Protistology 7 (2), 71–78 (2012)

Protistology

Distribution of soil testate amoeba assemblages along catenas in the northern taiga zone (Karelia, Russia)

Andrey N. Tsyganov, Elena A. Embulaeva and Yuri Mazei

Department of Zoology and Ecology, Penza State Pedagogical University, Penza, Russia

Summary

Topography is one of the main factors, which regulate composition and functioning of terrestrial ecosystems. However, the relationships between topography and soil protozoa remain poorly understood. We studied the distribution of testate amoeba assemblages in soil biotopes located at various topographic positions along two topographical gradients (catenas) in a forest site in the north taiga zone (Karelia, Russia). The variation in testate amoeba assemblages was estimated using univariate assemblage characteristics (the abundance and species number) and the species composition. The results of our study show that the species number increased from the upper to the lower catenary positions. This indicates the more favourable environmental conditions for testate amoebae in wet and nutrient rich low-lying accumulative positions. The species composition of testate amoeba assemblages changed along the catenas depending on the position of biotopes. The effects of topography on the species compositions decrease at the lower positions so that assemblages there have more similar composition. Our results show the important role of topography in regulation of spatial patterns of soil protozoa and demonstrate that other environmental variables can modify effects of topography.

Key words: catena, north taiga, soil, testate amoebae, topography

Introduction

Understanding how topography influences the distribution and the characteristics of soil protozoan communities at the landscape level is important for a better management of terrestrial ecosystems and preservation of biodiversity. Soil protozoa represent a common and diverse component of soil ecosystems (Foissner, 1987). They play an important role in soil decomposer food webs as secondary and higher level consumers. By grazing on bacteria, they increase bacterial turnover rates and thereby the release of nutrients immobilised in bacterial tissue (Bardgett and Griffith, 1997; Coûteaux and Darbyshire, 1998; Bonkowski, 2004). These feeding activities result in a greater availability of nutrients for plant uptake. Soil protozoa are very sensitive to soil properties such as moisture, particle size composition, concentrations of organic matter, nutrients, etc. (Foissner, 1987). At the landscape level, all these soil properties are strongly regulated by topography which is one of the main soil-forming factors (Bockheim et al., 2005).

Therefore, topography can be an important factor of the spatial distribution of soil protozoa at the landscape level as well. However, the relationships between topography and community characteristics of soil protozoa remain poorly understood.

One of the most interesting groups of soil protozoa for ecological studies is testate amoebae. Testate amoebae are free-living protozoa which are characterised by the presence of an external shell, sometimes referred to as a test. Empty shells of testate amoebae remain intact after organism death so that testate amoebae can be identified to the species level and enumerated in samples by 'direct' microscope counting (Foissner, 1987). This helps to avoid the difficulties associated with labour-intensive cultivation techniques which are necessary for studies of many other groups of protozoa. Testate amoebae constitute a considerable part of soil biota in terms of biomass and biodiversity (Schönborn, 1992; Finlay, 2002; Schröter et al., 2003; Esteban et al., 2006). They prey on a wide range of organisms, including bacteria, protozoa, microalgae, fungi and micrometazoa (Gilbert et al., 2000; Wilkinson and Mitchell, 2010). Testate amoebae are very sensitive to variation in substrate moisture (Lousier, 1974a, 1974b; Mazei and Tsyganov, 2007; Sullivan and Booth, 2011), temperature (Tsyganov et al., 2011, 2012), vegetation (Ledeganck et al., 2003; Sutton and Wilkinson, 2007), etc. Thus, testate amoebae can be used as model organisms for ecological studies on protozoa.

Numerous studies on soil and ecosystem patterns at the landscape level has shown that catena concept is a useful tool for understanding the role of topography in regulation of those patterns (Klink, 2002 and references therein). The concept of catena was first developed in soil science by Milne (1935) who defined it as a sequence of soils developed from similar parent material under similar climatic conditions but whose characteristics differ because of variations in topography (i.e. relief) or, more specifically, slope and drainage conditions. Subsequently, the soil concept was applied for ecological studies so that "soil sequence" could be replaced by "biotope sequence". Normally, the upper limit of catenas is defined by eluvial soils, which receive mainly atmospheric precipitation and are subjected to material removal due to downward water flows. The lower catena limits represent alluvial sites which accumulate water and materials and can be influenced by ground waters. The ecological catena concept can help to study the relationships between topography and soil protozoa while keeping the influence of the other factors, such as climate and parent material, constant.

So far, the distribution of soil testate amoebae along catenas has been studied by Bobrov (1999) and Rakhleeva (2000). These studies have shown that testate amoeba assemblages are characterised by well-defined patterns in biotope sequences along catenas. It has been also shown that the variation in testate amoeba assemblages depends on catena type. The aim of this work is to study the distribution of soil testate amoeba assemblages in the most typical regional ecosystem types located at various topographic positions along catenas in the north taiga zone (Karelia, Russia). This work focuses on the univariate assemblage characteristics and the species composition of testate amoeba assemblages. We expected to observe (1) the increasing species number from eluvial to alluvial positions along catenas; (2) and changes in species composition of testate amoeba assemblages.

Material and methods

Study site

The study was performed in a taiga area (the Black River village; 66°31'17''N, 32°58'07''E) located on the shore of the Kandalaksha Gulf, the White Sea (Karelia, Russia). Typical catenas in the area are characterized by pine (*Pinus sylvestris*) forest on elevated parts, by spruce (*Picea obovata*) and birch (*Betula pendula*) forests in transitional zones and by flood-meadows (dominated by *Carex* spp.) in alluvial (accumulative) parts. For this study, we selected two catenas which had slightly different accumulative parts. The first catena had a flood meadow located in the floodplain of a small river (the Black River). The second catena had a flood meadow which turned into a salt marsh located in the Graysnaya Bay (the Gryasnaya Guba).

Sampling strategy

Soil samples for testate amoeba analysis were collected on the 17 of June, 2007. At each catenary position, we dug three holes (1×1 m square) to reveal the profile of the upper soil layers. The holes were located in different micro-biotopes (i.e. litter, *Pleurozium schreberi* moss and *Cladonia* spp. lichen in the pine forests; litter, mosses *Hylocomnium splendens* and *Sphagnum* spp. in the spruce forests; litter and *Sphagnum* spp. moss in birch forests; litter in the meadows) in order to cover the natural heterogeneity of the sites. Then we sampled the litter (or moss/lichen) layer (A_0) and the upper 2 cm of the underlying layer (A_1) from a side of the

holes. Samples of 5×5 cm were cut out with a soil knife and were kept in sealed plastic bags until the analysis. This sampling strategy resulted in a total of 24 samples.

Testate amoeba analysis

The samples were prepared for counting testate amoebae following a modified version of water based sieving procedure (Hendon and Charman, 1997). Five grams of the substrate from each sample were mixed with arbitrary amount of water and were left soaking for 24 hours. After that, the mixture was thoroughly shaken for 10 min for extraction of testate amoebae from soil particles. The suspension was passed through sieves with mesh openings of 0.5 – 1 mm in order to remove big particles which can cover testate amoebae during counting. The sieving residue was gently washed with water. The mixture was left for sedimentation for 24 hours. After that, the supernatant was carefully poured off. The sedimentation was repeated once again so that the volume of the concentrate was 10 ml. Two millilitres of the concentrate were placed in a Petri dish and were diluted with arbitrary amount of water in order to obtain concentrations and volume suitable for microscopy. The suspension was left to settle down for several minutes. Then, testate amoebae were identified and counted by direct counting at a magnification of ×160 using a dissection light microscope Olympus CX41RF (Olympus Corporation, Japan). Two subsamples were analysed. A minimum total of 150 shells were counted in each sample. The obtained counts were calculated to 1 g of absolutely dry substrate weight.

Data analysis

Changes in testate amoeba assemblages were estimated using univariate assemblage characteristics and the species composition. The following assemblage characteristics were calculated: (1) the total abundance of testate amoebae (ind. g^{-1} absolutely dry substrate weight); (2) the total species number per biotope. The variation in the species composition was analysed using the species abundance matrix. The matrix was subjected to Principal Component Analysis (PCA) which is a useful tool for visualisation and description of changes in species composition. In order to eliminate unwarranted effects of rare species on the results of the multivariate analysis we removed species, which were encountered in only one sample before the analysis. The final data set for the multivariate analysis contained 29 taxa (see Table 1). After that, the species data were Hellinger-transformed (function 'decostand' in the package 'vegan', Oksanen et al., 2012). The Hellinger transformation helps to avoid problems arising from Euclidian distance when the distance between two site sharing no species in common can be smaller than between two sites sharing common species (Legendre and Gallagher, 2001). The numerical calculations and statistical analyses were performed in the R language environment (R Core Team, 2012).

Results

General observations

The analysis of the samples revealed 42 testate amoeba taxa belonging to 16 genera (Table 1). Living individuals were observed for 13 taxa only. The testate amoeba assemblage was dominated by six taxa: *Nebela collaris* (20.1%), *Euglypha rotunda* (12.4%), *Trinema complanatum* (7.4%), *Trigonopyxis arcula* (6.1%), *Nebela militaris* (6.1%), and *Centropyxis aerophila* v. *sphagnicola* (5.3%). All these species were also characterised by relatively high occurrence (> 30% of all samples, see Table 1) and therefore constituted the core of the testate amoeba assemblages at the site. The assemblages were also characterised by a considerable number of testate amoeba taxa (20 taxa) with low occurrence (they were encountered in less than 10% of the samples).

Univariate assemblage characteristics

The patterns of the total species number per biotope differed between the catenas. The first catena was characterised by the gradually increasing total species number per biotope from the pine forest to the meadow, i.e. from the eluvial position to the accumulation zone (Fig. 1, A). In the second catena, the total species number per biotope increased from pine forest till birch forest (from 15 to 31 taxa) and then drastically dropped down to 11 taxa in the meadow (Fig. 1, A). The variation in the abundance of testate amoebae was similar to the patterns in the total species number per biotope along the second catena but had no clear patterns along the first catena (Fig. 1, B).

Assemblage composition of testate amoebae

The results of the PCA indicate that the species composition of the testate amoeba assemblages

Table 1. Occurrence and mean abundances (ind. g^{-1} substrate weight) of testate amoebae in two catenas in the northern taiga zone (Karelia, Russia). The taxa are sorted in the descending order of their occurrence. The occurrence was calculated as the percentage of the number of samples in which the taxon was encountered. Species abundances which are greater than 5% of the mean total abundance in a biotope are shown in bold. Empty cells denote null concentrations. Species codes used in the figures are also indicated. Species marked with an asterisk were excluded from the multivariate analysis.

Species names	Codes	Catena 1 (freshwater flood-meadow)				Catena 2 (salt marsh)			
		Pine forest	Spruce forest	Birch forest	Flood-meadow	Pine forest	Spruce forest	Birch forest	Flood-meadow
Common species (occurrence >50%)									
Euglypha rotunda	*Eug.rot*	36.5	21.4	**125.0**	**114.8**	14.4	**627.7**	**520.0**	**125.1**
Trinema complanatum	*Trn.com*	**107.2**	14.6	**151.3**	**96.7**	29.1	37.9	**425.7**	**75.7**
Nebela collaris	*Neb.col*	**215.2**	38.8	**262.2**	**722.7**	**139.2**	**456.8**	**521.9**	**204.5**
Centropyxis aerophila	*Cen.aer*	38.9	**78.9**	**63.3**	**87.1**	22.0	14.8	92.3	7.2
Centropyxis aerophila v. *sphagnicola*	*Cen.aes*	7.9		36.2	69.1	12.4	**211.0**	**149.2**	**184.0**
Cyclopixis kahli	*Cyc.kah*	57.9	40.5	42.7	34.5	12.6	25.3	7.1	
Common species (occurrence 10–50%)									
Phryganela acropodia	*Phr.acr*	**140.5**	32.6	41.6	**95.1**	7.1		35.3	**81.8**
Trigonopixis arcula	*Tri.acr*	**101.9**	**387.6**			31.8	**232.4**	25.4	
Euglypha laevis	*Eug.lae*	**166.7**		25.8	34.0		72.9	**206.4**	
Nebela militaris	*Neb.mil*	7.9				**198.2**	**215.4**	**192.3**	**161.7**
Centropyxis sylvatica	*Cen.syl*	**210.7**	**102.3**	32.2	17.0	5.3		7.1	
Plagiopixis declivis	*Pla.dec*	10.4	43.9	25.8	**106.3**			98.6	
Tracheleuglypha dentata	*Tra.den*			**51.7**	36.1		96.0	49.8	
Arcella intermedia	*Arc.int*			10.4	8.5		**353.9**		
Corythion dubium v. *terricola*	*Cor.dut*		**87.7**			35.6	21.6	7.1	
Arcella catinus	*Arc.cat*		**142.1**	31.4		**440.5**	44.4		
Arcella arenaria	*Arc.are*		**258.4**				55.9	18.3	
Cyclopyxis eurystoma	*Cycl.eur*				**166.1**	7.3			
Euglypha ciliata	*Eug.cil*			10.5				92.5	20.4
Assulina muscorum	*Ass.mus*	**62.3**			18.1	28.8			
Arcella vulgaris	*Arc.vul*	7.9	43.9		17.0			31.7	
Heleophera sylvatica	*Hel.syl*			10.4	18.1			73.3	
Rare species (occurrence <10%)									
Trinema lineare	*Trn.lin*				54.2			56.4	
Corythion dubium v. *orbicularis*	*Cor.duo*						14.8	85.5	
Padaungiella wailesi	*Pad.wai*			**51.7**				7.1	
Centropyxis platystoma	*Cen.plt*							36.6	20.4
Cyclopyxis arcelloides	*Cyc.arc*			20.8				35.3	
Trinema enchelys	*Trn.ech*							35.3	20.4
Centropyxis plagiostoma	*Cen.pla*				8.5			7.1	
Arcella artocrea v. *pseudocatinus**	*Arc.arp*						34.3		
*Argynnia (Nebela) dentistoma**	*Arg.den*					14.4			
*Difflugia oblonga**	*Dif.obl*						108.2		
Euglypha rotunda v. *obliqua**	*Eug.roo*								**61.3**
Euglypha ciliata f. *glabra**	*Eug.cig*							42.7	

Table 1. (Continuation).

Species names	Codes	Catena 1 (freshwater flood-meadow)				Catena 2 (salt marsh)			
		Pine forest	Spruce forest	Birch forest	Flood-meadow	Pine forest	Spruce forest	Birch forest	Flood-meadow
*Centropyxis elongata**	*Cen.elo*							21.4	
*Euglypha inaquelis**	*Eug.ina*							21.4	
*Centropyxis aculeata**	*Cen.acu*							18.3	
*Nebela tincta**	*Neb.tin*							18.3	
Arcella dentata v. *trapezica**	*Arc.det*						12.6		
*Euglypha denticulata**	*Eug.den*						12.6		
*Nebela parvula**	*Neb.par*							7.1	

varied in the biotopes along the catenas and that this variation was catena-specific (Fig 2, A). The fist principal component explained 35.4% of the total variation in the species composition. This component was associated with changes in the species composition in the biotopes along the catenas (Fig 2, A). In both catenas, the eluvial parts (pine forest and spruce forest) were characterised by different species composition of testate amoeba assemblages whereas the alluvial parts (birch forest and meadow) had similar species composition (Fig 2, A). Therefore, three types of testate amoeba assemblages can be distinguished along the catenas. The second principal component explained 23.4% of the total variation in the species composition of the testate amoeba assemblages. The component was related to the differences between the catenas showing that the changes in the species composition in the biotopes were specific for each catena.

The species composition of testate amoebae in the pine forest on the first catena was characterised by species with wide ecological preferences *Centropyxis sylvatica, Euglypha laevis* and *Phryganella acropodia*. The spruce biotope located below on the catena had a specific species composition and was dominated by moss-dwelling species *Trigonopyxis arcula, Arcella arenaria* and *Arcella catinus*. The typical species in the birch and meadow biotopes on the first catena were *Nebela collaris, Trinema complanatum, Plagiopyxis declivis*. The pine biotopes on the second catena were dominated by *Arcella catinus* which was replaced by *Arcella intermedia* and *Nebela militaris* in the spruce biotopes. The birch and meadow biotopes on the second catena were characterised by *Centropyxis aerophila* v. *sphagnicola, Euglypha rotunda* and *Nebela collaris*.

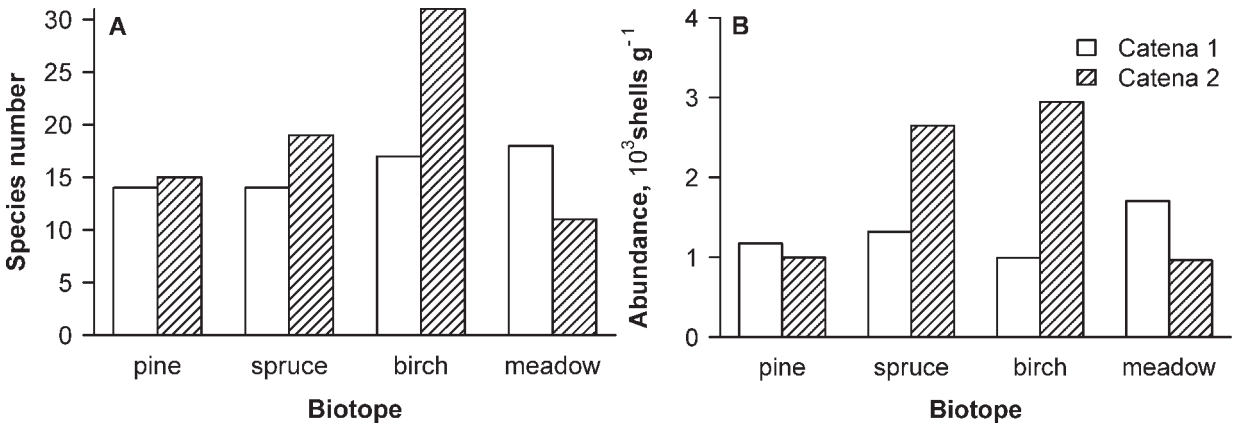

Fig. 1. Univariate characteristics (A – total abundance, B – the total species number) of soil testate amoeba assemblages in pine forest, spruce forest, birch forest and meadow biotopes located along two catenas in the north taiga zone.

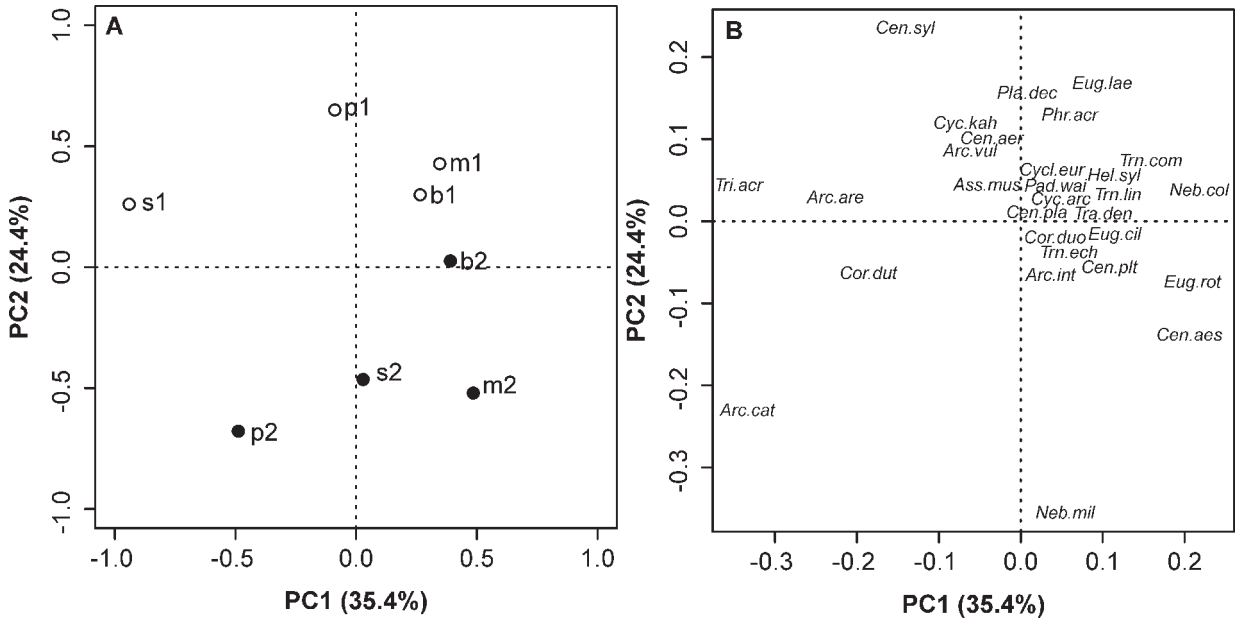

Fig. 2. Ordination diagrams illustrating the results of the analysis of principal components (PCA). A – Distance biplot of site scores (scaling 1). White circles represent the first catena; the black circles represent the second catena. The lowercase letters in the diagram indicate the investigated biotopes (p – pine forest, s – spruce forest, b – birch forest, m – meadow). B – Correlation biplot of species scores (scaling 2). The ordination was performed on the correlation matrix of the Hellinger-transformed abundances of the testate amoeba species which were encountered in more than one sample (see Table 1 for the species codes). The number in the parentheses is the proportion of the variation explained by each principal component.

Discussion

General observations

The testate amoeba assemblage at the site was characterised by relatively high taxonomic diversity and a considerable proportion of taxa with low occurrence. The assemblage was dominated by soil, moss-dwelling and ubiquitous species. The considerable proportion of moss-dwelling (*Nebela collaris, Nebela militaris, Trygonopyxis arculla*, etc.) species can be explained by the presence of reach moss vegetation in the biotopes on the studied catenas. The observed species were previously reported to be typical for soil and bog ecosystems in the studied region (Bobrov, 1999; Mazei and Bubnova, 2009; Mazei et al., 2009a, 2009b, 2010). Overall, the taxonomic composition of the testate amoeba assemblages at the site was typical for soil biotopes in the northern taiga zone suggesting that our findings can have bearing for other ecosystems beyond the studied location.

Univariate assemblage characteristics

The results show that the total species number of soil testate amoebae increases from eluvial to alluvial positions on catenas, however the patterns can be affected by local environmental conditions such as the negative influence of sea water. Previous studies demonstrated various types of the distribution of the species number along catenas (Rakhleeva, 1998, 2000; Bobrov, 1999). These patterns can be linear (either increasing or decreasing downwards), bell- or U-shaped. The downward increase in the species number which was observed in the present study can be explained by accumulation of water and nutrients which can sustain more diverse testate amoeba assemblages (Mitchell et al., 2000; Finlay and Fenchel, 2001). However, it is difficult to explain the absence of any edge effects at the transitional positions because ecotone communities of soil protozoa remain poorly understood. Therefore, the distribution of the species number of soil protozoa along catenas is a result of complex interaction of topography, local environmental conditions and edge effects.

Assemblage composition of testate amoebae

The results of our study indicate that the species composition of testate amoeba assemblages varies in the biotopes along the catenas and that this variation is catena-specific. The changes in the species composition were mostly related to the variation in

the proportions of moss- and *Sphagnum*-dwelling species which were replaced by soil species in some biotopes. However, it is difficult to distinguish any general trends in terms of species responses which could be directly linked to variation in environmental variables along catenas. Previous studies also reported that species composition of soil testate amoeba assemblages was related to topographical positions along catenas (Rakhleeva, 1998, 2000; Bobrov, 1999). The variation in the species composition was explained by changes in water regime and soil characteristics. In most cases, three types of testate amoebae assemblages which correspond to eluvial, transitional and alluvial catenary positions could be distinguished. Our results also demonstrate that the above mentioned positions on the studied catenas were characterised by specific species compositions of testate amoeba assemblages. Moreover, the accumulative positions and the transitional position right next to it were characterised by similar species composition that could be explained by influence of floods and ground waters.

Conclusions

Overall, our results demonstrate the total species number and the species composition of soil testate amoeba assemblages vary along catenas located in the northern taiga zone. The total species number decreases from the upper to the lower catenary positions as a result of more favourable environmental conditions for testate amoeba in wet and nutrient rich low-lying accumulative sites. However, topography-independent variation in environmental conditions, for example sea water influence, can considerably affect the patterns. Topographical position also influences species composition of testate amoeba assemblages and the effects of topography decrease at the lower positions so that assemblages there have more similar composition. Our results support the hypothesis about the important role of topography in regulation of spatial patterns of soil protozoa and show that other environmental variables can modify effects of topography.

Acknowledgements

We are thankful to Igor V. Burkovsky for the assistance and accommodation during the field campaign. This work was supported by the Russian Foundation for Basic Research (grant 10-04-00496-a) and grant of the President of Russian Federation (grant MD-4426.2012.4).

References

Bardgett R.D. and Griffith B. 1997. Ecology and biology of soil protozoa, nematodes and mircroarthropods. In: Modern Soil Microbiology (Eds: Elasas J.D. van, Wellington E. and Trevors J.T.). Marcell Dekker, New York, pp. 129-163.

Bobrov A.A. 1999. Ecological and geographical regularities in distribution and structure of testate amoebae (Protozoa: Testacea) communities. Moscow State Universty, Moscow (in Russian).

Bockheim J.G., Gennadiyev A.N., Hammer R.D. and Tandarich J.P. 2005. Historical development of key concepts in pedology. Geoderma. 124, 23-36.

Bonkowski M. 2004. Protozoa and plant growth: the microbial loop in soil revisited. New Phytol. 162, 617-631.

Coûteaux M.-M. and Darbyshire J.F. 1998. Functional diversity amongst soil protozoa. Appl. Soil Ecol. 10, 229-237.

Esteban G.F., Clarke K.J., Olmo J.L. and Finlay B.J. 2006. Soil protozoa – An intensive study of population dynamics and community structure in an upland grassland. Appl. Soil Ecol. 33, 137-151.

Finlay B.J. 2002. Global dispersal of free-living microbial eukaryote species. Science. 296, 1061-1063.

Finlay B.J. and Fenchel T. 2001. Protozoan community structure in a fractal soil environment. Protist. 152, 203-218.

Foissner W. 1987. Soil protozoa: fundamental problems, ecological significance, adaptations in Ciliates and Testateceans, bioindicators and guide to the literature. Prog. Protistol. 2, 69-212.

Gilbert D., Amblard C., Bourdier G., Francez A.-J. and Mitchell E.A.D. 2000. Le régime alimentaire des thécamoebiens. L'Année Biol. 39, 57-68.

Hendon D. and Charman D.J. 1997. The preparation of testate amoebae (Protozoa: Rhizopoda) samples from peat. Holocene. 7, 199-205.

Klink H.J. 2002. The Catena principle. In: Development and perspectives of landscape ecology (Eds: Bastian O. and Steinhardt U.). Kluwer Academic Publisher, Boston, pp. 93-100.

Ledeganck P., Nijs I. and Beyens L. 2003. Plant functional group diversity promotes soil protist diversity. Protist. 154, 239-249.

Legendre P. and Gallagher E.D. 2001. Ecologically meaningful transformations for ordination of species data. Oecologia. 129, 271-280.

Lousier J.D. 1974a. Response of soil Testacea to soil moisture fluctuations. Soil Biol. Biochem. 6, 235-239.

Lousier J.D. 1974b. Effects of experimental soil moisture fluctuations on turnover rates of Testacea. Soil Biol. Biochem. 6, 19-26.

Mazei Y.A. and Bubnova O.A. 2009. Species composition and community structure of testate amoebae in northern taiga *Carex-Sphagnum* bog (Karelia, Russia). Bull. Moscow Soc. Naturalists. Ser. Biol. 114, 15-23 (in Russian with English summary).

Mazei Y.A., Bubnova O.A. and Chernyshov V.A. 2009a. Testate amoebae community structure in *Sphagnum* quagmire in northern taiga bog (Karelia, Russia). Povolzhskiy Journal of Ecology. 2, 115-124 (in Russian with English summary).

Mazei Y.A., Bubnova O.A., Tsyganov A.N. and Chernyshov V.A. 2010. Testate amoebae community structure in ridge-lake wetland in northern taiga (Karelia, Russia). Izvestia Samarskogo Nauchnogo Tsentra RAS. 12, 99-102 (in Russian with English summary).

Mazei Y.A. and Tsyganov A.N. 2007. Species composition, spatial distribution and seasonal dynamics of testate amoebae community in a *Sphagnum* bog (Middle Volga region, Russia). Protistology. 5, 156-206.

Mazei Y.A., Tsyganov A.N. and Bubnova O.A. 2009b. The species composition and community structure of testate amoebae in *Sphagnum* bogs of northern Karelia (the White Sea Lowland). Zool. Zh. 88, 771-782.

Milne G. 1935. Some suggested units of classification and mapping particularly for East African soils. Soil Res. 4, 183-198.

Mitchell E.A.D., Buttler A., Grosvernier P., Rydin H., Albinsson C., Greenup A.L., Heijmans M., Hoosbeek M.R. and Saarinen T. 2000. Relationships among testate amoebae (Protozoa), vegetation and water chemistry in five *Sphagnum*-dominated peatlands in Europe. New Phytol. 145, 95-106.

Oksanen J., Blanchet F.G., Kindt R., Legendre P., Minchin P.R., O'Hara R.B., Simpson G.L., Solymos P., Stevens M.H.H., Wagner H. 2012. Vegan: Community ecology package. R package version 2.0-4. http://CRAN.R-project.org/package=vegan.

R Core Team. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.r-project.org/.

Rakhleeva A.A. 1998. Changes in structure and diversity of complexes of soil Testaceans (Protozoa) over mesorelief elements in the southern meshchera. Izv. Akad. Nauk Ser. Biol. 6, 725-731 (in Russian with English summary).

Rakhleeva A.A. 2000. Spatial distribution of testate amoebae (Testacea, Protozoa) in plain landscapes (South Meshchera). Moscow State Universty, Moscow (in Russian).

Schröter D., Wolters V. and Ruiter P.C. De 2003. C and N mineralisation in the decomposer food webs of a European forest transect. Oikos. 102, 294-308.

Schönborn W. 1992. The role of protozoan communities in fresh-water and soil ecosystems. Acta Protozool. 31, 11-18.

Sullivan M.E. and Booth R.K. 2011. The potential influence of short-term environmental variability on the composition of testate amoeba communities in *Sphagnum* peatlands. Microb. Ecol. 62, 80-93.

Sutton C.A. and Wilkinson D.M. 2007. The effects of Rhododendron on testate amoebae communities in woodland soils in north west England. Acta Protozool. 46, 333-338.

Tsyganov A.N., Aerts R., Nijs I., Cornelissen J.H.C. and Beyens L. 2012. *Sphagnum*-dwelling testate amoebae in subarctic bogs are more sensitive to soil warming in the growing season than in winter: the results of eight-year field climate manipulations. Protist. 163, 400-414.

Tsyganov A.N., Nijs I. and Beyens L. 2011. Does climate warming stimulate or inhibit soil protist communities? A test on testate amoebae in high-arctic tundra with Free-Air Temperature Increase. Protist. 162, 237-248.

Wilkinson D.M. and Mitchell E.A.D. 2010. Testate amoebae and nutrient cycling with particular reference to soils. Geomicrobiol. J. 27, 520-533.

Address for correspondence: Andrey N. Tsyganov. Department of Zoology and Ecology, Penza State Pedagogical University, Lermontov str. 37, 440026, Penza, Russia; e-mail: *andrey.tsyganov@bk.ru*