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Structural and functional characteristics of testate amoeba assemblages in terrestrial habitats of the Northern Eurasia

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Introduction

Belowground communities are essential components of terrestrial ecosystems, playing pivotal roles in nutrient cycling, carbon storage, and overall ecosystem functionality (Fitter, 2005; Dubey et al., 2019). Microbial organisms, particularly protists, are central to these communities, driving biogeochemical processes and shaping ecosystem dynamics (Geisen et al., 2017; Crowther et al., 2019; Sokol et al., 2022). Among belowground microorganisms, testate amoebae occupy a prominent position within mineral soil and peatland habitats (Lamentowicz, Mitchell, 2005; Mitchell et al., 2008; Coleman et al., 2024). Functioning as consumers and mixotrophs, they make critical contributions to belowground food web dynamics, carbon and nitrogen cycling (Potapov et al., 2021; Qin et al., 2022). Key environmental factors that strongly influence the composition and diversity of testate amoeba assemblages include moisture regime, organic matter content, and soil pH (Fournier et al., 2012; Arrieira et al., 2015; Fournier et al., 2016; Jassey et al., 2016; Koenig et al., 2018; Lamentowicz et al., 2020; Krashevska et al., 2020; Marcisz et al., 2020; Tsyganov et al., 2022). Despite their high ecological importance, testate amoeba assemblages in different terrestrial habitats and geographic regions remain insufficiently studied.

Existing knowledge of testate amoeba ecology has largely been based on traditional morphological taxonomic classifications (Bonnet, 1975; Todorov, Golemansky, 1995), which fail to fully capture the ecological roles and adaptive strategies of these organisms. A functional trait-based approach offers a promising alternative by linking organismal traits with environmental conditions and ecosystem functions, thereby providing new insights into the ecological strategies of testate amoebae (Fong et al., 2023). Recent studies have demonstrated the potential of this approach to reveal ecological patterns and adaptive strategies. For instance, trait-based analyses have uncovered important relationships between the morphological and physiological characteristics of testate amoebae and their adaptation to peatland and mineral soil habitats (Krashevska et al., 2020; Marcisz et al., 2020). These findings underscore the need to shift from traditional morphological classifications toward the study of functional diversity and ecological roles of testate amoebae.

The significant dependence of testate amoebae assemblages on environmental conditions is manifested at different scales from local variability within a habitat to continental-level heterogeneity, reflecting the influence of climatic and orographic gradients. However, comprehensive studies of various aspects of biodiversity (species composition, taxonomic α- and β-diversity, functional diversity), as well as mechanisms of community assembly and trait patterns across different terrestrial habitats along extensive geographical gradients have not yet been conducted.

Objective of the study: To perform a comparative assessment of the structural and functional organization of testate amoeba assemblages in terrestrial habitats of some regions of Middle Volga region, Western Siberia and Baikalia.

Specific tasks of the study:

1. Identify the main differences in the species composition and taxonomic diversity of sphagnum- and soil-dwelling testate amoeba assemblages taking into account regional specifics.

2. Develop a system of functional traits to describe the functional diversity of testate amoebae, develop a functional classification of testate amoebae.
3. Identify the main differences in the functional composition and diversity of sphagnum- and soil-dwelling testate amoeba assemblages taking into account regional specifics.
4. Perform a comparative analysis of assembly rules in sphagnum- and soil-dwelling testate amoeba assemblages.
5. Identify latitudinal distribution patterns of sphagnum- and soil-dwelling testate amoeba assemblages.

Scientific novelty. This study introduces several novel approaches and examines new objects in the field of testate amoebae ecology. By integrating both taxonomic and functional perspectives, it pioneers the development of a functional trait system and classification tailored to describe the ecological roles and diversity of testate amoebae. This functional framework advances over traditional morphology-based classifications, enabling a more detailed understanding of testate amoebae ecological strategies. Furthermore, we conducted a comparative analysis of the community assembly rules governing the sphagnum- and soil-dwelling testate amoeba assemblages, while considering regional and latitudinal variation. This provides a novel perspective on the community mechanisms of microbes across different environments. Focusing on latitudinal distribution patterns and regional specificity has further revealed previously unexplored dimensions in the ecology of testate amoeba assemblages, thereby fostering a more comprehensive understanding of their diversity and function. Overall, this study has significantly advanced our understanding of testate amoeba assemblages across diverse terrestrial habitats by introducing novel methodologies, frameworks and perspectives, which allow for a deeper interpretation of their ecological patterns.

Theoretical and practical importance. This study has important theoretical and practical value, as it deepens our understanding of the ecological strategies and community assembly mechanisms of testate amoeba assemblages in two terrestrial habitats. By revealing the patterns of taxonomic and functional diversity, this study lays the foundation for understanding how testate amoeba assemblages adapt to diverse ecological conditions and provides new insights into their role in soil ecosystem processes. The established functional trait classification scheme provides a novel framework for studying microbial communities, which allows researchers to more effectively link functional traits to environmental drivers. From a pragmatic standpoint, this research contributes to the advancement of the application of biological indicators. This can be attributed to the sensitivity of testate amoebae to environmental changes, thus enabling their use as indicators of water availability or shifts in climatic conditions. Additionally, the exploration of latitudinal diversity gradients and regional variations enhances our ability to predict microbial responses to global environmental changes, informing conservation strategies and sustainable soil management practices. This research bridges knowledge gaps in microbial ecology and provides tools for both theoretical exploration and practical application in environmental monitoring and ecosystem management.

Methodology and methods. The methodology of this study involves a multi-faceted approach to comprehensively analyze testate amoeba assemblages across the

Northern Holarctic realm. First, a trait-based classification system was developed by compiling a detailed database of 18 functional traits for 372 testate amoeba species. Hierarchical clustering, validated by silhouette width analysis, identified the ecologically meaningful functional groups. Second, to investigate differences in species composition and taxonomic diversity between sphagnum- and soil-dwelling testate amoeba assemblages across six regions, PCA-based ordination and permutational ANOVA were utilized to examine structural differences, while diversity metrics were assessed using the Scheirer-Ray-Hare rank test. Pairwise comparisons between habitat types within regions were conducted using the Wilcoxon rank-sum test. Third, linear mixed-effects models were used to evaluate environmental drivers of α- and β-diversity in sphagnum-dwelling testate amoeba assemblages. Concurrently, latitudinal distribution patterns were analyzed by applying multi-scale partitioning of β-diversity across multiple hierarchical levels (sample, microhabitat, ecosystem) within four climatic sub-zones of the West Siberian Plain for soil-dwelling testate amoeba assemblages. Together, these methods provided a robust framework for assessing the structural, functional, and biogeographical patterns of testate amoeba assemblages in contrasting terrestrial habitats.

Statements to defend:

1. The primary factor driving the structural and functional differences between soil- and sphagnum-dwelling testate amoeba assemblages is the characteristic moisture regime of mineral soils within the ecoregion. In forest-steppe ecoregions with insufficient soil moisture, sphagnum-dwelling assemblages are

more diverse compared to soil-dwelling assemblages. In contrast, in taiga and tundra ecoregions with adequate or excessive soil moisture, the diversity of soil-dwelling assemblages is higher.

2. Soil- and sphagnum-dwelling testate amoeba assemblages differ in their predominant functional traits. Sphagnum-dwelling assemblages are characterized by larger, elongated testate amoebae with a straight terminal aperture exhibiting minimal curvature. The predominant shell cover in these communities consists of organic particles and idiosomes.

3. The primary assembly rule shaping the structure of soil-dwelling testate amoeba assemblages is environmental filtering, whereas in sphagnum-dwelling assemblages, biotic interactions play a more significant role.

4. The α- and β-diversity of sphagnum-dwelling testate amoebae is influenced by climatic factors such as annual mean temperature and the seasonality of precipitation. For hollow assemblages, there is an inverse latitudinal diversity gradient, whereas for assemblages on hummocks, no latitudinal gradient is observed, reflecting the overall stressful conditions of this microhabitat.

Personal impact into results. During the course of this study, author reasoned the relevance of the thesis topic, set the aim and objectives of the research, performed the analysis, made generalizations and conclusions. Specifically, author developed a comprehensive database to catalog 18 functional traits for 372 testate amoebae species and constructed the abundance database from multiple source datasets, ensuring it was robust and suitable for detailed analysis. Second, author conducted the statistical analyses including writing scripts for analysis and visualization. Third, author described the results and provided the interpretation of these results, linking them to ecological theories and highlighting their significance in understanding testate amoebae community structure and function.

Confidence and testing the results. The findings and interpretations presented in this PhD thesis have been rigorously tested and validated through multiple channels of academic dissemination and peer review. The results have been shared and discussed at esteemed international conferences, allowing for feedback and validation from global experts in the field: 10th International Symposium on Testate Amoebae (2023), Madrid, Spain; International Scientific Online Seminar on Arctic and Subarctic Ecosystems (2023), online, Russia; International Conference "Current Trends and Achievements in Life Sciences" (2024), Shenzhen, China. These presentations have provided an opportunity for active engagement with the international research community, ensuring the results are tested against diverse perspectives.

Publications. The results have been reported in 5 publications in peer-reviewed scientific journals which are recommended for publication of results suitable for defense in the council MSU.015.3 for Specialty 1.5.15 – Ecology (biological sciences). In work [1], the author's contribution was 1.2 printed sheets (p.s.) out of 2.05 p.s.; in work [2], 1 p.s. out of 1.88 p.s.; in work [3], 0.45 p.s. out of 0.79 p.s.; in work [4] 1 p.s. out of 1.78 p.s.; in work [5] 0.15 p.s. out of 0.77 p.s.

Thesis structure and volume. This PhD thesis comprises a total of 8 chapters, spanning 157 pages. It includes 11 tables and 29 figures, which collectively illustrate and support the main findings of the study. The reference list consists of 196 sources, providing a comprehensive foundation for the research conducted.

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Chapter 1. Literature Review

1.1. Testate amoebae

Testate amoebae are unicellular eukaryotic microorganisms belonging to the phylum *Amoebozoa* and the order *Arcellinida*, though some species are also classified under *Rhizaria*, particularly within *Apodera* and *Euglyphida*. To date, over 2,000 species have been described (Mitchell et al., 2008a), yet many more remain undiscovered due to their microscopic size and extensive ecological distribution. Typically ranging from 10 to 500 µm in length, these protists exhibit considerable morphological diversity, primarily reflected in the structure of their protective shell (or test). This test can be composed of self-secreted silica or proteinaceous material, environmental particles (such as mineral grains or diatom frustules), or a combination of both. The structural composition of test reflects adaptations to specific environmental conditions (Marcisz et al., 2020).

These microorganisms inhabit a wide range of ecosystems, with their distribution spanning terrestrial, freshwater, and even some marine environments (Todorov, Bankov, 2019). They are particularly abundant in soil and peatlands, where they contribute to microbial food webs and organic matter decomposition. In terrestrial ecosystems, they thrive in mosses, leaf litter, and organic-rich soils, playing a key role in nutrient cycling (Smith et al., 2009). In freshwater habitats, they occur in periphytic communities, benthic sediments, and floating vegetation. Their presence in extreme environments, such as high-altitude peat bogs, arid desert soils, and polar tundra, highlights their adaptability to diverse climatic and edaphic conditions.

Ecologically, testate amoebae function as microbial predators, feeding primarily through phagocytosis on bacteria, ciliates, and organic detritus. Their trophic interactions influence microbial community structure and contribute to nutrient turnover. The life cycle of testate amoebae consists of an active trophic stage, in which they feed and grow, and a dormant cyst stage that enables survival under adverse conditions, such as drought or freezing temperatures (Todorov, Bankov, 2019). This dual-stage strategy enhances their resilience to environmental fluctuations, allowing them to persist in both stable and dynamic ecosystems.

1.1.1. Ecological roles

In ecological systems, testate amoebae play several key roles. As microbial predators, they primarily feed on bacteria, algae, and small protists, regulating microbial populations and contributing to nutrient cycling. Their feeding activities influence decomposition rates, particularly in soils rich in organic matter (e.g. peatlands), where they facilitate carbon sequestration and nitrogen cycling (Marcisz et al., 2020). In addition, testate amoebae indirectly influence the plants by regulating nutrient availability through interactions with other microorganisms and decomposers. Simultaneously, they make significant contributions to the structure and stability of soil ecosystems: the shells of testate amoebae accumulate over time, forming microhabitats for other soil microorganisms and affecting soil porosity and water-holding capacity. The role of testate amoebae in the carbon cycle is considered to be vital in peatlands. By helping to regulate the balance between carbon storage and release, they consequently influence the global carbon budget (Qin et al., 2022).

Due to their high sensitivity to environmental factors (such as humidity, pH and nutrient availability), testate amoebae have become reliable biological indicators for monitoring ecosystem health and detecting the impacts of climate change (Charman, 2001). This bioindicator capacity has led to their widespread use in palaeoecological studies, where fossil testate amoebae are analyzed to reconstruct historical climate patterns and environmental changes (Mitchell et al., 2008b; Qin et al., 2021). Changes in their assemblages often reflect broader ecological shifts, underlining their role in sustaining ecosystem balance and functionality.

Overall, testate amoebae are integral components of ecosystems, contributing to nutrient cycling, microbial regulation and soil structure formation. Their sensitivity to environmental conditions makes them excellent bioindicators, while their functional diversity plays a vital role in ecosystem processes.

1.1.2. Environmental drivers of testate amoebae assemblages

The community structure and diversity of testate amoebae are shaped by a complex interplay of environmental variables, including both abiotic and biotic factors. Among the abiotic factors, moisture is one of the most critical determinants, as testate amoebae are highly sensitive to water availability (Andrew et al., 2012; Islam et al., 2020). Sufficient moisture supports trophic activity, enhances nutrient availability, and stabilizes environmental conditions, which are essential for the survival and growth of these organisms. Conversely, desiccation imposes physiological stress, driving species with adaptations such as smaller test sizes or thicker shells to dominate in drier habitats.

pH is another key abiotic factor influencing testate amoeba assemblages (Lamentowicz, Mitchell, 2005). Acidic conditions typically favor species adapted to low pH environments, whereas neutral to alkaline conditions can support a broader range of species. Organic matter content also plays a significant role by providing the primary energy sources and substrates for microbial food webs. Most testate amoebae survive through heterotrophic feeding strategies, primarily consuming bacteria, fungi and detritus particles. Consequently, they require habitats abundant in organic resources. Soil texture further influences habitat suitability by regulating water retention and aeration. For instance, fine-grained soils like clay enhance water retention, while coarse-grained soils (such as sand) facilitate the formation of well-drained environments.

Biotic factors (e.g. interactions among microorganisms) further regulate the community structure of testate amoebae (Schlatter et al., 2015). Resource competition, predation and mutualistic symbiosis in microbial communities give rise to dynamic interactions that shape the diversity and functional traits of testate amoebae. Overall, these factors interact across spatiotemporal scales, jointly driving niche differentiation and community aggregation processes. A deeper understanding of the impacts of these factors can provide key insights into revealing the ecological functions and adaptive strategies of testate amoebae across various ecosystems.

1.2. Species diversity and composition

Biodiversity is the basis of life and the foundation for the survival and development of human society (Kumar, 2012). It is particularly important for the maintenance of ecosystem stability (Oliver et al., 2015). With the loss of species and habitats, the conservation of biodiversity on a global scale has become an urgent need (Rands et al., 2010; Turner et al., 2012; Lewin et al., 2022). From a narrower perspective, diversity is a key structural property of ecological communities which could be measured with a variety of metrics including species richness, taxonomic, phylogenetic and functional diversity indices (Magurran, McGill, 2011).

Species diversity refers to the richness and abundance of species within a community, it is crucial for maintaining ecosystem processes and stability (Hooper et al., 2002). Higher species diversity is associated with stronger ecosystem functions, because more diverse species can fulfill different ecological roles (such as participating in nutrient cycling, primary production and energy flow). Greater species diversity also enhances ecosystem resilience, enabling organisms to better withstand and recover from disturbances like climate fluctuations, habitat loss, or pollution. Species diversity is commonly categorized into three levels: α-, β-, and γ-diversity (Whittaker, 1960). Among the three levels, α-diversity refers to the diversity of species within a specific community, γ-diversity is the diversity of all species across a geographic region. However, β-diversity denotes the degree of variation in species composition between different communities (Anderson et al., 2011). It measures the rate that species change along environmental gradients or spatial distances. This concept also helps differentiate between local influences (e.g. environmental conditions and species interactions) and broader processes (e.g. dispersal limitations and historical factors) that shape species assemblages (Chase, Myers, 2011; Zhang et al., 2020b; Wu et al., 2021). Analyzing β-diversity patterns can help determine whether variations in community composition are driven mainly by habitat-specific factors or influenced by species dispersal from a wider regional species pool (Langenheder et al., 2012; Wang et al., 2017). Furthermore, β-diversity can highlight the strength of ecological gradients, which describe gradual environmental changes across different habitats or geographical areas (Kubota et al., 2014; Wang et al., 2020b).

Besides species diversity, species composition (the specific identity of species within a community) further influences ecosystem dynamics. Different species possess unique functional traits that drive key ecological processes. The presence of certain keystone species or functional groups can disproportionately affect ecosystem functioning (Davic, 2003). For example, in soil ecosystems, the presence of species involved in nitrogen fixation or organic matter decomposition can regulate nutrient availability and soil health. By quantifying species composition differences, these variations can be linked to specific environmental attributes, such as latitude, longitude, or temperature, providing insights into the mechanisms that influence species distribution and community assembly.

Changes in species diversity and community structure can trigger cascading effects within ecosystems. Species loss or alterations in species composition may reduce functional diversity, thereby weakening an ecosystem's capacity to perform key functions and adapt to environmental changes (Mori et al., 2013). Conversely, stable and diverse communities typically show functional redundancy (multiple species can perform similar ecological roles) which provides a buffer against species loss. Species diversity and community composition are fundamental elements influencing ecosystem function and resilience (Fischer et al., 2006), they jointly determine the range of ecological functions a biological community can perform. Moreover, species diversity and community composition directly influence a community's capacity to withstand environmental stresses, thereby affecting its ability to maintain system stability and sustainably provide ecosystem services.

1.2.1. Factors influencing species diversity and composition

Testate amoebae exhibit remarkable diversity across various habitats, with species richness per sample typically ranging from 3 to over 27, depending on environmental conditions (Smith et al., 2009; Tsyganov et al., 2015; Mazei et al., 2017b). These communities are highly sensitive to environmental gradients, making them valuable indicators for assessing habitat conditions and ecological changes. Previous research has emphasized the significant influence that local environmental factors, climate conditions, spatial isolation, and human interventions on the distribution patterns of testate amoebae diversity in different ecosystems (Fournier et al., 2012; Arrieira et al., 2015; Fournier et al., 2016; Jassey et al., 2016; Koenig et al., 2018; Lamentowicz et al., 2020).

The species diversity and composition of testate amoebae across ecosystems is driven by several key environmental factors, with moisture being the most critical in different habitats (Harnisch, 1927; Grospietsch, 1953; Meisterfeld, 1979; Mazei et al., 2007; Tsyganov et al., 2016). Wet habitats (such as peatlands and moss-covered areas) generally support higher species richness due to the stable water availability and rich organic content, which provide ideal conditions for growth and reproduction. In contrast, dry habitats (e.g. mineral soils) impose physiological stress, leading to reduced diversity and the dominance of drought-tolerant species. For example, the species richness of testate amoebae decreases significantly in arid environments (Mazei, Chernyshov, 2011).

Soil properties, such as texture, structure, pH and organic content, play a pivotal role in regulating moisture availability, which directly impacts the survival and distribution of microbial communities, including testate amoebae (Todorov, Bankov, 2019). For example, coarse-textured soils with poor water-holding capacity tend to support xerophilic species, whereas fine-textured soils with greater moisture retention provide a favorable environment for more hydrophilic species. Similarly, wetlands (e.g. peatlands) are notable for their ability to maintain consistently high moisture levels, independent of variations in precipitation. This stability promotes a rich diversity of testate amoebae adapted to waterlogged conditions.

In addition to soil properties, other factors (e.g. vegetation structure, light availability and microhabitat heterogeneity) can influence testate amoeba assemblages by shaping habitat conditions and resource availability (Todorov, Bankov, 2019). For instance, open habitats with high light availability (such as peat moss wetlands) often support a diverse array of mixotrophic species, which rely on light for photosynthesis in symbiosis with algal partners (Lamentowicz et al., 2020). Conversely, forested habitats with dense canopy cover tend to harbor lower diversity due to limited light and altered microclimatic conditions. Microhabitat heterogeneity further enhances diversity by providing a range of ecological niches. In moist habitats, the composition of testate amoebae is often uniform across similar microhabitats, such as mosses and lichens. However, the community structure can vary significantly across different habitat types (Tsyganov et al., 2015; Mazei et al., 2017a). These findings highlight the importance of localized environmental conditions in shaping testate amoeba assemblages.

Overall, the diversity and composition of testate amoebae are governed by a combination of moisture availability, light conditions, organic matter content, and habitat openness. These factors interact across spatial and temporal scales, emphasizing the importance of environmental heterogeneity in supporting biodiversity and maintaining ecosystem function.

1.2.2. Latitudinal and longitudinal gradients of species diversity

Among the many factors influencing ecological patterns, latitude and longitude are particularly important in large-scale studies because they shape other key environmental variables, such as climate, vegetation types, and soil properties. Geographical coordinates provide a framework that helps explain broad gradients in biodiversity and ecosystem functioning across regions. Microbial communities in soils possess significant importance, particularly concerning their spatial distribution across various habitats and geographical locations (Barberán et al., 2014). In light of the extensive global changes currently underway, it is crucial to understand how climatic factors influence the species diversity patterns within soil protist communities. Nevertheless, the examination of these diversity patterns along latitudinal or longitudinal gradients is still relatively underexplored (Hortal et al., 2015; Singer et al., 2019). Latitude and longitude predominantly shape climate variables (such as temperature and precipitation), which are fundamental in sculpting biological communities. The Latitudinal Diversity Gradient represents one of the most thoroughly documented biogeographical distributions of biodiversity on Earth, marked by a progressive decline in species richness as latitude increases (Willig et al., 2003; Condamine et al., 2012). This gradient is influenced by various factors, including climate stability, energy availability, and habitat heterogeneity. Understanding these gradients is crucial for predicting how biodiversity and ecosystem services may shift under global environmental changes. While this phenomenon has been extensively researched concerning larger organisms (Willig et al., 2003; Roll et al., 2017; Lawrence, Fraser, 2020), the distribution patterns of smaller organisms can differ markedly from those of larger species (Azovsky, Mazei, 2013; Azovsky et al., 2016; Azovsky et al., 2020). Research has shown that smaller organisms, including ants, fungi, and parasites, tend to exhibit higher species richness at elevated latitudes, influenced by climatic elements such as mean temperature and precipitation (Vasconcelos et al., 2018; Větrovský et al., 2019; Johnson, Haas, 2021). Additionally, certain studies have indicated a bimodal correlation between species richness and mean temperature, suggesting distinct cold and hot diversity peaks (Steidinger et al., 2020). Furthermore, evidence exists that mean annual temperature affects rare and abundant taxa in contrasting manners (Hou et al., 2020).

In addition to investigations into α-diversity patterns, various studies have revealed a negative correlation between β-diversity and latitude (Qian, Ricklefs, 2007; Qian, 2008; Soininen et al., 2018; Cao et al., 2021). However, research by

Alahuhta et al., (2017) indicated that regions at higher latitudes may display increased β-diversity. Moreover, several studies did not identify significant patterns along latitudinal gradients (Enkhtur et al., 2021; Mruzek et al., 2022). The primary factors influencing β-diversity are environmental variables like pH and temperature. Most of these studies concentrate on bacteria, mammals, and vascular plants, while research focused on soil microorganisms remains relatively limited, leading to uncertainties surrounding the global distribution of β-diversity among soil microbes.

Currently, studies on the biogeography of soil microorganisms are still inadequate. For example, some research has targeted specific habitats or regions, which could introduce biases and lead to incomplete knowledge regarding the true diversity and distribution of microbial life (Van Elsas et al., 2012; Větrovský et al., 2019; Hou et al., 2020). In order to systematically understand the geographical distribution patterns of soil microorganisms, we urgently need to conduct comprehensive research across broader geographic regions, habitat types and taxa. On the other hand, our understanding on the mechanisms that govern the formation and maintenance of microbial diversity remains incomplete (Chu et al., 2020). However, the capacity to precisely predict how ecosystems respond to environmental change is dependent on a comprehensive understanding of these mechanisms.

From the perspective of global distribution, most research indicates that species richness (α-diversity) in testate amoebae declines from tropical to polar regions (Beyens et al., 1986; Smith, Wilkinson, 1987; Lara et al., 2016). However, some studies have reported the opposite latitudinal pattern (Ju et al., 2014). Conversely, investigations into β-diversity latitudinal gradients in testate amoeba assemblages are limited, with no clear patterns currently identified. Also, testate amoebae exhibit significant taxonomic diversity across different habitats, particularly between sphagnum- and soil-dwelling testate amoeba assemblages. Species diversity in peatlands is typically higher, with a dominance of moisture-tolerant genera like *Arcella*, *Centropyxis*, and *Difflugia* (Mitchell et al., 2008a). In contrast, mineral soils, which tend to have lower moisture levels and organic matter, generally support a lower diversity of testate amoebae. These soils are often dominated by species adapted to drier conditions, such as *Euglypha* and *Trinema* (Bobrov et al., 1999). Differences in species composition reflect the contrasting environmental conditions in these habitats.

1.3. Trait-based framework

Trait-based ecology provides a powerful approach to understanding biodiversity and ecosystem functioning by emphasizing functional traits—measurable organismal characteristics that mediate species' responses to environmental conditions and their effects on ecosystem processes (Ellis et al., 2021). This framework has been widely applied in plant and animal ecology to explain species distributions, community assembly, and ecosystem stability (Reich et al., 2003; Larson et al., 2020). In microbial ecology, trait-based approaches are increasingly recognized as essential for linking microbial diversity to ecosystem functions, offering a predictive framework that transcends traditional taxonomy-based analyses (Lennon et al., 2012; Fournier et al., 2015; Marcisz et al., 2020;

Cébron et al., 2022).

Functional traits are broadly categorized into response traits and effect traits (Marcisz et al., 2020; Branco et al., 2023). Response traits determine how organisms respond to environmental variations, influencing community structure and resilience. Effect traits, by contrast, directly shape ecosystem functions such as organic matter decomposition, nutrient cycling, and carbon sequestration. Because ecological processes often involve multiple, interacting traits, studies that integrate both response and effect traits provide deeper insights into species' ecological roles and adaptive strategies (Fournier et al., 2015; Martini et al., 2021).

1.3.1. Trait-based framework in soil ecology

Soil ecosystems harbor diverse microbial communities that drive key biogeochemical processes, including nutrient cycling, decomposition, and soil structure maintenance (Jiao et al., 2018; Sokol et al., 2022). Trait-based approaches have advanced our understanding of microbial functions by linking species traits to environmental conditions and ecosystem processes (Jansson, Hofmockel, 2018; Gols, Harvey, 2023; Li et al., 2023). Compared to taxonomic classifications, functional traits offer a mechanistic perspective that enhances predictions of microbial responses to environmental change (Lennon et al., 2012; Fournier et al., 2015; Marcisz et al., 2020; Cébron et al., 2022).

Research on the functional traits of soil microorganisms has emerged as a growing and critical area of inquiry (Marcisz et al., 2020). Soil organisms interact with each other and respond to their environments through combinations of traits

(Treseder, Lennon, 2015; Malik et al., 2020). While single-trait studies provide valuable insights, the dynamic nature of ecological systems demands a broader perspective. Soil organisms adapt to environmental changes through multiple traits, each contributing to their overall adaptive strategies (Ho et al., 2017; Malik et al., 2020). In ecological communities, species often exhibit complementary traits that enable them to occupy distinct niches. Examining multiple traits simultaneously allows for a more comprehensive understanding of the trade-offs and adaptive strategies shaping their ecological roles (Reich et al., 2003; Larson et al., 2020). Furthermore, as environmental conditions fluctuate, single traits may not capture the full scope of organismal responses required for survival and reproduction in ever-changing environments (Fong et al., 2023). The study of multiple traits offers a broader perspective on the functional roles and ecological strategies of species (de Bello et al., 2010; Krause et al., 2014; Beauchard et al., 2017; Funk et al., 2017; Martini et al., 2021). In soil ecology, grouping organisms into functional categories based on multiple traits is essential for understanding microbial community structure and function. For example, researchers classify soil bacteria by traits such as morphology, metabolic pathways, biochemical characteristics, and genome properties (Lennon et al., 2012; Cébron et al., 2021). This classification helps identify functional groups involved in critical processes like nutrient cycling, organic matter decomposition, and carbon sequestration. Similarly, in soil protozoa ecology, traits like feeding behavior, morphology, size, and resistance to stressors are used to identify functional groups that drive community dynamics and trophic interactions (Fiore-Donno et al., 2019; Potapov et al., 2022). Ultimately, grouping soil organisms by functional traits provides valuable insights into their roles in ecosystem processes and their interactions within soil communities.

Diverse functional traits within a community optimize resource use, enhance ecosystem multifunctionality, and ensure adaptability to environmental changes through functional redundancy. This diversity provides ecological insurance, allowing ecosystems to maintain critical functions even in the face of disturbances (de Bello et al., 2021). Conversely, low functional diversity makes ecosystems more vulnerable to stress and reduces their capacity to recover. Thus, functional diversity is key to predicting ecosystem responses and guiding effective conservation and management strategies.

1.3.2. Functional traits of testate amoebae

The study of functional traits is especially relevant for testate amoebae, given their diverse morphologies and ecological strategies. These protists display a range of shell sizes, shapes, and compositions, along with behavioral and physiological adaptations that enable them to survive in different soil environments. These traits play essential roles in nutrient cycling and decomposition and make testate amoebae sensitive indicators of environmental shifts (Mitchell et al., 2008a). Response traits in testate amoebae include morphological plasticity, such as shell size, shape, and composition, as well as movement strategies and reproductive rates (Koenig et al., 2018; Krashevska et al., 2020; Marcisz et al., 2020; Zhang et al., 2020a). Effect traits, which reflect the impact of these organisms on their ecosystems, include feeding strategies and their position within trophic levels (Lansac-Tôha et al., 2014; Marcisz et al., 2020). Specific traits relevant to testate amoebae encompass characteristics such as test (shell) size/shape/composition and aperture features, all of which influence their ecological functions. Larger testate amoebae with wide apertures are typically associated with food web functioning, where they play a role in regulating microbial activity and nutrient cycling (Marcisz et al., 2020). In contrast, smaller species with more compact tests are often better adapted to drier conditions, reflecting their ability to conserve water (Krashevska et al., 2020). These functional traits not only help define the ecological roles of testate amoebae but also offer a framework for understanding their responses to environmental changes.

Recent studies have highlighted the importance of considering the functional traits of testate amoebae to better understand their ecological roles (van Bellen et al., 2018; Krashevska et al., 2020; Macumber et al., 2020; Marcisz et al., 2020; Zhang et al., 2020a; Branco et al., 2023). The size of the shells plays a crucial role in determining testate amoebae physical characteristics and abilities to acquire resources (Macumber et al., 2020; Marcisz et al., 2020). Shell size is particularly important for providing protection against environmental stressors. Larger shells offer better resistance to desiccation and predation, which enhances survival rates in harsh habitats (Macumber et al., 2020; Marcisz et al., 2020). Additionally, the size of the aperture can influence the types of prey the amoebae can capture and their feeding efficiency (Krashevska et al., 2020; Marcisz et al., 2020). Larger apertures allow for greater food intake and mobility, leading to improved nutrient absorption and faster growth. The overall shape of the shell in three-dimensional space is closely related to the specific environment in which the testate amoebae reside

(Macumber et al., 2020). Variations in aperture-related traits, such as its position, invagination degree, aperture rim, and the presence or absence of collars, further contribute to ecological success. These traits influence prey capture efficiency and offer protection from desiccation (Lahr et al., 2019). The presence or absence of internal partitions, spines or horns, as well as the type of shell covering, can also affect predator avoidance, drought adaptations, and ecological strategies, thereby impacting competitive interactions (van Bellen et al., 2018). Moreover, the feeding strategy of testate amoebae (e.g. mixotrophy and bacterivory) reflects their dietary preferences and foraging behavior.

Collectively, these morphological and behavioral traits represent adaptations to specific ecological pressures, promoting the ecological success of testate amoeba assemblages. In conclusion, the combination of physical traits and behavioral strategies in testate amoebae underpins their ability to survive, acquire resources, and differentiate their niches in complex ecosystems.

1.3.3. Existing morphological classification of testate amoebae

Historically, testate amoebae have been classified based on morphological traits, with Bonnet's system (Bonnet, 1975) being one of the most influential. The classification system for testate amoebae introduced by Bonnet (1975) is based solely on morphological features. This system organizes species primarily by the structure of their shells and apertures (e.g., shape, size, and ornamentation), providing valuable taxonomic insights. However, an exclusive focus on morphological traits can obscure key ecological functions, such as feeding strategies and habitat preferences, thereby limiting a deeper understanding of their ecological roles. In recent years, there has been a shift towards trait-based classification systems, which emphasize diverse functional traits rather than purely morphological features. Incorporating functional traits beyond shell morphology could advance our understanding of testate amoebae ecology (Koenig et al., 2018; Krashevska et al., 2020; Marcisz et al., 2020; Zhang et al., 2020a). These studies classified testate amoebae based on characteristics affecting ecological function, which include shell composition (siliceous or organic), shell/aperture size and feeding types. The functional trait-based classification system provides a more comprehensive understanding of the contribution of testate amoebae to ecosystem processes (particularly in regard to nutrient cycling and soil moisture regulation). By integrating a broader range of biological characteristics, we can more fully identify species niches and evaluate their contributions to ecosystem processes.

While existing classification systems provide valuable reference points, the discriminatory power of existing classification systems often falls short of fully revealing the ecological roles these organisms play across diverse environments. For instance, how shell composition influences microbial interactions and which specific functional traits determine testate amoebae's adaptability to environmental stresses remain critical areas requiring in-depth exploration. Furthermore, current classification systems frequently examine morphological characteristics or ecological roles in isolation, failing to integrate both into a unified framework. There is an urgent need to establish novel functional classification systems that incorporate broader traits, including morphological and ecological features, to more accurately reflect the diversity and ecological significance of testate amoebae. Such systems will provide new perspectives for understanding the roles of testate amoebae in various ecosystems (e.g. mineral soils and peatlands) while establishing a holistic framework for comprehensively evaluating their ecological contributions.

1.3.4. Functional diversity

Functional diversity refers to the range and distribution of functional traits within a community, it directly influences ecosystem processes (such as nutrient cycling, energy flow and resilience to environmental change) (Tilman, 2001). By contrast to taxonomic diversity, functional diversity facilitates a deeper understanding of species' roles within ecosystems and their contributions to the system's overall functioning. Microorganisms play a crucial role in regulating biogeochemical cycles, decomposing organic matter, and maintaining soil health. Consequently, functional diversity holds significant importance for soil microbial communities. It is also crucial to understand functional diversity from the perspective of community assembly and ecosystem processes in order to accurately predict how ecosystems respond to environmental change (Petchey, Gaston, 2006).

Functional diversity also exerts profound effects on ecosystem processes, resilience, and stability (Tilman, 2001). Higher functional diversity ensures the efficient operation of multiple ecological functions, including nutrient cycling, organic matter decomposition, and energy flow. Similarly, greater functional diversity underpins the maintenance of ecosystem multifunctionality (the synergistic enhancement of productivity and health through the coordinated action of diverse ecological processes). In addition, functional diversity enhances ecosystem resilience through the mechanism of functional redundancy (Mori et al., 2013). When multiple species perform similar ecological functions, this redundancy acts as an ecological insurance mechanism, enabling ecosystems to maintain critical functions even after disturbance and species loss. Conversely, ecosystems with low functional diversity are more vulnerable to disruption and less capable of adapting to environmental change. Furthermore, functional diversity influences resource use efficiency and niche differentiation. Therefore, functional diversity plays a key role in determining how ecosystems respond to stress, adapt to changing conditions, and sustain vital ecosystem services.

1.3.5. Functional diversity in soil ecology

The functional diversity of soil microorganisms profoundly influences ecosystem processes. Higher functional diversity is typically closely associated with enhanced ecosystem multifunctionality (i.e., the capacity of ecosystems to simultaneously maintain the stable operation of multiple key processes) (Valencia et al., 2015). Diverse functional traits within soil ecosystems can drive more efficient nutrient cycling, organic matter decomposition and turnover, and these processes are crucial for maintaining soil fertility and supporting plant growth. Moreover, functional diversity enhances ecosystem resilience by buffering external disturbances through its inherent functional redundancy (Mori et al., 2013). In systems with high functional redundancy, ecosystems are better equipped to maintain their normal functions even when confronted with environmental changes, due to the presence of multiple microbial species capable of performing similar ecological roles. For instance, in agricultural soils subjected to tillage, pesticide application, or nutrient depletion, the disappearance of certain microbial species may not necessarily lead to a significant decline in ecosystem processes if their functions can be compensated for by other species possessing analogous capabilities. In contrast, ecosystems with low functional diversity are more sensitive to disturbance. The loss of just a few key species can lead to the collapse of ecosystem functions (Hooper et al., 2002). This vulnerability is particularly pronounced in ecosystems reliant on specialised microbial communities, as specific functions are often performed by only a handful of species. The loss of such species triggers cascading effects, ultimately disrupting nutrient cycling and reducing soil productivity.

1.3.6. Functional diversity of testate amoebae

For testate amoebae, functional diversity is increasingly emerging as a crucial dimension in ecological research, and it complements traditional taxonomic approaches effectively. Several studies are utilising functional diversity research to delve deeper into the response patterns of these protists to environmental gradients and their functional roles within ecosystem processes (Arrieira et al., 2015; Koenig et al., 2018).

Although preliminary quantitative studies on the functional diversity of testate amoebae have been conducted, this field remains underdeveloped compared to other biological taxa. By employing metrics such as functional richness, functional evenness and functional dispersion, researchers are able to assess how trait variation contributes to ecosystem functioning (Arrieira et al., 2015; Koenig et al., 2018; Lamentowicz et al., 2020). For example, Lamentowicz et al., (2020) revealed how environmental factors (such as forest cover and light intensity) shape functional diversity by analysing functional traits and diversity of testate amoebae in peatlands. In addition, these studies employing trait research methods have revealed the adaptive responses of testate amoebae to specific habitat conditions (i.e., moisture gradients in soil and wetlands).

Despite the aforementioned advances, this field remains in urgent need of further research to standardise trait analysis methodologies and expand the theoretical framework for studying the functional diversity of testate amoebae. The integration of functional diversity systems into ecological research has the potential to enhance our comprehension of their ecological roles, adaptive capacity to environmental change, and contributions to macro-ecosystem processes.

1.4. Community assembly rules

Beyond the patterns of biodiversity, the rules governing community assembly also determine how species coexist and interact within ecosystems, which in turn shapes the structure and function of communities (Mittelbach, Schemske, 2015). Two primary processes, environmental filtering and biotic interactions, influence community assembly.

1.4.1. Theoretical framework of community assembly

Community assembly theory is a key framework in ecology that investigates how species aggregate into communities across space and time. The core of this theory lies in identifying the processes that shape community structure, which are often divided into two major categories: environmental filtering and biotic interactions. Environmental filtering refers to the process where environmental conditions select species that are adapted to specific ecological niches (D'Amen et al., 2018). These conditions may include abiotic factors such as climate, soil type, and moisture. Through environmental filtering, only species that can adapt to the specific environmental conditions will survive and reproduce, influencing the composition and functions of the community (Cornwell et al., 2006). For example, the acidic and high organic matter content of soils in wetlands often limit both species diversity and functional types within the community. In contrast, biotic interactions emphasize the role of species interactions (such as competition, predation, and symbiosis) in shaping community structure. These interactions not only regulate species abundance but can also influence the survival of populations and community stability (Wardle, 2006). For instance, the competitive exclusion hypothesis suggests that species with similar ecological niches find it difficult to coexist under limited resources (Armstrong, McGehee, 1980), which helps to explain reduced species diversity in certain communities. On the other hand, facilitative interactions can increase resource availability or improve environmental conditions, promoting species coexistence and enhancing community diversity (Tiunov, Scheu, 2005).

Another important theory in community assembly is the neutral theory (Hubbell, 1997, 2011). The neutral theory assumes that all species are ecologically equivalent in terms of population growth and survival, with no significant differences between them. This theory highlights the role of random dispersal and species migration in forming communities, especially in ecosystems with high species diversity. Additionally, community assembly theories include niche theory (Vandermeer, 1972; Adler et al., 2007). Niche theory emphasizes that functional differences between species along environmental gradients are the primary factors driving community structure, whereas the neutral-niche trade-off model integrates the effects of both stochastic processes and functional differences, providing a more comprehensive explanatory framework (Adler et al., 2007).

In summary, community assembly theory, through various ecological processes, reveals the importance of both environmental and species interactions in driving community structure and ecological function. Understanding these assembly rules in different ecosystems helps explain the spatial and temporal variation in biodiversity.

1.4.2. Habitat-specific community assembly rules

Environmental filtering represents the selection of species based on their ability to tolerate specific environmental conditions, while biotic interactions encompass processes like competition, predation, and mutualism, which occur between species and shape their coexistence. In soil microbial communities, both mechanisms operate simultaneously, but their relative importance can vary based on habitat-specific environmental factors such as soil moisture, nutrient availability, pH, and temperature (Gao et al., 2014; Zhang et al., 2018; Wang et al., 2020a).

Specifically, environmental filtering is a deterministic process that limits community composition based on abiotic factors. In soil environments, microorganisms must possess specific physiological traits that enable them to survive and thrive under local conditions. For example, in arid ecosystems, where water is scarce, microbial communities are dominated by drought-tolerant taxa, such as spore-forming bacteria or fungi that can withstand desiccation (Canarini et al., 2021; Gao et al., 2021). In contrast, waterlogged soils, such as those found in wetlands or peatlands, select for anaerobic microorganisms capable of functioning in low-oxygen environments, like methanogens and certain sulfate-reducing bacteria (Van der Valk, 2012; Tokarz, Urban, 2015). Soil pH is another key environmental filter. Strongly acidic or alkaline soils often exclude microorganisms that cannot adapt to such extremes, leading to a community dominated by taxa that can tolerate or even prefer these conditions (Torsvik, Øvreås, 2008). For instance, in highly acidic soils, acidophilic fungi and bacteria tend to dominate, while neutral to slightly alkaline soils support a more diverse range of bacteria and archaea. This process reflects how abiotic conditions act as a selective force, shaping community composition by excluding species that lack the necessary adaptations to persist in particular environments. Temperature is also a critical filter, especially in high-latitude or high-altitude ecosystems where cold conditions dominate. In these environments, microbial communities are often composed of psychrotolerant or psychrophilic species adapted to low temperatures (Margesin, Miteva, 2011). In contrast, in tropical soils, where temperatures are consistently high, microbial diversity tends to be greater, and thermal tolerance is less of a limiting factor

(Nottingham et al., 2018). The influence of environmental filtering is evident in the strong correlation between environmental gradients (e.g. temperature and moisture) and microbial community composition across different ecosystems.

In ecosystems with high biodiversity, biotic interactions like niche differentiation and mutualistic relationships play a crucial role in maintaining community stability and promoting coexistence (Peay, 2016; Bartomeus, Godoy, 2018; Kang et al., 2020). For example, mycorrhizal fungi form symbiotic relationships with plants, facilitating nutrient exchange and promoting plant growth, which in turn influences microbial communities in the rhizosphere. Similarly, in some soil ecosystems, predator-prey interactions between protozoa and bacteria regulate bacterial populations and contribute to nutrient cycling, thus influencing microbial diversity and abundance (Jousset, 2012; Nguyen et al., 2020). However, in highly stressful environments where resources are extremely limited or abiotic conditions are harsh, biotic interactions may play a secondary role compared to environmental filtering (Luzuriaga et al., 2012; Sommer et al., 2014). In these cases, the ability of species to tolerate extreme conditions becomes the overriding factor, and competition or mutualism is less influential. This dynamic is evident in extreme habitats like deserts, tundras, or high-salinity environments, where only a few specialized taxa can persist, and biotic interactions are often less intense.

In the context of testate amoebae, two main theoretical frameworks guide our understanding of these processes: environmental filtering and biotic interactions. Environmental filtering suggests that environmental conditions act as a selective force, favoring species with traits best suited to specific habitats. For example, testate amoebae in peatlands, which are rich in moisture and organic matter, are often dominated by species adapted to such conditions, while in mineral soils, drier environments filter for species with traits that enhance desiccation tolerance (Marcisz et al., 2020). In contrast, biotic interactions, such as competition, predation, and mutualism, can also shape community structure (Wang et al., 2020c; Ndayishimiye et al., 2023). These interactions may either reinforce or counteract the effects of environmental filtering. For instance, in peatlands with higher microbial activity, competition for resources may influence the dominance of certain testate amoeba species, while in nutrient-poor mineral soils, cooperative strategies such as niche partitioning may be more prominent.

Despite the progressive advancements of the aforementioned studies. However, there is a lack of a comparative analysis of assembly rules in sphagnum- and soil-dwelling testate amoeba assemblages.

1.5. Conclusions

Although all of the reviewed studies have advanced progress in the investigation of testate amoebae, several knowledge gaps remain unresolved. First, while previous studies have demonstrated the influence of habitat type on testate amoebae diversity and community structure, a comprehensive comparison integrating taxonomic composition, functional traits, and community assembly processes in different ecoregions across diverse habitats is still lacking. Second, the effects of longitudinal and latitudinal gradients on diversity patterns of testate amoebae across different regions have received limited attention. Addressing this gap is essential for understanding broader biogeographic patterns and predicting community responses to environmental change. Third, existing research has predominantly relied on morphology-based classifications, which may overlook the functional roles and adaptive strategies of testate amoebae. The application of a trait-based framework provides a promising avenue to bridge this gap, yet studies systematically linking specific traits to environmental gradients and ecosystem processes are still in their early stages.

This study aims to address these gaps by integrating functional trait analyses with taxonomic and ecological approaches to assess the structural and functional characteristics of sphagnum- and soil-dwelling testate amoeba assemblages. By investigating the key drivers of community composition and functional diversity, this research will contribute to a deeper understanding of testate amoebae ecology and their roles in soil ecosystem processes.

Chapter 2. Material and Methods

2.1. Source of data

The data we used include three main types: abundance data, climate data, and trait data.

2.1.1 Functional trait data

The first part is traits data. Collecting trait data for testate amoebae is essential to understand how these organisms adapt to diverse environmental conditions. Trait data allow us to identify specific characteristics that enable species to survive and thrive across various habitats (such as wetlands and mineral soils). By examining traits, we gain insights into the ecological roles of testate amoebae, their functional responses to environmental gradients, and their contributions to soil and ecosystem processes. The species list for trait database was compiled from three main sources, including peatland, lake, and mineral soil sample databases across Eurasia (Ivanovskii et al., 2023; Saldaev et al., 2023; Saldaeva et al., 2024); the pan-European peatland hydrology reconstruction database (Amesbury et al., 2016) and the North American peatland hydrology database (Amesbury et al., 2018). This list includes the most prevalent testate amoeba species from the Northern Holarctic realm, covering a broad spectrum of geographical regions and habitat types. Traits were chosen based on their ecological functionality and morphological relevance, reflecting the ecological strategies of testate amoebae. We collected traits data from the primary literature, online databases, or taxonomic keys. For quantitative traits, the maximum and minimum values were collected, and averages were calculated to ensure consistency. If only a single value was available for a trait, it was recorded as the average, while missing maximum and minimum values were left blank. Categorical traits were recorded directly from the literature descriptions. These traits are organized into five blocks (Table 1), reflecting both morphological characteristics and ecological functions.

The first block involves shell dimensions, including shell length, width, and depth, which provide indicators of testate amoeba size (Macumber et al., 2020; Marcisz et al., 2020). Shell length represents the distance from the aperture to the opposite end along the primary axis, while shell width is the widest point along the perpendicular axis, and shell depth denotes the thickness, measured perpendicular to both axes. Two ratios (R1 and R2) derived from these dimensions describe the shell's structural proportions. Specifically, R1 = shell width / shell length measures shell width relative to length, and R2 = shell depth / shell width represents the shape of the shell in a side-to-aperture view.

The second block addresses the overall shell shape (a categorical trait with eight variants), which encapsulates the three-dimensional form.

The third block includes eight traits related to the aperture. Aperture length is the longest dimension of the shell opening, and aperture width is its perpendicular measurement. Two ratios (R3 and R4) were utilized to describe aperture structure (Krashevska et al., 2020; Marcisz et al., 2020). R3 = aperture length / shell width reflects the relative size of the aperture compared to the shell, while R4 = aperture width / aperture length captures the aperture's shape. Additional categorical traits describe the aperture position, invagination, rim type, and the presence or absence of a collar.

The fourth block focuses on structural features, such as the existence of internal partitions, spines, horns, or shell coverings, which play roles in predator defense and competitive strategies (van Bellen et al., 2018; Marcisz et al., 2020).

Lastly, feeding behavior was used to characterize the trophic level of testate amoebae (Payne et al., 2016; Creevy et al., 2018).

Additionally, all testate amoeba species were assigned to 16 morphological types based on Bonnet's (1975) classification system.

Table 1. Description of functional traits of testate amoebae.

Block	Name	Description	Data Type	Range
Shell (test) dimensions	Shell length	First axis from the aperture of the shell to opposite side (unit: µm).	Numerical	5.50-410.50
	Shell width	Second axis is perpendicular to it and the maximum value in size (unit: µm).	Numerical	4.12-309.50
	Shell depth	Third axis is perpendicular to it and the second in size (unit: µm).	Numerical	3.88-309.50
	R1	The ratio between shell width and shell length (shell width / shell length).	Numerical	0.25-13.64
	R2	The ratio between shell depth and shell width (shell depth / shell width).	Numerical	0.20-1.00
Outline	Shell (test) shape	1-sphere, 2-hemisphere, 3-cylinder, 4-patelliform, 5- rectangular cuboid, 6-ovoid, 7-pyriform, 8-spiral.	Categorical	1-8
Aperture (Pseudostome)	Aperture length	The longest dimension of the opening of the shell (unit: µm).	Numerical	2.62-142.50
	Aperture width	The shorter dimension perpendicular to the aperture length (unit: µm).	Numerical	2.50-142.50
	R3	The ratio between aperture length and shell width (aperture length / shell width).	Numerical	0.10-1.09
	R4	The ratio between aperture width and aperture length (aperture width / aperture length).	Numerical	0.11-1.00
	Position of the aperture	1-straight terminal, 2-sub terminal, 3- central ventral, 4-shifted ventral, 5-amphistomic.	Categorical	1-5
	Degree of invagination of aperture	0-absent, 1-slightly, 2-strongly.	Categorical	0-2
	Aperture rim	1-straight, 2-curved, 3-lobbed, 4-denticular.	Categorical	1-4
	Presence/absence of collar	0-absence, 1- presence.	Binary	0-1
Structural features	Shell covering	1-organic, 2-xenosomes, 3-idiosomes, 4-cleptosomes.	Categorical	1-4
	Presence/absence of internal partitions	0-absence, 1- presence.	Binary	0-1
	Presence/absence of spines or horns	0-absence, 1- presence.	Binary	0-1
Trophic features	Feeding type	1-mixotrophy, 2-bacterivory, 3-predatory	Categorical	1-3

2.1.2 Abundance data

The second part is abundance data of testate amoebae, which were collected from a range of sampling sites spanning the Eurasian continent. The sampling sites cover a spatial range from 50 to 70°N and 28 to 158°E (Fig. 1) and encompass three distinct habitats (peatlands, mineral soils, lakes). Specifically, data from 6 sampling locations in Siberia (Zapolyarniy, Urengoi, Surgut and Tobolsk), European Russia (Penza region) and Baikalia were employed in a main study comparing sphagnum- and soil-dwelling testate amoeba assemblages. Data from 75 peatlands were analyzed for biogeographical patterns in sphagnum-dwelling testate amoeba assemblages (Fig. 1). In addition, data from 6 sampling locations in Western Siberia (Zapolyarniy, Urengoi, Surgut, Tobolsk, Tumen and Kurgan) were used to investigate the latitudinal gradient of *β*-diversity in soil-dwelling testate amoeba assemblages.

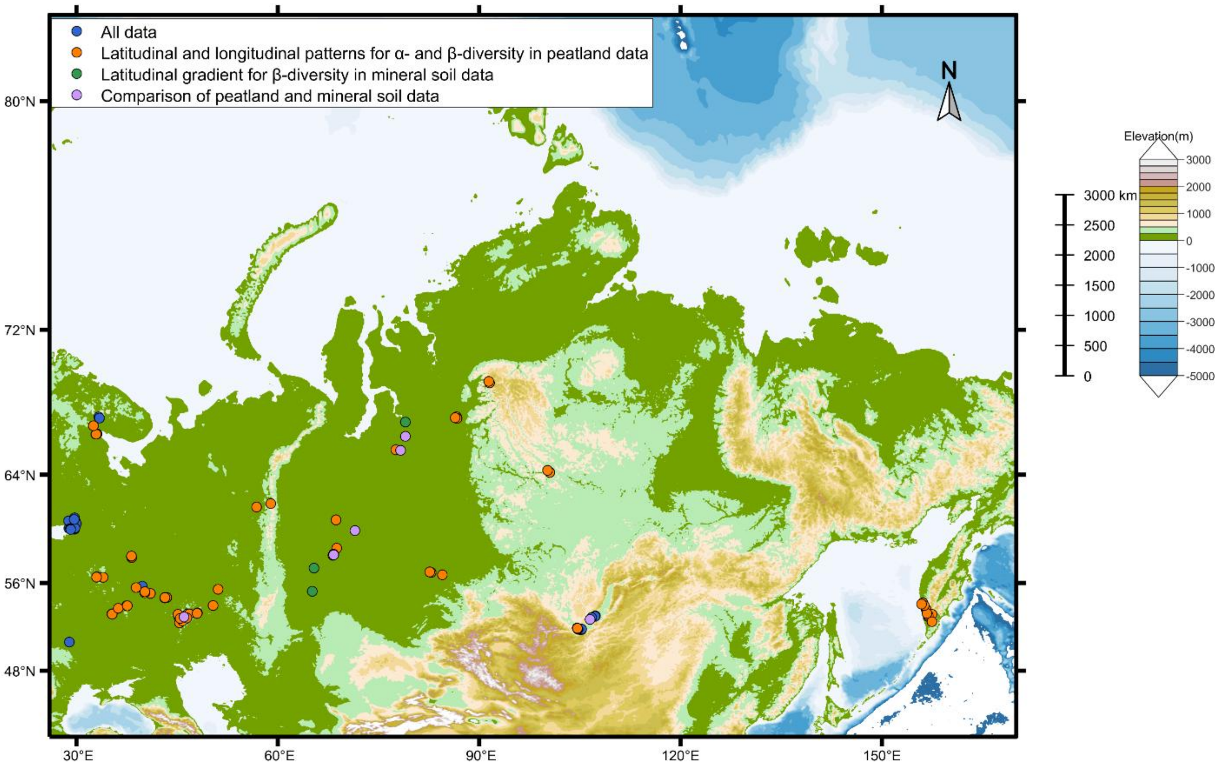

Fig 1. Location of sampling sites.

Samples were systematically collected from peatlands, forests and lakes across Eurasian continent, targeting both main terrestrial and freshwater habitats (Fig. 1). Sampling was carried out during the summer months during 2004 to 2020 and it was designed to capture the ecological variability within and across different habitat types, recognizing the importance of comprehensive coverage as a fundamental principle of ecological research. To achieve this, representative samples were carefully collected from key microhabitats, including sphagnum, moss, lichen and litter. For each habitat, adequately sized samples were taken in one to three replicates (Mazei et al., 2017a) to account for the inherent heterogeneity of these environments. This approach ensured that the sampling process adequately reflected the structural and functional complexity of the testate amoeba assemblages across diverse substrates. Samples were selected to represent the predominant substrate in each location. To preserve the quality of the samples, they were securely stored in plastic bags and kept in cool, dry conditions (Mazei et al., 2015). In total, 1635 samples were collected, of which 1115 were from peatlands, 91 samples were from lakes, while the remaining 429 samples were from mineral soils (forests). Previous studies have partially documented the testate amoeba data from these regions (Mazei, Tsyganov, 2007; Mazei, Bubnova, 2009; Mazei, Chernyshov, 2011; Mazei et al., 2012; Mazei et al., 2017a; Tsyganov et al., 2017; Mazei et al., 2020; Saldaev et al., 2023; Saldaeva et al., 2024; Su et al., 2024).

For the comparative study between sphagnum- and soil-dwelling testate amoeba assemblages, 170 sphagnum-dwelling samples and 150 soil-dwelling samples were selected. In peatlands, samples were taken from a range of microhabitats, including sphagnum-dominated peat, moss, lichen and various types of litter (such as *Carex spp*., *Eriophorum spp*., shrub vegetation, *Salix spp*. and *Phragmites australis*). In mineral soil samples were obtained from forest ecosystems and included six distinct microhabitats to account for small-scale spatial heterogeneity. These microhabitats included leaf litter near tree butts, litter under tree crowns, inter-crown spaces, and sites dominated by mosses, *Sphagnum sp*., and *Cladonia sp*. This detailed categorization of sampling habitats ensures comprehensive coverage of both soil types and their respective ecological contexts.

In the analysis of latitudinal gradient for α-diversity in sphagnum-dwelling testate amoeba assemblages, the dataset includes a total of 816 samples from peatlands, with 296 collected from hummocks, 314 from lawns, and 206 from hollows. Hummocks are elevated, well-drained microtopographic features typically dominated by sphagnum mosses and dwarf shrubs, creating relatively dry and stable habitats. In contrast, lawns and hollows are lower-lying areas with higher moisture levels; lawns have intermediate water tables and are often covered by sedges and grasses, while hollows being the wettest areas, are frequently inundated and characterized by the presence of aquatic or semi-aquatic vegetation.

In the study on latitudinal gradients in β-diversity, 111 samples from mineral soils were used with following four nested scales: sub-zone, ecosystem type, microhabitat and sample. In each sub-zone, between two and five ecosystem types were chosen to capture the diversity of vegetation. Sampling was conducted across six distinct microhabitats (including leaf litter near tree bases, beneath the canopy, in open spaces between crowns, and areas dominated by green moss, *Sphagnum sp.*

or *Cladonia sp.*). To account for fine-scale spatial variability, two to six microhabitats were sampled within each ecosystem by collecting surface material (~10 cm^3) from characteristic substrates at a depth of 1–3 cm. For every microhabitat, three replicate samples were gathered at intervals of several tens of meters.

For the analysis of testate amoebae, the samples were processed using a water-based extraction method (Mazei et al., 2011), involving wet sieving and shell concentration through sedimentation. Identification and counting of the amoebae were performed under light microscopy at magnifications of 200× and 400×. Species identification followed the taxonomic guide by Mazei, Tsyganov (2006), ensuring the highest possible taxonomic precision (Mitchell et al., 2014).

Crucially, Yuri Mazei, Andrey Tsyganov, Natalia Mazei, Viktor Chernyshov, Alexander Komarov, Kirill Babeshko, Elena Malysheva, Boris Levin and Damir Saldaev conducted fieldwork and collected samples, all data were provided by Yuri Mazei.

2.1.3. Climate data

The third part is climatic characteristics of the sampling sites. Due to the sampling regions covering wide latitudinal range, the climate types and vegetation characteristics represent significant diversity. The northern areas are primarily characterized by a polar climate, with long, cold winters and short, cool summers, and relatively low precipitation. Vegetation is mainly tundra and coniferous forest. The central region falls within a temperate continental climate, marked by significant seasonal temperature variations, with warm summers and harsh winters.

Precipitation is mainly concentrated in the summer, and vegetation consists largely of coniferous forests, mixed forests, and grasslands. The southern areas include forest-steppe, with hot summers and relatively mild winters, and moderate precipitation, also mostly occurring in summer. Vegetation here is predominantly grasslands and broadleaf forests. Overall, the annual temperature and precipitation of these sampling sites show a gradual increase from north to south, providing a diverse ecological background for studying the community structures of testate amoebae within these regions.

The main research sites (comparison of sphagnum- and soil-dwelling testate amoeba assemblages) cover a variety of geographic regions across Siberia (Zapolyarniy, Urengoi, Surgut and Tobolsk), European Russia (Penza) and Baikalia (Fig. 1), each featuring unique climatic and geographical characteristics (Trofimova & Balybina 2014). Four of the sampling areas in Western Siberia follow a north-south latitudinal gradient. Zapolyarniy and Urengoi, located near or within the Arctic Circle at high latitudes, experience extreme polar tundra climates. These areas are marked by long, severe winters and short, cool summers, with tundra vegetation such as mosses and lichens dominating due to the harsh environmental conditions, resulting in relatively uniform plant cover. In contrast, Tobolsk and Surgut, situated in the West Siberian Plain at lower latitudes, experience a subarctic climate, featuring long, cold winters and brief, mild summers. This climate supports taiga forests dominated by cold-hardy coniferous species such as spruces and larches. These regions also have low evaporation rates and relatively high humidity. Two other sampling locations were in the Eastern part of the Russian Plain (Middle Volga, Penza region) and near Lake Baikal in Eastern Siberia. These regions are positioned in warmer zones, distant from the Arctic Circle. Both the Baikalia and Middle Volga regions feature mixed forests and forest-steppe vegetation. The regions exhibit a temperate continental climate, characterized by cold winters, hot summers, significant annual temperature variations, concentrated precipitation, and pronounced seasonal changes.

Tobolsk, Surgut, and Urengoi fall within the West Siberian taiga ecoregion (Dinerstein et al., 2017), which is dominated by Retisols and Podzols. These soils are typically moist in the summer, due to their organic-rich topsoil layers and cool, humid climate, fostering a variety of microbial communities adapted to waterlogged environments. Zapolyarniy belongs to the Yamal-Gydan tundra ecoregion, known for permafrost-affected soils like Cryosols. Baikal and Penza are located in the South Siberian forest-steppe and East European forest-steppe ecoregions, respectively. These ecoregions are characterized by Phaeozems and Chernozems, which are generally well-drained, drier, and rich in organic matter, supporting microbial communities adapted to lower humidity and nutrient-rich conditions. Soil moisture regimes in these areas are primarily influenced by the regional climate. Soils at the Zapolyarniy, Urengoi, Surgut, and Tobolsk sites have a predominantly udic moisture regime, while those in the Baikal and Penza regions exhibit an ustic moisture regime (Soil Survey Staff, 1999).

For the analysis of latitudinal gradient for α- and β-diversity in sphagnum-dwelling testate amoeba assemblages, we collected climate features from the WorldClim (version 2.0) database, covering the period from 1970 to 2000 (https://www.worldclim.org), with a spatial resolution of 10 minutes. We used 19 standard WorldClim bioclimatic variables, which describe annual trends (e.g., mean annual temperature, annual precipitation), seasonality (e.g., temperature and precipitation seasonality), and extreme or limiting environmental factors (e.g., maximum temperature of the warmest month, precipitation of the driest month). Additionally, we included Potential Evapotranspiration (ET0) and Aridity Index, representing the atmospheric demand for water, obtained from the Global Aridity Index and Potential Evapotranspiration (ET0) database (version 3.0, spatial resolution of 30 seconds, 1970–2000) (Zomer et al., 2022). Using these data, we also calculated the Marsz Oceanity Index, which reflects the degree of maritime climate influence, and the Conrad-Pollak Continentality Index, which quantifies the extent of continental climatic effects (Andrade, Corte-Real, 2017). In total, we have 23 potential climate factors.

2.2. Community structure metrics

The community structure metrics include taxonomic diversity indices, functional diversity indices, community-weighted means for functional traits (CWMs) and null model metrics. Calculating community structure metrics provides crucial insights into the organization and functioning of ecological communities. These metrics allow researchers to understand how species and their traits contribute to ecosystem processes, predict responses to environmental changes, and assess biodiversity conservation needs. All community structure metrics are calculated using R (R Core Team, 2021).

2.2.1. Taxonomic diversity

Taxonomic diversity (e.g. α- and β-diversity) reveal the variety and distribution of species, which reflects the stability and resilience of ecosystems. To quantify diversity, we adopted the framework of Hill numbers D_q, which represent the "true diversity" or the number of equally abundant species that would yield the same diversity as observed in an empirical community (Hill, 1973; Chao et al., 2012). The Hill numbers are defined as:

$$D_q = \left[\sum_{i=1}^{S} {p_i}^{q}\right]^{\frac{1}{1-q}}$$

where S is the species richness, p_i is the relative abundance of i-th species and q is the order of diversity which specify the contribution of rare and abundant species to Hill number. For $q=0$, D_0 equals species richness S, reflecting the total number of species. For $q=1$, D_1 becomes the exponential of the Shannon index (e^H), where $H = -\sum_{i=1}^{S} p_i \log_2 p_i$, representing diversity weighted by species relative abundance. For $q=2$, D_2 equals the inverse Simpson index $D_2 = 1/\sum_{i=1}^{s} p_i^2$, emphasizing the dominance of abundant species. We also calculated the Pielou index $E = H/\ln S$ to quantify evenness.

For the comparison of organic and mineral soil communities, we calculated the above four indices (S, D_1, D_2, E) at sample level as taxonomic diversity indicators. Similarly, sample-level diversity was estimated with S, D_1 and E for the analysis of latitudinal gradient of α-diversity in sphagnum-dwelling testate amoeba assemblages.

For investigating the latitudinal gradient of β-diversity at nested scales in mineral soils, we quantified α-, β-, and γ-diversity across different hierarchical levels (climatic sub-zone, ecosystem, microhabitat and sample) using multiplicative partitioning, allowing for comparisons across scales:

$$^{\beta}D_q = \frac{^{\gamma}D_q}{^{\alpha}D_q}$$

where $^{\gamma}D_q$ corresponds to the effective diversity calculated for all samples pooled together and $^{\alpha}D_q$ is the mean effective diversity calculated at the sample level. Since $^{\beta}D_q$ strongly depends on the number of samples, this metric cannot be used to directly compare the β-diversity among communities with different number of samples. That's why we used similarity/differentiation measure C_{qN} proposed by Chao et al., (2012):

$$C_{qN} = \frac{\left(^{\beta}D_q\right)^{q-1} - \left(\frac{1}{N}\right)^{q-1}}{1 - \left(\frac{1}{N}\right)^{q-1}}$$

where N is the number of samples and q is the order of diversity. This measure is applicable to compare communities with different number of samples. C_{qN} is a similarity measure which is always in the range $[0,\ 1]$. To get a differentiation (β-diversity) measure we subtracted it from the unity: $1 - C_{qN}$.

To adopt multiplicative partitioning for several levels of hierarchical sampling we calculated β-diversity (both $^{\beta}D_q$ and $1 - C_{qN}$) for each sub-zone, ecosystem and microhabitat. To do this, we aggregated samples at each level and considered β-diversity among ecosystems within sub-zone, among microhabitats within ecosystem and among replicate samples within microhabitat. Then, we averaged corresponding components to get estimates for three scale levels. We calculated normalized beta diversity by using the package 'vegan' (Oksanen et al., 2013).

For the analysis of latitudinal gradient for β-diversity in sphagnum-dwelling testate amoeba assemblages, we also used the $1 - C_{qN}$ framework, the zeroth-order and first-order β-diversity within microhabitats were calculated using $1\text{-}C_{0N}$ and $1\text{-}C_{1N}$, respectively.

Table 2. Notation system and α- and β-diversity measures.

Notation	**Explanation**	**Formula**
N_i	The abundance of the i species	
N	The sum of abundance values of all species	
P_i	The relative abundance of the i species	$P_i = N_i/N$
q	Diversity order	
D_q	Hill number	$D_q = \left[\sum_{i=1}^{S} P_i^q\right]^{\frac{1}{1-q}}$
S	Species richness	$S = D_0$
H	Shannon index	$H = -\sum_{i=1}^{S} P_i \, log_2 \, P_i$
D_1	Exponential of the Shannon index	$D_1 = e^H$
D_2	Inverse Simpson index	$D_2 = 1 \Big/ \sum_{i=1}^{S} P_i^2$
E	Pielou evenness index	$E = H/\ln S$
${}^{\beta}D_q$	Multiplicative β-diversity	${}^{\beta}D_q = \frac{{}^{\gamma}D_q}{{}^{\alpha}D_q}$
$1\text{-}C_{qN}$	Normalized multiplicative β-diversity	$1 - C_{qN} = 1 - \frac{\left({}^{\beta}D_q\right)^{q-1} - \left(\frac{1}{N}\right)^{q-1}}{1 - \left(\frac{1}{N}\right)^{q-1}}$

2.2.2. Functional diversity

Functional diversity metrics capture the range of functional traits represented within a community, indicating its potential to perform various ecological roles under different environmental conditions. These metrics were derived based on the functional distances between testate amoeba species. These distances were calculated using the Gower distance (Gower, 1971) as it accommodates a mix of trait types:

$$GD_{ij} = \frac{\sum_{k=1}^{p} d_{ijk}\delta_{ijk}}{\sum_{k=1}^{p} \delta_{ijk}}$$

$$d_{ijk} = \begin{cases} 1 - \left|x_{ik} - x_{jk}\right|/R_k & \mathit{Quantitative\ variables} \\ 1\{x_{ik} = x_{jk}\} & \mathit{Qualitative\ variables} \end{cases}$$

where GD_{ij} is the Gower distance between two species i and j. p represents the total number of traits being considered for the calculation. A quantity δ_{ijk} is also computed: if x_i and x_j can be compared along trait k, then δ_{ijk} is 1. If x_i and x_j cannot be compared along trait k (such as due to missing values), δ_{ijk} is set to zero. R_k represents the range of the numeric traits (difference between maximum and minimum value) in the dataset.

When calculating Gower distances, we used all the traits listed in Table 1. Traits were grouped into five blocks (shell dimensions, outline, aperture, structural features, trophic features), and equal weight was assigned to each category (Table 1). Within these blocks, trait weights were distributed in proportion to the number of traits. The Gower distance was computed using the gowdis() function from the ‘FD’ package (Laliberté et al., 2014).

Functional diversity metrics were computed using a distance-based framework that included principal coordinates analysis (PCoA) from functional distances. The resulting PCoA axes were used as new "traits" to calculate three functional diversity metrics. Functional richness (FRic) was calculated using the convex hull volume, which represents the smallest geometric shape encompassing all species in the functional trait space, capturing the range of functional traits within the community. Functional evenness (FEve) was computed as the normalized sum of the branch lengths of a minimum spanning tree, which is a network connecting all species in the functional space with the shortest total distance, weighted by species abundances. This metric quantifies the uniformity of species distribution within the occupied trait space. Functional divergence (FDiv) reflects the extent to which species abundances are concentrated toward the edges of the functional space, indicating how traits are distributed in relation to resource use or ecological strategies within the community (Villéger et al., 2008; Laliberté, Legendre, 2010).

2.2.3. Community-weighted means (CWMs)

The community-weighted means (CWMs) for functional traits provide information on the average traits in the testate amoeba assemblages, offering a direct link between species composition and ecosystem functions. Each sample was described by mean trait values:

$$CWMs = \sum_{i=1}^{n} p_i \times trait_i$$

p_i is the relative abundance of species i, $trait_i$ is the trait value of species i. For quantitative traits, community-weighted means (CWMs) were computed using species abundances as weights (Peres-Neto et al., 2017). For categorical traits, the proportions of each category were calculated. Functional diversity indices and community-weighted means of functional traits were calculated with the dbFD function from the ‘FD’ package (Laliberté et al., 2014).

2.2.4. Null model metrics

Furthermore, we employed a null model framework to assess the mechanisms governing community assembly. Mean pairwise functional distances between species were computed for each sample (simple and abundance-weighted versions):

$$MPD = \begin{cases} \dfrac{\sum_{i\neq i}^{S} GD_{ij}}{S(S-1)/2} & simple \\ \dfrac{\sum_{i\neq i}^{S} p_i p_j GD_{ij}}{S(S-1)/2} & abundance - weighted \end{cases}$$

where GD_{ij} refers to Gower distance, S is species richness, p_i and p_j are the relative abundances of species i and j in the community. The observed MPD values were compared to those generated by the null model, which simulates species distribution at random across samples (Webb, 2000; Cadotte, Davies, 2016). An independent swap null model was selected due to its suitability for quantitative data, its reliability in avoiding type I errors, and its widespread availability in common software (Miller *et al.* 2017). The standardized effect size was then computed by subtracting the null model mean from the observed MPD and dividing the result by the standard deviation of the null model (Webb, 2000; Cadotte, Davies, 2016):

$$SES.MPD = \frac{MPD_{observed-mean(MPD_{null})}}{sd(MPD_{null})}$$

Positive SES.MPD values indicate higher functional diversity than expected by chance (functional overdispersion), supporting the hypothesis that biotic interactions (e.g., competitive exclusion or facilitation) play a dominant role in community assembly. Conversely, negative SES.MPD values suggest that species within the community are more similar than expected by random distribution (functional clustering), which is typically attributed to environmental filtering. For SES.MPD calculations, we used the ‘independentswap’ null model with 999 randomizations via the ses.mpd function in the ‘Picante’ package (Kembel et al., 2010).

2.3. Statistical analysis

All data analysis was carried out using the R software (R Core Team, 2021). For the development of the system of trait-based functional groups, hierarchical clustering was performed with Ward linkage method to categorize the 372 testate amoeba species (Murtagh, Legendre, 2014), which generates a nested structure of bifurcating divisions. Dendrograms were used to visualize the clustering results. The Ward clustering was executed through the hclust function in ‘stats’ package (R Core Team, 2021). To determine the optimal number of functional groups, the silhouette method was applied. For each species, its cluster membership was evaluated using the silhouette width, a metric that quantifies how similar an individual is to its own cluster compared to other clusters. The silhouette width ranges from -1 to 1, where values close to 1 indicate a species is well-matched to its cluster, values around 0 suggest it lies on the boundary between clusters, and negative values imply potential misclassification. The silhouette widths were then averaged across all species to assess the overall quality of clustering. The classification with the highest mean silhouette width was deemed optimal (Rousseeuw, 1987). We tested group numbers ranging from 2 to 50 and selected the best partition based on the silhouette results. The average silhouette width was calculated using the silhouette() function from the ‘cluster’ package (Maechler et al., 2013).

Principal Coordinate Analysis (PCoA) was conducted to visualize the differences between functional groups based on the Gower distances, producing both 2D and 3D ordination diagrams. The PCoA was implemented via the cmdscale() function from the ‘stats’ package (R Core Team, 2021). To better interpret the PCoA-derived functional space, relationships between trait values and the first three PCoA axes (PC1, PC2, PC3) were examined. For quantitative traits, linear regression was used, while for binary traits, logistic regression was performed with a generalized linear model employing a binomial residual distribution. We then simultaneously mapped these species into both our newly developed functional groups and the established morphological groups to facilitate a comparison between the two. To visually represent the proportion of species from each traditional group within the newly defined functional groups, we created a stacked bar chart. By analyzing the mapping of species in both classification schemes, we evaluated the level of alignment between the functional and morphological groupings.

For the comparison of sphagnum- and soil-dwelling testate amoeba assemblages, we applied PCA-based ordination and permutational ANOVA (Anderson, 2014) to examine variations in species composition across different terrestrial habitats and geographic regions. Principal components were computed using the rda function from the ‘vegan’ package (Oksanen et al., 2013) based on Hellinger-transformed species relative abundances (Legendre, Gallagher, 2001).

Permutational ANOVA (PERMANOVA) was performed based on Bray-Curtis dissimilarities matrix using the adonis2 function, also from the ‘vegan’ package (Oksanen et al., 2013). Habitat type, region, and their interaction were considered as factors in PERMANOVA. Statistical significance was evaluated through 9999 permutations. To analyze all community structure metrics, we employed non-parametric methods using the Scheirer Ray Hare rank test, implemented through the scheirerRayHare function in the ‘rcompanion’ package (Mangiafico, 2017). A two-way analysis was conducted to test the effects of habitat type, region, and their interaction. Given our emphasis on the impact of habitat type, comparisons between sphagnum- and soil-dwelling testate amoeba assemblages within each region were performed using the rank-based Wilcoxon test. Additionally, we conducted single-sample tests to assess whether SES.MPD deviated significantly from zero, indicating either clustering (negative SES.MPD) or overdispersion (positive SES.MPD). These tests were also performed using rank-based Wilcoxon methods.

For the analysis of latitudinal gradient of α- and β-diversity in sphagnum-dwelling testate amoeba assemblages, we filter the appropriate climate factors as explanatory variables as the first step. Collinearity among 23 climatic variables considered as potential predictors was examined using the Variance Inflation Factor (VIF). Only factors with a VIF of less than 10 were retained as fixed effect factors in further analyses and models, along with microhabitat type. Second, we applied linear mixed-effects models to explore the relationship between community diversity metrics (S, D_1, E) and environmental factors, with peatland ID included as a random factor. For each diversity metric, we conducted three types of analysis.

Initially, we analyzed the effect of microhabitat, including post hoc comparisons between microhabitats. Then, we modeled the relationship with environmental predictors separately. Finally, we constructed models with multiple predictors. The quantitative environmental factor models included microhabitat type as well as the interaction between environmental predictors and microhabitats. In single-predictor analyses, we considered the effects of predictors within each of the three microhabitats separately (when the interaction between predictors and microhabitat was significant) or the effects of predictors across microhabitats (when the interaction was not significant). When the interaction was significant, we also tested the hypothesis of slope coefficients differing from zero and conducted multiple comparisons of slope coefficients across different microhabitats. For multi-predictor analyses, we used a stepwise backward selection procedure to construct a simplified model. For all models, we reported the marginal R^2, representing the variance explained by the fixed factors. Mixed-model analyses were conducted using the "lmerTest" (Kuznetsova et al., 2017) and "MuMIn" packages (Barton, 2012) in R (R Core Team, 2021); post hoc comparisons were performed using the glht() function from the "multcomp" package (Hothorn et al., 2008).

For latitudinal gradient analysis of β-diversity in mineral soils, we calculated $1 - C_{qN}$ metrics (q = 0, 1, 2, 3) and performed the null model analysis of $1 - C_{qN}$ metrics by a randomization procedure (9999 permutations) with the oecosimu function in the 'vegan' package (Oksanen et al., 2013) to test the statistical significance of β-diversity at three scale levels. The observed metrics were compared to the expected values in a null model. Since our raw data were individual cell counts and we calculated abundance-based diversity metrics we used individual-based null-model which preserve both row (sample) and column (species) sums. The model is based on swapping random sub-matrices (Gotelli, Entsminger, 2003; Ulrich, Gotelli, 2010). Randomizations were run at the scale of initial samples. For each set of randomizations mean (expected) value of the metric was calculated. Significance of the difference between observed and expected values was calculated as the proportion of null-model values, which have a more extreme deviation from the expected value than an observed value.

Chapter 3. Functional groups of testate amoebae

3.1. Description of functional traits[1]

The trait data have been collected from the primary literature for 372 species of testate amoebae, including the most frequently observed species within the Northern Holarctic realm. The database accounts for 100% of the species from all samples, 97% of the species listed in the pan-European peatland database, and 100% from the North American peatland database. Consequently, this dataset is considered representative of the most widely distributed testate amoeba species in the Northern Holarctic. Missing data are limited to extreme numerical trait values when specific range information was unavailable. In such instances, average values are provided, which ensuring the database includes a complete set of traits for all 372 species. Genera with the highest species diversity include *Difflugia* (81 species), *Euglypha* (35 species), and *Centropyxis* (31 species) (Fig. 2). In contrast, 19 genera are represented by only one species. The selected species span a wide range of geographic regions and habitat types, ensuring comprehensive representation. Each species is described by a collection of trait measurements, offering extensive information on key functional traits that reflect their ecological roles and behaviors. This trait database provides valuable insights into the morphological, physiological, and behavioral attributes of testate amoebae.

To more intuitively present the distribution characteristics of 18 traits for testate

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[1] The results presented in this section are published in the work:
Su J., Mazei Y.A., Tsyganov A.N., Chernyshov V.A., Komarov A.A., Malysheva E.A., Babeshko K.V., Mazei N.G., Saldaev D.A., Levin B., Yakimov B.N. Functional traits data for testate amoebae of Northern Holarctic realm // Scientific Data. 2024. V. 11. P. 1028. https://doi.org/10.1038/s41597-024-03874-0 (Q1, IF SRJ 1.867, EDN: WZJVLK, 0.79/0.45 p.s.)

amoebae, we used histograms and frequency bar charts to display the distributions of numerical and categorical traits, respectively. The distribution of 18 traits could be summarized in five main blocks. Firstly, for the majority of species, shell dimensions (shell length, width, and depth) typically range from 3 to 200 micrometers, with distributions of all three dimensions skewed rightward (Fig. 3a-3c). Over half of the species exhibit an R1 (shell width / shell length) value below one, indicating a strip-like form (Fig. 3d), while most species share equal width and depth, as shown by an R2 (shell depth / shell width) value of one (Fig. 3e). Secondly, ovoid and pyriform shell shapes are the most prevalent, while rectangular cuboid forms are less common (Fig. 4). Thirdly, more than half of the species have apertures averaging less than 50 micrometers in size (Fig. 3f-3g). The distribution of the R3 (aperture length / shell width) ratio is approximately symmetric around a median of 0.39 (Fig. 3h), and most species display a circular aperture, reflected by an R4 (aperture width / aperture length) value of one (Fig. 3i). In addition, more than half of the species possess terminal apertures that are straight, lacking invagination, with either straight or curved rims and no collar (Fig. 4). Fourthly, xenosome and idiosome shell coverings are widespread, and internal structures such as partitions, spines, or horns are generally absent (Fig. 4). Finally, the majority of these species primarily feed on bacteria (Fig. 4).

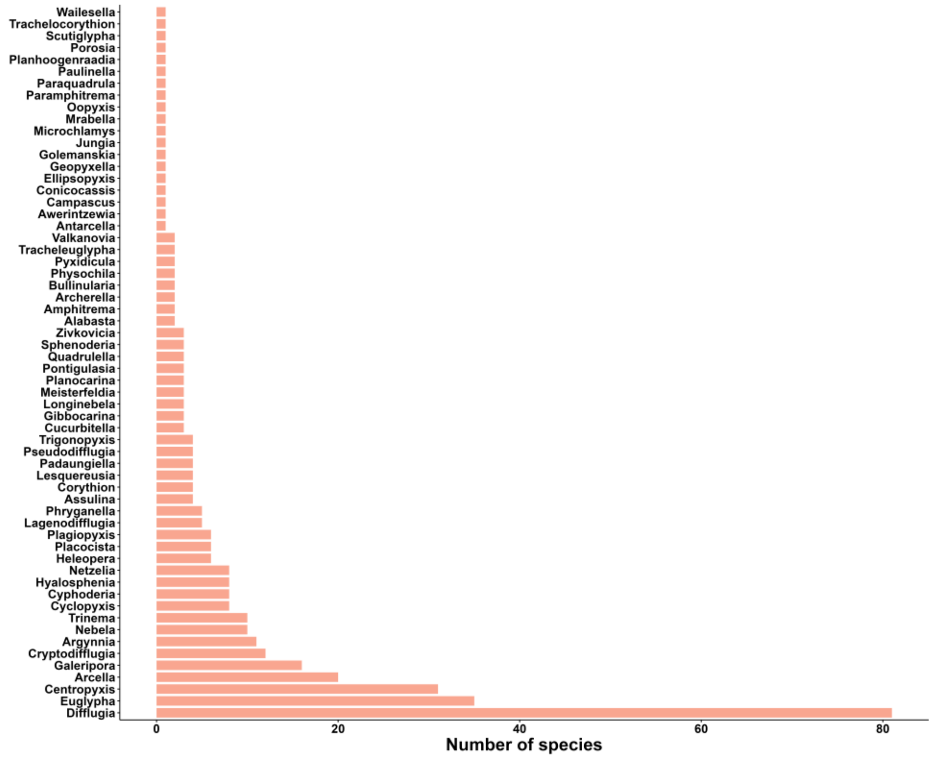
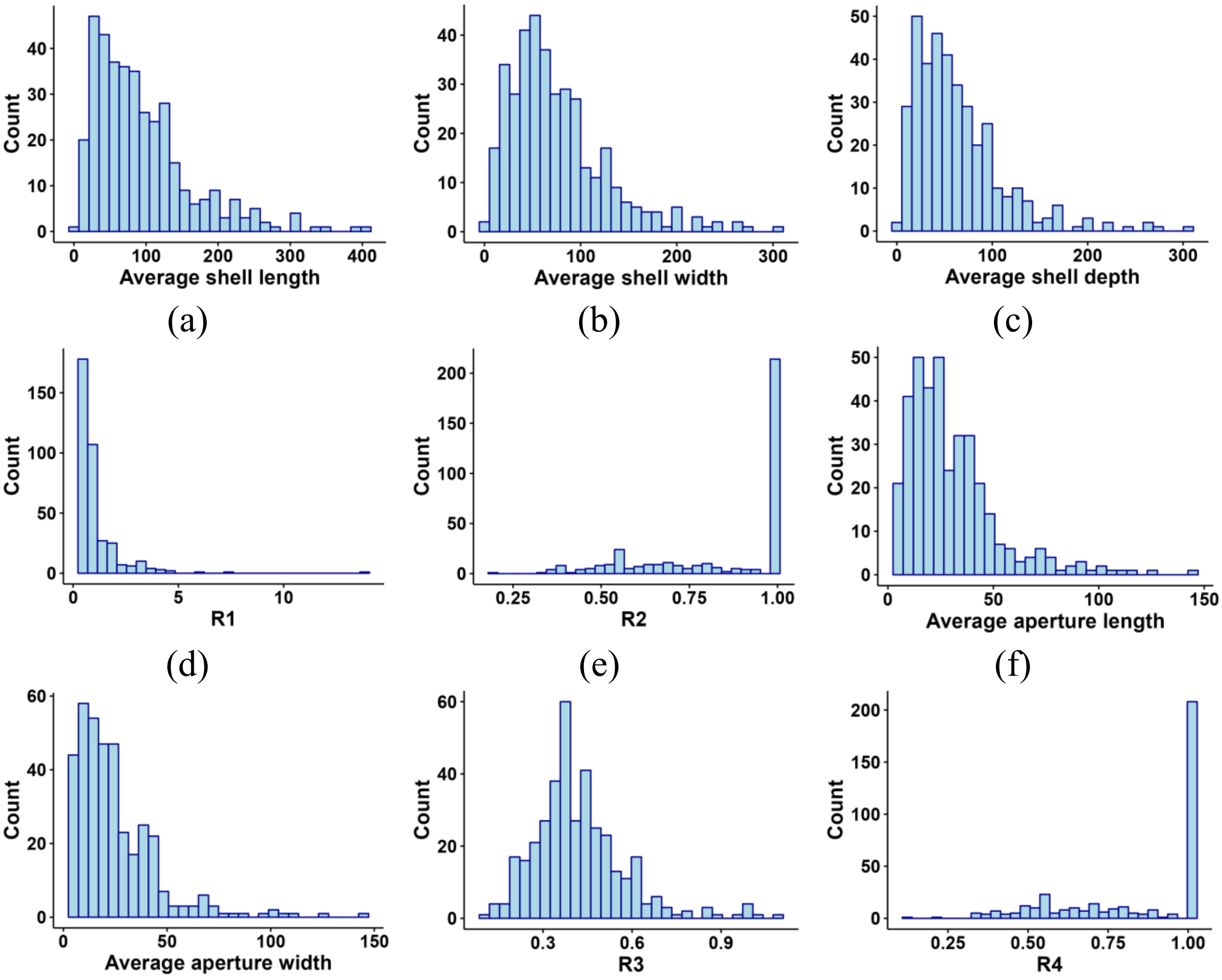


Fig 2. Number of species in each genus for trait data table.



(a) (b) (c)

(d) (e) (f)

(g) (h) (i)

Fig 3. Histogram of distribution for the numerical traits.

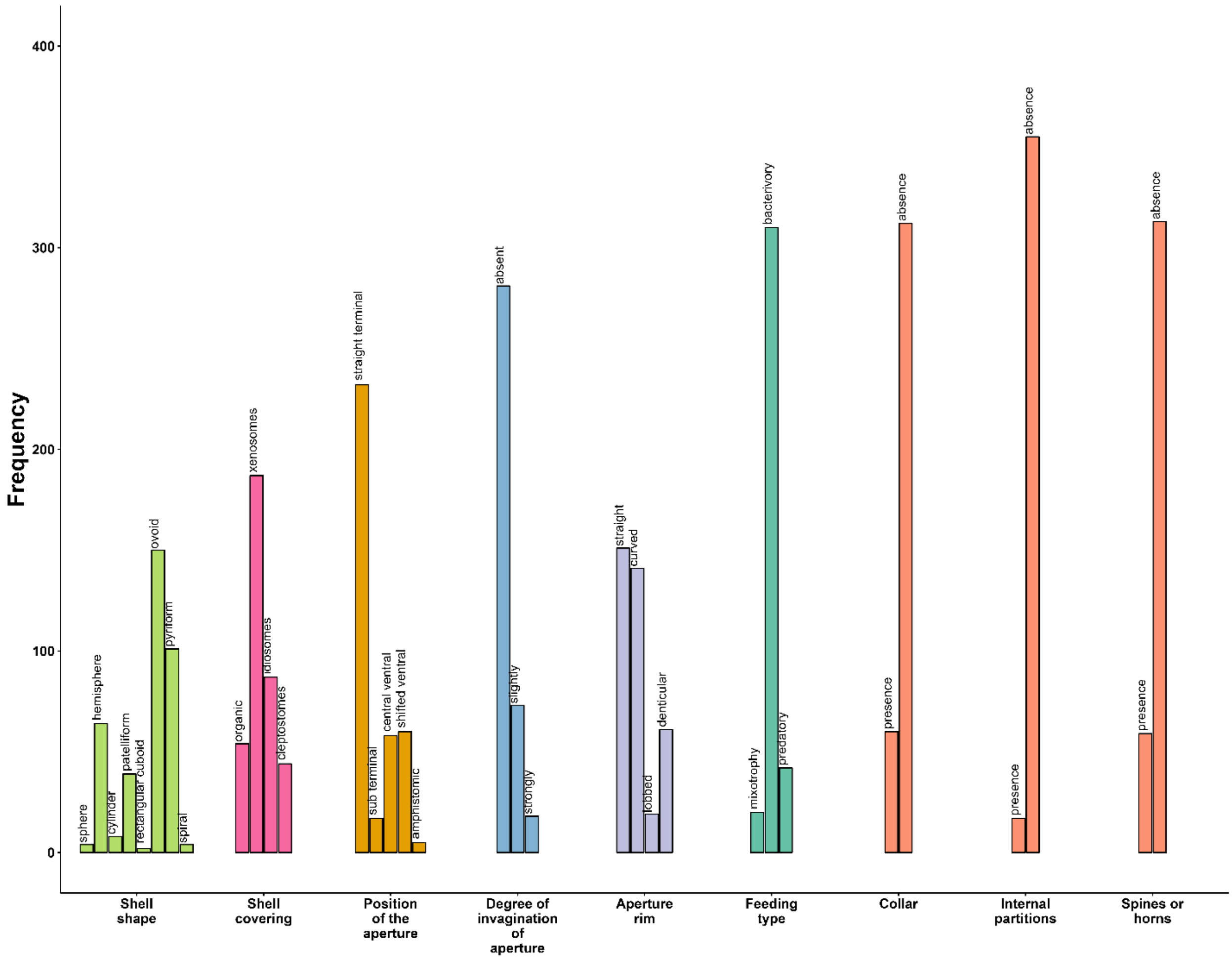


Fig 4. Bar plots of distribution for the categorical and binary traits.

3.2. Functional groups based on traits

Functional groups based on traits will provide more comprehensive ecological role information for testate amoebae. Cluster analysis was conducted to classify species into distinct functional groups based on 18 traits. Based on hierarchical clustering, we used the silhouette width method to determine the optimal number of groups. The silhouette width analysis of 372 testate amoeba species indicates that the optimal solution is clustering into seven functional groups (Fig. 5). These seven groups vary significantly, ranging from 12 to 138 species. An overall group summary is provided in Table 3, which presents the following characteristics of the seven functional groups.

Group 1 is characterized by the predominance of species with relatively large body sizes and pyriform shell shapes featuring cleptostome coverings, preying primarily on smaller testate amoeba species (predatory). In contrast, Group 2 includes the largest testate amoebae sizes across all groups. Over 50% of the species in this group exhibit a straight terminal aperture with collars and lack invagination, while their shells are covered with xenosomes. The majority of species in Group 1 are mixotrophic and lack internal partitions or spines. Group 3 shares similar traits with Group 1, but differs in having xenosome shell coverings and a bacterivorous feeding strategy. Group 4 is akin to Group 2, differing mainly in its aperture characteristics, which feature a curved rim and the absence of a collar, alongside a bacterivorous feeding type. Group 5 species are marked by hemisphere shell shapes, shifted ventral aperture positions, and xenosome coverings. Unlike Groups 2 and 4, Group 6 is represented by smaller morphotypes, with patelliform shapes and straight aperture rims. While internal infolding occurs at the aperture, the degree of invagination remains relatively mild, with a central ventral aperture position and organic shell covering. Group 7 is the most populous, encompassing 138 species and subspecies, distinguished by minimal aperture sizes and ovoid shell shapes.

The distribution of species and their corresponding functional groups within the functional space, as generated by PCoA, is illustrated in Figs 6a and 6b. The first three principal components account for a significant portion (56.9%) of the total variation within this functional space. The first principal coordinate serves as the primary axis of variation, explaining 26.3% of the variance, and differentiates between Groups 1, 4, and the combination of Groups 5-6. The second axis, accounting for 19.3% of the variation, distinguishes Group 7 from Groups 5 and 6, while the third axis, explaining 11.3% of the variation, differentiates Groups 3, 4, and 6. Therefore, a three-dimensional representation is necessary to adequately portray the functional groups of testate amoebae.

The seven functional groups identified via hierarchical clustering highlight key adaptations of testate amoebae to varying environmental conditions. Larger species, particularly those in Groups 1 and 2, exhibit traits that enhance resilience to environmental stressors, including straight terminal apertures without invagination. These groups predominantly consist of species with larger shells and complex structural features, such as collars or cleptostome coverings, which likely relate to environmental filtering and adaptation (Schönborn, 1989; van Bellen et al., 2018). The mixotrophic nature of Group 2 and the predatory behavior of Group 1 underscore the diversity of foraging strategies, enhancing the ecological success of these species in nutrient-poor environments.

Conversely, smaller morphotypes in Group 6 are typified by patelliform shells and central ventral apertures, traits potentially linked to adaptations for drier conditions (Marcisz et al., 2020). Group 7, with the highest species count, is notable for its small body and aperture sizes positioned at the straight terminal. The reduced shell size enables these species to adapt to unfavorable environmental conditions and facilitate rapid reproduction in new habitats (Macumber et al., 2020). Moreover, the smaller aperture size may reflect specific adaptations to prey size or feeding strategies (Krashevska et al., 2020). Collectively, these observations suggest that our defined functional groups hold significant ecological relevance.

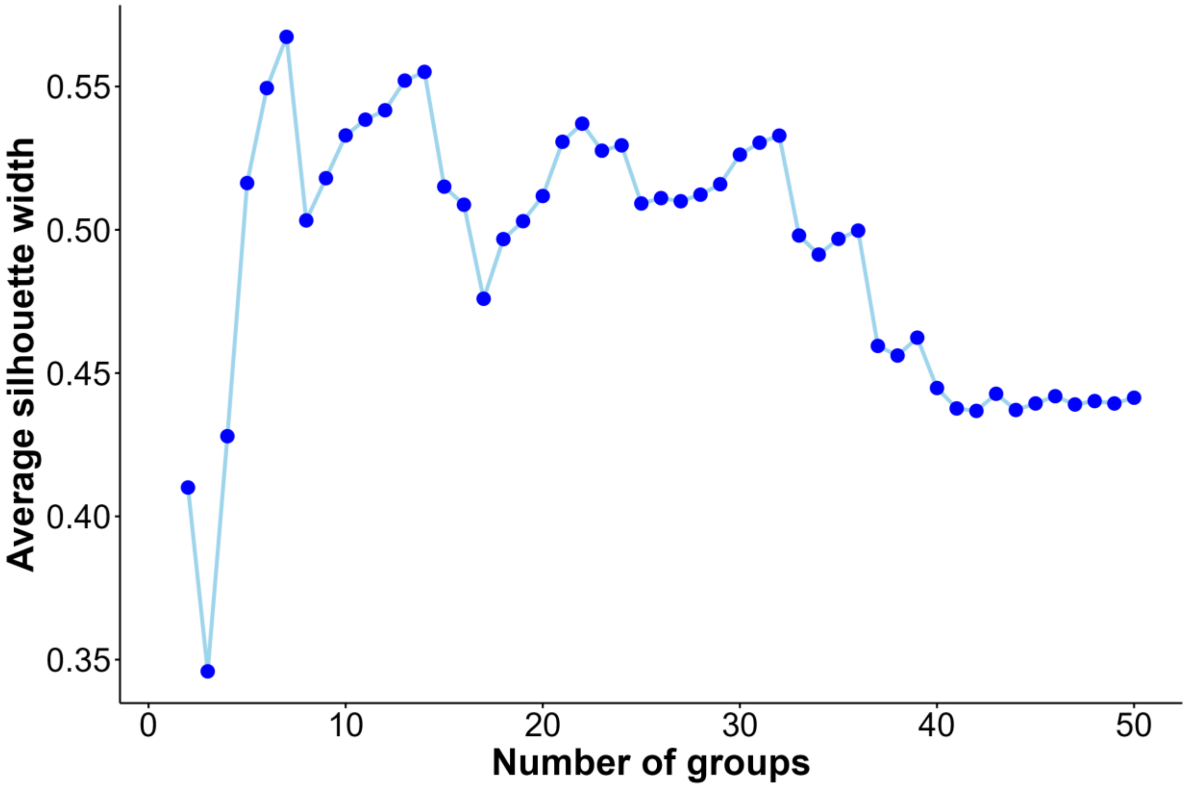
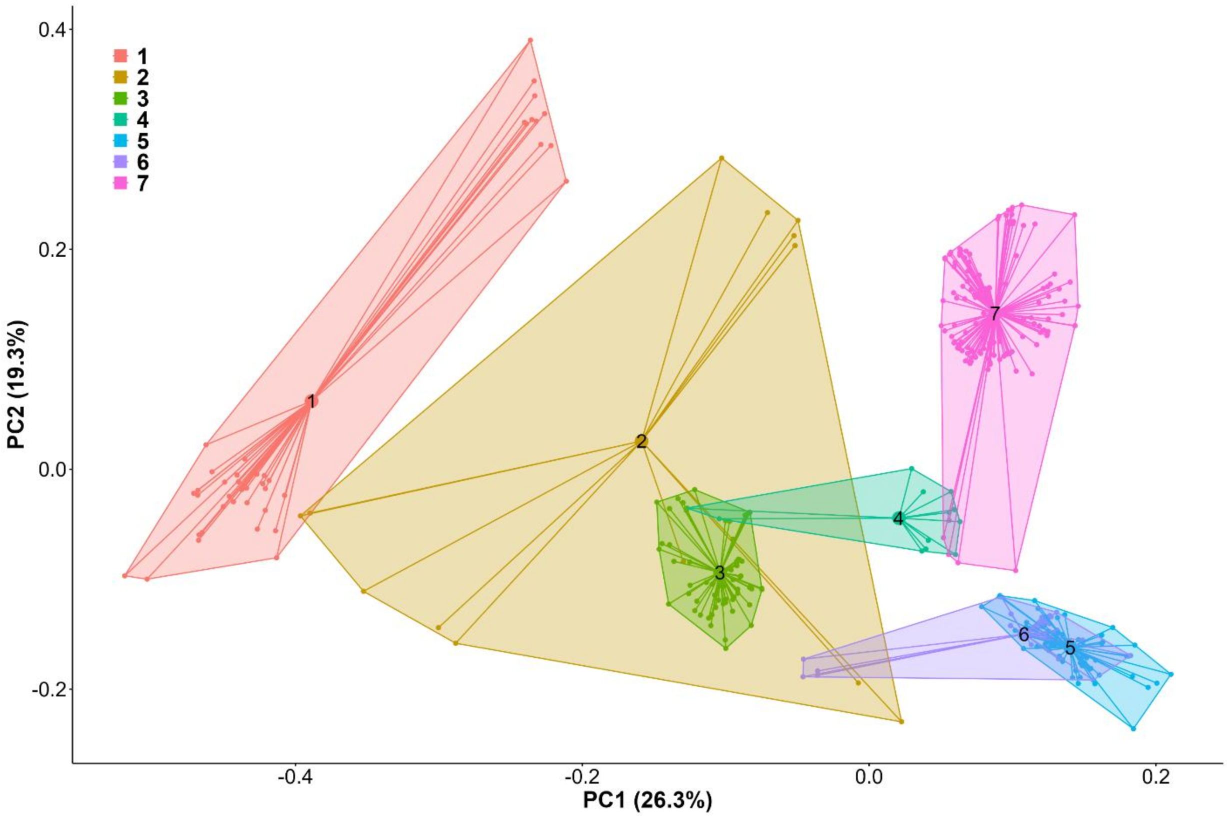
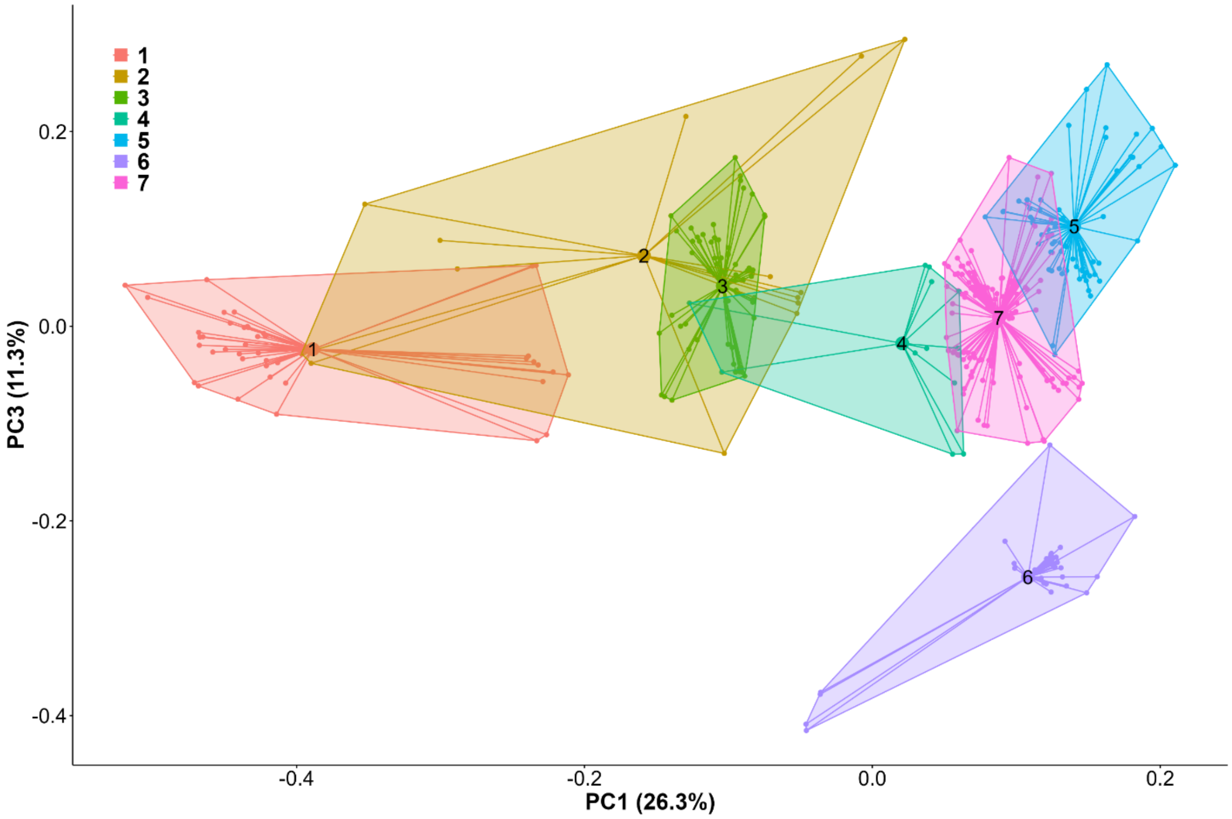


Fig 5. Relationship between the number of groups and the average silhouette width based on Ward's hierarchical clustering, the peak occurs when the number of groups is 7.



(a)



(b)

Fig 6. Functional groups (FG) in 2D functional space. (a) PC1 vs PC2, (b) PC1 vs PC3.

Table 3. Trait values of the seven identified functional groups.

FG	1	2	3	4	5	6	7
n	42	14	65	12	62	39	138
Shell length, µm	145	172	127	134	67	40	77
Shell width, µm	91	131	72	70	97	96	51
Shell depth, µm	59	110	62	51	88	96	41
R1 (shell width / shell length)	0.64	0.80	0.58	0.57	1.74	2.87	0.70
R2 (shell depth / shell width)	0.66	0.83	0.89	0.76	0.92	1.00	0.81
Shell (test) shape	pyriform	NA	pyriform	cylinder	hemisphere	patelliform	ovoid
Aperture length, µm	34	51	29	26	41	28	23
Aperture width, µm	23	44	26	23	35	28	18
R3 (aperture length / shell width)	0.38	0.40	0.43	0.39	0.46	0.29	0.46
R4 (aperture width / aperture length)	0.66	0.83	0.89	0.79	0.86	1.00	0.81
Position of the aperture	straight terminal	straight terminal	straight terminal	NA	shifted ventral	central ventral	straight terminal
Degree of invagination of aperture	absent	absent	absent	absent	slightly	slightly	absent
Aperture rim	curved	NA	NA	curved	NA	straight	NA
Presence/absence of collar	absence	presence	absence	absence	absence	absence	absence
Shell covering	cleptostomes	xenosomes	xenosomes	NA	xenosomes	organic	NA
Presence/absence of internal partitions	absence	absence	absence	absence	absence	absence	absence
Presence/absence of spines or horns	absence	absence	absence	absence	absence	absence	absence
Feeding type	predatory	mixotrophy	bacterivory	bacterivory	bacterivory	bacterivory	bacterivory

FG is a functional group. n represents the number of species for each group. Mean values are provided for quantitative traits. For categorical traits, dominating category is reported when its frequency in the group exceeds 50%. If no dominant category exists within a particular group, NA is indicated.

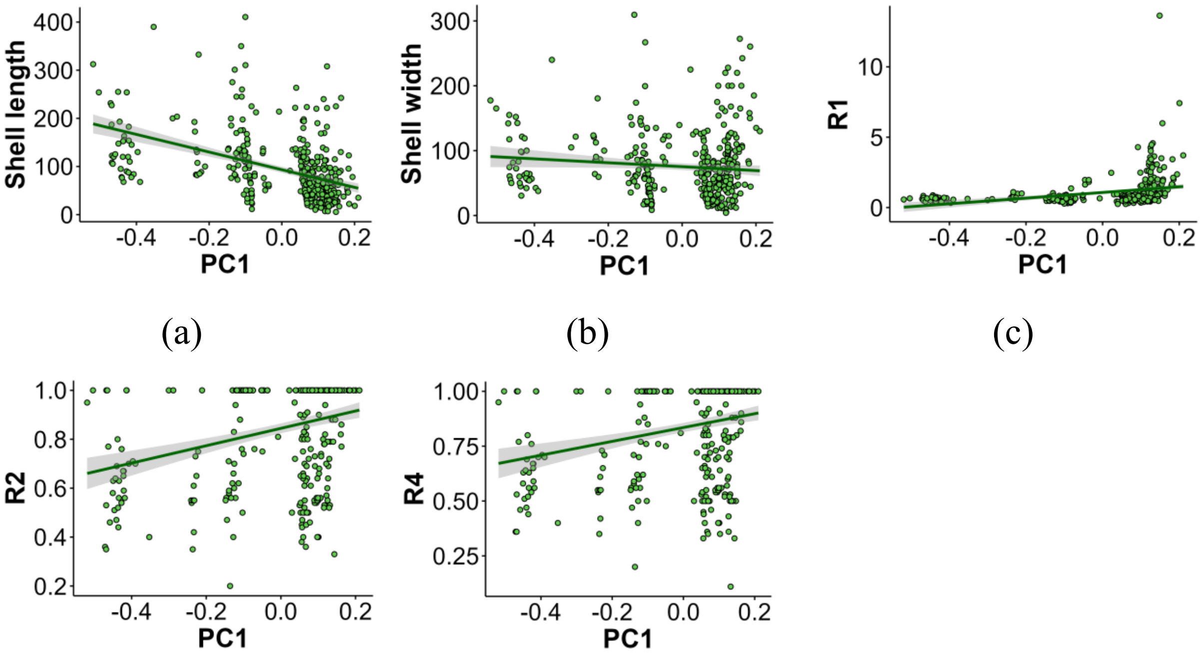
3.3. Trait distribution along PCoA axes

To more clearly display trait distribution along the PCoA axes, relationships between trait values and the first three PCoA axes (PC1, PC2, PC3) were examined. For quantitative variables, only the significant relationships with the PCoA axes were illustrated graphically. In the case of categorical variables, all trait categories exhibiting probabilities greater than 80% along a given PCoA axis were included in the plots.

For PC1 axis , lower values along the PC1 axis corresponded strongly with higher probabilities for seven distinct traits (Figs. 7a, 7b, 8b, 8c, 8d, 8f, 8i). Species positioned on the left side of the PCoA plot (Fig. 6) typically displayed characteristics such as larger shell length and width, pyriform shape, straight terminal apertures without invagination, cleptostome coverings, spines, and predation as their feeding type. Groups 1 and 2 (Table 3) encompassed species sharing all these traits and occupied a trait space with low PC1 values (Fig. 6). Conversely, other traits were linked to higher PC1 values (Figs. 7c-7e, 8a, 8e, 8g, 8h). Species found on the right side of the PCoA functional space (Fig. 6) were more likely to exhibit traits such as higher R1 (shell width / shell length), R2 (shell depth / shell width), and R4 (aperture width / aperture length) values, hemispherical test shapes, shifted ventral apertures with slight invagination, and a bacterivorous feeding strategy. Groups 4-7, positioned furthest to the right on the ordination plot, included species that shared many of these characteristics (Fig 6).

For PC2 axis, lower values along the PC2 axis were significantly associated with nine traits (Figs. 9a-9g, 10a, 10d). Species located at the lower end of the PCoA plot (Fig. 6a) generally possessed wide and thick shells, large apertures (in both length and width), higher R1 (shell width / shell length), R2 (shell depth / shell width), and R4 values, hemispherical test shapes, and central ventral apertures. Groups 3-6 (Table 3) included species that shared these traits and were situated at the bottom of the trait space (Fig. 6a). In contrast, another set of three traits correlated with higher PC2 values (Figs. 10b, 10c, 10e). Species at the upper end of the PCoA plot (Fig. 6a) were more likely to exhibit traits such as denticular aperture rims, straight terminal apertures, and idiosome shell coverings. Groups 1 and 7 (Table 3), located at the top of the ordination plot, comprised species sharing many of these features.

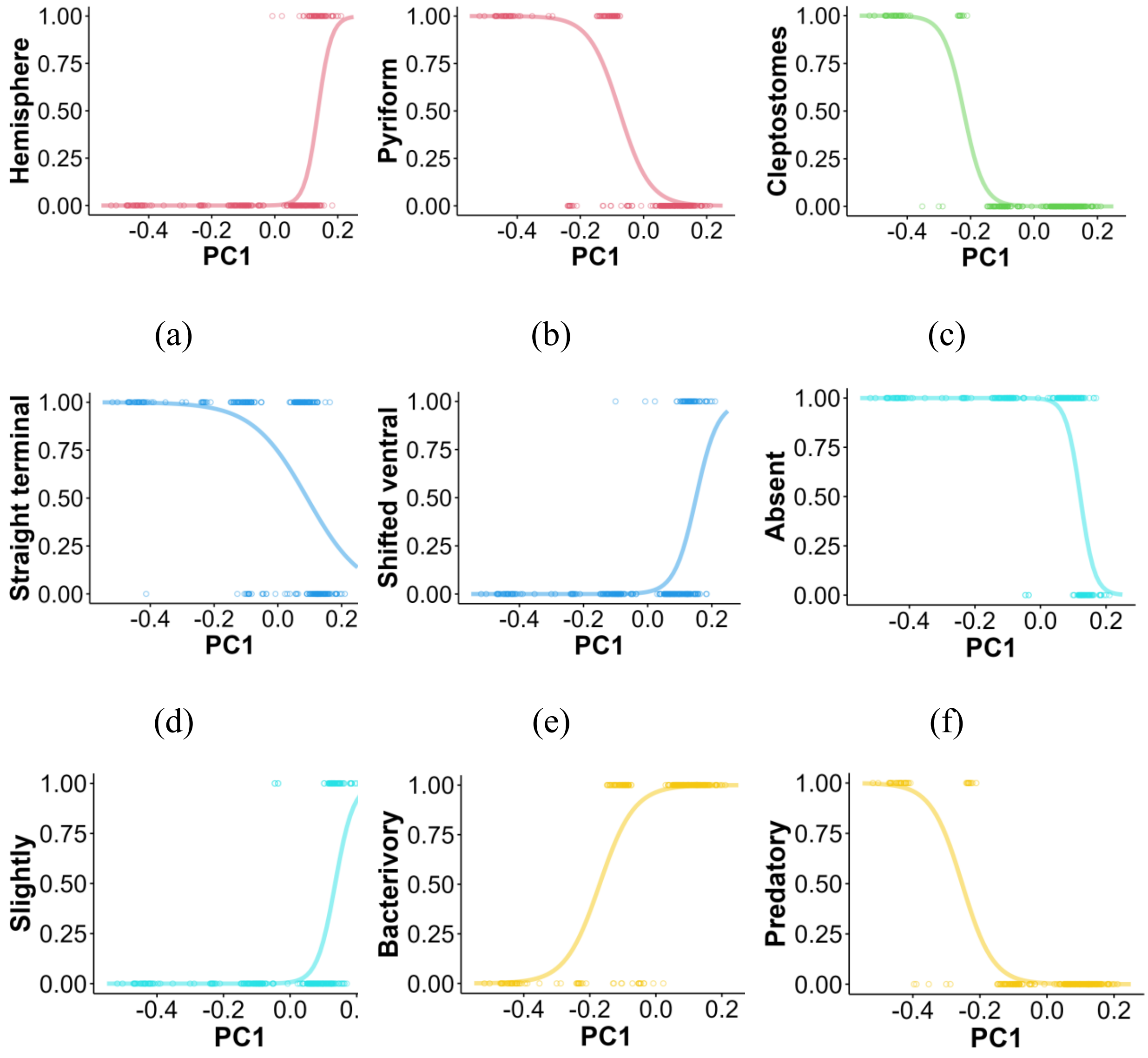
However, higher values along the PC3 axis were strongly linked to traits such as larger body sizes (including all shell and aperture dimensions), higher R3 (aperture length / shell width) values, hemispherical test shapes, absence of aperture invagination, xenosome shell coverings, and the presence of spines (Figs. 11a-11e, 11g, 12a, 12c, 12e, 12g, 12h). Groups 3, 5, and 7 (Table 3) consisted of species that shared these traits and occupied areas of the trait space characterized by high PC3 values (Fig. 6b). Conversely, species in Group 6 (Table 4), which exhibited higher R1 (shell width / shell length) values, straight aperture rims, central ventral apertures, and organic shell coverings (Figs. 11f, 12b, 12d, 12f), were situated in areas with lower PC3 values (Fig. 6b).



(a) (b) (c)

(d) (e)

Fig 7. Trait distribution along PC1. If the trait is quantitative, the y-axis represents its own. If the trait is categorical data, the y-axis denotes the traits with a probability of occurring > 80% at some value of PC1. These were quantitative variables (a-e).

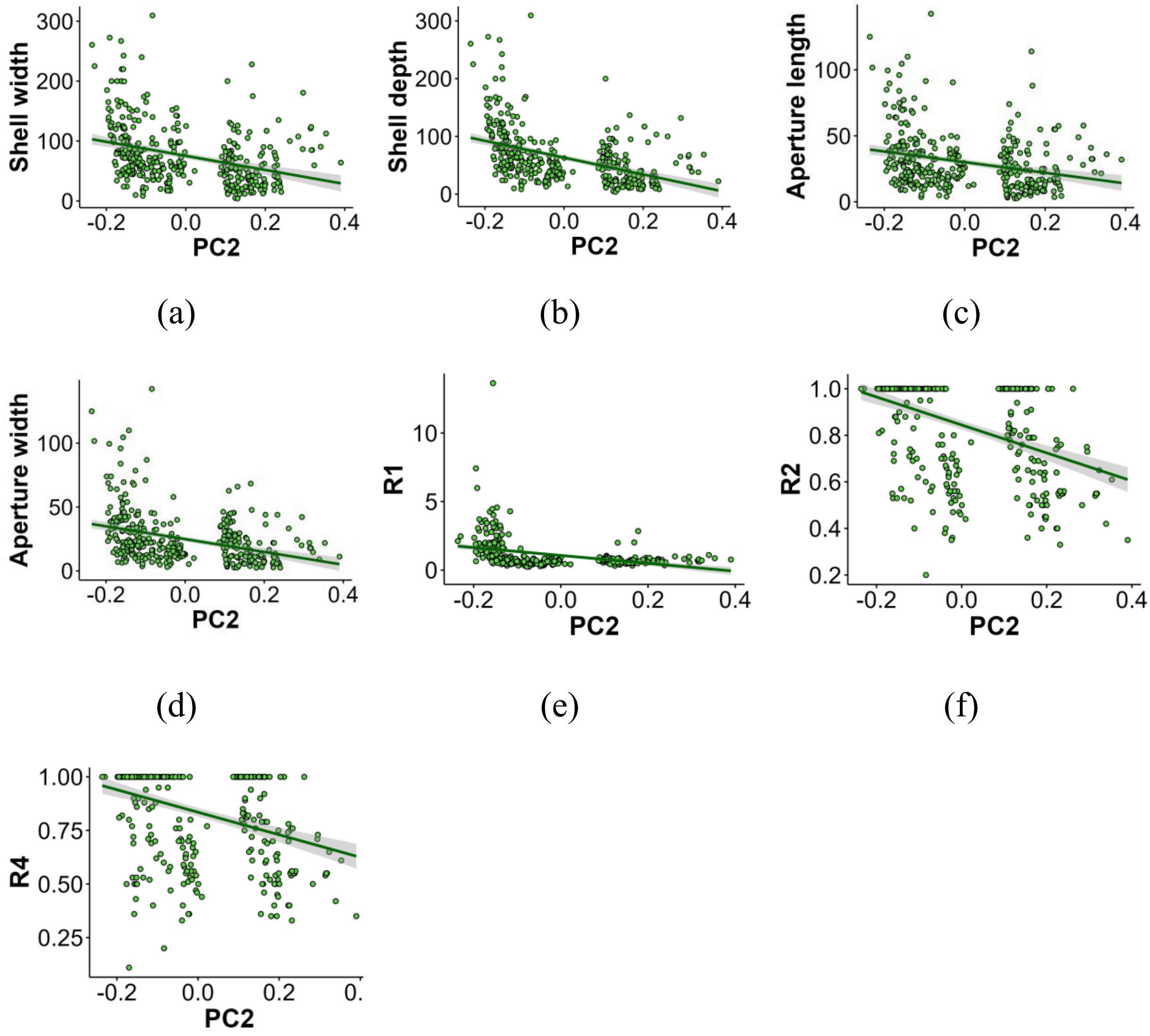


(a) (b) (c)

(d) (e) (f)

(g) (h) (i)

Fig 8. Trait distribution along PC1. If the trait is quantitative, the y-axis represents its own. If the trait is categorical data, the y-axis denotes the traits with a probability of occurring > 80% at some value of PC1. These were categorized multivariate variables (a-i). a-b: shell shape, c: shell covering, d-e: position of the aperture, f-g: degree of invagination of aperture, h-i: feeding type.

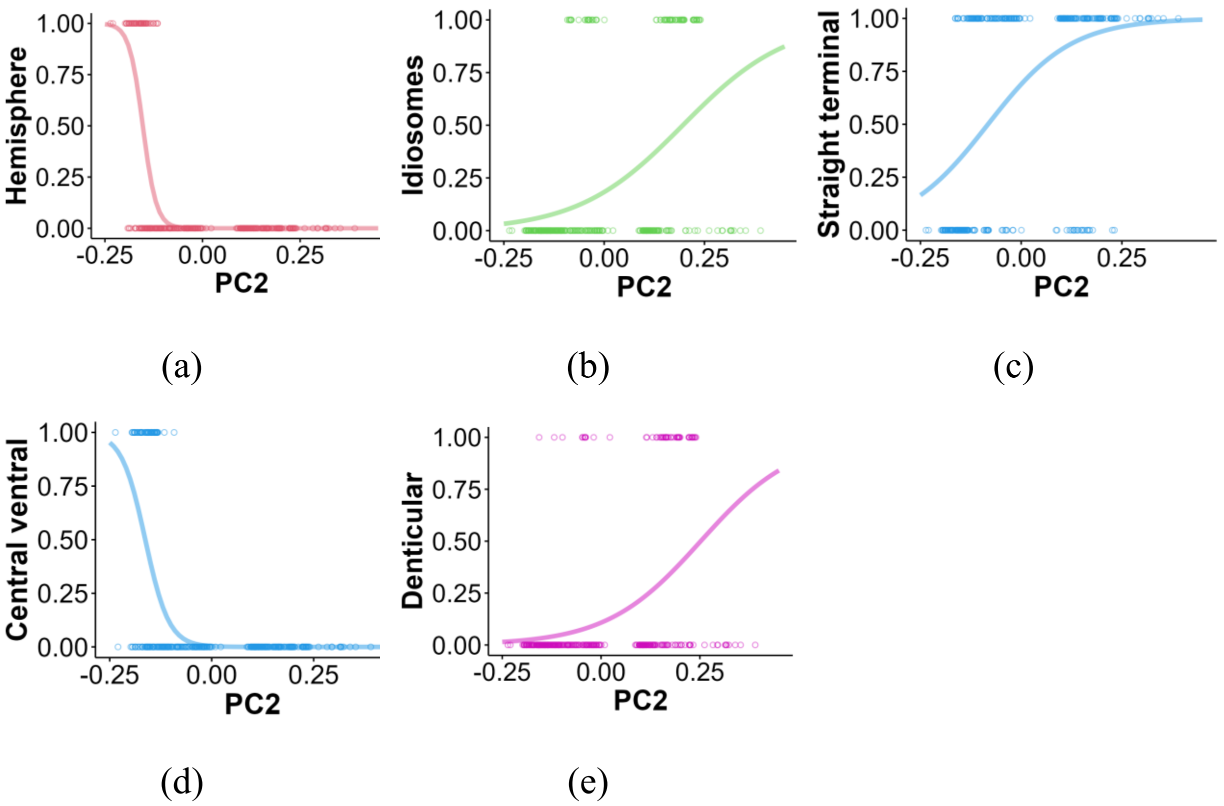


(a) (b) (c)

(d) (e) (f)

(g)

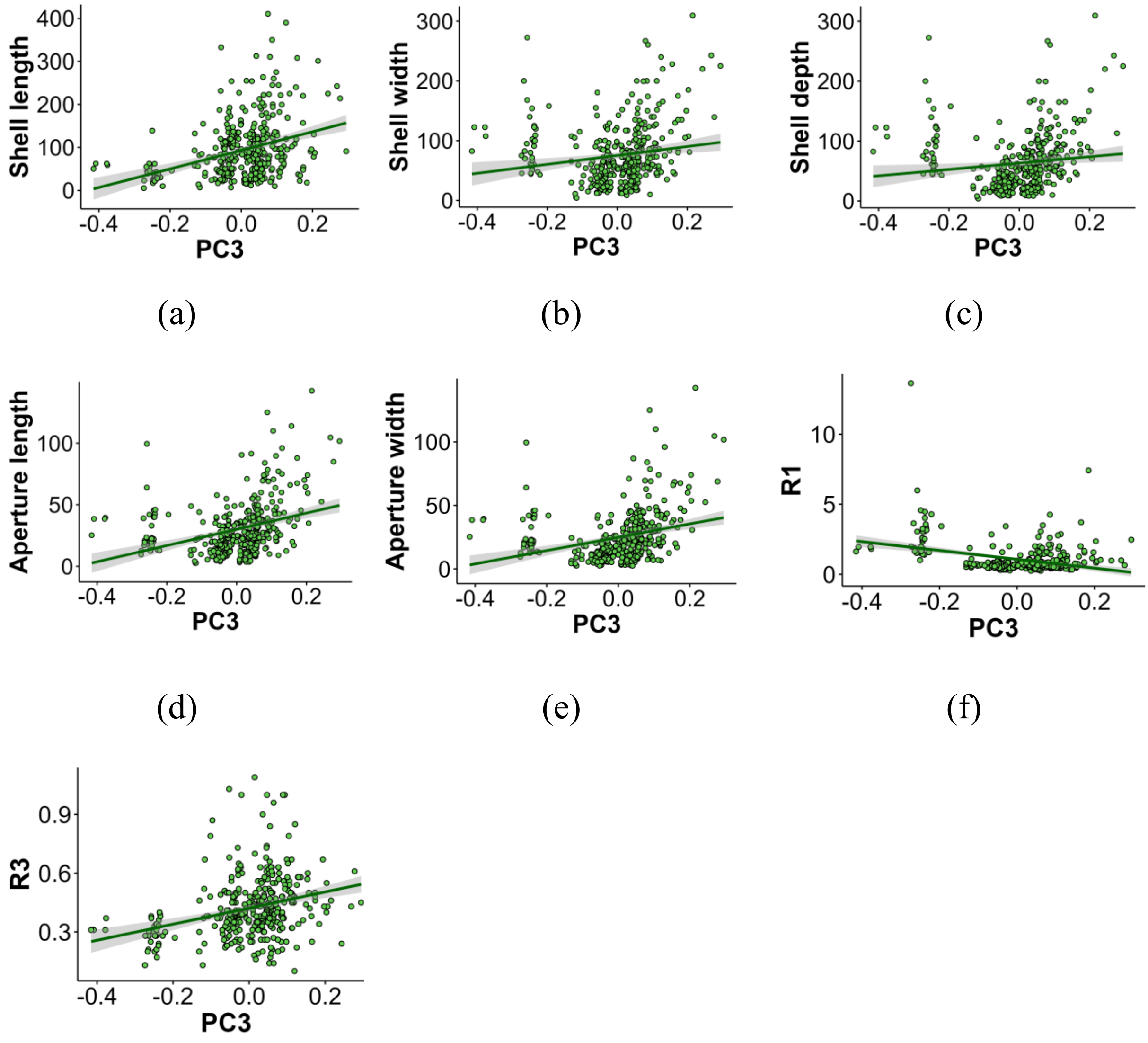
Fig 9. Trait distribution along PC2. If the trait is quantitative, the y-axis represents its own. If the trait is categorical data, the y-axis denotes the traits with a probability of occurring > 80% at some value of PC2. These were quantitative variables (a-g).



(a) (b) (c)

(d) (e)

Fig 10. Trait distribution along PC2. If the trait is quantitative, the y-axis represents its own. If the trait is categorical data, the y-axis denotes the traits with a probability of occurring > 80% at some value of PC2. These were categorized multivariate variables (a-e). a: shell shape, b: shell covering, c-d: position of the aperture, e: aperture rim.

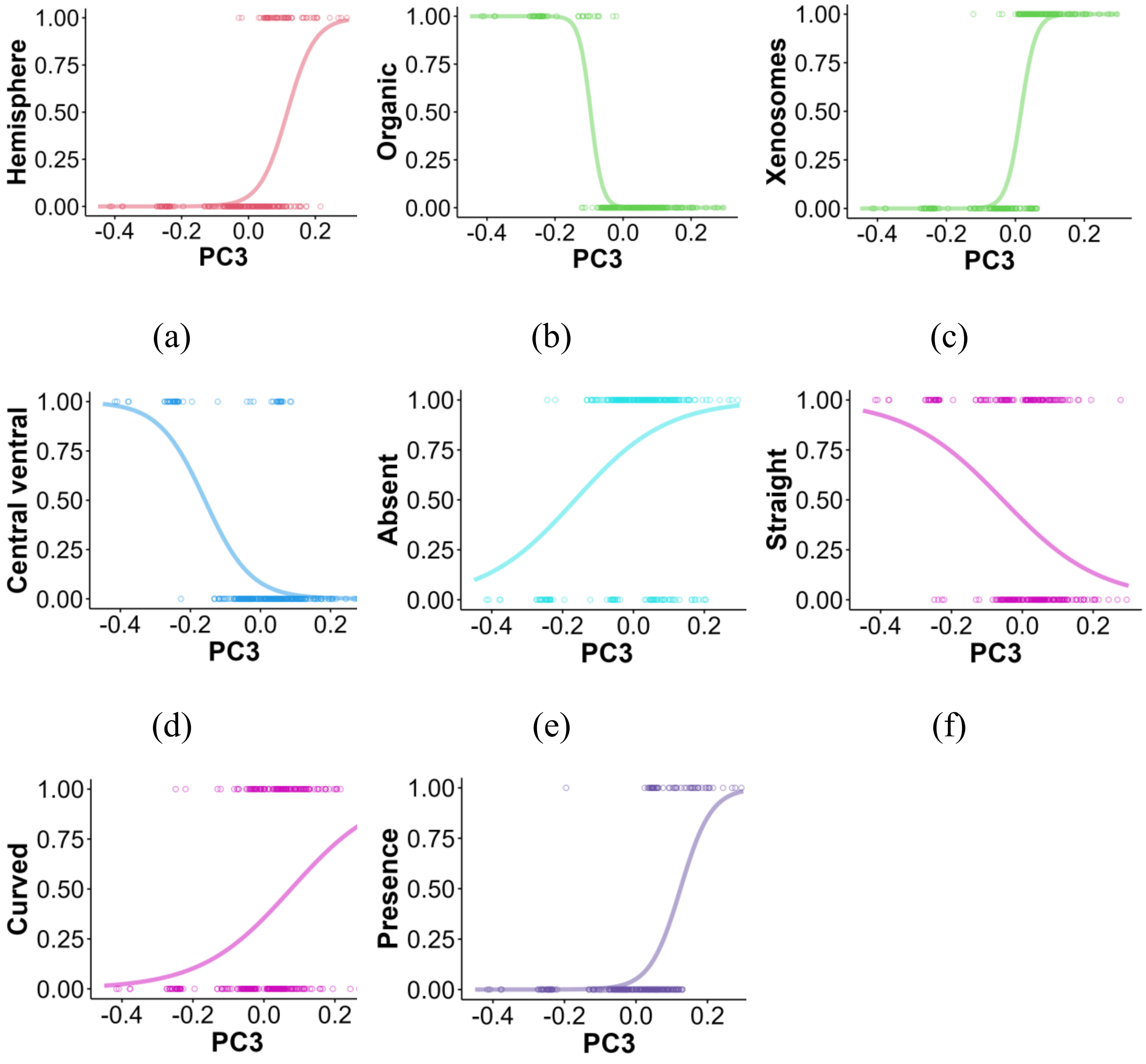


(a) (b) (c)

(d) (e) (f)

(g)

Fig 11. Trait distribution along PC3. If the trait is quantitative, the y-axis represents its own. If the trait is categorical data, the y-axis denotes the traits with a probability of occurring > 80% at some value of PC3. These were quantitative variables (a-g).



(a) (b) (c)

(d) (e) (f)

(g) (h)

Fig 12. Trait distribution along PC3. If the trait is quantitative, the y-axis represents its own. If the trait is categorical data, the y-axis denotes the traits with a probability of occurring > 80% at some value of PC3. These were categorized multivariate variables (a-g) and binary classification variables (h). a: shell shape, b-c: shell covering, d: position of aperture, e: degree of invagination of aperture, f-g: aperture rim, h: presence of spines/horns.

3.4. Comparing functional groups to Bonnet classification

When comparing functional groups to the existing classification by Bonnet (1975), we noted both similarities and differences. Among the seven functional groups, four were primarily dominated by specific morphological types. Specifically, Groups 1-3 and 7 consisted mainly of simple acrostomy (ACS) shaped species, while Group 6 was represented by arcella (ARC) shaped species. Group 5 was the most diverse, encompassing representatives of eight different shapes (Fig. 13). Traditional groups were not confined to single functional groups; for example, the arched acrostomy (ACA) and simple acrostomy (ACS) shapes appeared across six different functional categories, whereas cotylostomy (COT), cryptostomy with visor (CRV), ellipsostomy (ELL), and plagiostomy with visor (PLV) were restricted to a single functional group.

The functional groups identified in our research offer a more ecologically relevant framework compared to Bonnet's traditional morphological classification (Bonnet, 1975). Our method highlights critical traits, including shell size, shape, aperture features, and feeding strategies. In our comparison, we observed several areas of alignment and divergence. For instance, species placed in Bonnet's arcella (ARC) and simple acrostomy (ACS) categories largely aligned with our Groups 6 and 1. However, we also identified significant overlap, as certain traditional morphological categories (like arched acrostomy and simple acrostomy) spanned multiple functional groups, indicating that Bonnet's classification may overlook aspects of ecological diversity. Conversely, some morphological types, such as cotylostomy (COT) and cryptostomy with visor (CRV), were confined to a single functional group, reflecting more specific ecological roles. By incorporating ecological traits, our classification elucidates the functional roles and ecological niches of testate amoebae more effectively than a purely morphology-based approach. For example, species with larger, robust shells that exhibit predatory behaviors occupy distinct ecological niches compared to smaller, patelliform species that primarily feed on bacteria. This distinction underscores how ecological pressures influence species traits, providing a refined framework for understanding the adaptive strategies and environmental interactions of testate amoebae.

In conclusion, this trait-based classification enhances our capacity to link testate amoebae functional diversity to ecological processes, improving our understanding of their roles in various ecosystems. The framework developed here lays the groundwork for future studies in microbial ecology, particularly concerning environmental changes and habitat-specific adaptations.

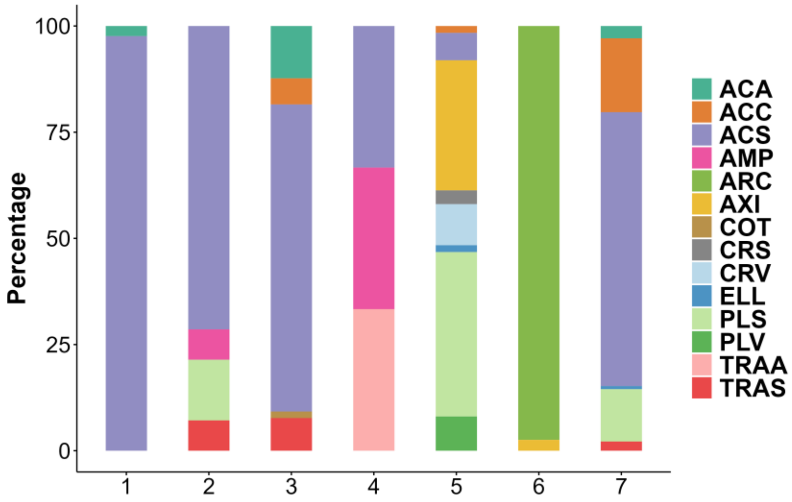


Fig 13. Composition (as % of the total species in each functional group) of seven functional groups compared to the traditional morphological classification (Bonnet 1975). Multicolored bars represent functional groups that contain more than one morphological group. The traditional morphological groups of testate amoebae: ACA - arched acrostomy; ACC - compressed acrostomy; ACS - simple acrostomy; AMP - amphystomy; ARC - arcella; AXI - axial; COT - cotylostomy; CRS - simple cryptostomy; CRV - cryptostomy with visor; ELL - ellipsostomy; PLS - simple plagiostomy; PLV - plagiostomy with visor; TRAA - arched trachelostomy; TRAS - simple trachelostomy.

3.5. Conclusions

This chapter was devoted to the development of trait-based functional groups system for testate amoebae across Northern Holarctic realm. We developed a comprehensive database of 18 functional traits for 372 testate amoebae species and applied silhouette width analysis to identify seven distinct functional groups based on hierarchical clustering method. The seven functional groups represent distinct ecological adaptations of testate amoebae to various environmental conditions. Groups 1 and 2 consist mainly of species with large shells and complex structural adaptations (e.g. straight terminal apertures without invagination, collars or cleptostomes covering), many species in these two groups prefer wetter environments (e.g. fresh water, wet sphagnum and organic sediment). Groups 3-5 are represented by medium-sized species. Group 6 is characterized by patelliform shell shape with organic alveolar covering and central ventral aperture, its members represent adaptations to dry conditions and allow to occupy micropores within the soil matrix, particularly in fine-textured mineral soils. Group 7 contains the largest number of species, which have the smallest body size and aperture size (straight terminal position). These characteristics enable the group to occupy a variety of soil microhabitats, making them versatile contributors to different soil processes.

To verify the structure of the functional space, we demonstrated a clear association between the distribution of traits and PC axes. Lower PC1 values strongly aligned with higher probabilities of traits like larger shell dimensions, pyriform shape, straight terminal aperture, cleptostomes covering, presence of spines, and predation as a feeding type. Lower PC2 values were associated with traits such as wide, thick shells, large apertures, higher shell-to-aperture ratios R1, R2, R4, and hemispherical shapes. Higher PC3 values corresponded to larger body size, absence of aperture invagination, xenosomes shell coverage, presence of spines, and specific shell-to-aperture ratio R3.

We also compared the functional groups derived from our trait-based classification with Bonnet's traditional morphological classification. While some correspondences were observed, our results reveal that the trait-based framework provides a more ecologically informative perspective by capturing the functional diversity and ecological roles of testate amoebae. This approach emphasizes key traits such as shell size, shape, aperture characteristics, and feeding strategies, offering deeper insights into the adaptive strategies and their contributions to soil processes. Overall, these groups highlight the functional diversity and ecological roles of testate amoebae.

Chapter 4. Ecoregional patterns in sphagnum- and soil-dwelling testate amoeba assemblages[2]

4.1. Taxonomic composition and diversity

Investigation of taxonomic composition and diversity of ecological communities is a conventional approach providing basic insights into the distribution and structural characteristics of testate amoeba species within ecosystems, reflecting how assemblages respond to changes in environmental conditions.

To compare sphagnum- and soil-dwelling testate amoeba assemblages, we selected 320 samples across six temperate-zone regions. A total of 177 testate amoeba species and subspecies were recorded, with 110 species recorded in mineral soils and 157 in peatland environments. Species richness ranged from 1 to 60 per sample (mean ± standard deviation: 14.3 ± 8.9).

A two-way analytical framework was applied, testing the significance of habitat type, regional differences, and their interaction. To specifically evaluate the influence of habitat type, pairwise comparisons between peatland and mineral soil samples within each region were conducted.

4.1.1. Community composition

To analyse differences between habitat types and regions at the level of species composition, we performed PERMANOVA based on Bray-Curtis dissimilarities. PERMANOVA results confirmed the significant influence of all three factors

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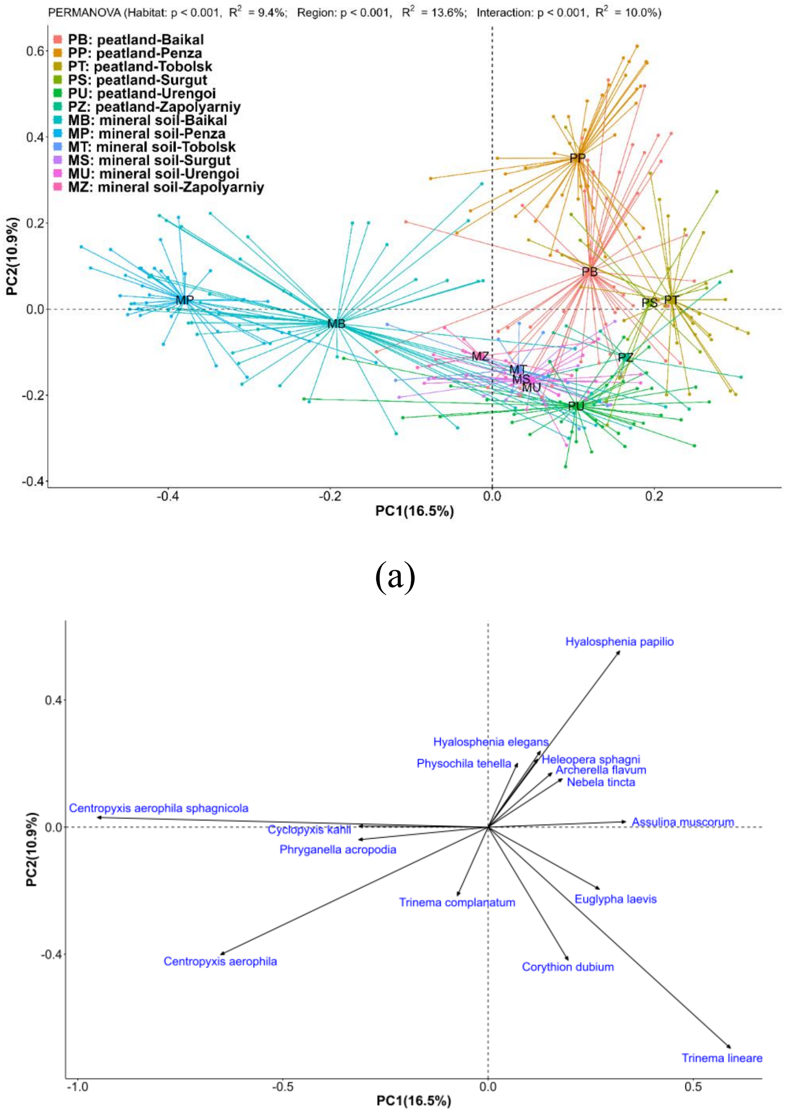
[2] The results presented in this chapter are published in the work:
Su J., Mazei Y.A., Tsyganov A.N., Mazei N.G., Chernyshov V.A., Komarov A.A., Babeshko K.V., Mitchell E.A.D., Shimano S., Krasilnikov P., Saldaev D.A., Yakimov B.N. Ecoregional patterns of protist communities in mineral and organic soils: assembly processes, functional traits and diversity of testate amoebae in Northern Eurasia // Soil Biology and Biochemistry. 2025. V. 208. 109841. https://doi.org/10.1016/j.soilbio.2025.109841 (Q1, IF SRJ 3.982, 2.05/1.2 p.s.)

($p < 0.001$): habitat type, region, and their interaction. Region had the strongest impact (R^2 = 13.6 %), which is understandable given the large latitudinal and longitudinal scope of the study. The effect of habitat type was similar (R^2 = 9.4 %), while the significance of the interaction term (R^2 = 10 %) suggests that the direction of differences between habitat types varies by region. Pairwise tests showed significant differences among most group pairs, except between Zapolyarniy and Urengoi in peatland samples ($p = 0.055$). Figure 14 presents a PCA-based ordination diagram. In Figure 14a, samples from similar habitat types and regions are depicted with different colors, and groups are connected to their centroid using a spider plot to highlight group centers. Figure 14b displays projections of the 15 most influential species in the ordination space, indicated by the length of their arrows. The first two principal components together explain over a quarter of the total variation (27.4 %) in species composition, indicating high β-diversity across the assemblages. The first principal component separates soil-dwelling testate amoeba assemblages, located on the left side of the ordination, from sphagnum-dwelling testate amoeba assemblages on the right. In soil-dwelling testate amoeba assemblages, *Centropyxis aerophila sphagnicola* and *Centropyxis aerophila* dominated (17.4 % and 16.6 % of total abundance in soil samples, respectively), whereas sphagnum-dwelling testate amoeba assemblages were primarily composed of *Trinema lineare* (17.2 %) and *Hyalosphenia papilio* (7.7 %). *Corythion dubium* (7 % in soils and 3.8 % in peatlands) was present in both environments in Western Siberia. For soil-dwelling testate amoeba assemblages, the first principal component also highlights the contrast between the Penza and Baikal regions on the left and Western Siberia on the right. For sphagnum-dwelling testate amoeba assemblages, the second principal component reflects this same contrast, with Penza and Baikal shifted upward and Western Siberia downward. This difference is largely driven by the dominance of *Hyalosphenia papilio* (11.8 %) in Penza and Baikal peatlands and *Trinema lineare* (28.3 %) in Western Siberia. Additionally, the contrast between sphagnum- and soil-dwelling testate amoeba assemblages within each region varies considerably, being greatest in Penza, less pronounced in Baikal, and least significant in Western Siberia.

The composition of sphagnum- and soil-dwelling testate amoeba assemblages differed significantly. Peatlands, characterized by high moisture and abundant organic matter, were dominated by species like *Trinema lineare* and *Hyalosphenia papilio*, which thrive in wet, nutrient-rich conditions. In contrast, mineral soils, generally drier and poorer in organic matter, were dominated by *Centropyxis aerophila sphagnicola* and *Centropyxis aerophila*, species that can withstand drier, less stable environments with fewer available resources. These findings underscore the impact of habitat-specific factors on microbial community structures, with moisture and organic matter being key drivers that influence resource availability and habitat suitability for testate amoebae (Harnisch, 1927; Grospietsch, 1953; Meisterfeld, 1979; Mazei et al., 2007; Tsyganov et al., 2016). The high β-diversity observed highlights the species' adaptability and specialization in their respective habitats.

Moreover, the variability in contrasts between sphagnum- and soil-dwelling testate amoeba assemblages across regions highlights the role of regional climatic and environmental factors. The strongest contrast observed in the Penza region suggests that regional climate, likely more temperate, amplifies habitat differences. Conversely, smaller contrasts in Baikal and Western Siberia suggest more uniform conditions across habitats, reducing community distinctions. The significant regional influence, as shown by PERMANOVA, indicates that large-scale biogeographical factors, such as latitude and longitude, also shape microbial community structure, with these variables influencing species distribution and dominance in different habitats. These findings are consistent with prior research showing the critical role of habitat-specific factors (e.g., moisture, organic matter) in structuring microbial communities (Eskelinen et al., 2009; Wang et al., 2017; Liu et al., 2020; Su et al., 2020).



(a)

(b)

Fig 14. Ordination biplot for the principal component analysis (PCA) based on Hellinger-transformed relative abundances of testate amoebae. Arrows represent fifteen species with the greatest contribution to the results of ordination.

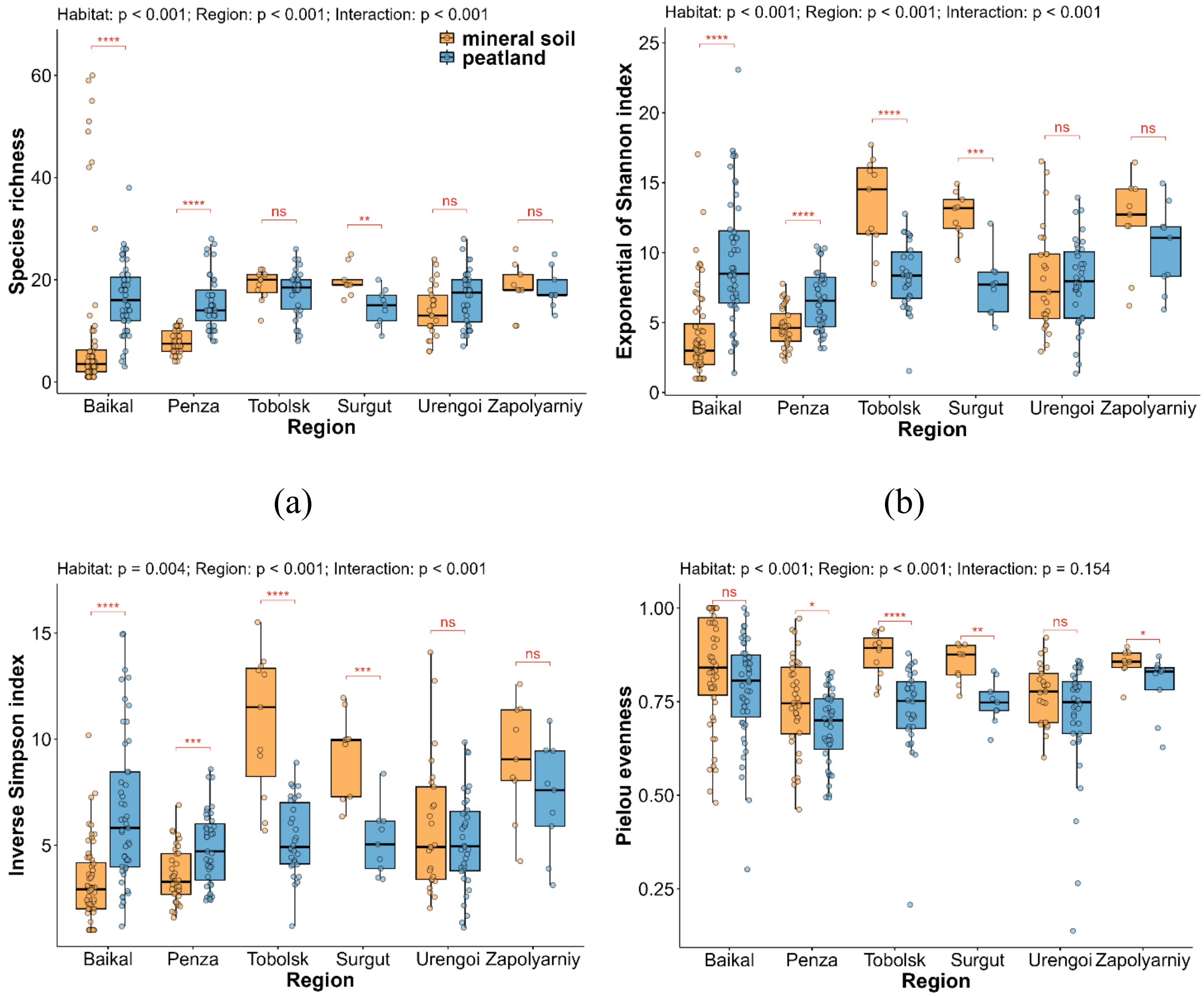
4.1.2. Species diversity

In addition to community composition, taxonomic diversity indices integrating both species richness and abundance patterns provide an important insight into structural complexity of assemblages.

The results of the overall tests, including p-values for the effects of habitat type, region, and their interaction on all taxonomic diversity, functional diversity and traits metrics, are displayed in Figures 15-18 (for selected metrics) and in the Tables 4-7 (for all metrics).

All four taxonomic diversity metrics are significantly influenced by both region and habitat type. The interaction effect is significant for species richness, Shannon diversity, and Simpson diversity, but not for Pielou evenness (Fig. 15). This indicates that the impact of habitat type varies by region concerning taxonomic diversity (species richness, exponential to Shannon index, and inverse Simpson index). Quantitative diversity metrics, specifically the exponential to Shannon index and the inverse Simpson index, are significantly higher in peatlands than in mineral soils in the Baikal and Penza regions; however, the opposite trend is observed in the Western Siberian regions, with significant differences noted in two out of the four regions (Fig. 15b, 15c). This contrasting pattern between Penza/Baikal and the four Western Siberian regions is evident across various metrics, which we label as inconsistent. We define a pattern as inconsistent if there is at least one significant difference in the Baikal or Penza regions and at least one significant difference in the Western Siberian regions in opposing directions. The inconsistent pattern also applies to species richness (Fig. 15a). In contrast, Pielou evenness shows a consistent trend across all regions, being significantly higher in soil-dwelling testate amoeba assemblages than in sphagnum-dwelling assemblages across all six regions, with significant differences found in four regions (Fig. 15d). We categorize this pattern as consistent. A consistent pattern is identified if there is at least one significant difference in the same direction between the Baikal or Penza regions and the Western Siberian regions or if there is a significant overall effect of habitat type with a non-significant interaction effect. All other instances are considered uncertain.

The effect of habitat on taxonomic diversity is regionally dependent. Quantitative diversity metrics were significantly greater in sphagnum-dwelling testate amoeba assemblages compared to soil-dwelling assemblages in the Baikal and Penza regions, while the reverse was observed in Western Siberia. This regional contrast underscores the importance of ecoregional conditions in shaping taxonomic diversity (Qian et al., 2020; Frasconi Wendt et al., 2021; Wu et al., 2021). Wet mineral soils typical of tundra and taiga ecoregions offer sufficient moisture akin to peatlands, coupled with higher habitat heterogeneity, resulting in increased diversity (Voroney, 2007). Conversely, the dry mineral soils found in forest-steppe ecoregions present harsh conditions for testate amoebae, leading to lower diversity. The consistently higher Pielou evenness in soil-dwelling testate amoeba assemblages across all regions suggests a more uniform community structure, likely reflecting reduced competitive exclusion and more stable environmental conditions.



(a) (b)

(c) (d)

Fig 15. Boxplots of taxonomic diversity metrics for sphagnum- and soil-dwelling testate amoeba assemblages across different regions. The symbols display the significance of the pairwise difference between two habitat types within regions. (****) - $p < 0.0001$, (***) - $0.0001 < p < 0.001$, (**) - $0.001 < p < 0.01$, (*) - $0.01 < p < 0.05$, (ns) - $p > 0.05$.

Table 4. Pairwise comparisons: median value of taxonomic diversity metrics in six regions.

	Variable	**Baikal**		**Penza**		**Tobolsk**		**Surgut**		**Urengoi**		**Zapolyarniy**	
		mineral soil	peatland	mineral soil	peatland	mineral soil	peatland	mineral soil	peatland	mineral soil	peatland	mineral soil	peatland
Taxonomic diversity	Species richness	**3.5***	**16**	**7.5***	**14**	20	18.5	**19***	**15**	13	17.5	18	17
	Exponential of Shannon index	**3***	**8.5**	**4.6***	**6.6**	**14.5***	**8.4**	**13.2***	**7.7**	7.2	8.0	12.7	11.1
	Inverse Simpson index	**2.9***	**5.8**	**3.3***	**4.7**	**11.5***	**4.9**	**10.0***	**5.0**	4.9	4.9	9.0	7.6
	Pielou evenness	0.84	0.81	**0.75***	**0.70**	**0.89***	**0.75**	**0.88***	**0.75**	0.78	0.75	**0.86***	**0.83**

Asterisks (*) indicate that the value differs significantly between the sphagnum- and soil-dwelling testate amoeba assemblages (bold fonts).

4.2. Functional diversity and traits

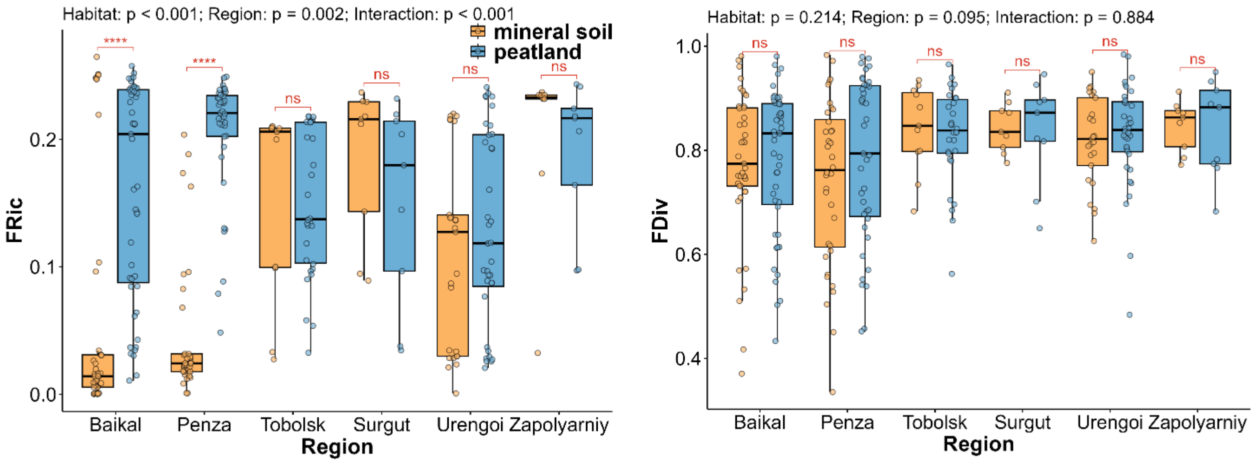
Compared to taxonomic diversity, functional diversity and traits hold greater ecological significance as they reflect species' roles and adaptations within ecosystems. Functional traits provide insights into how organisms interact with their environment, influence ecosystem processes, and respond to environmental changes, offering a deeper understanding of ecosystem function and resilience.

4.2.1. Functional diversity

We applied the same analytical approach as used for taxonomic diversity, with functional diversity indices as the dependent variable and habitat type, region, and their interaction as independent variables. Among the functional diversity metrics, only functional richness showed a significant influence from habitat type in the overall analysis. This metric exhibited an inconsistent pattern similar to that of taxonomic diversity, being higher in sphagnum-dwelling testate amoeba assemblages compared to soil-dwelling assemblages in the Baikal and Penza regions, while in Western Siberian regions, it was higher in soil-dwelling testate amoeba assemblages than in sphagnum-dwelling assemblages (although differences were not significant in all four regions, the presence of contrasts among regions is supported by the significant interaction term in the overall analysis and the consistent direction of differences in the four Western Siberian regions, Fig. 16a). Functional evenness was significantly greater in soil-dwelling testate amoeba assemblages than in sphagnum-dwelling assemblages solely in the Penza region, but the overall effect of habitat type remained insignificant (Table 5). There were no significant differences in functional divergence between sphagnum- and soil-dwelling testate amoeba assemblages across any of the regions (Fig. 16b).

Functional diversity metrics, particularly functional richness, revealed distinct variations between sphagnum- and soil-dwelling testate amoeba assemblages. In the Baikal and Penza regions, sphagnum-dwelling testate amoeba assemblages exhibited higher functional richness, indicating that these habitats foster a more diverse environment that supports a wider array of functional traits. The optimal local moisture conditions in peatlands likely create various microhabitats that cater to different functional niches, enhancing functional diversity (Marcisz et al., 2020). Conversely, the increased functional diversity observed in soil-dwelling testate amoeba assemblages within Western Siberia may relate to soil properties. In these regions, both peatlands and mineral soils are consistently moist, which reduces the impact of limiting factors. Thus, a significant mineral fraction within organic matter may contribute to greater heterogeneity (Wander, 2004), potentially driving the higher functional diversity.

These findings indicate that the functional diversity of testate amoebae is significantly shaped by local habitat conditions, which are influenced by broader regional factors (Marcisz et al., 2020). This underscores the importance of considering both biotic and abiotic factors when investigating the functional ecology of microbial communities.



(a) (b)

Fig 16. Boxplots of functional diversity metrics for sphagnum- and soil-dwelling testate amoeba assemblages across different regions. The symbols display the significance of the pairwise difference between two habitat types within regions. (****) - $p < 0.0001$, (***) - $0.0001 < p < 0.001$, (**) - $0.001 < p < 0.01$, (*) - $0.01 < p < 0.05$, (ns) - $p > 0.05$.

Table 5. Pairwise comparisons: median value of functional diversity metrics in six regions.

	Variable	Baikal		Penza		Tobolsk		Surgut		Urengoi		Zapolyarniy	
		mineral soil	peatland	mineral soil	peatland	mineral soil	peatland	mineral soil	peatland	mineral soil	peatland	mineral soil	peatland
Functional diversity	FRic	**0.01***	**0.20**	**0.02***	**0.22**	0.21	0.14	0.22	0.18	0.13	0.12	0.23	0.22
	FEve	0.59	0.64	**0.55***	**0.41**	0.59	0.62	0.64	0.58	0.58	0.58	0.64	0.60
	FDiv	0.774	0.833	0.763	0.793	0.847	0.839	0.835	0.873	0.816	0.840	0.863	0.883

Asterisks (*) indicate that the value differs significantly between the sphagnum- and soil-dwelling testate amoeba assemblages (bold fonts).

4.2.2. Functional traits

We utilized the same analytical framework as for functional traits, treating the community-weighted means (CWMs) of functional traits as the dependent variable, while habitat type, region, and their interaction were included as independent variables.

The functional traits of testate amoebae are significantly influenced by habitat type (Table 6). While some traits display consistent patterns, many exhibit inconsistencies, and others show no clear trends (Table 6). Overall biovolume consistently appears larger in peatlands compared to mineral soils (Fig. 17a). In contrast, key linear dimensions such as shell length and width (Fig. 17b) show inconsistent patterns, being larger in peatlands in the Baikal and Penza regions, but smaller in Western Siberia. Shell depth presents an uncertain pattern. The ratio R1 (shell width / shell length) consistently indicates a smaller size in peatlands, suggesting a more elongated form (Fig. 17c). Ratio R2 (shell depth / shell width) has an inconsistent pattern, being smaller in peatlands in Baikal and Penza regions (indicating a more elliptical shape) but larger in Western Siberia (suggesting a more circular shape).

Aperture length shows an inconsistent trend: it is longer in Baikal iapeatlands compared to mineral soils but shorter in Western Siberian peatlands. However, the aperture is consistently wider in mineral soils. The relative aperture size, measured by ratio R3 (aperture length / shell width), is smaller in Penza and Baikal peatlands than in mineral soils, yet larger in Western Siberian peatlands. Ratio R4 (aperture width / aperture length), which reflects aperture shape, has an uncertain pattern.

Most categorical traits show consistent trends (Table 7). Peatlands have a consistently higher proportion of patelliform and ovoid shapes (Fig. 18a), along with a smaller proportion of hemispherical shapes. The prevalence of pyriform shapes is uncertain, being more frequent in Baikal and Penza peatlands, but showing insignificant differences between peatlands and mineral soils in Western Siberia.

Peatlands are characterized by a consistently higher proportion of amoebae with straight terminal apertures and a lower proportion of those with central ventral apertures (Fig. 18c). Shifted ventral apertures are the most common overall, but their prevalence varies by region: significantly smaller in Baikal, Penza, and Tobolsk peatlands, while higher in Urengoi. The absence of invagination is the most frequent aperture type, with region-specific proportions, but no significant differences between peatlands and mineral soils in any region. Slightly invaginated apertures are significantly more common in peatlands. Although direct comparisons between peatlands and mineral soils do not yield significant differences in any region (Table 7), we regard the overall pattern as consistent due to the insignificance of the interaction between region and environment type. Strongly invaginated apertures are less frequent, with a median proportion present only in Penza and Tobolsk mineral soils, where they differ significantly from peatlands.

The proportion of testate amoebae with curved aperture rims is consistently lower in peatlands, while denticular rims are consistently more frequent (Fig. 18d). Straight aperture rims show an inconsistent pattern, being more common in Baikal peatlands but less so in Western Siberian peatlands compared to mineral soils. Aperture collars are typically absent, demonstrating inconsistent patterns; they are significantly more frequent in Baikal and Penza peatlands compared to mineral soils, but less frequent in Western Siberian peatlands.

Organic and idiosome shell coverings are consistently more prevalent in peatlands, whereas xenosome coverings are more common in mineral soils (Fig. 18b). Spines and horns, while infrequent overall, are consistently more prevalent in peatlands. Bacterivorous testate amoebae dominate the studied environments, with this feeding type being consistently less common in peatlands compared to mineral soils. Mixotrophs, on the other hand, are consistently more frequent in peatlands. The predatory type shows an uncertain pattern, being significantly more common in Baikal and Penza peatlands but not significantly different between Western Siberian mineral soils and peatlands (Fig. 18e).

The functional traits of testate amoebae exhibit both consistent and inconsistent differences between mineral soils and peatlands, reflecting the impact of varying environmental conditions and ecological processes. Consistently, testate amoebae in peatlands tend to have larger shell volumes, which may be adaptations to anoxic and water-saturated environments (McKeown et al., 2019; Macumber et al., 2020). The larger shell volume could facilitate buoyancy and oxygen storage, enhancing survival in low-oxygen environments (McKeown et al., 2019; Macumber et al., 2020). Moreover, the higher levels of organic matter in peatlands can provide abundant resources, supporting larger-bodied amoebae (McKeown et al., 2019; Macumber et al., 2020). In contrast, mineral soils, characterized by better aeration and lower moisture, support testate amoebae with smaller shell volumes, reflecting adaptations to more oxygenated and less waterlogged conditions (Nisbet, 2012).

Shell coverings vary significantly across habitat types, influenced by the availability of silica and other minerals, which can fluctuate in both peatlands and mineral soils (van Bellen et al., 2018; Marcisz et al., 2020). The predominance of organic and idiosome shell coverings in peatlands is due to the high availability of organic materials and specific ecological conditions (van Bellen et al., 2018; Marcisz et al., 2020). Peatlands' high moisture content, low pH, and abundant organic matter create ideal conditions for amoebae to construct their shells from available organic materials and idiosomes internal secretions that form the shell. This adaptation likely confers advantages in buoyancy and structural integrity within the water-saturated, acidic environment of peatlands. Conversely, xenosome coverings are more frequent in mineral soils, which are less acidic and contain a higher proportion of mineral particles. Xenosomes are made from exogenous materials such as mineral grains and detritus, readily available in mineral soils, enabling testate amoebae to build robust shells that withstand varying physical and chemical conditions (Todorov, Bankov, 2019).

The differentiation in shell coverings highlights the amoebae's ecological strategy to optimize survival and reproduction in distinct habitats, showcasing their ability to effectively exploit available resources and adapt to specific environmental pressures (Marcisz et al., 2020). Thus, the contrasting prevalence of shell types between peatlands and mineral soils emphasizes how habitat-specific conditions influence the morphological adaptations of testate amoebae.

These differences underscore how testate amoebae have evolved unique morphological adaptations to enhance their survival and reproduction in diverse habitats (Marcisz et al., 2020). Previous studies have demonstrated that testate amoebae display a range of morphologically adaptive traits related to their living environment (e.g. moisture conditions and substrate types) (Bonnet, 1975; Korganova, 2003; Todorov, Bankov, 2019). These studies reveal intrinsic connections between the life forms of testate amoebae and their habitat conditions, with specific morphological characteristics often corresponding to ecological niches. The patterns observed in this research further substantiate the highly adaptable and responsive environmental capabilities of testate amoebae.

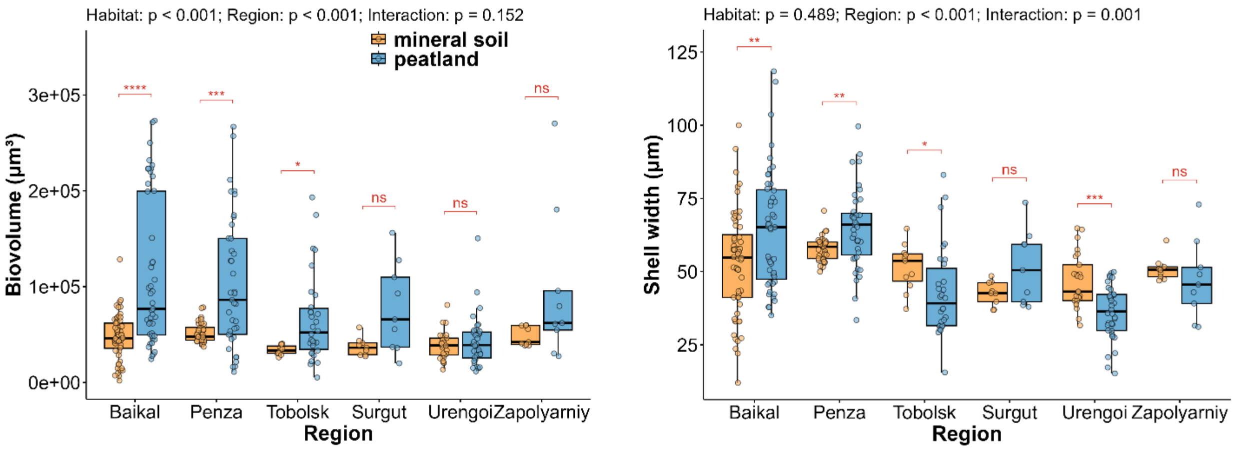
However, numerous traits display inconsistent patterns. Take shell length, shell width, the ratio of shell depth to width (R2) and aperture length as examples: these traits are larger in peatlands from Baikal and Penza, while being smaller in Western Siberia. The increased shell length, width, R2 (shell depth / shell width), and aperture length in these regions may result from more stable and favorable environmental conditions, including consistent water chemistry, nutrient availability, and reduced environmental stressors (Krashevska et al., 2020; Marcisz et al., 2020). Such conditions promote the growth and development of larger and more robust testate amoebae.

Conversely, smaller values of these morphological traits may reflect harsher environmental conditions, such as fluctuations in water levels, temperature extremes, and lower nutrient availability, imposing physiological constraints on amoebae and resulting in smaller and less robust forms (Krashevska et al., 2020; Marcisz et al., 2020). This variation highlights how regional environmental factors influence the phenotypic plasticity of testate amoebae, illustrating their adaptation strategies to diverse ecological niches.

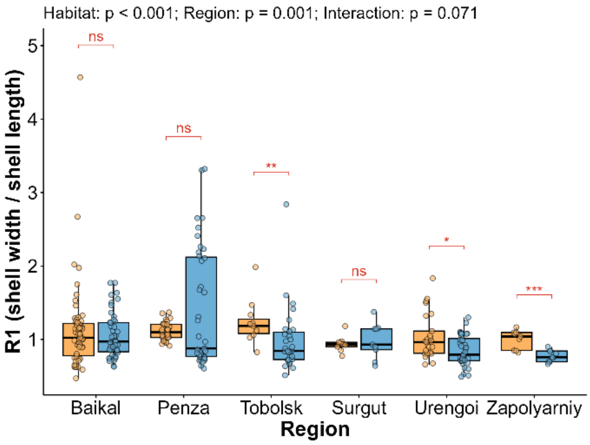
In forest-steppe ecoregions (Penza and Baikal), peatlands seem to offer more favorable habitats for testate amoebae compared to mineral soils characterized by Phaeozems and Chernozems, whereas in taiga ecoregions, Podzols are more beneficial than organic soils. Various soil types can influence the functional traits of testate amoebae due to differences in soil properties, including moisture, pH, and organic matter content, which create distinct microhabitats that select for specific traits in these microorganisms (Soil Survey Staff, 1999; Lavelle, Spain, 2002; Grandy et al., 2009). For example, Phaeozems are typically dry and fertile soils found beneath deciduous forests with well-developed horizons (Soil Survey Staff, 1999), while Chernozems are dry, black soils associated with grasslands, particularly in temperate regions (Soil Survey Staff, 1999). In contrast, Podzols are usually acidic soils found in coniferous forests, characterized by a leached upper horizon and organic matter accumulation (Soil Survey Staff, 1999). Histosols, often found in taiga regions, are organic-rich soils formed under waterlogged conditions (Soil Survey Staff, 1999). The combination of these two soil types may create a balanced environment for microbial communities.

Certain traits lack distinct patterns. For example, the degree of invagination in testate amoebae apertures does not show clear trends between peatlands and mineral soils. This inconsistency could arise from localized environmental factors, such as microtopography and vegetation cover, creating heterogeneous conditions within each habitat type (Koenig et al., 2018).

In summary, the functional traits of testate amoebae display considerable variability across peatlands and mineral soils, influenced by environmental conditions such as water-logged status, nutrient availability, and oxygen levels (Prośków et al., 2018; Shuai et al., 2018; Maebe et al., 2021). The larger biovolumes observed in peatlands suggest adaptations for buoyancy and oxygen storage, while inconsistent shell dimensions and aperture characteristics reflect regional adaptations to local hydrological and substrate conditions. Categorical traits, including shell shapes and aperture types, reveal consistent patterns indicative of selective advantages in various environments, while feeding strategies vary with nutrient gradients. These findings highlight the complex interplay of ecological principles that drive microbial adaptations to diverse habitats.



(a) (b)



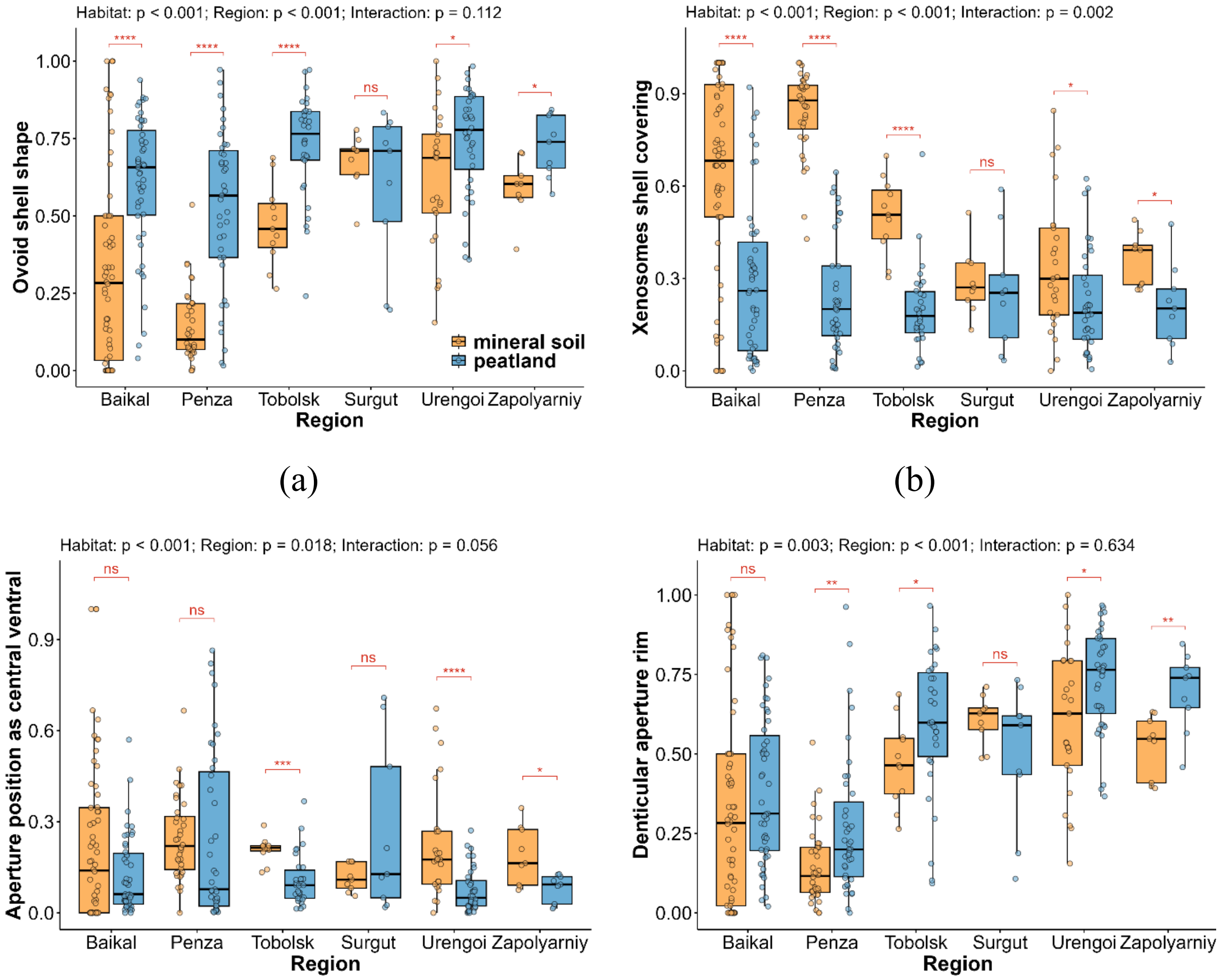
(c)

Fig 17. Boxplots of functional traits (community-weighted means for numeric traits) for sphagnum- and soil-dwelling testate amoeba assemblages across different regions. The symbols display the significance of the pairwise difference between two habitat types within regions. (****) - $p < 0.0001$, (***) - $0.0001 < p < 0.001$, (**) - $0.001 < p < 0.01$, (*) - $0.01 < p < 0.05$, (ns) - $p > 0.05$.

Table 6. Pairwise comparisons: median value of for numeric traits in six regions.

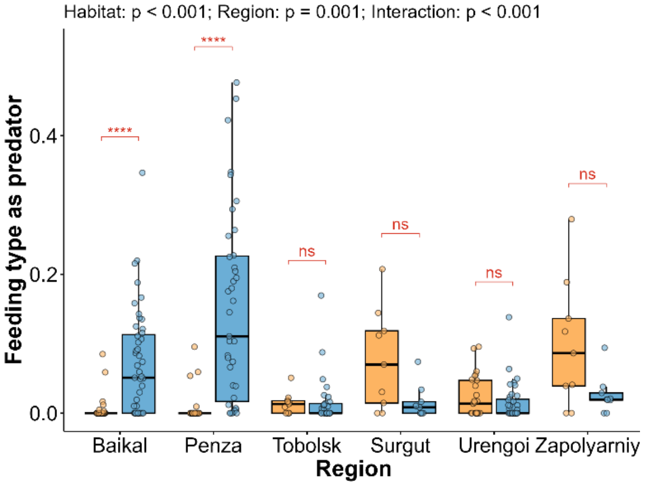
Trait	Metric/category	Baikal		Penza		Tobolsk		Surgut		Urengoi		Zapolyarniy	
		mineral soil	peatland	mineral soil	peatland	mineral soil	peatland	mineral soil	peatland	mineral soil	peatland	mineral soil	peatland
Overall size	Biovolume	**46161***	**76874**	**47772***	**86197**	**33305***	**52097**	36312	65836	38760	38995	42180	62121
Shell size	Shell length	**52.6***	**62.9**	**55.2***	**75.4**	48.4	48.8	52.1	53.4	**51.3***	**47.4**	55.7	59.0
	Shell width	**54.8***	**65.2**	**58.5***	**66.0**	**53.7***	**39.2**	42.6	50.5	**43.2***	**36.4**	50.6	45.5
	Shell thickness	42.2	43.4	45.4	42.1	**47.1***	**33.1**	33.3	36.4	**38.0***	**27.7**	36.6	34.1
	R1	1.02	0.97	1.10	0.88	**1.18***	**0.84**	0.93	0.93	**0.96***	**0.79**	**1.04***	**0.76**
	R2	0.86	0.82	**0.79***	**0.66**	0.92	0.87	**0.79***	**0.89**	0.81	0.83	0.77	0.86
Aperture size	Aperture length	**22.8***	**26.6**	26.1	25.4	**22.8***	**16.7**	18.8	22.6	**17.4***	**14.7**	**22.3***	**18.7**
	Aperture width	18.1	17.8	**20.3***	**18.0**	**17.8***	**13.5**	14.2	15.7	**13.3***	**11.7**	**16.8***	**12.7**
	R3	0.44	0.43	**0.45***	**0.41**	0.44	0.44	0.43	0.45	**0.40***	**0.44**	0.46	0.43
	R4	**0.85***	**0.72**	**0.79***	**0.66**	0.84	0.87	0.79	0.85	0.81	0.83	0.77	0.85

Asterisks (*) indicate that the value differs significantly between the sphagnum- and soil-dwelling testate amoeba assemblages (bold fonts).



(a) (b)

(c) (d)



(e)

Fig 18. Boxplots of functional traits (community-weighted means for proportions of specific variants for categorical traits) for sphagnum- and soil-dwelling testate amoeba assemblages across different regions. The symbols display the significance of the pairwise difference between two habitat types within regions. (****) - $p < 0.0001$, (***) - $0.0001 < p < 0.001$, (**) - $0.001 < p < 0.01$, (*) - $0.01 < p < 0.05$, (ns) - $p > 0.05$.

Table 7. Pairwise comparisons: median value of categorical traits in six regions.

Trait	**Metric/category**	**Baikal**		**Penza**		**Tobolsk**		**Surgut**		**Urengoi**		**Zapolyarniy**	
		mineral soil	peatland	mineral soil	peatland	mineral soil	peatland	mineral soil	peatland	mineral soil	peatland	mineral soil	peatland
Position of the aperture	straight terminal	**0***	**0.50**	**0.06***	**0.79**	**0.20***	**0.43**	0.42	0.23	0.24	0.23	0.31	0.40
	sub terminal	0	0	0	0	0	0	0	0	0	0	0	0
	central ventral	0.14	0.06	0.22	0.08	**0.21***	**0.09**	0.11	0.13	**0.18***	**0.05**	**0.16***	**0.09**
	shifted ventral	**0.69***	**0.37**	**0.69***	**0.03**	**0.62***	**0.42**	0.52	0.31	**0.55***	**0.70**	0.49	0.50
	amphistomic	0	0	0	0.002	0	0.008	0	0.018	0	0	0	0
Degree of invagination of aperture	absent	0.57	0.65	0.83	0.90	0.42	0.50	0.64	0.34	0.51	0.41	0.57	0.46
	slightly	0.33	0.35	0.12	0.10	0.53	0.49	0.34	0.66	0.49	0.59	0.43	0.54
	strongly	0	0	**0.04***	**0**	**0.04***	**0**	0	0	0	0	0	0
Type of aperture rim	straight	**0.14***	**0.28**	0.23	0.23	**0.31***	**0.18**	0.17	0.22	0.13	0.11	**0.26***	**0.12**
	curved	**0.50***	**0.19**	**0.62***	**0.36**	0.21	0.10	0.17	0.09	0.14	0.11	0.18	0.11
	lobbed	0	0	0	0	0	0	0.005	0.008	0	0	0.019	0.038
	denticular	0.28	0.31	**0.12***	**0.20**	**0.46***	**0.60**	0.63	0.59	**0.63***	**0.76**	**0.55***	**0.74**
Presence of collar	absence	**1.00***	**0.90**	**1.00***	**0.69**	0.96	0.91	0.88	0.97	**0.97***	**1.00**	0.98	0.95
	presence	0	0.10	0	0.31	0.04	0.09	0.12	0.03	0.03	0	0.02	0.05
Shell (test) shape	sphere	0	0	0	0	0	0	0	0	0	0	0	0
	hemisphere	**0.67***	**0.15**	**0.88***	**0.08**	**0.51***	**0.09**	0.26	0.19	**0.30***	**0.15**	**0.28***	**0.17**
	cylinder	0	0	0	0.002	0	0.008	0	0.018	0	0	0	0
	patelliform	**0***	**0.03**	**0***	**0.03**	**0.01***	**0.04**	**0.01***	**0.05**	0.01	0.00	0.00	0.01
	rectangular cuboid	0	0	0	0	0	0	0	0	0	0	0	0
	ovoid	**0.28***	**0.66**	**0.10***	**0.57**	**0.46***	**0.77**	0.71	0.71	**0.69***	**0.78**	**0.60***	**0.74**
	pyriform	**0***	**0.04**	**0***	**0.13**	0.02	0.03	0.02	0.04	0.01	0.02	0.09	0.04
	spiral	0	0	0	0	0	0	0	0	0	0	0	0
Type of shell covering	organic	**0***	**0.08**	**0***	**0.33**	**0.01***	**0.14**	**0.01***	**0.26**	0.01	0.01	**0***	**0.03**
	xenosomes	**0.68***	**0.26**	**0.88***	**0.20**	**0.51***	**0.18**	0.27	0.25	**0.30***	**0.19**	**0.39***	**0.20**
	idiosomes	**0.28***	**0.43**	**0.12***	**0.20**	**0.46***	**0.60**	0.63	0.59	**0.63***	**0.77**	**0.55***	**0.74**
	cleptostomes	**0***	**0.05**	**0***	**0.11**	0.01	0	0.12	0.02	0.01	0	0.09	0.03
Presence of spines or horns	absence	**1.00***	**0.97**	**1.00***	**0.95**	**1.00***	**0.94**	0.98	0.98	**1.00***	**0.98**	0.99	0.97
	presence	0	0.03	0	0.05	0	0.06	0.02	0.02	0	0.02	0.01	0.03
Feeding type	mixotrophy	0	0	0	0.02	0	0.04	0.02	0.02	0	0	0	0.02
	bacterivory	**1.00***	**0.90**	**1.00***	**0.72**	**0.99***	**0.95**	0.88	0.97	0.99	1.00	0.91	0.95
	predator	**0***	**0.05**	**0***	**0.11**	0.01	0	0.07	0.01	0.01	0	0.09	0.02

Asterisks (*) indicate that the value differs significantly between the sphagnum- and soil-dwelling testate amoeba assemblages (bold fonts).

4.3. Community assembly rules

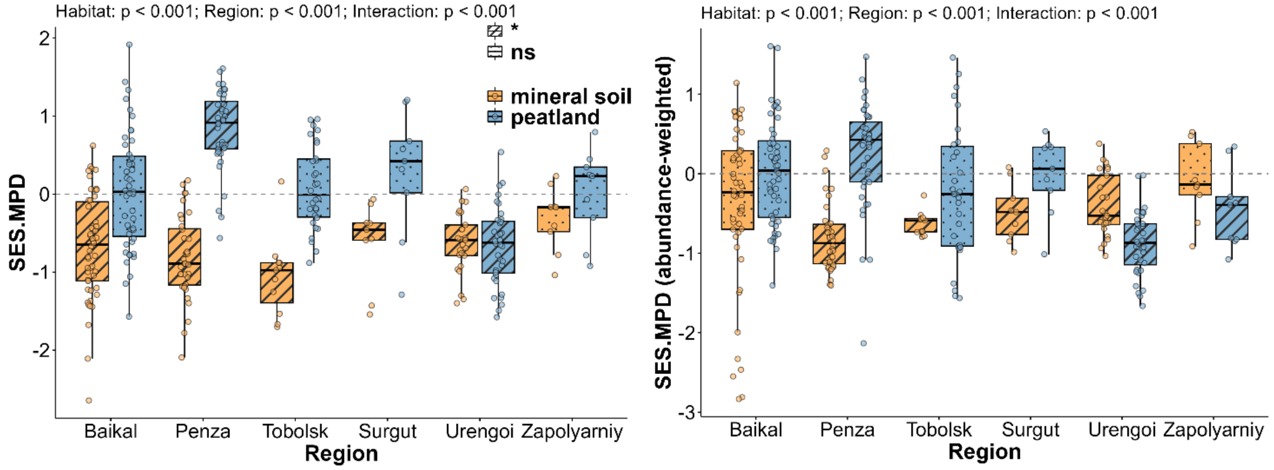
In addition to biodiversity pattern studies, understanding the main community assembly rules is ecologically significant, as it helps explain how species composition is shaped by environmental factors, interactions, and evolutionary processes. It also provides insights into the mechanisms driving biodiversity patterns and the functioning of ecosystems, offering a deeper understanding of how communities develop and respond to changes.

The two-way analysis of SES.MPD metric evaluated the effects of habitat type, region, and their interaction. Focusing on habitat type, we compared sphagnum- and soil-dwelling testate amoeba assemblages within each region using Wilcoxon tests. We also performed tests for clustering (negative SES.MPD) or overdispersion (positive SES.MPD) using single-sample tests.

Null model analysis indicated a pronounced contrast in the assembly mechanisms of t sphagnum- and soil-dwelling testate amoeba assemblages. The non-weighted SES.MPD metric consistently shows higher values in sphagnum-dwelling testate amoeba assemblages compared to those in soil-dwelling assemblages (Table 8, Fig. 19). In all studied regions, soil-dwelling testate amoeba assemblages exhibit assembly primarily influenced by environmental filtering, with functional clustering reflected in a median SES.MPD significantly below zero. Conversely, peatland communities demonstrate a positive median SES.MPD (except in Urengoi), suggesting evidence of functional overdispersion, though this is significantly different from zero only in the Penza region. Hence, biotic interactions emerge as the main driver in peatland community assembly.

The weighted SES.MPD metric tends to be lower than the non-weighted counterpart in peatlands. The median weighted SES.MPD values are negative for mineral soil communities across all regions and for half of the peatland communities. Significant functional clustering was identified in mineral soil communities across four regions, while peatland communities in Urengoi also showed this pattern. Notably, significant functional overdispersion was detected solely in Penza peatlands. There were significant differences in weighted SES.MPD between mineral soils and peatlands in Penza and Urengoi, with opposing directions of difference.

The assembly processes of testate amoeba assemblages in peatlands and mineral soils appear to stem from both habitat filtering and biotic interactions. The null model analyses of mean pairwise distances shed light on the relative significance of these assembly drivers. In mineral soils, negative standardized effect sizes (SES.MPD) imply that community structure is predominantly influenced by environmental constraints (Chase et al., 2011; Fournier et al., 2012; Arrieira et al., 2015), while positive SES.MPD values in peatlands indicate a greater impact from biotic interactions. Nevertheless, regional variations exist (e.g., in Urengoi, environmental constraints prevail in both mineral and peatland communities), underscoring the importance of regional factors in shaping microbial community structures.



(a) (b)

Fig 19. Boxplots of null model analysis metrics (median SES.MPD) for sphagnum- and soil-dwelling testate amoeba assemblages across different regions. Box hatching displays the significance of the difference from zero.

Table 8. Pairwise comparisons: median value of null model analysis metrics in six regions.

Type	**Variable**	**Baikal**		**Penza**		**Tobolsk**		**Surgut**		**Urengoi**		**Zapolyarniy**	
		mineral soil	peatland	mineral soil	peatland	mineral soil	peatland	mineral soil	peatland	mineral soil	peatland	mineral soil	peatland
SES.MPD	simple	**-0.69***	**0.04**	**-0.85***	**0.92**	**-1.01***	**0.01**	**-0.49***	**0.42**	-0.59	-0.63	-0.19	0.23
	abundance-weighted	-0.20	0.05	**-0.82***	**0.41**	-0.59	-0.24	-0.57	0.05	**-0.50***	**-0.90**	-0.13	-0.44

Asterisks (*) indicate that the value differs significantly between the sphagnum- and soil-dwelling testate amoeba assemblages (bold fonts).

4.4. Conclusions

This chapter have been devoted to identifying the differences in the species composition and taxonomic diversity of sphagnum- and soil-dwelling testate amoeba assemblages across six regions. We have performed PCA-based ordination and permutational ANOVA to analysis differences between habitat types and regions at the level of species structure. Diversity metrics, functional traits metrics and null model metrics (SES.MPD) were analyzed by Scheirer Ray Hare rank test for testing the effects of habitat type, region and their interaction, while the comparison between *sphagnum* and soil-dwelling testate amoeba assemblages within each region through simple rank-based Wilcoxon test.

The following results were obtained through our analysis. First, we have shown that the structure differed significantly between sphagnum- and soil-dwelling testate amoeba assemblages. Peatlands, characterized by abundant moisture and high levels of organic material, were dominated by species such as *Trinema lineare* and *Hyalosphenia papilio*, which thrive in nutrient-rich, waterlogged conditions. Conversely, mineral soils, typically drier and less enriched in organic content, were dominated by *Centropyxis aerophila*. These species exhibit strong resilience to the arid and unstable conditions prevalent in mineral soils, effectively utilizing the scarce resources available. This distinct separation underscores the pivotal role of habitat-specific factors in shaping microbial communities.

Second, taxonomic diversity metrics (including species richness, Shannon, and Simpson indices) revealed significant effects of ecoregion and habitat type, with interaction of factors indicating that habitat type influences diversity differently across regions. Peatlands generally supported higher diversity than mineral soils in the Baikal and Penza regions, while the reverse was observed in Western Siberia, highlighting the role of ecoregional conditions. Wet mineral soils in tundra and taiga regions provided sufficient moisture and habitat heterogeneity to enhance diversity, whereas dry mineral soils in forest-steppe ecoregions resulted in low diversity. These patterns emphasize that taxonomic diversity is shaped by the interplay of habitat type and regional environmental factors.

Third, functional diversity metrics (such as functional richness) exhibited notable differences between sphagnum- and soil-dwelling testate amoeba assemblages. In the Baikal and Penza regions, sphagnum-dwelling testate amoeba assemblages demonstrated higher functional richness suggesting that these habitats provide a more heterogeneous environment supporting a broader range of functional traits. The functional traits of testate amoebae demonstrate notable variation between sphagnum- and soil-dwelling testate amoeba assemblages, shaped by environmental factors such as water saturation, nutrient levels, and oxygen availability. The larger cell volumes observed in sphagnum-dwelling testate amoeba assemblages likely represent adaptations for flotation and oxygen retention, while variability in shell size and aperture features indicates region-specific responses to hydrological and substrate conditions. Consistent patterns in traits like shell morphology and aperture types suggest selective advantages in distinct environments, whereas feeding behaviors shift in response to nutrient availability. These observations highlight the intricate relationships among ecological factors that influence microbial adaptation to varied habitats.

Fourth, the assembly rules of sphagnum- and soil-dwelling testate amoeba assemblages are influenced by both environmental filtering and biotic interactions. Analyses using null models of mean pairwise distances (SES.MPD) shed light on the relative contribution of these processes. In soil-dwelling testate amoeba assemblages, negative SES.MPD values indicate that environmental factors primarily shape community composition, whereas positive SES.MPD values in sphagnum-dwelling testate amoeba assemblages suggest a greater role of biotic interactions. Nevertheless, regional variations exist; for instance, in Urengoi, environmental constraints appear to govern community structure in both assemblages. All findings collectively underscore the critical roles of soil moisture regime and ecological processes in shaping testate amoeba assemblages.

Chapter 5. Latitudinal and longitudinal gradient patterns in species diversity in testate amoebae *α*- and *β*-diversity

The latitudinal and longitudinal gradient patterns of *α*- and *β*-diversity in different habitat types provide insights into how environmental factors, such as climate and soil properties, influence the distribution and composition of species. These gradients help explain how species diversity changes across geographical regions and between different habitats, offering important ecological information about community assembly, adaptation to local conditions, and the role of biotic and abiotic factors in shaping biodiversity. Understanding these patterns is crucial for predicting how ecosystems respond to environmental changes.

5.1. Latitudinal and longitudinal patterns in sphagnum-dwelling testate amoeba assemblages[3]

To identify latitudinal distribution patterns of sphagnum-dwelling testate amoeba assemblages, we first selected a set of samples from 75 peatlands. 296 samples were collected from hummocks, 314 from lawns, and 206 from hollows. Second, we calculated the diversity indices (S, D_1, E, $1\text{-}C_{0N}$, $1\text{-}C_{1N}$) based on relative abundance data. Third, we considered the climate characteristics extracted from WorldClim (version 2.0) database to explain the variation in species diversity and structure of

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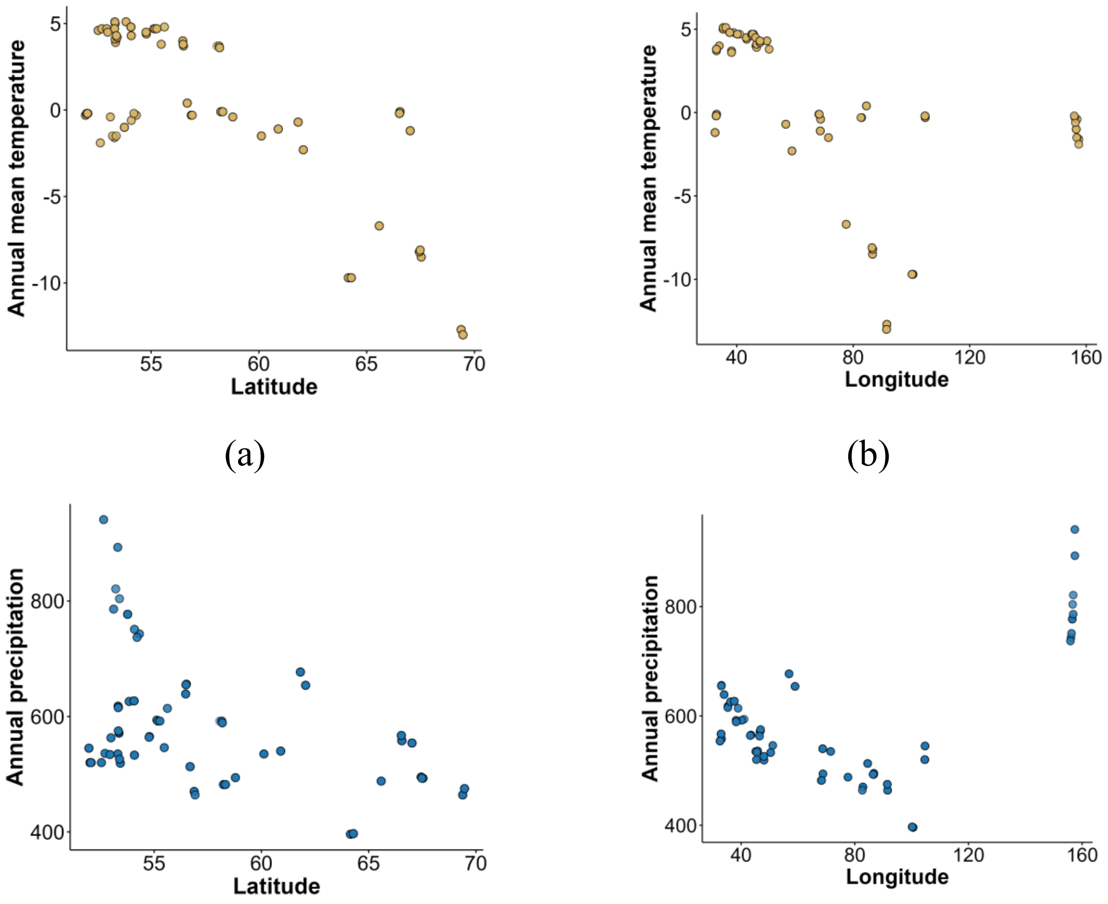
[3] The results presented in this section are published in the works:

Saldaev D., Babeshko K., Chernyshov V., Esaulov A., Gu X., Kriuchkov N., Mazei N., Saldaeva N., Su J., Tsyganov A., Yakimov B., Yushkovets S., Mazei Y.A. Biodiversity of Terrestrial Testate Amoebae in Western Siberia Lowland Peatlands // Data. 2023. V. 8. P. 173. https://doi.org/10.3390/data8110173 (Q2, IF SRJ 0.480, EDN: FCUMAC, 0.77/0.15 p.s.)

Su J., Mazei Y.A., Tsyganov A.N., Mazei N.G., Chernyshov V.A., Komarov A.A., Babeshko K.V., Mitchell E.A.D., Shimano S., Saldaev D.A., Yakimov B.N. Continental-Scale α- and β-Diversity Patterns of Terrestrial Eukaryotic Microbes: Effect of Climate and Microhabitat on Testate Amoeba Assemblages in Eurasian Peatlands // Journal of Biogeography. 2025. V. 52. e15082. https://doi.org/10.1111/jbi.15082 (Q1, IF SRJ 1.438, EDN: SJTXLM, 1.88/1 p.s.)

testate amoeba assemblages along the latitude and longitude. We selected climate factors with a VIF < 10 and incorporating microhabitat type as fixed effects in linear mixed-effects models. Community diversity metrics (S, D_1, E, $1\text{-}C_{0N}$, $1\text{-}C_{1N}$) were examined in relation to microhabitat, individual environmental predictors, and combined predictors, with peatland ID as a random factor. For each diversity metric, we conducted three types of analysis. Initially, we analyzed the effect of microhabitat, including post hoc comparisons between microhabitats. Then, we modeled the relationship with environmental predictors separately. Finally, we constructed models with multiple predictors.

On the whole, precipitation and temperature are primarily influenced by geographic regions. The latitudinal gradient is linked to a gradual northward decline in both annual mean temperature and precipitation levels (Fig. 20a, 20c). Longitudinal effects show a more complex pattern, with mean annual temperature and total precipitation gradually decreasing between 40° and 120°E due to increased climate continentality, then sharply rising beyond 120°E, influenced by the maritime climate of the Kamchatka Peninsula (Fig. 20b, 20d). Then, variance inflation factor (VIF) values indicated high collinearity among most climatic variables, so only five factors with VIFs below 10 (annual mean temperature, isothermality, temperature seasonality, annual precipitation, and precipitation seasonality) were selected as potential predictors for further analysis.



(a) (b)

(c) (d)

Fig 20. Annual mean temperature and annual precipitation in relation to latitude and longitude.

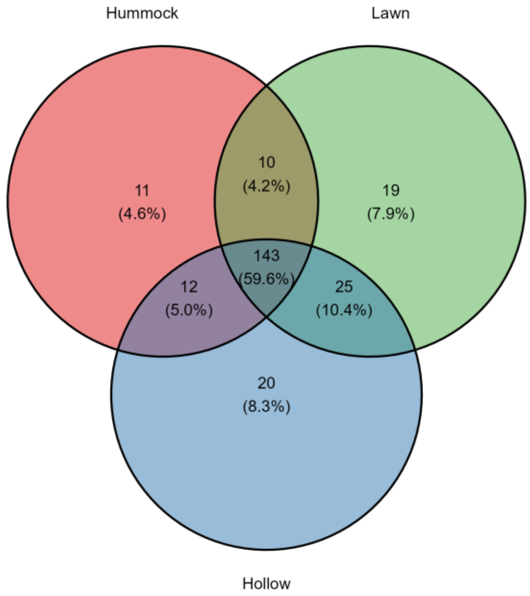
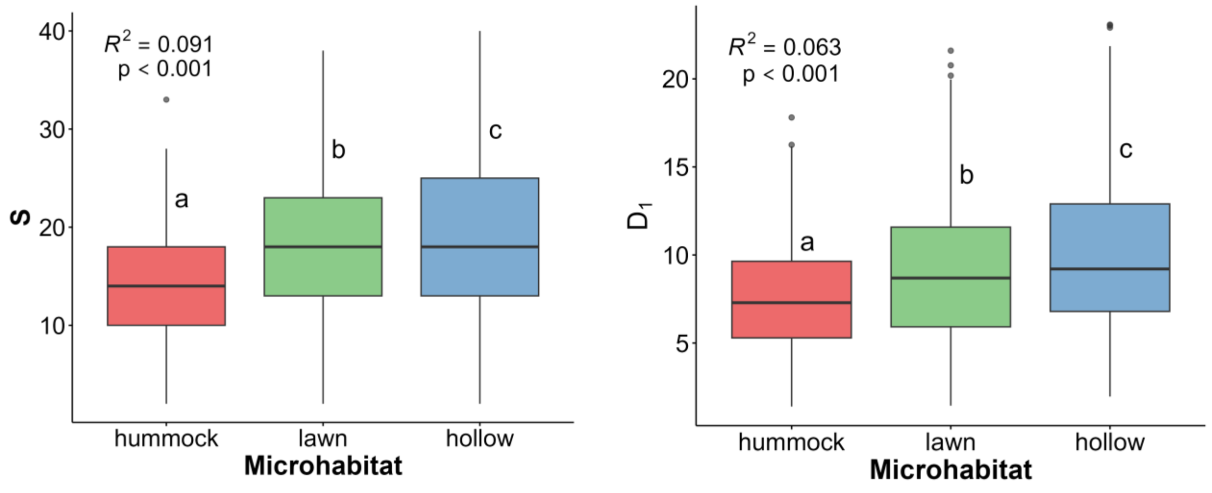


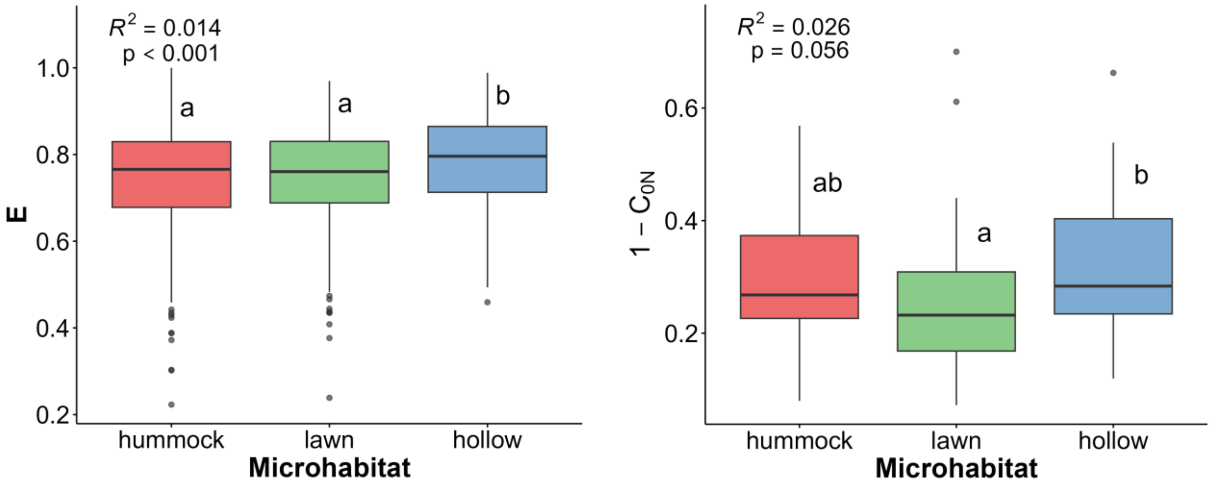
Fig 21. Venn diagram which shows the number of species and the proportion to total species in three microhabitats (hummock, lawn, hollow).

We recorded a total of 240 testate amoeba taxa, highlighting distinct community structures across microhabitats: 176 species in hummocks, 197 in lawns, and 200 in hollows (Fig. 21). Species richness and the exponential Shannon index varied significantly across the three microhabitats, increasing from hummocks to hollows (Figs. 22a, 22b), while evenness was notably higher in hollows compared to hummocks and lawns (Fig. 22c). In contrast, β-diversity was lowest in lawns, showing a significant reduction compared to hollows (Figs. 22d, 22e).

Species richness of testate amoeba assemblages increased in a northerly direction (Table 9, Fig. 23a), with this effect being microhabitat-specific; it was most pronounced in hollows and lawns, while absent in hummocks. The relationship between longitude and species richness was not significant, as the overall model was significant, but the only noteworthy term was the interaction with microhabitat type, with no slopes differing from zero. A negative correlation was observed between species richness and both mean annual temperature and annual precipitation (Table 9, Figs. 23b-c). The correlation between testate amoeba diversity and mean annual temperature varied by microhabitat, being strongest in hollows and insignificant in hummocks (Table 9). Among all significant predictors, mean annual temperature exhibited 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 9), explained 18.4% of the variance in species richness, indicating that mean annual temperature was the best predictor of testate amoeba species richness.



(a) (b)



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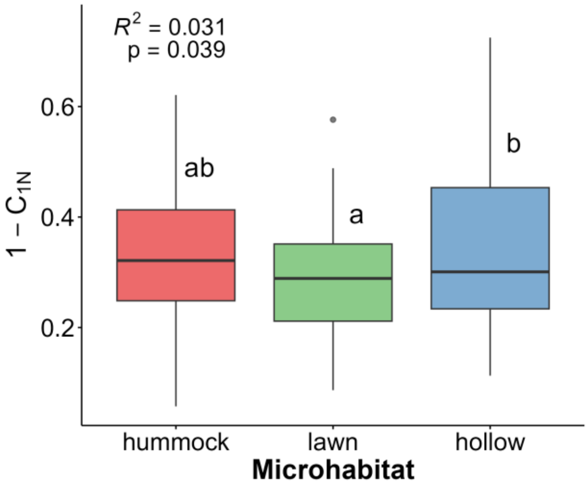


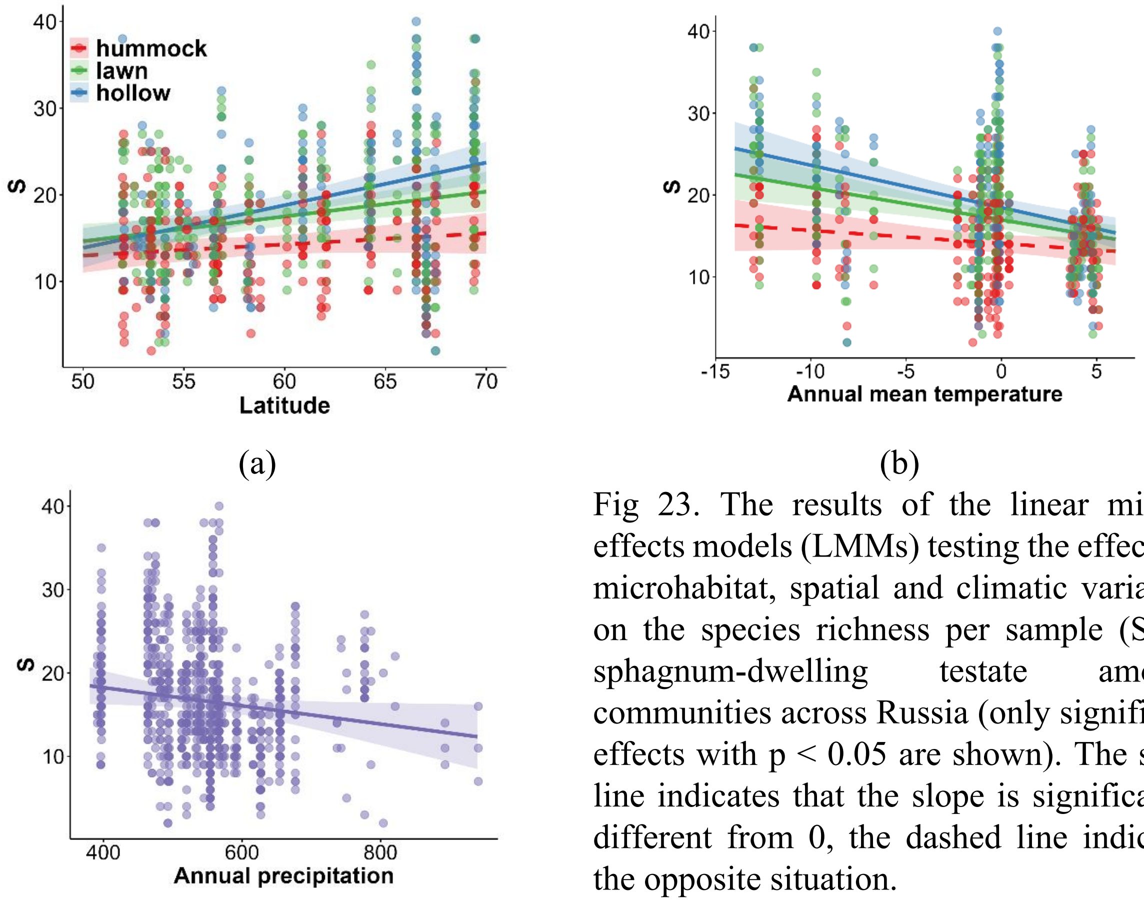
(e)

Fig 22. 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 assemblages 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 9. 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. 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).

Variable	**Single-predictor model**				**Multiple-predictor model**		
	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			
Annual mean temperature					-	-	0.031
Isothermality					-	-	
Temperature seasonality					-	-	
Annual precipitation					-	-	
Precipitation seasonality	-0.0015^{a}	0.00001^{ab}	0.0024^{b}	0.056	-	-	



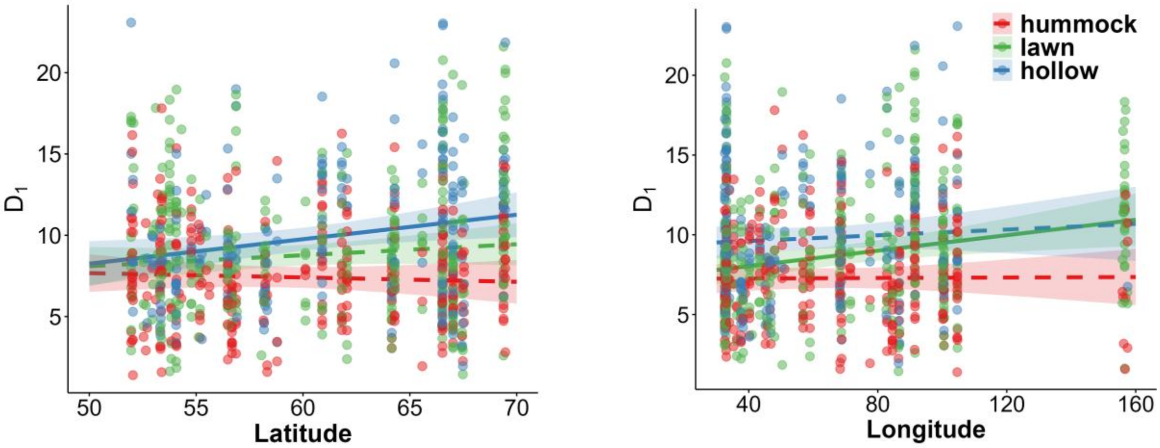
(a)

(b)

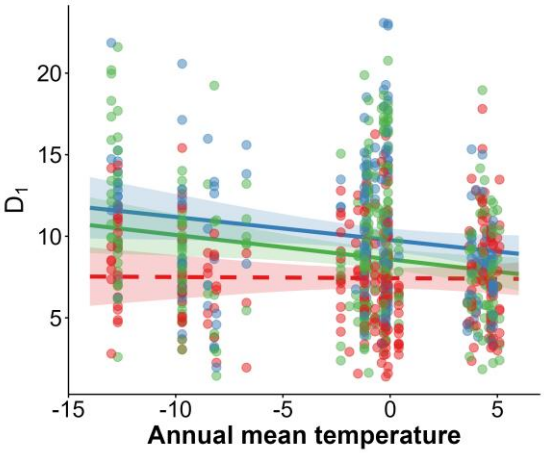
(c)

Fig 23. 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.

The Shannon diversity index D_1 varied both latitudinally and longitudinally. Similar to species richness, the correlation between D_1 and latitude differed among microhabitats, increasing with latitude in hollows but remaining constant in hummocks (Table 9, Fig. 24a). Conversely, the D_1 index increased towards the east, significantly so only for lawns. Among climatic factors, only mean annual temperature was significant in single-predictor models (Fig. 24c), though this was not significant for hummocks (Table 9). The fixed effects in the parsimonious multiple-predictor model, which included mean temperature and temperature seasonality (Table 9), accounted for 10.2% of the variance in the D_1 index.



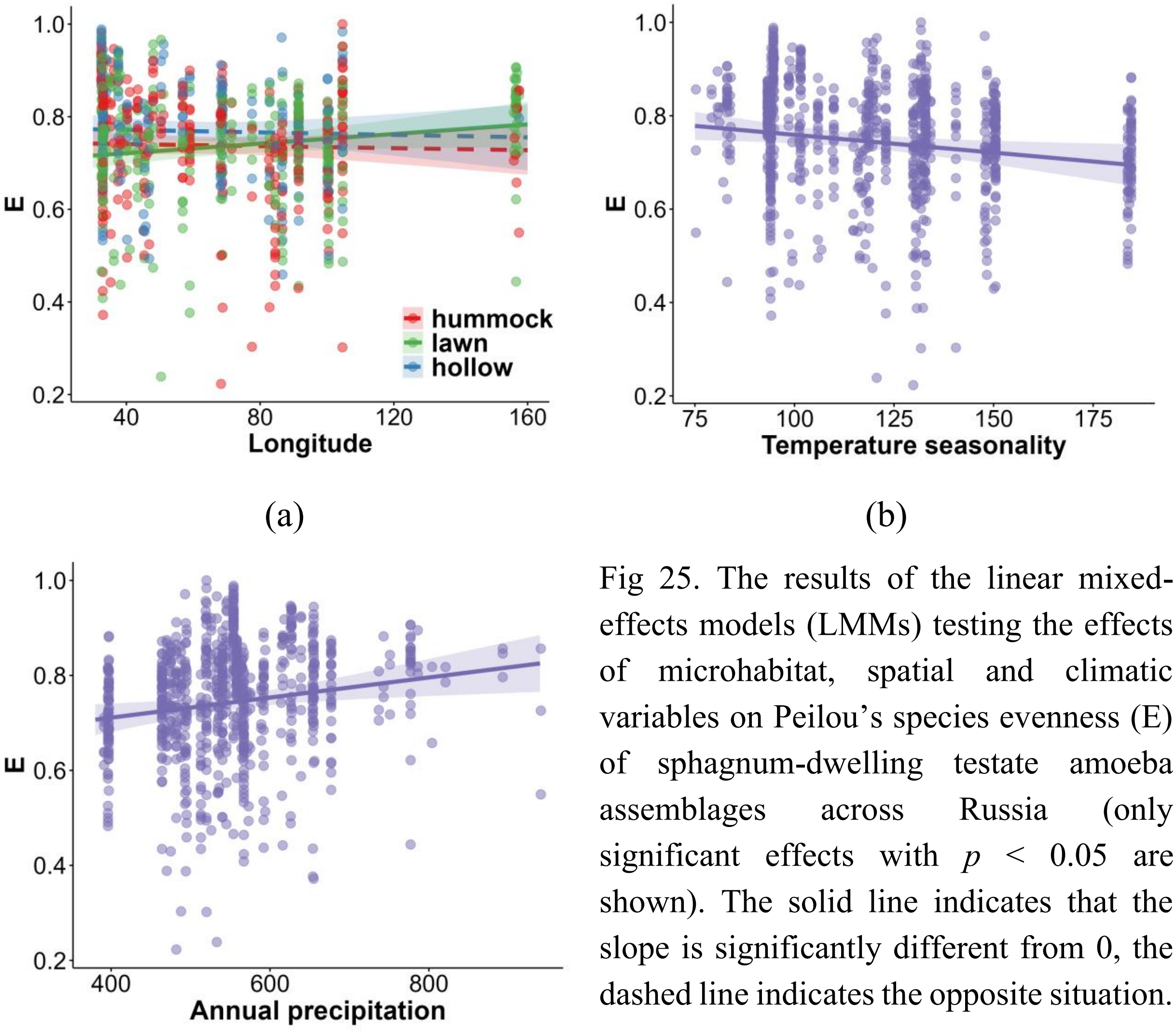
(a) (b)



(c)

Fig 24. The results of the linear mixed-effects models (LMMs) testing the effects of microhabitat, spatial and climatic variables on the exponential Shannon diversity index (D_1) of sphagnum-dwelling testate amoeba assemblages 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.

Pielou evenness E showed a positive correlation with longitude, being significant for lawns but not for hummocks and hollows (Table 9, Fig. 25a). Additionally, E was negatively correlated with temperature seasonality and positively correlated with annual precipitation (Figs. 25b, 25c). The parsimonious model comprised only annual precipitation, so its performance aligns with the single-predictor model.



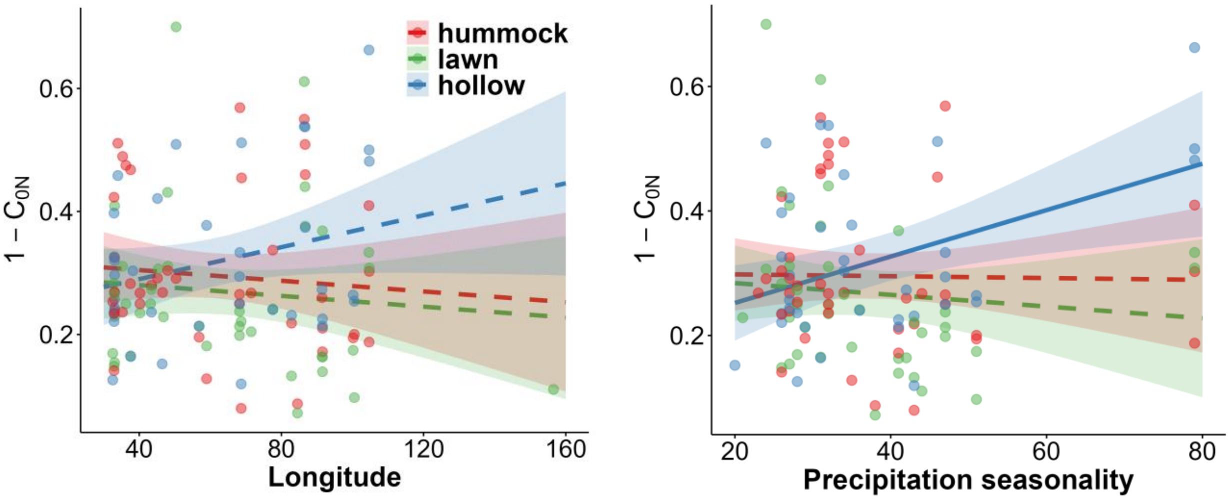
(a)

(b)

(c)

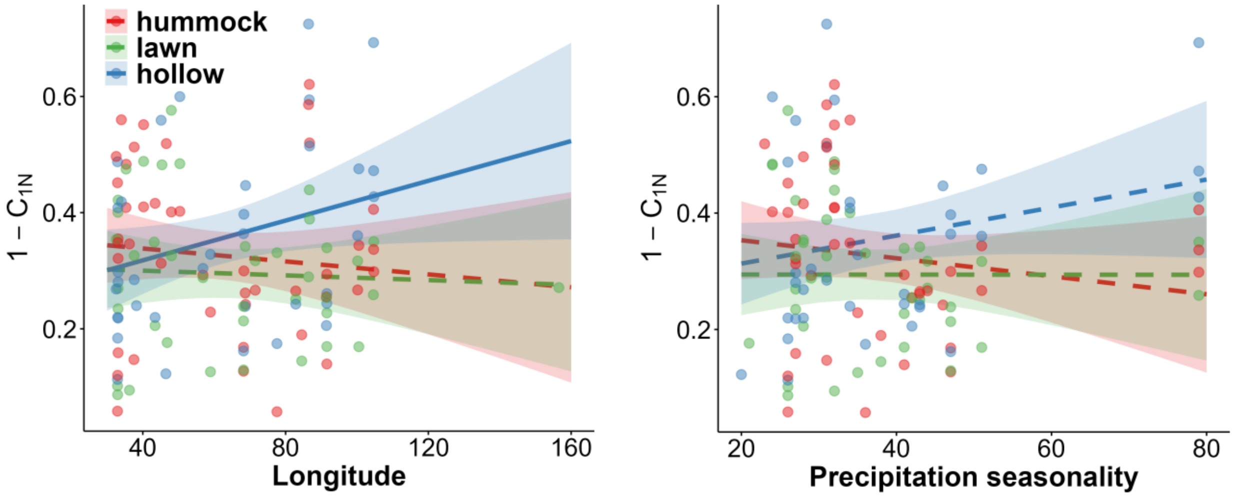
Fig 25. The results of the linear mixed-effects models (LMMs) testing the effects of microhabitat, spatial and climatic variables on Peilou's species evenness (E) of sphagnum-dwelling testate amoeba assemblages across Russia (only significant effects with $p < 0.05$ are shown). The solid line indicates that the slope is significantly different from 0, the dashed line indicates the opposite situation.

In contrast to α-diversity metrics and evenness, the analysis of β-diversity revealed significantly fewer correlations. Zeroth-order β-diversity ($1 - C_{0N}$) showed a positive dependency on precipitation seasonality, which was significant only for hollows (Table 9, Fig. 26). However, the parsimonious multiple-predictor model did not include precipitation seasonality but rather incorporated isothermality and temperature seasonality. Additionally, first-order β-diversity ($1 - C_{1N}$) positively depended on longitude solely for hollows (Table 9, Fig. 27). Both models included a significant interaction term, contrasting the slopes for hummocks and hollows, with the effect being negative for hummocks and positive for hollows. All climatic factors were excluded from the parsimonious model for 1 - C_{1N} (Table 9).



(a) (b)

Fig 26. 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 assemblages 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.



(a) (b)

Fig 27. The results of the linear mixed-effects models (LMMs) testing the effects of microhabitat, spatial and climatic variables on the first order β-diversity ($1 - C_{1N}$) of sphagnum-dwelling testate amoeba assemblages 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.

5.2. Latitudinal gradient β-diversity patterns in soil-dwelling testate amoeba assemblages[4]

To study latitudinal distribution β-diversity patterns of soil-dwelling testate amoeba assemblages, we first selected a set of samples following nested scales in four sub-zones. 18 samples were collected from northern forest-tundra sub-zone, 52 samples from forest-tundra sub-zone, 21 samples from taiga sub-zone, and 30 samples

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[4] The results presented in this section are published in the work:
Su J., Mazei Y.A., Tsyganov A.N., Chernyshov V.A., Mazei N.G., Saldaev D.A., Yakimov B.N. Multi-scale beta-diversity patterns in testate amoeba communities: species turnover and nestedness along a latitudinal gradient // Oecologia. 2024. V. 205. P. 691-707. https://doi.org/10.1007/s00442-024-05602-2 (Q1, IF SRJ 0.966, EDN: RZNXWB, 1.78/1 p.s.)

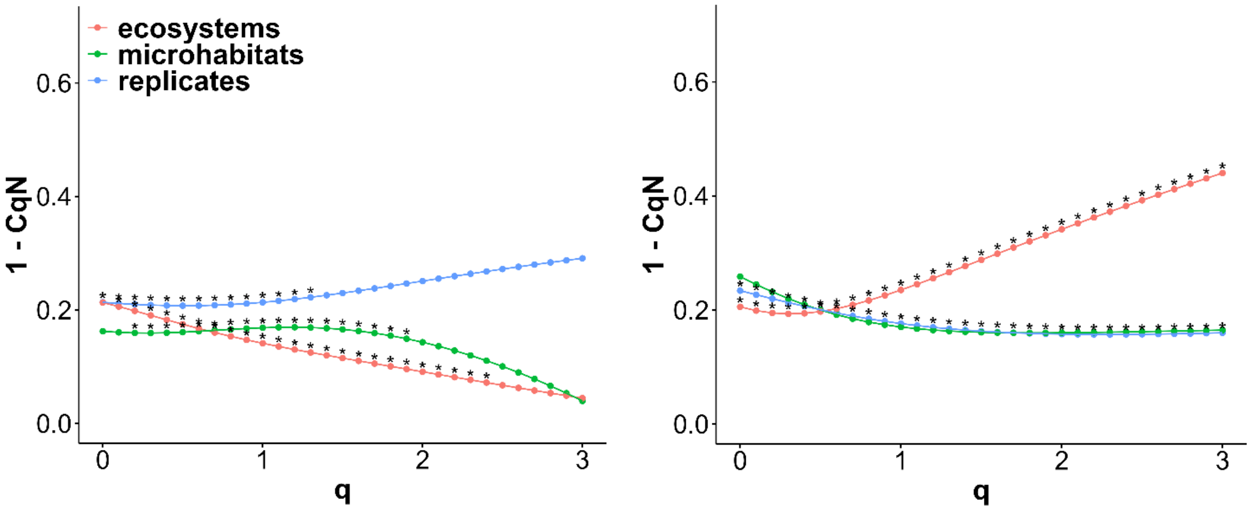
from sub-taiga sub-zone (Table 10). In total, 74 species and subspecies of testate amoebae were identified. Samples contained 10 to 293 individuals (87.6 ± 51.1, mean ± sd). Species richness varied from 1 to 26 species (15.5 ± 5.52). Second, we calculated β-diversity $(1 - C_{qN})$ for each sub-zone, ecosystem and microhabitat (Table 10) by using multiplicative partitioning method. Third, we utilized β-diversity profiles to visualize these patterns, which plot $1 - C_{qN}$ against the corresponding diversity order q (ranging from 0 to 3).

Table 10. Sampling sites

Sub-zone	**Sampling area**	**Latitude, °N**	**Longitude, °E**	**Ecosystems**	**Microhabitats**	**Samples**
northern forest-tundra	Zapolyarniy	67.233	79.017	*Larix* forest	litter (tree butt)	3
					Sphagnum sp.	3
					Cladonia sp.	3
				Betula forest	litter (tree butt)	3
					litter (intercrown)	3
					green moss	3
forest-tundra	Urengoi	65.550	78.300	*Larix-Pinus sibirica-Betula* forest	litter (tree butt)	3
					litter (intercrown)	3
				Pinus sylvestris forest	litter (tree butt)	3
					Cladonia sp.	3
				Pinus sibirica-Betula forest	litter (tree butt)	3
					Cladonia sp.	3
				Larix-Pinus sibirica forest	litter (tree butt)	3
					Cladonia sp.	3
				Larix forest	green moss	3
					Sphagnum sp.	3
					Cladonia sp.	3
					litter (tree butt)	3
					litter (undercrown)	3
					litter(intercrwon)	3
taiga	Surgut	60.117	71.500	*Pinus sibirica* forest	green moss	3
					litter (tree butt)	3
					litter (undercrown)	3
					litter(intercrwon)	3
	Tobolsk	58.267	68.333	*Abies-Picea-Pinus* forest	litter (tree butt)	3
					litter (undercrown)	3

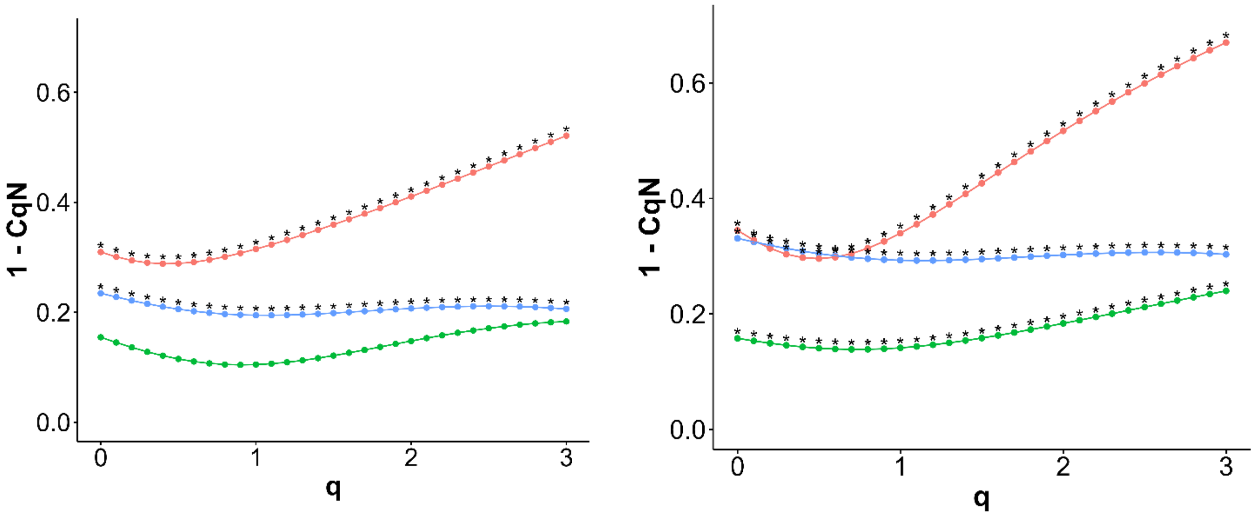
					litter(intercrwon)	3
sub-taiga	Tumen	57.217	65.400	*Populus-Betula* forest	green moss	3
					litter (tree butt)	3
					litter (undercrown)	3
					litter(intercrwon)	3
	Kurgan	55.300	65.150	*Betula* forest	litter (tree butt)	3
					litter (undercrown)	3
					litter(intercrwon)	3
				Pinus sylvestris forest	*Cladonia* sp.	3
					green moss	3
					litter	3

The analysis of β-diversity profiles reveals that the forest-tundra, taiga, and sub-taiga sub-zones exhibited high β-diversity among ecosystems but low β-diversity among microhabitats across most diversity orders (q). Conversely, in the northern forest-tundra zone, the highest contribution was observed in among-replicate β-diversity, with the lowest contribution in among-ecosystem β-diversity. However, these differences among scales varied depending on the influence of abundant species (i.e., the diversity order q). Generally, a higher contribution of abundant species (i.e., greater q values) led to increased β-diversity among ecosystems, while β-diversity among microhabitats and among replicates converged. For instance, in the typical forest-tundra zone (Fig. 28b) at $q = 0$ (where species abundances are disregarded), among-microhabitat β-diversity is the highest, followed by among-replicate β-diversity, with among-ecosystem β-diversity being the lowest. As q values exceed 0.5, both among-microhabitat and among-replicate diversities decrease and soon align, while among-ecosystem diversity increases, eventually becoming the dominant component. Similar trends are observed in the taiga and sub-taiga sub-zones (Fig. 28c and 28d), except that among-replicate β-diversity consistently surpasses among-microhabitat β-diversity at all q levels. In the northern forest-tundra (Fig. 28a), among-replicate β-diversity remains relatively stable across various q values, while among-microhabitat and among-ecosystem β-diversity decline as q increases.



(a) northern forest-tundra

(b) forest-tundra



(c) taiga

(d) sub-taiga

Fig 28. Multiplicative partitioning of testate amoeba diversity in the northern forest-tundra zone (a), forest-tundra zone (b), taiga (c) and sub-taiga (d). Lines are diversity profiles for three scale levels. Points marked with an asterisk represent the significant cases compared to expected results in the null model analysis.

When comparing profiles across the four sub-zones, a distinct latitudinal gradient in among-ecosystem β-diversity emerges (Fig. 29). The $1\text{-}C_{qN}$ value is highest in the southern (sub-taiga) sub-zone and decreases towards the north. Latitudinal differences are less evident for lower diversity orders. The corresponding among-ecosystem β-diversity values are similar between sub-taiga and taiga, as well as between northern and typical forest-tundra. No consistent latitudinal gradient was observed for among-microhabitat and among-replicate β-diversity.

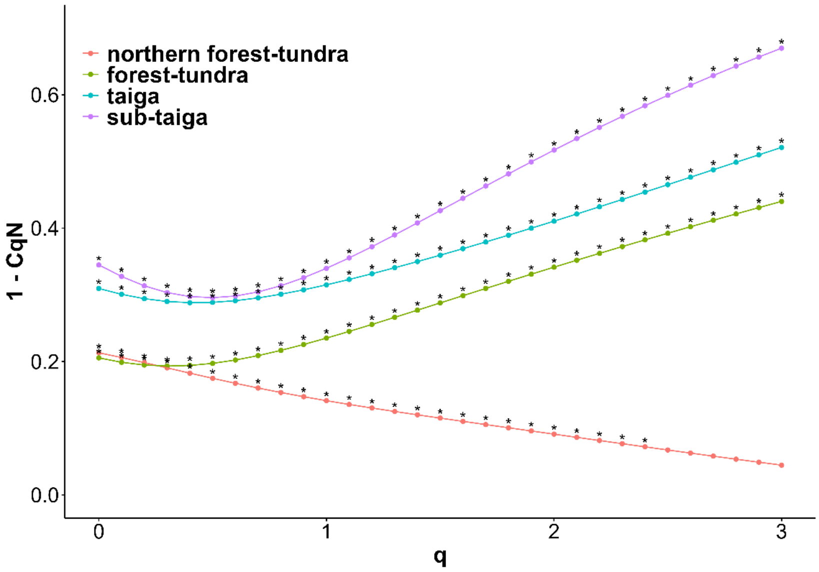


Fig 29. Among-ecosystem β-diversity of testate amoeba assemblages in Western Siberia. Lines are diversity profiles for four sub-zones. Points marked with an asterisk represent the significant cases as compared to expected results in the null model analysis.

A null-model analysis of $1\text{-}C_{qN}$ values was conducted to assess deviations from random expectations (Table 11). Overall, β-diversity among ecosystems was significantly higher than expected, indicating that the elevated β-diversity among ecosystems in all four sub-zones could not be attributed solely to differences in α-diversity, species composition, or microhabitat composition. In contrast, β-diversity among replicates was significantly lower than expected in all sub-zones, suggesting a homogeneous testate amoeba composition within microhabitats. Results for among-microhabitat β-diversity varied among sub-zones: it was significantly lower than expected in the sub-taiga but higher than expected in the northern forest-tundra, with no significant deviation from expectation in the typical forest-tundra and taiga. The null-model analysis results were consistent across different diversity orders (q), with changes only in significance levels but no reversals (where a component is significantly lower than expected for one q value but higher for another q).

Table 11. Null-model analysis of $1 - C_{qN}$

q	northern forest-tundra		forest-tundra		taiga		sub-taiga	
	observed	expected	observed	expected	observed	expected	observed	expected
	among sample replicates							
0	0.214***	0.325	0.234***	0.381	0.235***	0.346	0.331***	0.443
1	0.213***	0.274	0.176***	0.310	0.195***	0.322	0.293***	0.435
2	0.251 ns	0.248	0.158***	0.288	0.207***	0.376	0.302***	0.512
3	0.291 ns	0.226	0.160*	0.278	0.206***	0.451	0.303***	0.601
	among microhabitats							
0	0.163 ns	0.141	0.259 ns	0.232	0.155 ns	0.174	0.158***	0.231
1	0.169***	0.104	0.170 ns	0.151	0.105 ns	0.122	0.141*	0.177
2	0.143 ns	0.088	0.160 ns	0.113	0.148 ns	0.165	0.184*	0.261
3	0.040 ns	0.056	0.165 ns	0.071	0.183 ns	0.229	0.240*	0.374
	among ecosystems							
0	0.213***	0.068	0.206***	0.090	0.310***	0.128	0.345***	0.127
1	0.141***	0.040	0.235***	0.005	0.315***	0.042	0.340***	0.056
2	0.091*	0.026	0.342***	-0.068	0.410***	0.043	0.517***	0.091
3	0.045 ns	0.006	0.440***	-0.196	0.521***	0.054	0.670***	0.151

Null-model analysis of $1 - C_{qN}$ for three levels: among sample replicates, among microhabitats, among ecosystems. The observed values were compared to the expected under the null model based on 9999 randomizations: (***) - P < 0.001, (**) - P < 0.01, (*) - P < 0.05, (ns) - P > 0.05.

5.3. Conclusions

This chapter have been devoted to identify latitudinal distribution patterns of sphagnum- and soil-dwelling testate amoeba assemblages. We have performed linear mixed-effects models to explore potential environmental influences on α- and β-diversity in sphagnum-dwelling testate amoeba assemblages and multi-scale partitioning of β-diversity for 111 samples across multiple hierarchical levels (including sample, microhabitat, and ecosystem, within four climatic sub-zones of the West Siberian Plain) in soil-dwelling testate amoeba assemblages.

In sphagnum-dwelling testate amoeba assemblages, our analysis revealed a notable inverse latitudinal gradient in α-diversity, which was negatively associated with mean annual temperature. This pattern was strongly evident in lawn and hollow microhabitats but absent in hummocks. Longitude, reflecting a gradient in precipitation seasonality, emerged as a significant factor influencing β-diversity, particularly within hollow habitats. These results highlight the role of climatic variables, such as mean annual temperature and precipitation seasonality, in shaping large-scale α- and β-diversity patterns of testate amoebae. The lack of a discernible pattern in hummocks likely reflects the dominant influence of microhabitat stressors (including low moisture and pH).

In soil-dwelling testate amoeba assemblages, our findings demonstrate that the taxonomic β-diversity of these assemblages peaks at the inter-ecosystem scale, particularly when abundance-weighted metrics are used. This study reveals that diversity patterns of terrestrial testate amoebae along the nested microhabitat hierarchy and latitudinal gradient in the West Siberian Plain are predominantly shaped by spatial and environmental heterogeneity at the ecosystem level. Rare species played a major role in driving β-diversity across all hierarchical levels, with their influence being most pronounced in northern sub-zones. Collectively, these results underscore the scale- and latitude-dependent roles in shaping the β-diversity of terrestrial microbial communities.

Concluding remarks

This study presents a comparative analysis of sphagnum- and soil-dwelling testate amoeba assemblages across different regions of Northern Eurasia. A novel functional group classification system, developed based on 18 traits, offers an alternative to traditional morphology-based approaches. This system enables a deeper understanding of the ecological roles, adaptive strategies, and functional niches of species, thereby improving the interpretation of testate amoebae responses to environmental change. Such an approach provides a foundation for a more mechanistic understanding of microbial ecology, allowing for the identification of generalizable patterns in trait–environment relationships across ecosystems. It also lays the groundwork for integrating testate amoebae into broader functional frameworks alongside plants, fungi, and other components of the soil biota. Future studies could combine functional trait data with molecular approaches (e.g., environmental DNA and transcriptomics) to elucidate the genetic basis of traits and link community functional structure to ecosystem processes such as organic matter decomposition and carbon sequestration.

Our results revealed substantial taxonomic and functional differences between sphagnum- and soil-dwelling testate amoeba assemblages, largely driven by regional environmental conditions, particularly soil moisture and climate. Differences in average trait values, such as shell size and aperture characteristics, reflect adaptations to distinct moisture regimes. The contrasting patterns of diversity between peatland and mineral soil habitats across ecoregions: higher diversity in peatlands in drier forest-steppe zones versus higher diversity in mineral soils in the wetter taiga and tundra, which highlight the central role of moisture availability in shaping testate amoeba assemblages. These findings illustrate how microeukaryotic communities respond to macroecological gradients and emphasize water availability as a key driver of community structure. The data support the use of testate amoebae as indicators of moisture conditions across habitat types and climatic zones. Future research should focus on long-term monitoring along moisture gradients to assess community resilience and detect threshold responses to wetting and drying processes. Integrating remotely sensed soil moisture data with in situ functional trait measurements will enhance the predictive capacity of models forecasting testate amoeba assemblages responses to climate-driven hydrological changes at the landscape scale.

We also demonstrated that the dominant ecological processes underlying community assembly differ between habitat types: testate amoeba assemblages in mineral soils are primarily shaped by abiotic filtering, while those in peatland habitats are more influenced by biotic interactions. These differences suggest that testate amoebae exhibit habitat-specific sensitivity to environmental changes, resulting in divergent response trajectories. This observation contributes to the development of microbial community assembly theory by highlighting how habitat context modulates the balance between stochastic and deterministic processes. Promising directions for future research include experimental approaches to test the strength and reversibility of these processes, as well as the development of mechanistic models that integrate trait-based assembly processes with disturbance regimes.

Our analysis also revealed the presence of latitudinal diversity gradients, including a decline in β-diversity with increasing latitude in soil-dwelling testate amoeba assemblages and a negative α-diversity gradient in sphagnum-dwelling testate amoeba assemblages in microtopographic depressions (hollows). These large-scale biogeographic patterns shed light on the combined influence of historical biogeography, climatic variability, and habitat specialization on microbial distributions. They also raise important questions about how these gradients may shift under accelerated warming in high-latitude regions. Future research should incorporate paleoecological data and fossil testate amoebae to reconstruct historical biogeographic shifts and identify long-term drivers of diversity. Comparative studies between the Northern and Southern Hemispheres may further test the universality of latitudinal diversity patterns, contributing to the development of a unified theory of microbial biogeography.

Conclusions

1. A comparison of the taxonomic structure and diversity of sphagnum- and soil-dwelling testate amoeba assemblages in the Middle Volga region, Western Siberia, and Baikalia revealed pronounced differences. Sphagnum-dwelling testate amoeba assemblages were dominated by *Trinema lineare* and *Hyalosphenia papilio*, whereas *Centropyxis aerophila sphagnicola* and *Centropyxis aerophila* prevailed in soil-dwelling testate amoeba assemblages. The taxonomic diversity between habitat types varied significantly across regions: sphagnum-dwelling testate amoeba assemblages exhibited higher diversity in forest-steppe ecoregions, while soil-dwelling testate amoeba assemblages were more diverse in the taiga and tundra.

2. A classification system for testate amoebae of the Northern Holarctic was developed, dividing species and subspecies into seven functional groups based on 18 traits. Compared to traditional morphology-based classifications, this trait-based system provides a more informative framework for understanding ecological roles and strategies.

3. Community-weighted mean trait values of testate amoebae differed significantly between peatland and mineral soil habitats. Sphagnum-dwelling testate amoebae were characterized by larger shell size, more elongated shell shape, narrower apertures, and a predominance of organic shells with endogenous siliceous plates (idiosomes).

4. The assembly of sphagnum- and soil-dwelling testate amoeba assemblages is driven by a combination of abiotic and biotic mechanisms. Abiotic environmental filtering plays a dominant role in soil-dwelling testate amoeba assemblages, whereas biotic interactions are more influential in sphagnum-dwelling testate amoeba

assemblages.

5. The moisture regime of mineral soils across different ecoregions is a key factor underlying the structural and functional differentiation between sphagnum- and soil-dwelling testate amoeba assemblages. In forest-steppe regions, where soil moisture is limited, sphagnum-dwelling testate amoeba assemblages display higher diversity. In contrast, the sufficient soil moisture of taiga and tundra supports greater diversity in soil-dwelling testate amoeba assemblages.

6. The α- and β-diversity of sphagnum-dwelling testate amoeba assemblages is influenced by climatic variables such as mean annual temperature and precipitation seasonality. Communities in moist hollow microhabitats exhibit a positive latitudinal diversity gradient, while such a gradient is absent in drier hummock microhabitat, likely reflecting the stressful conditions of the latter. Soil-dwelling testate amoeba assemblages show a negative latitudinal gradient in β-diversity at the scale of ecosystems, but this pattern does not hold at the scale of microhabitat or within microhabitat variation.

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