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RESEARCH ARTICLE

Continental-Scale α- and β-Diversity Patterns of Terrestrial Eukaryotic Microbes: Effect of Climate and Microhabitat on Testate Amoeba Assemblages in Eurasian Peatlands

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ABSTRACT

Aim: The role of environmental factors that shape the large-scale distribution of eukaryotic microbes remains understudied. We aimed to disentangle the impacts of latitudinal and longitudinal gradients on the distribution of *Sphagnum*-dwelling testate amoebae in mires and to understand the influence of environmental factors related to both local habitats (hummock—lawn—hollows) and regional climates.

Location: A range from temperate to subarctic and from the European part to the Far East of Russia (51°–70°N, 32°–158°E).

Taxon: Testate amoeba (Arcellinida, Euglyphida, and Amphitremida).

Methods: We analysed the testate amoeba (TA) composition and abundance data from 816 samples collected in 75 peatlands. Linear mixed-effects models and redundancy analysis were applied to determine the likely environmental drivers of TA α- and β-diversity.

Results: We identified a significant reversed latitudinal gradient in α-diversity which negatively correlated with the mean annual temperature. This gradient is microhabitat-specific, being prominent in lawn and hollow microhabitats, but not in hummocks. Longitude, which corresponds mainly to a gradient of precipitation seasonality, was a significant predictor of TA β-diversity, especially in hollows.

Main Conclusions: Our findings identify climatic factors (e.g., mean annual temperature and precipitation seasonality) as likely shaping the continental-scale TA α- and β-diversity patterns, emphasising the microhabitat-specific nature of these relationships. The absence of pattern in hummocks is interpreted as evidence for a predominant microhabitat stress (i.e., low moisture and pH) in this habitat.

1 | Introduction

Soil environment is highly heterogeneous, varying significantly from local to global scales and influenced by microenvironmental conditions over short periods (e.g., precipitation) to seasonal or longer time frames. This heterogeneity explains the very high biodiversity of soils (Andersen, Chapman, and Artz 2013; Anthony, Bender, and van der Heijden 2023).

Soil microbiota plays a vital role in maintaining soil health and ecosystem functioning by regulating the decomposition of organic matter, cycling nutrients, and contributing to the global carbon cycle (Garbeva, Van Veen, and Van Elsas 2004; Geisen et al. 2018). The diversity of soil microorganisms is particularly important because it underpins these functions, enhancing ecosystem stability, resilience to disturbances, and the efficiency of biogeochemical processes. For instance, diverse microbial communities are better equipped to adapt to environmental changes and maintain critical functions such as nutrient availability and carbon sequestration. Therefore, understanding soil microbial diversity is essential for developing effective ecosystem management and climate change mitigation strategies (Singh et al. 2010; Jansson and Hofmockel 2020).

One of the most important aspects of microbial assemblages in soils is their spatial distribution across different habitats and geographical regions (Barberán et al. 2014). Considering the magnitude of ongoing global change, it is of high importance to determine how climate factors affect the pattern of species diversity for soil protist communities. However, the patterns of their species diversity along latitudinal or longitudinal gradient remain poorly investigated (Hortal et al. 2015; Singer et al. 2019). Latitude and longitude primarily determine climate factors (e.g., temperature and precipitation), which in turn are key drivers for shaping biological communities. The latitudinal diversity gradient is one of the best-documented (and significant) biogeographical patterns of biodiversity distribution on Earth, characterised by a gradual decrease in species richness with increasing latitude. This pattern is well-studied for macroscopic organisms (Willig, Kaufman, and Stevens 2003; Roll et al. 2017; Lawrence and Fraser 2020). However, the distribution patterns of small organisms may differ significantly from larger organisms (Hillebrand 2004; Azovsky and Mazei 2013; Azovsky, Tikhonenkov, and Mazei 2016; Azovsky et al. 2020). These studies found the greater species richness at high latitudes for small size organisms (e.g., ants, fungi, and parasites), which driven by climate factors (e.g., mean temperature and precipitation) (Vasconcelos et al. 2018; Větrovský et al. 2019; Johnson and Haas 2021). Moreover, some studies indicated the bimodal relationship between species richness and mean temperature for ectomycorrhizal fungi, with separate cold- and hot-diversity optima (Steidinger et al. 2020). Apart from this, there is evidence that mean annual temperature has opposite impacts on the rare and abundant taxa in bacterial communities (Hou et al. 2020).

Besides studies on patterns of α-diversity (species diversity within a single community or habitat), numerous studies have indicated that β-diversity (the variation in species composition between communities or habitats) exhibits a negative correlation with latitude (Qian and Ricklefs 2007; Qian 2008; Soininen, Heino, and Wang 2018; Cao et al. 2021). However, Alahuhta et al. (2017) found that regions at higher latitudes had greater β-diversity. Furthermore, some studies did not identify relevant patterns along the latitudinal gradient (Enkhtur et al. 2021; Mruzek et al. 2022). The main driving factors for β-diversity are environmental factors (e.g., pH and temperature). All these investigations primarily focus on bacteria, mammals, and vascular plants, with research on soil microbes still being relatively scarce, therefore, the global distribution pattern of β-diversity for soil microbes remains unclear.

Currently, the biogeographic studies for soil microorganisms are still insufficient. For instance, some investigations have focused on specific regions or habitats, resulting in potential biases and incomplete knowledge regarding the true diversity and distribution of microbes (Van Elsas et al. 2012; Větrovský et al. 2019; Hou et al. 2020). To gain a more holistic understanding of their biogeography, it is essential to conduct studies that encompass a broader range of geographic locations, habitats, and taxa. Another limitation is that we still know little of the mechanisms that sustain the diversity of microorganisms (Chu et al. 2020), which is critical in the prediction of ecosystem responses to environmental change.

Peatlands play a critical role in carbon sequestration and biodiversity conservation, serving as significant global carbon sinks and unique habitats for diverse organisms (Joosten, Tapio-Biström, and Tol 2012; Roucoux et al. 2017). They also provide ideal model systems for ecological studies on the patterns and drivers of diversity and biogeography at the continental scale due to their widespread distribution and consistent environmental characteristics across wide geographical gradients (Booth and Zygmunt 2005; Schneider, Kutzbach, and Wilmking 2012). Peatlands encompass diverse types (including bogs, fens, and transitional mires), each characterised by distinct hydrological regime, nutrient availability, and vegetation type. Within these systems, microhabitats such as hummocks, lawns, and hollows create fine-scale environmental heterogeneity, which significantly influences the species diversity of microorganisms. These microhabitats vary in water table depth, pH, and organic matter content, creating gradients that support diverse ecological niches. For instance, hummocks, being elevated and relatively dry, often host drought-tolerant species, whereas hollows, which are wetter and nutrient-rich, favour hydrophilic and nutrient-demanding organisms (Eve, Pensa, and Portsmuth 2011). This micro-scale variation promotes niche partitioning, reduces competition, and enhances community complexity, contributing significantly to the overall biodiversity of peatland systems. Microorganisms are integral to peatland functioning, as they drive key processes such as organic matter decomposition, nutrient cycling, and carbon dynamics. These microbial communities directly influence peatland ecosystem stability, resilience, and capacity for long-term carbon storage. Despite their importance, large-scale patterns of microbial biodiversity and biogeography in peatlands remain poorly understood, limiting our ability to predict their responses to environmental change (Burdman et al. 2021). Testate amoebae are abundant and diverse microorganisms in peatlands where they play key roles as microbial predators as well as primary producers (for mixotrophic species) (Jassey et al. 2013, 2015). However, they are mostly studied as ecological indicators, of current and past environmental conditions, especially water table depth (Amesbury et al. 2018; Swindles et al. 2019). Moreover, testate amoebae contribute to nutrient cycling and organic matter decomposition, influencing overall ecosystem dynamics (Wilkinson and Mitchell 2010; Qin et al. 2022).

The primary objective of our study is to characterise the macroscale patterns of *Sphagnum* peatland testate amoeba diversity across microhabitats (hummock, lawn, and hollow) at a continental scale (in relation to climate). Using a unique compiled data set covering microhabitat gradients as well as a broad

geographical area, we assessed which environmental variables best explain diversity patterns and whether these relationships varied among microhabitats.

2 | Materials and Methods

2.1 | Study Area

We compiled testate amoeba species abundance data of *Sphagnum*-dwelling testate amoeba communities collected in 75 peatland ecosystems across Russia (Figure 1), including the European part, Western and Central Siberia, and Kamchatka. The overall spatial coverage of the data set ranges from 51° to 70°N and from 32° to 158°E. The studied sites are generally located in the main area of peatland distribution, that is, the boreal forest and temperate broadleaf and mixed forests biomes, including several locations in tundra (Dinerstein et al. 2017). The samples were collected between 2003 and 2020 in several types of peatlands including fens, bogs, blanket bogs, transitional mires, and aapas. Some of those data were previously used for the studies on local communities of testate amoebae (Ivanovskii et al. 2023; Mazei, Tsyganov et al. 2017; Mazei and Bubnova 2007; Mazei, Tsyganov, and Bubnova 2007a; Mazei, Tsyganov, and Bubnova 2007b; Mazei, Tsyganov, and Bubnova 2009; Payne et al. 2021; Saldaev et al. 2023; Saldaeva et al. 2024; Tsyganov et al. 2015; Tsyganov et al. 2017). The study area is characterised by diverse climatic conditions and vegetation with the mean annual temperature of −13°C to +5°C and the mean annual precipitation between 396 and 941 mm year^{-1} (1970–2000, https://www.worldclim.org). The minimal temperature of the coldest month (January) varies from −41.7°C to −8.9°C and the maximum temperature of warmest month (July) from +11.7°C to +26.1°C. The potential evapotranspiration ranges from 396 to 991 mm/year.

2.2 | Sampling and Testate Amoeba Analysis

Samples were collected in a summer season from June to August, aiming to cover the entire diversity of microhabitats for testate amoebae within each site, that is, hummocks, lawns, and hollows. These microhabitats form a microtopographic gradient in peatland ecosystems (Rydin, Jeglum, and Bennett 2013) and are characterised by various vegetation types and surface wetness regimes that greatly determine the structure of testate amoeba communities. The microhabitats were defined following Rydin, Jeglum, and Bennett (2013) with modifications. Hummocks are raised 25–50 cm above the lowest level, characterised by dwarf shrubs and are generally the driest microhabitats. The lawns are 5–20 cm above water table mostly and generally represent flat and firm surfaces of vegetation dominated by *Cyperaceae* and a diverse moss cover. The hollows are the wettest microhabitats with a water table depth ranging from −5 to 5 cm. They are characterised by the predominance of bryophytes and a sparse cover of cyperaceous plants. The samples of an approximate volume of 10 cm^3 were extracted from the moss cover with scissors. The sampling depth varied from 6 to 18 cm depending on the aims of the original studies and sample substrates. When moss layers were sampled separately the data were merged per sampling location.

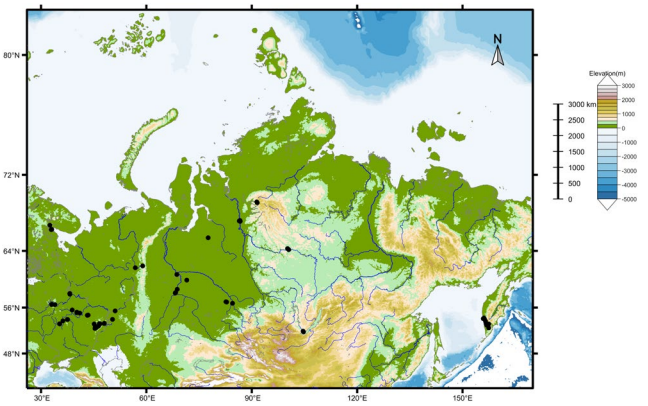

FIGURE 1 | Map of the study area with the black points marking the location of the studied peatlands. The full list of sites and summary characteristics are given in Table S1.

The samples of appropriate size (Mazei, Tsyganov et al. 2017) were prepared for testate amoeba analysis following the water-based technique (Mazei, Blinokhvatova, and Embulaeva 2011) which includes wet sieving and concentrating the shells by sedimentation. Testate amoebae were identified and counted under light microscopy at a magnification of 200× and 400×. The species identification of testate amoebae was performed following Mazei and Tsyganov (2006) up to the highest possible taxonomic resolution (Mitchell et al. 2014). In total, 816 samples were included in the database with 296 samples collected in hummocks, 314 in lawns, and 206 in hollows (Table S1).

2.3 | Climate Characteristics

To explain the variation in species diversity and structure of testate amoeba communities along the latitude and longitude, we considered the climate characteristics extracted from the WorldClim (version 2.0) database for 1970–2000 (Fick and Hijmans 2017; https://www.worldclim.org) with the spatial resolution of 10′. We used the 19 standard WorldClim bioclimatic factors (Table S2). We also considered potential evapotranspiration obtained from the Global Aridity Index and Potential Evapotranspiration (ET0) Database (version 3.0, the spatial resolution is 30″, 1970–2000 period) (Zomer, Xu, and Trabucco 2022). Based on this data, we also calculated the Marsz Oceanity Index (Andrade and Corte-Real 2017) and the Conrad-Pollak Continentality Index (Andrade and Corte-Real 2017).

2.4 | Community Structure Metrics

We considered several species diversity metrics including α-diversity, β-diversity, and evenness. The α-diversity at the sample level was estimated using species richness (S) and exponential Shannon Diversity Index (D_1) which was calculated as $D_1 = e^H = e^{(-\sum p_i \bullet \log p_i)}$, where H is the regular Shannon diversity and p_i is the relative abundance of species i. S and D_1 indices correspond to effective diversities of zeroth and first order, respectively (Hill 1973; Chao, Chiu, and Hsieh 2012). Evenness was quantified as Pielou index $E = H / lnS$.

The β-diversity among samples within microhabitats was calculated using $1 - C_{0N}$ and $1 - C_{1N}$ (Chao, Chiu, and Hsieh 2012), for zeroth and first order, respectively:

$$C_{0N} = \frac{\frac{S}{\overline{S}} - N}{1 - N} = 1 - \frac{{}^{0}D_{\beta} - 1}{N - 1}$$

$$C_{1N} = 1 - \frac{H_{\gamma} - H_{\alpha}}{\log N}$$

where N is the number of samples and 0, 1 is the order of diversity, S indicates the total number of species in the combined samples inside microhabitat, and $\overline{S}$ shows the mean number of species per sample. H_{α} is the average Shannon diversity over samples, and H_{γ} is the Shannon diversity in the pooled sample representing microhabitat. Zeroth-order β-diversity is derived from the Sørenson index, emphasising species presence/absence and turnover rates. In contrast, first-order β-diversity is based on the Horn homogeneity measure, which accounts for species abundance, making it sensitive to the commonness or rarity of species. These indices were chosen because they are normalised and suitable for comparing β-diversity in communities with different numbers of samples.

2.5 | Statistical Analyses

The available numerical environmental variables which were considered as potential predictors were checked for collinearity using variance inflation factor (VIF). Only those with VIF < 10 were retained in further analyses and models together with the microhabitat type as fixed effect factors. To explore the relationships between the community diversity metrics and environmental factors, we applied linear mixed-effects models with the peatland ID included as a random factor. For each diversity metric, we conducted three types of analyses. First, we analysed the effect of microhabitat considering also post hoc comparisons among microhabitats. Then, we modelled relations with the environmental predictors separately. Finally, we constructed models with multiple predictors. Models with quantitative environmental factors included microhabitat type and interaction terms of environmental predictors with microhabitat. For single-predictor analysis, we considered the predictor effect either separately for the three microhabitats (when the interaction between predictor and microhabitat was significant), or without differentiation by microhabitat (when the interaction was insignificant). When the interaction was significant, we also tested hypotheses about the difference of slope coefficients from zero, and conducted multiple comparisons of slope coefficients among microhabitats. For multiple-predictor analyses, we constructed parsimonious models using a stepwise backward selection procedure. For all models, we report a marginal coefficient of determination, which represents the variance explained by the fixed factors. Mixed-model analyses were performed in R (R Core Team 2021) using packages 'lmerTest' (Kuznetsova, Brockhoff, and Christensen 2017) and 'MuMIn' (Barton 2023); function glht() in 'multcomp' package (Hothorn, Bretz, and Westfall 2008) was applied for post hoc comparisons of metric values among microhabitats; function emtrends() in 'emmeans' package (Lenth 2023) was applied to implement post hoc comparisons of slopes among microhabitats.

The relationship between environmental factors and community structure was analysed using redundancy analysis (RDA) based on Hellinger-transformed relative abundance data (Legendre and Gallagher 2001). As for analyses of diversity metrics, several models were produced. First, we analysed the effect of microhabitat on community structure with a partial RDA model to control for site effects. This model was produced with sample-level data. Due to the need for control of the random effect of peatland in RDA models with environmental predictors, these models were produced based on data aggregated at the level of microhabitat ($n = 183$). We performed RDAs for each environmental predictor separately and for five climatic predictors and their interaction with microhabitats. Finally, to address the differences among microhabitats, the analysis was performed separately for hummocks ($n = 67$), lawns ($n = 66$), and hollows ($n = 50$). In the latter case, we constructed a parsimonious model by a stepwise backward selection procedure. RDAs were performed in R using package 'vegan' (Oksanen et al. 2013).

3 | Results

3.1 | General Characteristics of Climatic Patterns

The latitudinal trend is associated with a northward gradual decline in annual mean temperature and annual precipitation (Figure S1a,c). The effects of longitude have more complicated patterns so that mean annual temperature and total annual precipitation progressively decrease between 40° and 120°E, reflecting the increasing continentality of the climate, and then they sharply increased beyond 120° E due to maritime climate at Kamchatka peninsula (Figure S1b,d). According to VIF values (Table S2), most of the climatic factors were highly collinear to each other so that only five factors with VIF < 10 (annual mean temperature, isothermality, temperature seasonality, annual precipitation, and precipitation seasonality) were retained as potential predictors in further analyses (Table 1).

3.2 | Effects of Microhabitat on Taxonomic Diversity of Testate Amoeba Assemblages

A total of 240 taxa of testate amoeba were identified: 176 in hummocks, 197 in lawns, and 200 in hollows (Figure S2). Species richness and the exponential Shannon index significantly differed among the three microhabitats increasing from hummocks to hollows (Figure 2a,b), whereas evenness was significantly greater in hollows as compared to hummocks and lawns (Figure 2c). In contrast, β-diversity was the lowest in lawns, where it is significantly lower as compared to hollows (Figure 2d,e).

3.3 | Effects of Climatic Factors on Diversity of Testate Amoeba Assemblages

Species richness of testate amoeba assemblages increased northwards (Table 2, Figure 3a) but the effect was

TABLE 1 | Description of independent variables included in the analysis as predictors, variance inflation factor (VIF) and ranges of values.

Variable	Unit	Description	VIF	Range
Latitude	°N	—	—	51–70
Longitude	°E	—	—	32–158
Annual mean temperature	°C	The annual mean temperature.	3.12	–13-5
Isothermality	Per cent	It quantifies how large the day-to-night temperatures oscillate relative to the summer-to-winter (annual) oscillations.	2.96	16–24
Temperature seasonality	°C	The amount of temperature variation over a given year (or averaged years) based on the standard deviation (variation) of monthly temperature averages.	5.55	75–185
Annual precipitation	Mm	The sum of all total monthly precipitation values.	2.91	396–941
Precipitation seasonality	Per cent	A measure of the variation in monthly precipitation totals over the course of the year.	1.97	20–79

microhabitat-specific being the most pronounced in hollows and lawns and absent in hummocks. The relationship between longitude and species richness was non-significant (although the overall model was significant, the only significant term was the interaction with the microhabitat type but none of the slopes differed from zero). Species richness was negatively correlated to mean annual temperature and annual precipitation (Table 2, Figure 3b,c). The correlation of TA diversity and mean annual temperature was microhabitat-specific being highest in hollows and insignificant in hummocks (Table 2). Among all significant predictors, mean annual temperature provided the highest predictive power ($R^2 = 0.179$). The fixed effects in the parsimonious multiple-predictor model which included only mean annual temperature and temperature seasonality (Table 2) explained 18.4% of species richness variance. Thus, mean annual temperature was the best predictor of testate amoeba species richness.

The Shannon index D_1 varied both latitudinally and longitudinally. As for species richness, the correlation between D_1 and latitude varied among microhabitats, increasing with latitude in hollows but not in hummocks (Table 2, Figure S3a). By contrast, the D_1 index increased eastwards, significantly so only for lawns. Among the climatic factors only mean annual temperature was significant in single-predictor models (Figure S3c), this was insignificant for hummocks (Table 3). The fixed effects in the parsimonious multiple-predictor model which included mean temperature and temperature seasonality (Table 2) explained 10.2% of variance for the D_1 index.

Pielou evenness E was positively correlated to longitude, and significantly so for lawns but not for hummocks and hollows (Table 2, Figure 4a). Besides, E was negatively correlated to temperature seasonality and positively correlated to annual precipitation (Figure 4b,c). The parsimonious model included only annual precipitation, so its performance corresponds to single-predictor model.

In contrast to the α-diversity metrics and evenness, the analysis of β-diversity revealed far fewer significant correlations. Zeroth-order β-diversity $1 - C_{0N}$ positively depended on precipitation seasonality, this effect being significant only for hollows (Table 2, Figure 5b). However, the parsimonious multiple-predictor model did not include precipitation seasonality but isothermality and temperature seasonality. Nevertheless, first-order β-diversity $1 - C_{1N}$ positively depended on longitude only for hollows (Table 2, Figure S4c). Both models had a significant interaction term and there was contrast between slopes for hummocks and hollows (the effect being negative for hummocks and positive for hollows). All climatic factors were eliminated from the parsimonious model for $1 - C_{1N}$ (Table 2).

3.4 | Species Structure of Testate Amoeba Assemblages

In the RDAs, the microhabitat and climatic variables and their interaction terms significantly explained the community composition of testate amoebae ($p < 0.001$, Table 3). Although the proportion of the explained variance was low in the models with single predictors (4.2%–6.5%), models with a set of climate predictors explained a greater proportion of the variability (9.1%–13.1%).

To consider the potential differences among microhabitats (due to the significant interaction with the climate variables, Table 3), we also performed separate RDAs with climatic predictors separately for hummocks, lawns, and hollows (Figure 6). In all microhabitats, the variation in the community species structure along the first RDA axis was related to precipitation seasonality which was considerably correlated with temperature seasonality in lawns and hollows. In all biotopes, these variables were positively related to a greater proportion of the small-size eurybiotic taxon *Trinema lineare*, which might be considered as *r*-strategist (species with fast rate of resource acquisition and fast reproduction) taking an advantage of unstable environmental conditions in various types of microhabitats. This species was associated with another *r*-strategist, *Euglypha laevis*, in hummocks and lawns, whereas in hollows, it was observed together with *Trinema enchelys* and *Centropyxis aerophila*.

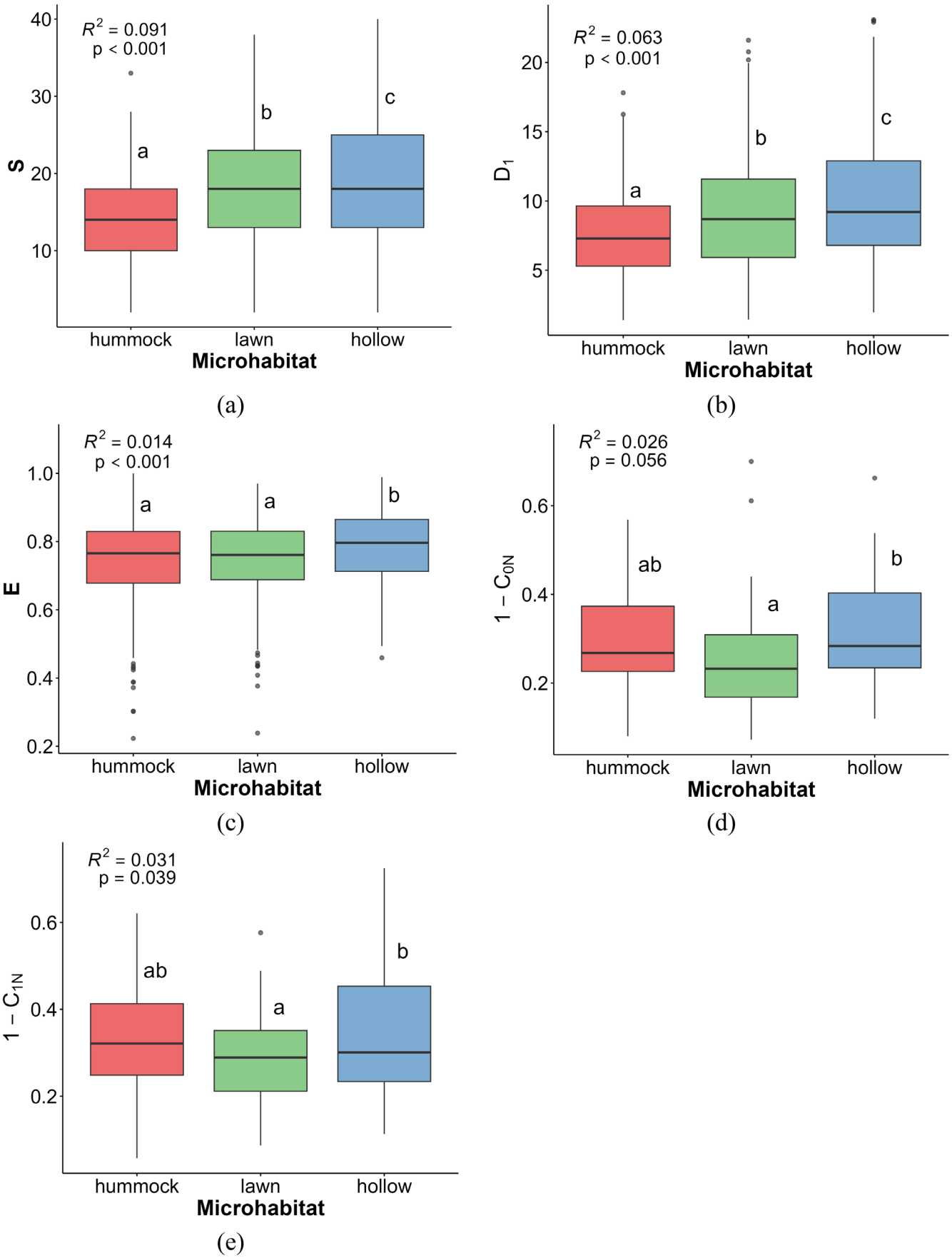

FIGURE 2 | Diversity metrics (S – species richness per sample, D_1—exponential Shannon diversity index, E—Pielou evenness, $1 - C_{0N}$ and $1 - C_{1N}$: β-diversity) of testate amoeba communities in three microhabitat types across Russia. The R^2 values are based on linear mixed-effects models (LMMs). Letters mark the significance of the pairwise post hoc comparisons among microhabitats ($p < 0.05$).

TABLE 2 | Single- and multiple-predictor linear mixed-effects models (LMMs) testing the effects of spatial and climatic variables on the community diversity metrics of *Sphagnum*-dwelling testate amoebae along microtopographical gradient in peatlands across Russia. For the single-predictor models, regression coefficients for three microhabitats are reported when interaction with microhabitat is significant, otherwise a single regression coefficient (when the predictor effect is significant) or nothing (when predictor effect is insignificant) is reported.

	Single-predictor model				Multiple-predictor model		
Variable	**Hummock**	**Lawn**	**Hollow**	R^2	**Effect**	**Interaction**	R^2
Species richness S							
Latitude	0.129[a]	0.287[a]*	0.492[b]*	0.170			
Longitude	−0.008[a]	0.028[b]	0.025[ab]	0.103			
Annual mean temperature	−0.159[a]	−0.395[b]*	-0.516[b]*	0.179	+	+	0.184
Isothermality					−	−	
Temperature seasonality					+	+	
Annual precipitation		−0.011*		0.115	−	−	
Precipitation seasonality					−	−	
Exponential of Shannon diversity D_1							
Latitude	−0.027[a]	0.067[ab]	0.151[b]*	0.079			
Longitude	0.001[a]	0.024[b]*	0.009[ab]	0.083			
Annual mean temperature	−0.007[a]	−0.150[b]*	−0.141[ab]*	0.088	+	+	0.102
Isothermality					−	−	
Temperature seasonality					+	+	
Annual precipitation					−	−	
Precipitation seasonality					−	−	
Pielou evenness E							
Latitude							
Longitude	−0.0001[a]	0.0005[a]*	−0.0001[a]	0.023			
Annual mean temperature					−	−	0.039
Isothermality					−	−	
Temperature seasonality		−0.0008*		0.046	−	−	
Annual precipitation		0.0002*		0.039	+	−	
Precipitation seasonality					−	−	
Zeroth-order β-diversity $1 - C_{0N}$							
Latitude							
Longitude	−0.0004[a]	−0.0004[a]	0.0013[a]	0.051			
Annual mean temperature					−	−	0.083
Isothermality					+	+	
Temperature seasonality					+	+	
Annual precipitation					−	−	
Precipitation seasonality	−0.0001[a]	−0.0009[a]	0.0037[b]*	0.085	−	−	
First-order β-diversity $1 - C_{1N}$							
Latitude							
Longitude	−0.0006[a]	−0.0002[ab]	0.0017[b]*	0.062			

(Continues)

TABLE 2 | (Continued)

Variable	Single-predictor model				Multiple-predictor model		
	Hummock	Lawn	Hollow	R^2	Effect	Interaction	R^2
Annual mean temperature					–	–	0.031
Isothermality					–	–	
Temperature seasonality					–	–	
Annual precipitation					–	–	
Precipitation seasonality	−0.0015[a]	0.00001[ab]	0.0024[b]	0.056	–	–	

Note: Letters display significance of slope difference among microhabitats. Asterisk (*) indicates that the slope significantly differs from zero. Multiple-predictor models were built based on five climatic variables as potential predictors (+ indicates the inclusion of the predictor main effect and the interaction with microhabitat into the parsimonious model).

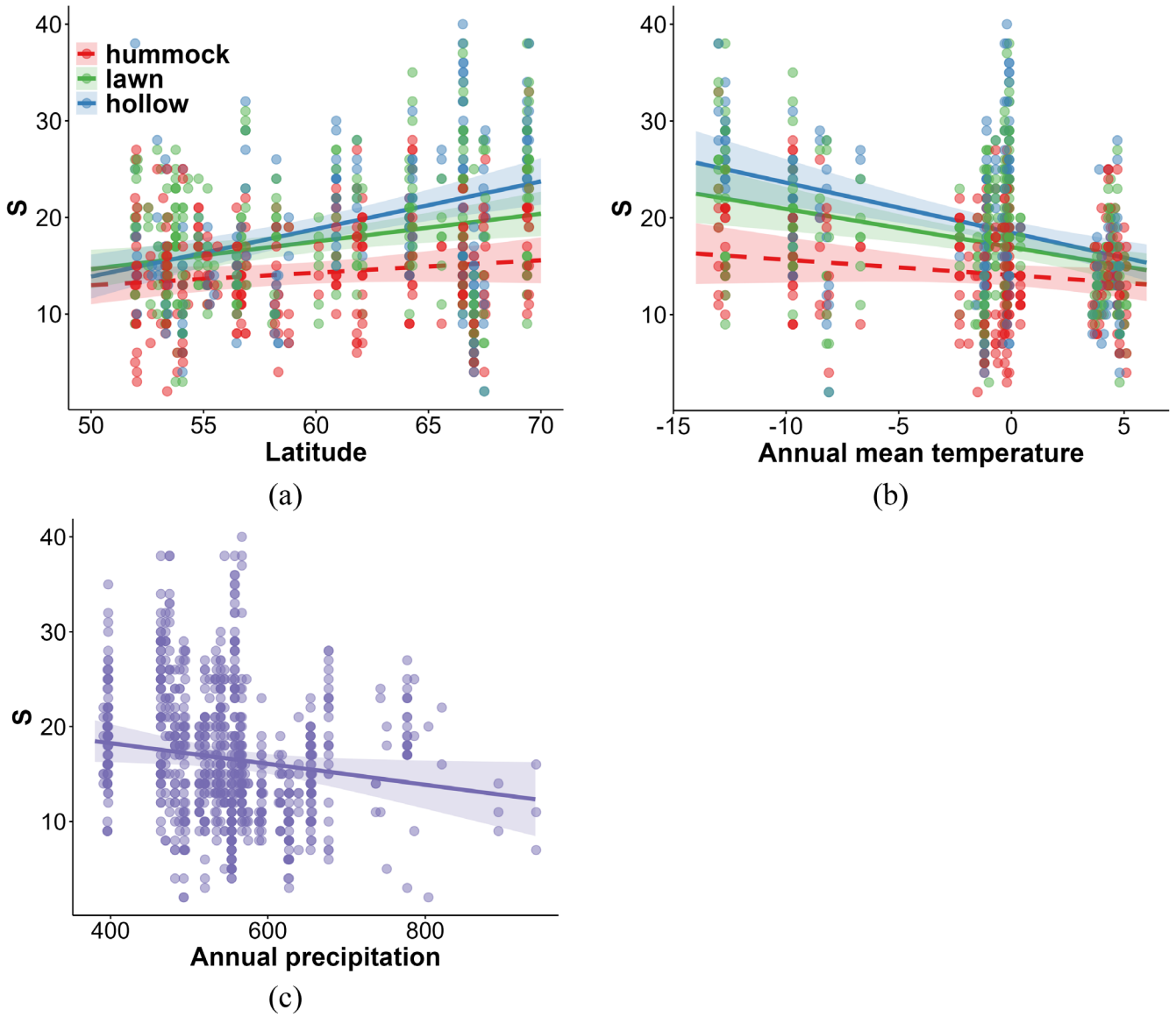

FIGURE 3 | The results of the linear mixed-effects models (LMMs) testing the effects of microhabitat, spatial and climatic variables on the species richness per sample (S) of Sphagnum-dwelling testate amoeba communities across Russia (only significant effects with $p < 0.05$ are shown). The solid line indicates that the slope is significantly different from 0, the dashed line indicates the opposite situation.

In all microhabitats, the clustering of samples on the other side of the first RDA axis was positively related to annual precipitation. This probably indicates the importance of this climatic factor in the regulation of local surface wetness of the microhabitats. In all microhabitats, increased annual precipitation resulted in the greater proportion of hydrophilic *Nebela collaris*

TABLE 3 | Results of redundancy analysis (RDA). The dependent variable for all models was the Hellinger-transformed relative abundances of testate amoebae. In model 1, microhabitat was included as independent variable and site (peatland ID) as a random variable. In all other models the variables shown and their interactions were included in the models.

Model	Variables	DF	Variance	*F*	*p*	R^2_{adj}
Model 1	Microhabitat	2	0.017	14.723	0.001	0.024
Model 2	Latitude	1	0.015	17.940	0.001	0.051
	Microhabitat	2	0.020	12.053	0.001	
	Interaction	2	0.006	3.563	0.001	
Model 3	Longitude	1	0.013	14.800	0.001	0.047
	Microhabitat	2	0.020	11.937	0.001	
	Interaction	2	0.006	3.344	0.001	
Model 4	Annual mean temperature	1	0.025	30.314	0.001	0.065
	Microhabitat	2	0.021	12.359	0.001	
	Interaction	2	0.005	3.176	0.001	
Model 5	Isothermality	1	0.020	23.943	0.001	0.058
	Microhabitat	2	0.021	12.348	0.001	
	Interaction	2	0.006	3.349	0.001	
Model 6	Annual precipitation	1	0.022	25.937	0.001	0.058
	Microhabitat	2	0.020	12.028	0.001	
	Interaction	2	0.004	2.470	0.001	
Model 7	Precipitation seasonality	1	0.011	12.719	0.001	0.042
	Microhabitat	2	0.020	11.835	0.001	
	Interaction	2	0.004	2.148	0.001	
Model 8	Temperature seasonality	1	0.020	24.340	0.001	0.054
	Microhabitat	2	0.020	12.029	0.001	
	Interaction	2	0.003	1.769	0.001	
Model 9	Annual mean temperature	1	0.025	32.621	0.001	0.131
	Isothermality	1	0.009	11.118	0.001	
	Temperature seasonality	1	0.011	13.712	0.001	
	Annual precipitation	1	0.010	13.507	0.001	
	Precipitation seasonality	1	0.013	16.758	0.001	
	Microhabitat	2	0.019	12.511	0.001	
	Interaction with annual mean Temperature	2	0.005	3.346	0.001	
	Interaction with isothermality	2	0.004	2.495	0.001	
	Interaction with temperature Seasonality	2	0.004	2.352	0.001	
	Interaction with annual Precipitation	2	0.004	2.518	0.001	
	Interaction with precipitation Seasonality	2	0.004	2.768	0.001	

(Continues)

TABLE 3 | (Continued)

Model	Variables	DF	Variance	*F*	*p*	R^2_{adj}
Model 10 (hummock)	Annual mean temperature	1	0.021	10.087	0.001	0.091
	Isothermality	1	0.015	6.957	0.001	
	Annual precipitation	1	0.011	5.236	0.001	
	Precipitation seasonality	1	0.018	8.739	0.001	
	Temperature seasonality	1	0.007	3.415	0.001	
Model 11 (lawn)	Annual mean temperature	1	0.033	16.967	0.001	0.112
	Isothermality	1	0.012	6.226	0.001	
	Annual precipitation	1	0.017	8.783	0.001	
	Precipitation seasonality	1	0.011	5.736	0.001	
	Temperature seasonality	1	0.013	6.829	0.001	
Model 12 (hollow)	Annual mean temperature	1	0.041	12.554	0.001	0.124
	Isothermality	1	0.021	6.423	0.001	
	Annual precipitation	1	0.019	5.933	0.001	
	Precipitation seasonality	1	0.015	4.571	0.001	
	Temperature seasonality	1	0.015	4.557	0.001	

Abbreviations: DF, degrees of freedom; R^2_{adj}, adjusted explanatory; R^2 model.

and *Hyalosphenia papilio*. In hummocks, this was associated with greater relative abundances of *Assulina muscorum* and *Alabasta militaris* (both are indicators of dry/moderately wet conditions), in lawns with *Hyalosphenia elegans* and *Archerella flavum* and in hollows with *Heleopera sphagni*. The latter apparently requires greater wetness and stability of hydrological regime. Surprisingly, a well-known hydrophilic species *Archerella jollyi* seems to be more resistant to unstable hydrological regime (it is associated with precipitation seasonality in all three microhabitats) in comparison to *Hyalosphenia papilio* and *Heleopera sphagni* (these species are negatively correlated with precipitation seasonality).

The second RDA axis was negatively related to mean temperature and isothermality in hummocks only, but no specific taxa for these conditions can be identified. In other microhabitats, the second RDA axis is related to the factors not included in the analysis which might be water characteristics in permanently flooded microhabitats (basically aquatic conditions) as shown by greater proportions of *Arcella rotundata* and *Physochila tenella*.

4 | Discussion

The study allows us to discuss the large-scale spatial patterns of local diversity (α-diversity) and species turnover (β-diversity) of soil eukaryotic microbes along latitudinal (51°–70°N) and longitudinal (32°–158°E) gradients. The issue was addressed using a morphospecies approach to *Sphagnum*-dwelling testate amoeba assemblages in three main types of microhabitats (hollow, lawn, and hummock) in peatland ecosystems.

Our results indicate that α-diversity (i.e., species richness and diversity) of testate amoebae varies along the microtopographical gradient increasing from hummocks to hollows. Although peatland surface microtopography has long been known to host distinct testate amoeba assemblages (De Graaf 1956; Tolonen, Warner, and Vasander 1992), to date only a few studies have directly investigated the patterns of testate amoeba assemblages in this regard (Sullivan and Booth 2011; Niinemets, Pensa, and Charman 2011; Tsyganov et al. 2016; Stastney and Black 2020). The available studies report either similar patterns of species richness and diversity distribution (Heal 1961; Lamentowicz et al. 2010; Mieczan 2010; Roe, Elliott, and Patterson 2017) or opposite ones (Stastney and Black 2020; Marcisz, Fournier, et al. 2014; Marcisz, Lamentowicz, et al. 2014). It seems that surface wetness is the main driver of species diversity of testate amoebae in the microforms because hummocks are generally the driest sites as their surface is more distant from the water table (Bragazza, Alber, and Gerdol 1998; Robroek et al. 2007; Rydin, Jeglum, and Bennett 2013). As a result, testate amoebae require more adaptations (e.g., resistant cysts, reduced shell size, or specialised pseudostome structure, etc.) for successful survival in these microhabitats (Schönborn 1965), which limits the number of species can thrive in hummocks and lawns as shown by lower richness values in our results. However, in some cases these patterns of the surface wetness can be disturbed due to the greater control of atmospheric precipitation on surface wetness in maritime climate (as it was reported by Stastney and Black 2020 for an Irish bog). The lower species richness in hollows was explained by the stresses other than water availability, for example, prey scarcity (Stastney and Black 2020). Besides, Sullivan and Booth (2011) reported that although the surfaces of hummocks are more distant from the water table, the compact growth form

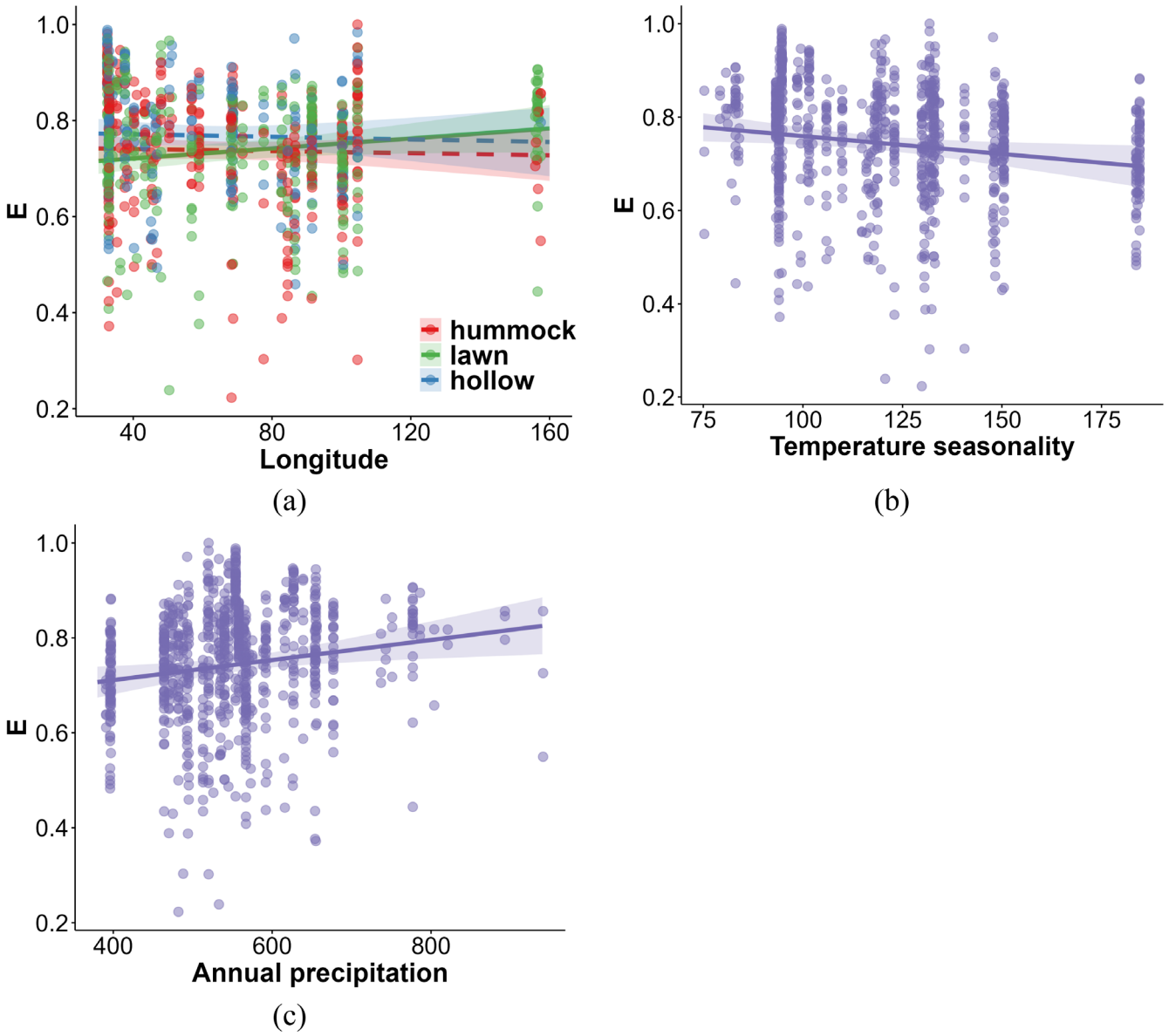

FIGURE 4 | The results of the linear mixed-effects models (LMMs) testing the effects of microhabitat, spatial and climatic variables on Peilou's species evenness (E) of *Sphagnum*-dwelling testate amoeba communities across Russia (only significant effects with $p < 0.05$ are shown). The solid line indicates that the slope is significantly different from 0, the dashed line indicates the opposite situation.

of many hummock dwelling *Sphagnum* species (e.g., *S. fuscum*) allows for a greater water-holding capacity and seasonal moisture stability as opposed to hollows where *Sphagnum* species often are less compact and less dense (e.g., *S. cuspidatum*). Overall, despite the numerous possible mechanisms for the effect of microrelief on species richness diversity of testate amoeba assemblages, our data indicate that when considered on the large spatial scale within the territory dominated by the continental climate, the effects of surface moisture-related water-table depth seem the most plausible. However, the influence of surface humidity and, as a result, the distribution of testate amoeba communities in different forms of microrelief in certain cases may not be the leading factor. In rich fens, unlike bogs, the key drivers structuring testate amoeba communities are related to nutrient status (Lamentowicz, Lamentowicz, and Payne 2013) where pH, conductivity, Ca, and Mg concentrations are principal. But even in such ecosystems, the water level remains one of the major factors.

Given the differences in the diversity characteristics of testate amoeba assemblages in various microhabitats, it is not surprising that their responses to climatic characteristics varied among microhabitat type. Our results demonstrate that species richness of testate amoeba assemblages increased northwards in hollows and lawns, this increase was mostly driven by reduced mean annual temperature. A previous global study showed that molecular α-diversity of Euglyphid testate amoeba in forest soil litter increased with temperature and decreased with latitude and substrate C/N ratio (Lara et al. 2016), that is, the patterns were similar to those of macroscopic organisms. However, regional studies based on a greater diversity of studied substrates and testate amoeba groups showed somewhat different patterns. For example Fernández et al. (2016) reported a unimodal trend of species richness (all habitat types are combined) along a latitudinal gradient (17°–56°S) in SW South America that was mostly explained by water-energy balance, which refers to the

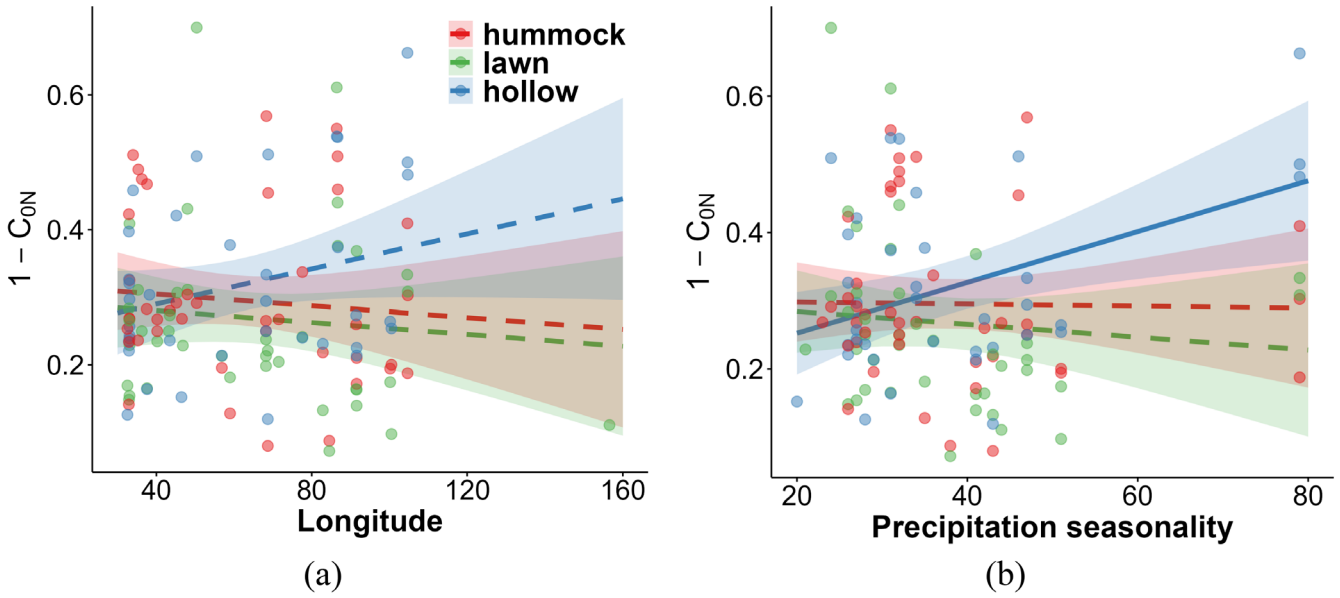

FIGURE 5 | The results of the linear mixed-effects models (LMMs) testing the effects of microhabitat, spatial and climatic variables on the zeroth order β-diversity ($1 - C_{0N}$) of *Sphagnum*-dwelling testate amoeba communities among samples inside microhabitat across Russia (only significant effects with $p < 0.05$ are shown). The solid line indicates that the slope is significantly different from 0, the dashed line indicates the opposite situation.

combined availability of water and ambient energy (e.g., temperature), which jointly influence the physiological processes and reproductive success of testate amoebae, as represented by actual evapotranspiration. This pattern was explained by a combination of the ancestral adaptation of testate amoebae to warm, humid climates and past climate changes that set up permanent harsh abiotic conditions northward and southward from mid-latitudes (Fernández et al. 2016). Another study on freshwater testate amoebae from lacustrine bottom surface sediments along a latitudinal gradient in China (23°–50°N) revealed that the biomass of testate amoebae significantly decreased northwards, while the Shannon index and species richness presented an opposite trend (Ju et al. 2014). However, the latter was suspected to be an artefact of the altitudinal distribution of the study sites.

Increased species diversity with the latitude (a.k.a. 'reversed latitudinal diversity gradient') was observed for other organism types in many regions, for example, ants in neotropical savanna (Vasconcelos et al. 2018), birds in Finnish peatlands (Järvinen, Kouki, and Häyrinen 1987), parasites (Johnson and Haas 2021). In some cases, these patterns were controlled by climatic drivers or reflected the biotopic origin of the group (e.g., distribution of forest ants in savannas; Vasconcelos et al. 2018). Early studies on the biogeographical patterns of testate amoebae in the southern hemisphere reported a broad trend of decreasing species richness with increasing latitude and with declining mean temperatures of the warmest month (Smith and Wilkinson 1987; Smith 1996). Similarly, the mean temperature of the warmest month was positively correlated to testate amoeba species richness in 10 physiographic regions of Tibet and Yunnan (Yang et al. 2006). However, monthly mean temperatures are an extremely crude indicator of habitat suitability within soils, wetlands and freshwater habitats; there are doubtless many exceptions to the general trend (Vincke et al. 2006); detailed microclimate data would be necessary to establish such a relationship with precision. In our case, the patterns were observed for various microhabitats of the same ecosystem, that is, peatlands, which are known to be strongly controlled by climatic conditions (e.g., water supply excess) and to have greater abundance and diversity at high latitudes (Tarnocai and Stolbovoy 2006). Furthermore, the northward progression also introduces permafrost, leading to a greater surface heterogeneity within peatland ecosystems (Pokrovsky et al. 2020). Therefore, despite the important role of climatic factors controlling the latitudinal diversity patterns of *Sphagnum*-dwelling testate amoebae they might also be attributed to the greater area and diversity of peatlands in the north. The future studies should account for the effects of biotope area on diversity patterns of testate amoebae.

Our results indicate that species richness and diversity of testate amoebae in hummocks were less sensitive to climatic effects as compared to the wetter types of microhabitats (i.e., hollows and lawns). The susceptibility of various peatland microforms to climate effects remains debated in the literature (Stastney and Black 2020), mainly because the bog microtopography is a result of complex interplay among climate, local hydrological regime, vegetation and peat properties (Nungesser 2003). The hummocks are generally considered to be less sensitive to climatic variation (Mauquoy and Barber 2002) as hollows experience drought more frequently and more severe. When hollows dry, *Sphagnum* species desiccate and become dormant but rehydrate and thrive when moisture level restores, whereas hummock species strongly resist desiccation, but when they do dry, they recover poorly (Nungesser 2003). Because hummock mosses grow further above the water table than in hollows, they have adaptations that allow them to tolerate (and even create) dry conditions (Robroek et al. 2009; Mazziotta et al. 2019). On the other hand, due to overall elevated shape, hummocks are rarely flooded. Another possible explanation of relative stability of testate amoeba assemblages in hummocks is that these microhabitats harbour just a fraction of adapted species, which seems to be a finite fraction of the regional diversity. However,

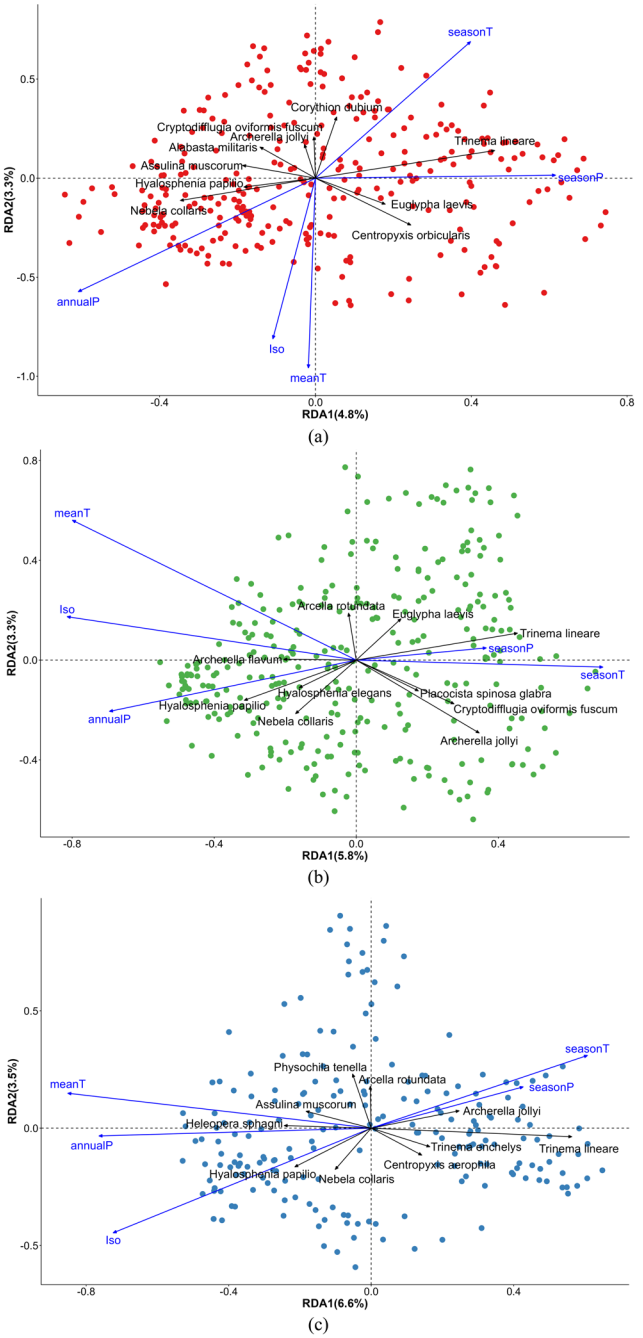

FIGURE 6 | The ordination biplots based on the redundancy analysis (RDA, Hellinger-transformed relative abundances) of *Sphagnum*-dwelling testate amoeba communities in (a) hummocks (67 peatlands: 296 samples), (b) lawns (66 peatlands: 314 samples) and (c) hollows (50 peatlands: 206 samples) of peatland ecosystems. Black arrows represent 10 species with the greatest contribution to the results of ordination (measured by the length of the arrow: Square root of the sum of squares of the species RDA loadings). Blue arrows show climatic factors selected for the parsimonious model. Abbreviations for the five climate factors: MeanT—annual mean temperature; Iso—isothermality; annualP—annual precipitation; seasonP—precipitation seasonality; seasonT—temperature seasonality.

a recent study (Stastney and Black 2020) based on palaeoecological data indicate that a significant correlation of water table depth reconstructed based on subfossil testate amoebae in hummock microhabitats with instrumental temperature and precipitation factors exists. That might present a challenge to the assumption that hummocks record a 'complacent' climatic signal (Barber 1993; Barber et al. 1998), at least in terms of testate amoeba species composition data, if not other proxy indicators such as peat humification or plant macrofossils are used (Väliranta et al. 2012; Payne and Blackford 2008). Nevertheless, there remains a suspicion that not all surface microforms are equally responsive to climatic variability, so the specific climate-sensitivity of various components of those microhabitats should be studied further in details. The overall recommendation remains that palaeoecological investigations should target intermediate bog microforms as the most diverse and sensitive in terms of testate amoeba assemblages.

Our results indicate that all of three microhabitats share high number of species (59.6%). The reason for such a high overlap may be the seasonal dynamics of communities, in particular when peatlands are more waterlogged in the spring season and drier in summer. Such dynamics may lead to the short-term development of hydrophilous species in typical arid biotopes and vice versa (i.e., hummocks). Another potential reason may be the vertical transfer of empty shells as a result of fluctuations of mire water tables. Lawns harboured the most homogeneous assemblages in terms of species composition as compared to the hummocks and hollows. The same patterns were observed in the studies of testate amoeba diversity at the spatial mesoscale within peatlands in a broadleaved forest region (Mazei and Tsyganov 2007) which showed the intermediate locations of the *Sphagnum*-dominated vegetation mat were the most homogeneous in terms of species structure of testate amoeba assemblages. It has been previously shown that hummocks provide a variety of microsites (Vasander 1984), thereby exhibiting a wider variety of species of bryophytes and vascular plants. The same can be applied to hollows which might provide diverse environmental conditions for microorganisms taking into account their high sensitivity to climatic conditions, and possible variation in water table depth and sampling location. This is further supported by our results which showed that both zeroth- and first-order β-diversity positively depended on precipitation seasonality in hollows, that is, heterogeneity of species structure of testate amoeba assemblages increased both in terms of species incidence and abundance with precipitation seasonality. Similar controls on β-diversity of Euglyphid testate amoeba were shown by Lara et al. (2016), who demonstrated that β-diversity was correlated with pH, isothermality and temperature of the coldest month of the year (Lara et al. 2016). The β-diversity patterns observed in our study display both consistencies and inconsistencies when compared to other large-scale studies of β-diversity gradients. The longitudinal gradient of β-diversity has been reported for stream fish assemblages (Zhang et al. 2022). In addition, Su et al. (2024) reported a negative latitudinal gradient of among-ecosystem β-diversity in testate amoeba communities of mineral soils, emphasising the influence of latitude on community composition. In contrast, our study highlights the role of longitudinal gradients, particularly for first-order β-diversity at the sample level in hollows. This indicates that longitudinal variation may shape unique community assembly processes, potentially driven by regional climatic stability or dispersal barriers. Such differences could stem from variations in environmental heterogeneity across regions, as well as disparities in

sampling scales or methodological approaches. Overall, these findings underline the importance of considering multiple geographic and environmental factors when analysing β-diversity, as they may interact in complex ways to influence microbial community structures.

We determined microhabitat-specific responses of the species structure of testate amoeba assemblages to climatic variables. Again, the species structure of testate amoeba assemblages in hollows was the most sensitive to climatic variables with the total explained variance of 12.4%, which is smallest compared to lawns (11.2%) to hummocks (9.1%). These results support the previous findings of high sensitivity of species structure of testate amoeba assemblages in various types of microhabitats (Stastney and Black 2020), but point that lawns and hollows remain the preferable target for palaeoecological reconstructions based on this group of organisms. The most important variable that accounted for this variation was precipitation seasonality that was considerably correlated with temperature seasonality in lawns and hollows. These climatic variations favoured small-sized ubiquitous taxa *Trinema linear*e which was accompanied by *Euglypha laevis* in hummocks and lawns and larger-sized *Trinema enhelys* and *Centropyxis aerophila* in hollows. Small-sized species of testate amoebae are known to demonstrate opportunistic behaviour (Marcisz et al. 2020) as they are able to reproduce faster than the larger-sized organisms. Interestingly, the larger-sized testate amoeba species were observed in wetter microhabitats. In all microhabitats increased annual precipitation resulted in the greater proportion of hydrophilic *Nebela collaris* and *Hyalosphenia papilio*, which were observed together with *Assulina muscorum* and *Alabasta militaris* in hummocks, with *Hyalosphenia elegans* and *Archerella flavum* in lawns and with *Heleopera sphagni* in hollows. These ecological preferences of the taxa revealed in these studies correspond well to the previously reported one, however these findings indicate their potential relation of the taxa to atmospheric precipitation and show that hydrophilic taxa can potentially increase their abundance in hummocks provided by the favourable environmental conditions (Bobrov, Charman, and Warner 1999; Booth 2002; Tsyganov et al. 2017).

5 | Conclusions

Our study contributes to the understanding of the impact of climatic factors on the large-scale distribution of soil microorganisms, focusing on *Sphagnum*-dwelling testate amoebae in various microhabitats of peatland ecosystems. We found that α-diversity of *Sphagnum*-dwelling testate amoebae positively correlated with latitude, with the most pronounced effects observed in hollows and lawns, while being absent in hummocks. Mean temperature emerged as the primary driver of α-diversity, with negative impacts from both mean temperature and annual precipitation. Furthermore, longitude emerged as a significant predictor of β-diversity, particularly influenced by precipitation seasonality in hollows. Overall, our study highlights the complex interplay between environmental factors, spatial gradients, and microhabitat specificity in shaping the distribution patterns of *Sphagnum*-dwelling testate amoebae, providing valuable insights for understanding ecosystem dynamics and conservation strategies in peatland ecosystems.

Author Contributions

Yuri A. Mazei conceived the study and secured funding. Yuri A. Mazei, Andrey N. Tsyganov, Edward A.D. Mitchell, Satoshi Shimano, Kirill V. Babeshko, and Natalia G. Mazei conducted fieldwork. Victor A. Chernyshov, Kirill V. Babeshko, and Alexander A. Komarov conducted microscopic analysis. Andrey N. Tsyganov, Jiahui Su, Basil N. Yakimov, and Yuri A. Mazei constructed a database for analysis, Basil N. Yakimov designed statistical analysis. Basil N. Yakimov and Jiahui Su conducted statistical analysis and wrote the first draft of the manuscript. All authors made substantial contributions to the analysis, interpretation of data and editing of the manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in Zenodo at https://doi.org/10.5281/zenodo.13149556.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.