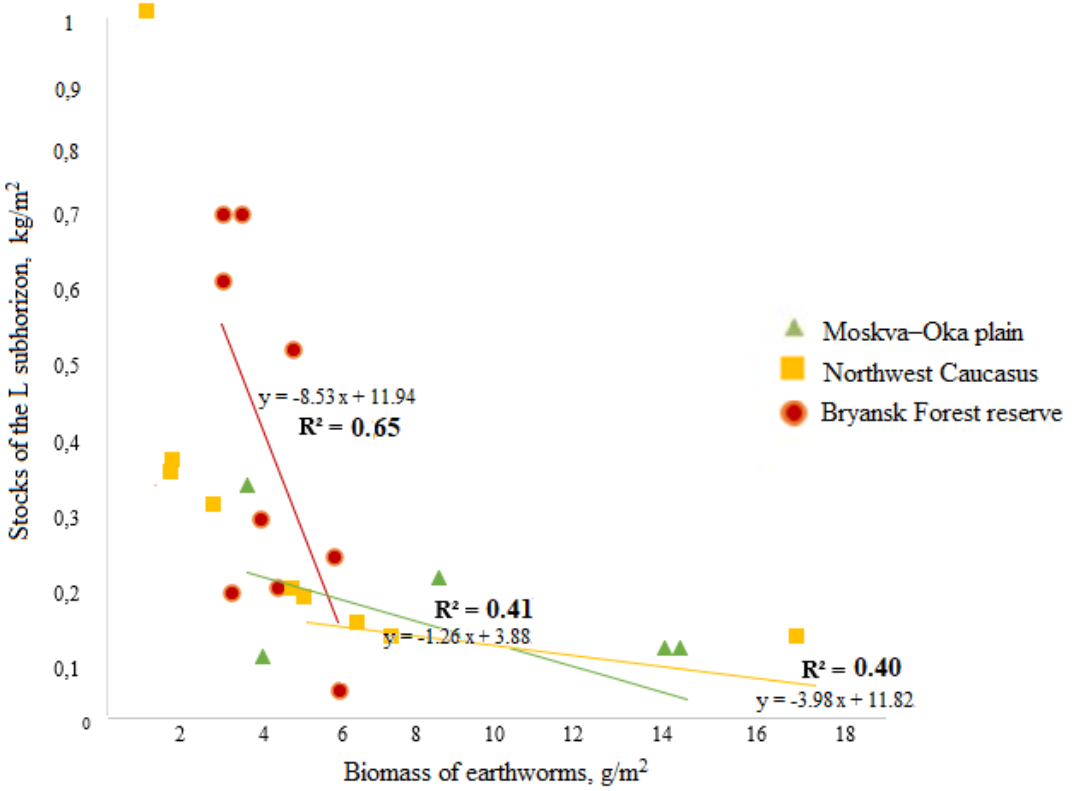

Figure 2. Dependence of the stock of litter L subhorizon on the biomass of epigeic, epi-endogeic and anecic earthworm species

The lack of mineral forms of nitrogen is one of the crucial limiting factors of plant mineral nutrition, since up to 90% of this element in soils is in the form inaccessible to plants (Mengel, 1996). The activity of earthworms is known to result in soil enrichment with nitrogen forms available for plants. Earthworm coprolites are rich with urea and ammonium ions. Digestive enzymes of earthworms boost the activity of nitrifying and ammonifying bacteria thus reducing the loss of free nitrogen, which is fixed in the form of compounds, ammonium nitrogen going into nitrites and nitrates (Kozlovskaja, 1976). Experiments with (Q R U G H Q V N L R G L which live in dark gray soil under broadleaf forests, have shown that the soil is enriched with active forms of amino nitrogen available for absorption by plant roots, as well as with free and bound amino acids (Kozlovskaja et al., 1983; Striganova et al., 1989). In experiments with epi-endogeic and endogeic earthworms it was shown that ammonium contained in earthworm coprolites is able to modify soil nitrification, causing long-term cumulative effects that are vastly superior to their direct effect (Bitjuckij et al., 2007). In experiments with anecic earthworms, it was shown that the available nitrogen content in the soil increased by 0.03 mg/kg for every 0.1 g of earthworm biomass (Andriuzzi et al., 2016). In natural ecosystems, the flow of soil nitrogen through earthworm populations amounts to dozens of kilograms per hectare per year (Lee, 1985; Parmelee and Crossley, 1988). Also, the soil is enriched with nitrogen through the death of earthworms: their annual mortality rate is on average 60% of the total population (Lavelle et al., 1998). In the soils of Central Europe, the nitrogen yield reaches 24 g/m^2 after the death of earthworms, which is comparable to the annual dose of mineral nitrogen fertilizers (100–200 kg of N per 1 ha). Earthworm biomass containing 65–75% of protein decomposes quickly in the soil, but nitrogen bound by microorganisms is washed out more slowly (Lee, 1985; Makeschin, 1997; et al.).

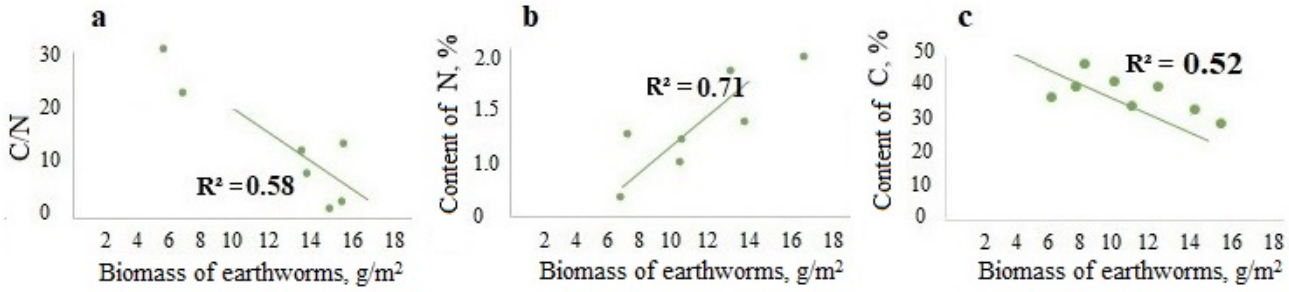

Figure 3. Dependence of the C/N ratio (a), nitrogen content (b) and carbon content (c) in the **L subhorizon of litter** on the biomass of **epi-endogeic** earthworms in the forests of the Moskva–Oka plain

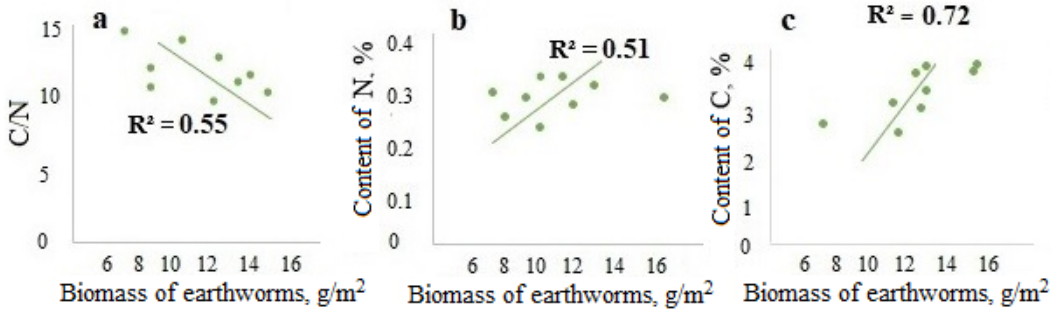

Figure 4. Dependence of the C/N ratio (a), nitrogen content (b) and carbon content (c) in **A horizon** on the biomass of **epi-endogeic** earthworms in the forests of the Moskva–Oka plain

Earthworms contribute to a significant decrease in the C/N ratio in the soil due to their direct and indirect influence on the mineralization and humification of organic matter. Thanks to earthworms there is a three-fold decrease in the C/N ratio in the soil as compared to the litter fall (Striganova, 1968). There is experimental evidence of a significant decrease of the C/N ratio under the influence of different morpho-ecological groups of earthworms not only in forest soils. For epi-endogeic earthworms, this has been shown in vermicompost (Talashilkar et al., 1999), and for endogeic earthworms – in agricultural fields (Sandor, Schrader 2007; McDaniel et al. 2013).

Earthworms are more often classified as nitroliberants, i.e. soil organisms that have a strong influence on nitrogen migration (Kozlovskaja, 1976; Zhukov et al., 2000), primarily due to the humification of organic matter in the soil. However, earthworms as primary litter decomposers and secondary decomposers of dead plant residues also affect the migration of carbon in soils, so they can also be attributed to the group of carboliberants (mineralizing agents). According to our and literature data, the influence of different morpho-ecological groups of earthworms on the nitrogen content and the C/N ratio is similar in the horizons of their activity: the nitrogen content increases, the C/N ratio decreases. However, a differential functional approach is required in regard to the effect of earthworms on carbon content. The latest global meta-analysis shows that the presence of not only epigeic and anecic groups, but also of endogeic earthworms leads to a decrease in organic matter in the litter horizon, with the strongest effect being exerted by anecic earthworms (Huang et al., 2020).

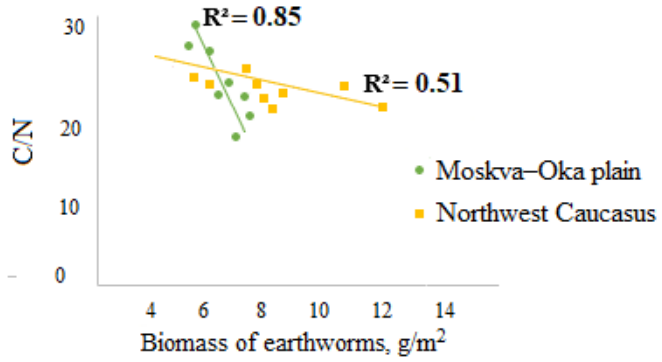

Figure 5. Dependence of the C/N ratio in **A horizon** on the biomass of **endogeic** earthworms in the forests of the Moskva–Oka plain and the Northwest Caucasus

Our study shows a possible significant negative effect of the group of epi-endogeic earthworms (*L. rubellus*) on litter store and the content of organic carbon in it. It is known that this species is often confined to rich soils and a high content of organic matter (Zhukov, 2004; Zhukovskaja et al., 2005, etc.). We have identified the relationship between the biomass of the epi-endogeic *L. rubellus* and increased carbon content in the humus horizon. This is probably due to the high trophic activity of these earthworms and high quality of rapidly decomposing litter fall (birch, linden, hazel). No significant correlations between the biomass of endogeic species and the level of carbon accumulation were revealed, but there is a general trend towards decreased organic carbon content in the humus horizon with an increase in the biomass of this group of species. Endogeic species feed on humus (Perel', 1979; Zhukov, 2004); their coprolites show a decrease in the total mass of organic matter and an increase in ash content by 2–3% as compared to the soil (Lavelle, Martin, 1992; Angst et al., 2017). Endogeic species are not involved in active movement of litter and transfer of organic carbon to the underlying horizons. To obtain convincing results, more field experiments in forest soils are needed, and we intend to continue our research in this area.

CONCLUSIONS:

1. With the change in the succession status of forests, the species composition and the set of morpho-ecological groups of earthworms become more complex, but there is no consistent replacement of any one group by others.
2. The species richness, diversity of morpho-ecological groups, and biomass of earthworms with similar granulometric composition of soils is determined by the litter quality: the most favorable type of litter fall for maintaining the functional diversity of earthworms is the mixed litter of broadleaf and coniferous species of the tree canopy, undergrowth, and shrubs.
3. Ambiguous effects of earthworms of different morpho-ecological groups on carbon accumulation in forest soils were revealed. Negative correlations were found between the total biomass of epigeic, epi-endogeic, and anecic earthworm species and the litter carbon content. In the humus horizon, the biomass of epi-endogeic species was positively correlated with the carbon content. This study revealed no relationship between the carbon content of the soil and the earthworm anecic species.
4. Indicators associated with carbon accumulation, i.e. the C/N ratio and the nitrogen content, show similar (unidirectional) correlations with the biomass of earthworms in the horizons of their activity: with an increase in the biomass of earthworms of different morpho-ecological groups, the C/N ratio decreases, whereas the nitrogen content increases.

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REFERENCES

Abaturov B.D., Pochvoobrazujushhaja rol' zhivotnyh v biosfere (Soil-forming role of animals in the biosphere), *Biosfera i pochvy*, Moscow: Nauka, 1976. pp. 53-69.

Alban D.H., Berry E.C., Effects of earthworm invasion on morphology, carbon, and nitrogen of a forest soil, *Appl. Soil Ecol*., 1994, Vol. 1, pp. 243-249.

Andriuzzi W.S., Schmidt O., Brussaard L., Faber J.H., Bolger T., Earthworm functional traits and interspecific interactions affect plant nitrogen acquisition and primary production, *Applied Soil Ecology,* 2016, Vol. 104, pp. 148-156.

Angst S., Mueller C.W., Cajthaml T., Angst G., Lhotakova Z., Bartuska M., Spaldonova A., Frouz J., Stabilization of soil organic matter by earthworms is connected with physical protection rather than with chemical changes of organic matter, *Geoderma*, 2017, Vol. 289, pp. 29-35.

Begon M., Harper J.L., Townsend C.R., *Ecology: Individuals, Populations and Communities*. Oxford: Blackwell Scientifi c Publications, 1986, 1068 p.

Berezina O.G., Struktura naselenija kollembol (Hexapoda, Collembola) reliktovogo lipovogo lesa (Gornaja Shorija, Kemerovskaja oblast') (The spatial structure of springtails community (Hexapoda, Collembola) of the southern forest-steppe of Western Siberia), *Evraziatskij jentomologicheskij zhurnal,* 2016, Vol. 15, No 6, pp. 583-590.

Bitjuckij N.P., Solov'eva A.N., Lukina E.I., Olejnik A.S., Zavgorodnjaja Ju.A., Demin V.V., Byzov B.A., Jekskrety dozhdevyh chervej stimuljator mineralizacii soedinenij azota v pochve (Stimulating Effect of Earthworm Excreta on the Mineralization of Nitrogen Compounds in Soil), *Pochvovedenie*, 2007, No 4, pp. 468-473.

Bohlen P.J., Pelletier D.M., Groffman P.M., Fahey T.J., Fisk M.C., Influence of earthworm invasion on redistribution and retention of soil carbon and nitrogen in northern temperate forests, *Ecosystems*, 2004, Vol. 7, pp. 13-27.

Burtelow A.E., Bohlen P.J., Groffman P.M., Influence of exotic earthworm invasion on soil organic matter, microbial biomass and denitrification potential in forest soils of the northeastern United States, *Appl. Soil Ecol.*, 1998, Vol. 9, pp. 197-202.

Curry J.P., Factors affecting the abundance of earthworms in soils. In: Edwards C.A. (Ed.). *Earthworm Ecology*, 2nd ed., CRC Press, Boca Raton, FL, 1994, pp. 91-113.

Frouz J., Liveckova M., Albrechtoa J., Chronakova A., Cajthaml T., ... & Simackova H. Is the effect of trees on soil properties mediated by soil fauna? A case study from post-mining sites, *Forest Ecology and Management*, 2013, Vol. 309, pp. 87-95.

Geras'kina A.P., Preobrazovanija kompleksa dozhdevyh chervej v hode poslerubochnyh sukcescij v lesah Severo-Zapadnogo Kavkaza (Transformations of earthworm communities during post-logging successions in the forests of the Northwest Caucasus), *Forest science issues*, 2018, No 1, pp. 1-14.

Gilyarov M.S., *Metody pochvenno-zoologicheskih issledovanij* (Methods of soil and zoological research), Moscow: Nauka, 1975, 304 p.

Gleixner G., Soil organic matter dynamics: a biological perspective derived from the use of compound-specific isotopes studies, *Ecological Research*, 2013, Vol. 28, No 5, pp. 683-695.

Goncharov A.A., *Struktura troficheskih nish v soobshhestvah pochvennyh bespozvonochnyh (mezofauna) lesnyh jekosistem* (The structure of trophic niches in the communities of soil invertebrates (mesofauna) of forest ecosystems. Candidate's biol. sci. thesis), Moscow: IPJeJe, 2014, 177 p.

Hirth J.R., Li G.D., Chan K.Y., Cullis B.R., Long-term effects of lime on earthworm abundance and biomass in an acidic soil on the south-western slopes of New South

Wales, Australia, Applied Soil Ecology, 2009, Vol. 43, pp. 106-114.

Hoeffner K., Monard C., Santonja M., Cluzeau D., Feeding behaviour of epi-anecic earthworm species and their impacts on soil microbial communities, *Soil Biology and Biochemistry,* 2018, Vol. 125, pp. 1-9.

Holdsworth A.R., Frelich L.E., Reich P.B., Leaf litter disappearance in earthworm-invaded northern hardwood forests: role of tree species and the chemistry and diversity of litter, *Ecosystems,* 2012, Vol. 15, No 6, pp. 913-926.

Huang W., Gonzalez G., Zou X., Earthworm abundance and functional group diversity regulate plant litter decay and soil organic carbon level: A global meta-analysis, *Applied Soil Ecology*, 2020, Vol. 150, pp. 1-15.

Klassifikacija i diagnostika pochv Rossii (Classification and diagnostics of Russian soils), Shishov L.L., Tonkonogov V.D., Lebedeva I.I., Gerasimova M.I. (Compl.), Smolensk: Ojkumena, 2004, 342 p.

Kozlovskaja L.S., Archegova I.B., Rakova H.N., Biohimicheskoe vozdejstvie pochvennyh bespozvonochnyh na rastitel'nye ostatki (Biochemical effects of soil invertebrates on plant debris), *Bolotnye biogeocenozy i ih izmenenija v rezul'tate antropogennogo vozdejstvija*, Leningrad: Nauka, 1983, pp. 24-26.

Kozlovskaja L.S., *Rol' pochvennyh bespozvonochnyh v transformacii organicheskogo veshhestva bolotnyh pochv* (The role of soil invertebrates in the transformation of organic matter of bog soils), Leningrad, 1976, 211 p.

Kuznecova A.I., Lukina N.V., Tihonova E.V., Gornov A.V., Gornova M.V., Smirnov V.E., Geras'kina A.P., Shevchenko N.E., Teben'kova D.N., Chumachenko S.I., Akkumulyaciya ugleroda v peschanyh i suglinistyh pochvah ravninnyh hvojno-shirokolistvennyh lesov v hode poslerubochnyh vosstanovitel'nyh sukcessij (Carbon stock in sandy and loamy soil of coniferous-deciduous forestsat the different stages of successions), *Pochvovedenie*, 2019, No 7, pp. 803-816.

Lavelle P., Martin A., Small-scale and large-scale effects of endogeic earthworms on soil organic matter dynamics in soils of the humid tropics, *Soil Biology and Biochemistry,* 1992, Vol. 24, No. 12, pp. 1491-1498.

Lavelle P., Pashanasi B., Charpentier F., Gilot C., Rossi J.-P., ...& Bernier N., Large-scale effects of earthworms on soil oranic matter and nutrient dynamics, Edwards C.A. (Ed.), *Earthworm ecology*, St. Lucie Press, 1998, pp.103-122.

Lee K.E., *Earthworms. Their ecology and relationships with soils and land use*, Academic Press, 1985, 411 p.

Lukina N.V., Tihonova E.V., Shevchenko N.E., Gornov A.V., Kuznecova A.I., … & Shanin V.N., *Akkumuljacija ugleroda v lesnyh pochvah i sukcessionnyj status lesov* (Carbon accumulation in forest soils and forest succession status), N.V. Lukina (Ed.), Moscow: KMK, 2018, 232 p.

Makeschin F., Earthworms (Lumbricidae: Oligochaeta): Important promoters of soil development and soil fertility, G. Benckiser (Ed.), *Fauna in soil ecosystems. Recycling processes, nutrient fluxes and agricultural production,* Florida: CRC Press, 1997, pp. 173-223.

McDaniel J.P., Stromberger M.E., Barbarick K.A., Cranshaw W., Survival of *Aporrectodea caliginosa* and its effects on nutrient availability in biosolids amended soil, *Applied soil ecology,* 2013, Vol. 71, pp. 1-6.

Mengel K., Turnover of organic nitrogen in soils and its availability to crops, *Plant and Soil*, 1996, Vol. 181, pp. 83-96.

Metodicheskie ukazanija po kolichestven-nomu opredeleniju obema pogloshhenija parnikovyh gazov (Guidelines for the quantification of greenhouse gas absorption), *Rasporjazhenie Minprirody Rossii 30.06.2017*, No 20-r, 108 p.

Moore J.-D., Ouimet R., Bohlen P.J., Effects of liming on survival and reproduction of two potentially invasive earthworm species in nothern forest Podzol, Soil Biology and Biochemistry, 2013, Vol. 64, pp. 174-180.

Nacional'nyj atlas pochv Rossijskoj Federacii (National Atlas of Soils of the Russian Federation), Shoba S.A., Aljabina I.O.,

Urusevskaja I.S., Chernova O.V., Moskow: Astrel', 2011, 632 p.

Novara A., Rühl J., La Mantia, T., Gristina L., La Bella, S., Tuttolomondo T., Litter contribution to soil organic carbon in the processes of agriculture abandon, *Solid Earth,* 2015, Vol. 6, No 2, pp. 425-432.

Parmelee R.W., Crossley Jr., Earthworm production and role in the nitrogen cycle of a no-tillage agroecosystem on the Georgia piedmont, *Pedobiologia,* 1988, Vol. 32, pp. 353-361.

Perel' T.S., *Rasprostranenie i zakonomernosti raspredelenija dozhdevyh chervej fauny SSSR* (Distribution and distribution patterns of earthworms of the fauna of the USSR), Moskow: Nauka, 1979, 272 p.

Pulleman M.M., Six J., Uyl A., Marinissen J.C.Y., Jongmans A.G., Earthworms and management affect organic matter incorporation and microaggregate formation in agricultural soils, *Appl. Soil Ecol.*, 2005, Vol. 29, pp. 1-15.

Sandor M., Schrader S., Earthworms affect mineralization of different organic amendments in a microcosm study, *Bulletin of University of Agricultural Sciences and Veterinary Medicine Cluj-Napoca. Agriculture,* 2007, Vol. 63, pp. 442-447.

Sariyildiz T., Effects of tree canopy on litter decomposition rates of *Abies nordmanniana*, *Picea orientalis* and *Pinus sylvestris*, *Scandinavian journal of forest research*, 2008, Vol. 23, No. 4, pp. 330-338.

Sariyildiz T., Küçük M., Litter mass loss rates in deciduous and coniferous trees in Artvin, northeast Turkey: Relationships with litter quality, microclimate, and soil characteristics, *Turkish journal of Agriculture and Forestry,* 2008, Vol. 32, No. 6, pp. 547-559.

Shevchenko N.E., Kuznecova A.I., Teben'kova D.N., Smirnov V.E., Geras'kina A.P., Gornov A.V., Tihonova E.V., Lukina N.V., Sukcessionnaya dinamika rastitel'nosti i zapasy pochvennogo ugleroda v hvojno-shirokolistvennyh lesah severo-zapadnogo Kavkaza (The succession dynamics of vegetation and carbon stocks in coniferous-deciduous forests of the north-western Caucasus), *Lesovedenie*, 2019, No 3, pp. 163-176.

Striganova B.R., Issledovanie roli mokric i dozhdevyh chervej v processah gumifikacii razlagajushhejsja drevesiny (Investigation of the role of woodlice and earthworms in the processes of humification of decaying wood), *Pochvovedenie*, 1968, №. 8, pp. 85-90.

Striganova B.R., Kozlovskaja L.S., Chernobrovkina N.P., Kudrjasheva I.V., Pishhevaja aktivnost' dozhdevyh chervej i soderzhanie aminokislot v temnoseroj lesnoj pochve (Alimentative activity of earthworms and content of aminoacids in the dark grey forest soil), *Pochvovedenie*, 1989, No 5, pp. 44-51.

Striganova B.R., *Pitanie pochvennyh saprofagov* (Nutrition of soil saprophages), Moskow: Nauka, 1980, 243 p.

Striganova B.R., Sukcessii zhivotnogo naselenija pochvy v processe pervichnogo pochvoobrazovanija (Successions of the animal population of the soil in the process of primary soil formation), *Rannjaja kolonizacija sushi*, Moskow: PIN RAN, 2012, pp. 177-195.

Suarez E.R., Fahey T.J., Yavitt J.B., Groffman P.M., Bohlen P.J., Patterns of litter disappearance in a northern hardwood forest invaded by exotic earthworms, *Ecological Applications,* 2006, Vol. 16, No 1, pp. 154-165.

Talashilkar S.C., Bhangarath P.P., Mehta V.B., Changes in chemical properties during composting of organic residues as influenced by earthworm activity, *Journal of the Indian Society of Soil Science*, 1999, Vol. 47, pp. 50-53.

Vsevolodova-Perel' T.S., *Dozhdevye chervi fauny Rossii. Kadastr i opredelitel'* (Earthworms of Russia. Cadastr and key-book.), Moskow: Nauka, 1997, 101 p.

Vsevolodova-Perel' T.S., Gryuntal' S.Yu., Kudryasheva I.V., Nadtochij S.E., Golovach S.I., Matveeva A.A., Osipov V.V., Karpachevskij L.O., Rastvorova O.G., *Struktura i funkcionirovanie pochvennogo naseleniya dubrav Srednerusskoj lesostepi* (The structure and functioning of the soil population of the

oak forests of the Central Russian forest-steppe). Moscow: Nauka, 1995, 152 p.

World Reference Base for Soil Resources, *International soil classification system for naming soils and creating legends for soil maps. World Soil Resources Reports*, IUSS Working Group. Rome: FAO, 2015, 203 p.

Zhukov A.V., Dozhdevye chervi kak komponent biogeocenoza i ih rol' v zooindikacii (Earthworms as a component of biogeocenosis and their role in zooindication), *Ґruntoznavstvo*, 2004, Vol. 5, No 1-2, pp. 44-57.

Zhukov A.V., Jekologicheskoe raznoobrazie zhivotnogo naselenija pochv pojmennyh biogeocenozov reki Samara (Ecological diversity of the animal population in the soils of floodplain biogeocenoses of the Samara River), *Visnik Dnipropetrovs'kogo universitetu. Biologija. Ekologija*, 2000, No 7. pp. 73-79.

Zhukovskaja E.A., Kodolova O.P., Pravduhina O.Ju., Varne A.Zh., Bolotecki j N.M., Issledovanie geneticheskogo raznoobrazija dozhdevogo chervja Lumbricus rubellus Hoff. (Oligochaeta, Lumbricidae) (Study of genetic diversity of earthworm *Lumbricus rubellus* Hoff. (Oligochaeta, Lumbricidae), *Izvestija Rossijskoj akademii nauk. Serija biologicheskaja*, 2005. No 5. pp. 625-627.

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