Testate Amoeba Functional Traits and Their Use in Paleoecology

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This review provides a synthesis of current knowledge on the morphological and functional traits of testate amoebae, a polyphyletic group of protists commonly used as proxies of past hydrological changes in paleoecological investigations from peatland, lake sediment and soil archives. A trait-based approach to understanding testate amoebae ecology and paleoecology has gained in popularity in recent years, with research showing that morphological characteristics provide complementary information to the commonly used environmental inferences based on testate amoeba (morpho-)species data. We provide a broad overview of testate amoeba morphological and functional traits and trait-environment relationships in the context of ecology, evolution, genetics, biogeography, and paleoecology. As examples we report upon previous ecological and paleoecological studies that used trait-based approaches, and describe key testate amoebae traits that can be used to improve the interpretation of environmental studies. We also highlight knowledge gaps and speculate on potential future directions for the application of trait-based approaches in testate amoeba research.

Keywords: protists, functional traits, morphological traits, ecology, peatlands, lakes, soils, trait-based approaches

INTRODUCTION

Paleoecological reconstructions based on subfossil species assemblage data are commonly used to reconstruct past environmental changes over long time-scales (from hundreds of years to millennia) (Willis and MacDonald, 2011; Roberts, 2013). Assuming that species ecological requirements are stable over time, the main premise in paleoecology is that changes in species assemblages over time similarly reflect past environmental changes within a study site or region (Birks et al., 2016). While this approach informs on changes in key abiotic drivers of ecosystem processes (e.g., peatland water table depth, air temperature, pH, nutrient loading, road salt and

metal contamination in lakes), it does not provide direct evidence for functional changes. The functional trait approach aims to link community composition to ecological drivers and the functional consequences of these changes. This approach, which was first developed to better understand modern community structure has been increasingly used to infer long-term changes in ecosystem functioning (Walker and Cwynar, 2006; Luoto and Ojala, 2018; Peppe et al., 2018; van der Sande et al., 2019).

A functional trait, as defined by Violle et al. (2007), is any morphological, physiological or phenological feature measurable (or identifiable) at the individual level. These measurements need not refer to environmental variables or any other levels of organization (population, community, or ecosystem) (McGill et al., 2006; Violle et al., 2007; Nock et al., 2016; Céréghino et al., 2018). As such, functional traits can vary both within (intraspecific) and between (interspecific) species and can be further classified into two categories: (1) effect traits, which drive these changes in ecosystem functions; and (2) response traits, which drive the response of community structure to changes in environmental conditions (Lavorel and Garnier, 2002; Naeem and Wright, 2003; Suding et al., 2008). Response traits are adaptive to a specific environmental pressure, as they provide a higher fitness to the organisms that possess it.

Trait-based approaches are used to gain a mechanistic understanding of key processes in community ecology (Díaz and Cabido, 2001). They have predictive capabilities, and as such, have been adopted by a wide array of researchers through the last decade to, for example, explain the distribution of species along various abiotic gradients (e.g., Kaustuv et al., 2001; Berg et al., 2010; Diamond et al., 2011), the processes underlying the assembly of species into communities (e.g., Kraft et al., 2008; Jung et al., 2010; Kraft and Ackerly, 2010), the relationship between ecological community structure and ecosystem functions and services (e.g., de Bello et al., 2010; Lavorel and Grigulis, 2012; Robleño et al., 2018), and the impact of climate change on species assemblages (Bjorkman et al., 2018; Henn et al., 2018). The response/effect traits framework has been used in various fields including ecological restoration (Laughlin, 2014), environmental change prediction (Suding et al., 2008), and ecosystem services (Lavorel and Grigulis, 2012). In general, trait-based approaches are expected to lead to generalized predictions across organizational and spatial scales, independent of taxonomy (Shipley et al., 2016; Robroek et al., 2017). Across fossil records, species are gained or lost, and are sometimes not easy to identify due to non-optimal preservation of fossil material. However, certain traits remain and can be similarly influenced by environmental conditions regardless of species identity. Therefore, the trait approach is a powerful way of gaining insight on how past changes influenced communities functions and related ecological processes (Lamentowicz et al., 2019). In turn, its use may improve predictions on how future species assemblages and their function will change along with current climate change in response to emerging environmental stressors (e.g., climate change; Heilmeier, 2019).

The first trait-based paleoecological studies focused on plant macrofossils and pollen, and explored the response of life-history traits to environmental and climate changes (Lacourse, 2009;

Butterfield et al., 2019; Birks, 2020). Trait-based approaches appeared to be particularly suited for application to testate amoebae, a polyphyletic group of protists. These unicellular amoeboid organisms are protected by a test (shell), whose shape, ornamentation and composition are characteristic for each species and used for morphology-based species identification. The tests can be preserved over millennia in peat (Charman, 2001) and lake sediments (Patterson and Kumar, 2002), and fossils strikingly similar to some modern taxa date to the Neoproteozoic (Porter and Knoll, 2000; Porter et al., 2003; Porter, 2011). Past environmental conditions can be inferred based on the observation of testate amoeba community makeup and previous knowledge on individual species ecological requirements. Testate amoebae are commonly used as proxies for peatland water table depth (DWT; Booth, 2002; Booth et al., 2004) and pH (Booth, 2001), the two major environmental gradients in peatlands (Hájek et al., 2006; Rydin and Jeglum, 2006), as well as lake trophic status (Patterson et al., 2012; Watchorn et al., 2013; Nasser et al., 2020b). Testate amoeba community composition data and associated measurements of environmental variables have been used to determine the environmental preferences of each species. Training sets have been developed across different geographical regions for both peatland and lake taxa in both the Northern and the Southern Hemisphere (Woodland et al., 1998; Wilmshurst et al., 2003; Lamentowicz and Mitchell, 2005; Booth, 2008; Patterson et al., 2012; Qin et al., 2012). These have been used to develop statistical models (transfer functions) for the reconstruction of long-term environmental changes based on species community data (Birks, 2012).

Testate amoeba tests can be used to measure several morphological traits, while knowledge of species' ecological preferences can provide additional relevant measures, e.g., trophic status of particular species or their hydrological preferences (Fournier et al., 2012; Céréghino et al., 2018). As such, testate amoeba functional traits in lake sediment and peat records constitute unique ecological archives of past changes in community structure that can be related to past environmental conditions and/or ecosystem functions. Several studies have successfully used trait-based approaches to investigate past trends in functional diversity (Marcisz et al., 2020), and to reconstruct past environmental conditions (Fournier et al., 2015; Lamentowicz et al., 2015; Marcisz et al., 2016; Gałka et al., 2017; van Bellen et al., 2017). This review summarizes the current knowledge of functional traits in testate amoebae and outlines some open questions and options for future applications in paleoecology.

Benefits of Testate Amoeba Functional Trait-Based Approaches in Paleoecology

In the specific context of paleoecology, the use of testate amoeba trait-based approaches has several notable advantages:

(1) **Improved mechanistic understanding and predictability of ecological processes**. Testate amoebae are important top predators in the microbial food web (Gilbert and Mitchell, 2006; Jassey et al., 2013b). They contribute to soil nutrient

cycling (Wilkinson and Mitchell, 2010), especially the cycles of C, N, and Si in soils (Schröter et al., 2003; Nguyen-Viet et al., 2004; Aoki et al., 2007; Jassey et al., 2015; Puppe, 2020). Their community structure is also strongly correlated to peatland water table depth, soil moisture regime (Woodland et al., 1998; Mitchell et al., 1999; Sullivan and Booth, 2011), shade/hydrology (Marcisz et al., 2014b; Lamentowicz et al., 2020), and chemistry (Tolonen et al., 1992; Hajkova et al., 2011; Singer et al., 2018); contaminant runoff into lakes (Neville et al., 2014; Roe and Patterson, 2014; Gavel et al., 2018); sea level change (Patterson et al., 1985; Charman et al., 1998, 2002); and has been shown to respond to experimental water table changes both in the field (Marcisz et al., 2014a) and in mesocosm studies (Koenig et al., 2017, 2018b). Testate amoeba community dynamics and how they relate to ecosystem functions is a dynamic field of research, although many knowledge gaps remain (but see Fournier et al., 2012; Jassey et al., 2013a, 2015; Lamentowicz et al., 2013a; Macumber et al., 2017). Investigation of past long-term changes in both testate amoeba assemblages and traits could be used to better understand community assembly rules, trait-filtering over time, and – most importantly – the possible existence of critical transitions of community functions, and thus of past ecosystem functioning. This would help to better understand current community dynamics and enable predictions of future environmental changes under ongoing global warming.

(2) **Independence from taxonomic bias and improved transferability of models across biogeographic regions and temporal and spatial scales**. Most soil life have not yet been described and this knowledge gap is larger for the smaller organisms (prokaryotes, protists and other microeukaryotes) (Decaëns, 2010). Testate amoebae have been thoroughly studied due to the well-defined morphological characteristics of the test that usually permits species-level identification for living and dead specimens. Their morphological identification can thus be considered simpler than for many other microbial groups. However, species boundaries, and the definition of species (Schlegel and Meisterfeld, 2003) requires additional research. Morphologic analysis and more recently molecular analysis has explored the phenotypic plasticity and cryptic diversity among several groups (Medioli et al., 1987; Wanner, 1999; Kosakyan et al., 2012; Singer et al., 2018; Macumber et al., 2020). This clearly illustrates the need for basic taxonomic research as a prerequisite for interpretations of the ecology and/or biogeography of taxa (Heger et al., 2009). The degree to which current taxonomic issues undermine the use of testate amoebae in palaeoecology is unclear, but *in silico* experiments in which the identity of morphologically similar species was switched, showed the potentially significant impact of inadequate baseline taxonomic research (Payne et al., 2011). One informal solution to overcome this problem would be to lump species into morphospecies and species complexes in ecological and paleoecological studies.

This approach is principally used with small taxa, e.g., reporting *Corythion* and *Trinema* species as *Corythion-Trinema* type although they can be identified based on scale shape (oval vs. round) (Charman et al., 2000; Amesbury et al., 2016, 2018). However, merging taxa into larger complexes or morphospecies that possess different functional traits results in the loss of potentially useful ecological information, especially when focusing on species responses along narrow ecological gradients. Moreover, using a lower taxonomic resolution in paleoecological studies makes it impossible to fully exploit insights derived from observational or experimental studies that would have been possible if a higher taxonomic resolution was used. As described below in section "Lacustrine Environments" another approach widely utilized since the 1980s within the lacustrine testate amoebae research community is to designate informal infrasubspecific 'strains' associated with test morphologies, not necessarily linked to formal taxa, but which can be linked to specific environmental stressors. During multivariate statistical analysis, this ecophenotypic approach permits delineation of subtle environmental gradients that would not otherwise be possible (Patterson and Kumar, 2002). Alternatively, using testate amoebae functional traits in addition to, and not instead of, species data in paleoecology provides complementary information and reduces the risk associated with taxonomic confusion as the measurements of traits are less ambiguous than formal taxonomic criteria. The resulting transfer functions would potentially enable broader interpretations of community changes and functional processes over long time-scales.

(3) **A useful additional tool for multi-proxy paleoecological reconstructions**. Paleoecological investigations and interpretations often use several biological and geochemical proxies to obtain a wide range of information about past environmental changes. For instance, pollen, spores, plant macrofossils, and charcoal are commonly analyzed to reconstruct past vegetation changes, fires, and human impact over time (Schwörer et al., 2014; Feurdean et al., 2020), whereas geochemical data are used to assess changes in entire lake basins (Bonk et al., 2016; Lu et al., 2017; Jensen et al., 2020). Within projects involving a multi-proxy approach testate amoeba species assemblage data provide quantitative hydrological (e.g., Mitchell et al., 2001; Booth et al., 2012; Lamentowicz et al., 2015) and pH (Mitchell et al., 1999; Lamentowicz et al., 2008; Patterson et al., 2013); road salt contamination (e.g., Roe et al., 2010); nutrient loading (e.g., Patterson et al., 2012; Gavel et al., 2018), and mining induced metal contamination (e.g., Kihlman and Kauppila, 2009, 2010; Nasser et al., 2020b) reconstructions. Integrating trait-based approaches in multi-proxy investigations can provide information on ecological processes and may also help to elucidate functional roles based on correlations with other proxies. These then need to be tested in observational or experimental studies, illustrating a linkage between neo-ecology and paleoecology (Hunter, 1998; Rull, 2010;

Buma et al., 2019). Moreover, multi-proxy data can elucidate long-term trait-environment relationships, giving an insight into eco-evolutionary processes at time scales beyond the range of ecological studies.

A Functional Characterization of Testate Amoebae

Functional traits have been well studied in various taxonomic groups such as plants (Weiher et al., 1999; Diaz et al., 2004; Wright et al., 2004; Cornwell et al., 2008; Kleyer et al., 2008; Kattge et al., 2020), invertebrates (Andriuzzi and Wall, 2018; Céréghino et al., 2018), birds (Bregman et al., 2014), and mammals (Porto et al., 2013). In the case of testate amoebae, some functional traits relevant to understanding the response of these organisms to environmental changes and their functional role in the soil ecosystem have also been identified (Fournier et al., 2012, 2015; Jassey et al., 2013a, 2015, 2016; Lamentowicz et al., 2015; Marcisz et al., 2016; Koenig et al., 2017). Traits can be measured on tests preserved in lake sediments and peat and are thus relevant for paleoecological studies. However, much work still needs to be done to: (1) quantitatively link these traits to organisms' fitness under different conditions; (2) assess trade-offs among functional traits; (3) identify effect traits of specific ecosystem functions; (4) resolve the problem of collinearity among traits (cf. Lamentowicz et al., 2015); and (5) to relate traits to key factors such as climate.

Trait-based approaches have been increasingly applied in testate amoeba studies. It is therefore useful to provide a synthesis of the field of testate amoeba functional ecology and paleoecology and to outline some proposed future research avenues. Section "Current Knowledge and Characterization of Traits of Testate Amoebae" presents the current state of knowledge about testate amoeba traits linked to ecological, evolutionary, genetic and biogeographic contexts. Section "Description of Key Testate Amoeba Traits for Paleoecology" highlights the key traits and their significance to paleoecology, showcases the potential of using traits in long-term studies, emphasizes both the advantages, as well as the strengths and limitations of their application in paleoecology. Section "Conclusion, Knowledge Gaps and Perspectives for the Use of Testate Amoeba Traits in Paleoecology" summarizes knowledge gaps and future perspectives for the use of testate amoeba traits in paleoecology. A list of relevant testate amoeba functional traits and their characterization are presented in **Table 1** and **Figures 1–3**.

CURRENT KNOWLEDGE AND CHARACTERIZATION OF TRAITS OF TESTATE AMOEBAE

Testate Amoeba Traits and Ecological Roles Before "Functional Traits"

Early ecological studies on testate amoebae assessed the distribution of species in various ecosystems and later attributed the environmental gradients to which particular species assemblages were correlated (Penard, 1902; Harnisch, 1925;

Sandon, 1927). The traits of testate amoebae in these studies were generally based on their taxonomic descriptions, in the context of well-defined, measurable taxonomy, usually based at the individual level and used comparatively across species (Nock et al., 2016). At the same time, the first attempts were made to develop ecological typologies of plant and animal species aimed at associating the performance of different species to ecologically relevant features of their morphology or physiology. The terms "guilds" (Schimper, 1903; Clements, 1905) and "life forms" (Raunkiaer, 1934) were introduced first by plant ecologists and similar attempts were subsequently made by zoologists e.g., Koepcke (1956), see Laureto et al. (2015). Unfortunately, the available information relating to the ecological preferences of testate amoebae was insufficient then to make any broad generalizations; therefore their functional role in ecosystem processes was rarely explicitly stated. For example, Deflandre (1937) reported that the largest species of all genera were purely aquatic. Other, early community ecology studies identified soil water content and pH as important factors explaining the distribution of testate amoebae in *Sphagnum* bogs (Bartoš, 1940, 1946; de Graaf, 1956, 1957; Bonnet, 1961a). Several studies observed that the variation in test size of certain species was related to the water content of the habitat (Jung, 1936; Heal, 1961, 1963). Bonnet (1961a) recognized that the tests of soil-dwelling testate amoebae were not only smaller in size than those from wetter biotopes, but that they were also different in shape. He observed that in wet *Sphagnum* mosses, tests were generally ovoid or pyriform, whereas in dry mosses and soils they are hemispherical or sub-hemispherical. Bonnet (1959) also noted that soil-dwelling species of *Centropyxis* Stein, 1859 lacked the characteristic hollow "horns" commonly found in aquatic species (e.g., *C. aculeata* Ehrenberg, 1832).

By the mid-1970s the terms "guild" (Root, 1967) and "functional groups" (Cummins, 1974) were formalized in ecological studies with the latter term having a more general connotation [see Blondel (2003) for a discussion of the key differences between the terms]. In line with this approach, Bonnet (1975) classified testate amoebae into sixteen morphological types according to the shape and symmetry of the tests and the structure of the aperture (or pseudostome). The morphological types were found to be closely related to the habitat types and could be used as indicators of ecological conditions and in understanding morphological evolutionary trends (Schönborn, 1989). For instance, species with a terminal and comparatively large aperture of acrostomic and trachelostomic morphological types were observed to be dominant in aquatic habitats and wet mosses. In dry habitats the proportion of species with a slit-like opening (compressed acrostomic type), with an aperture covered by an anterior visor or lip (plagiostomic or cryptostomic types) or by modified complex structures (propylostomic and diplostomic types) was found to be higher. The cotylostomic morphotype was determined to be characterized by an enlarged collar around the aperture which is used for fixation in unstable coastal marine interstitial biotopes (Schönborn, 1989). However, the application of this classification in subsequent functional ecology studies was limited.

TABLE 1 | List of relevant testate amoeba functional traits explored so far in ecological and palaeoecological studies.

Trait (unit; if relevant)	Description	Trait function, ecological meaning, link to ecosystem functions (if known)		Used in paleo?	References
Test (shell) size					
Biovolume (μm^3)	Volume of the test	Related to the metabolic rate and the capacity of the food web to process energy	Size features of testate amoebae are linked to dissolved organic carbon and nitrogen in peatlands, and thus related to C and nitrogen cycles. Small species better overcome difficult conditions and colonize new habitats faster than large ones as they are lighter	Yes	Lousier, 1974; Wanner and Xylander, 2005; Laggoun-Défarge et al., 2008; Fournier et al., 2012, 2015; Jassey et al., 2013a,b, 2016; Fiałkiewicz-Kozieł et al., 2015; Lamentowicz et al., 2015; Arrieira et al., 2016; Krashevska et al., 2016, 2020; Marcisz et al., 2016, Marcisz et al., 2020; Gałka et al., 2017; Koenig et al., 2017, 2018a,b; McKeown et al., 2019; Macumber et al., 2020
Length/size/shell size (μm)	Length of the test	Larger taxa have longer generation times than small taxa and are thus expected both to be more sensitive to perturbation and to recover more slowly from perturbations		Yes	
Height (μm)	Height of the test	–		No	
Width/breadth (μm)	Width of the test	–		No	
Diameter (μm)	Diameter of the test	–		No	
Body range (μm)	(body length species x – maximum body length within the community)/minimum body length within the community	-		Yes	
Centroid size	Geometric morphometrics: square root of the non-weighted sum of squared distances from the joint centroid to landmarks.	Large, pyriform taxa are associated with low nutrients, benthic habitats and mixotrophy.		Yes	Macumber et al., 2020, this issue
Test construction					
Test material origin/ composition/type	(1) tests made of secreted biosilica plates (idiosomes), (2) organic-coated idiosomes (tests with thick organic coating), (3) proteinaceous tests, (4) tests built from recycled organic or mineral particles (xenosomes, agglutinated)	May allow an environmental filter to operate, in relation to the availability of the different substrates (e.g., mineral particles of adequate size, fungal hyphae, silica) or the relative cost of building a self-secreted test by comparison with an agglutinated one; Availability of material and/or prey to construct the test. Source of material appear to be a major regulator of abundance and repartition of testate amoeba along *Sphagnum*		Yes	Lamentowicz et al., 2009a; Fournier et al., 2012; Gomaa et al., 2012; Fiałkiewicz-Kozieł et al., 2015; Krashevska et al., 2016, 2020; Schwind et al., 2016a,b; Koenig et al., 2017, 2018a,b; van Bellen et al., 2018 Marcisz et al., 2019, 2020

(Continued)

TABLE 1 | Continued

Trait (unit; if relevant)	Description	Trait function, ecological meaning, link to ecosystem functions (if known)	Used in paleo?	References
Test shape/morphology/outline	Test shapes: discoid, pyriform, globular, circular, oviform, flask-shaped	In lake Arcellinida, taxa with discoid and hemispherical tests are associated with planktic/epiphytic habitats.	No	Gomaa et al., 2012; Lansac-Tôha et al., 2014; Lahr et al., 2019; Krashevska et al., 2020; Macumber et al., 2020
	Geometric morphometrics: principal component scores and shape models.	In lake Arcellinida, taxa with large pyriform tests are associated with oxygenated benthic habitats, taxa with oviform tests with epiphytic habitats, and taxa with globular tests with planktic/epiphytic habitats.	Yes	Macumber et al., this issue
Presence of a neck	Yes or no	Important trait in Arcellinida	No	Gomaa et al., 2012; Lahr et al., 2019
Test compression	Compressed, sub-spheric, spheric, hemispherical	An adaptation to living in a thin water film and allowing the amoebae to remain active longer when the soil moisture content decreases; Survival potential in drier situations and thus potential contribution to the food web in dry conditions	Yes	Lousier, 1974; Fournier et al., 2012, 2015, 2016; Koenig et al., 2017, 2018a; Krashevska et al., 2020
Test aperture (pseudostome)				
Aperture position	Position of the aperture within the test: acrostomic, plagiostomic, axial	Protected/hidden apertures are interpreted as adapted to decreasing soil moisture content; Aperture position represents the ability to survive in thin water film and thus the ability to remain active and contribute to the food web in dry conditions	Yes	Bonnet, 1964; Lousier, 1974; Chardez and Lambert, 1981; Laggoun-Défarge et al., 2008; Fournier et al., 2012; Krashevska et al., 2012, 2020; Jassey et al., 2013a,b; Fiałkiewicz-Kozieł et al., 2015; Fournier et al., 2015; Lamentowicz et al., 2015; Marcisz et al., 2016; Koenig et al., 2017, 2018a,b; Marcisz et al., 2020
Aperture shape	Shape of the aperture can be circular, oval, slit-like, irregular	In lake Arcellinida, *Netzelia* sp. with teeth-like apertures have been observed to be planktic carnivores and have been found to be associated with the rise of other planktic carnivores such as *Daphnia* sp. highlighting success of strategy.	Yes	Han et al., 2011; Gomaa et al., 2012; Macumber et al., this issue; Lahr et al., 2019; Krashevska et al., 2020
Aperture size (μm)	Width of the shell aperture	Related to prey size and food web functioning	Yes	Jassey et al., 2013a,b, 2016; Meyer et al., 2013; Gomaa et al., 2014; Fournier et al., 2015; Marcisz et al., 2016; Koenig et al., 2017, 2018a,b; Krashevska et al., 2020; Marcisz et al., 2020

(Continued)

TABLE 1 | Continued

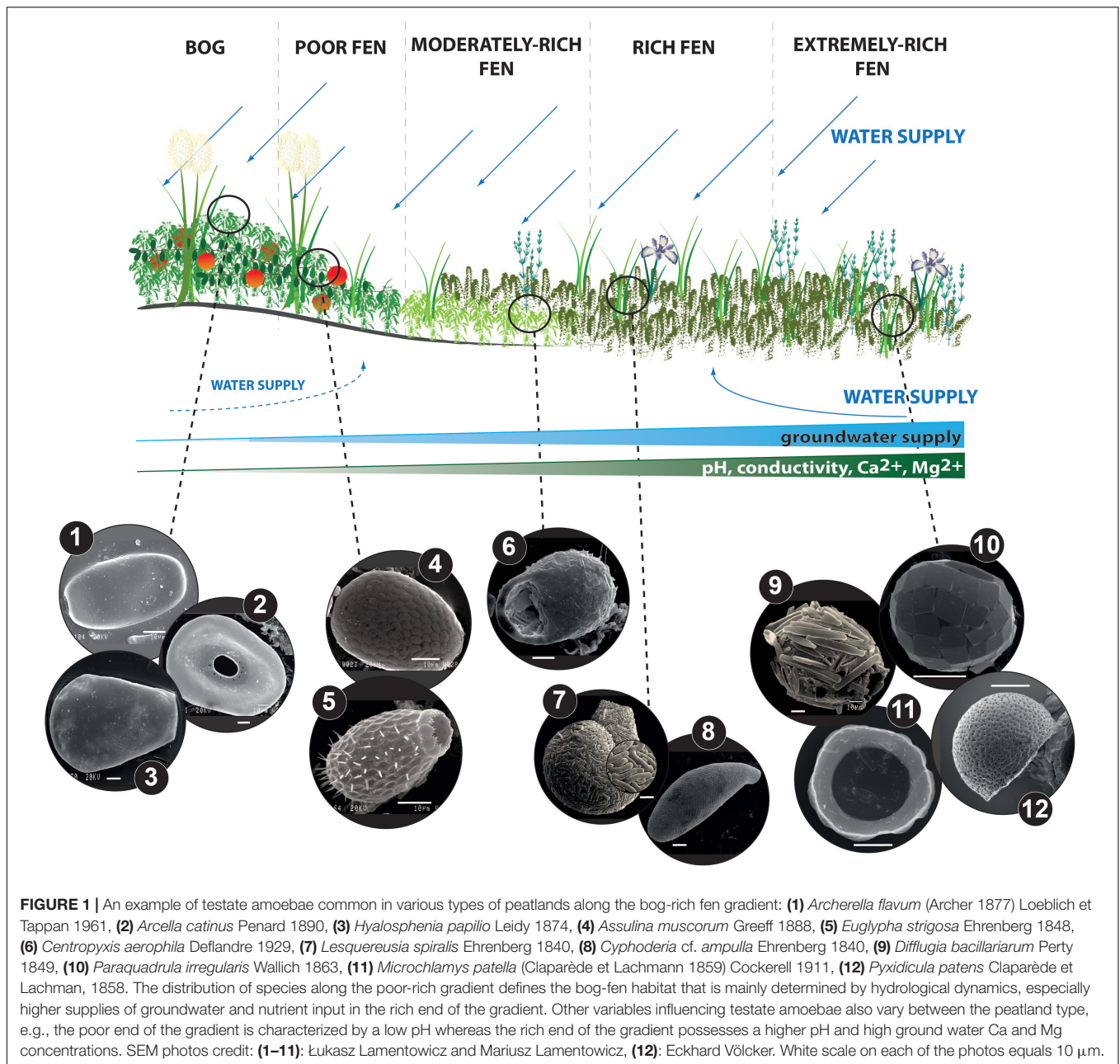| Trait (unit; if relevant)	Description	Trait function, ecological meaning, link to ecosystem functions (if known)	Used in paleo?	References
Phylogeny				
Pseudopod type	Lobose, filose	This trait was used as lobose/filose TA index where lobose TA represent K-strategic species whereas filose TA represent r-strategic species. More developed communities are dominated by K-strategic lobose TA.	No	Mattheeussen et al., 2005; Wanner and Xylander, 2005; Beyens et al., 2009; Fournier et al., 2012;
Phylogeny	Euglyphida vs. Arcellinida; "Pyriform" vs. "Lanceolate" vs. other	Different evolutionary stable strategy to cope with environmental settings	No	Fournier et al., 2012; Krashevska et al., 2020; Macumber et al., 2020
Trophy				
Trophic status (heterotrophy/ mixotrophy)	Presence or not of photosynthetic endosymbionts	Mixotrophy is strongly related to the presence of wet *Sphagnum* and carbon sequestration in peatlands. It can also be used as a proxy for species survival in extremely oligotrophic conditions in *Sphagnum* capitula. Among lake Arcellinida, mixotrophy, especially in large pyriform taxa may indicate oligotrophy, clear water and an oxygenated benthic environment.	Yes	Heal, 1964; Schönborn, 1965; Yeates and Foissner, 1995; Gilbert et al., 2000, 2003; Jassey et al., 2012, 2015; Krashevska et al., 2012, 2020; Marcisz et al., 2014b, 2015, 2016, 2019, 2020; Fournier et al., 2015; Payne et al., 2016; Gałka et al., 2017; Koenig et al., 2017, 2018a,b; Ratcliffe et al., 2017; Creevy et al., 2018; van Bellen et al., 2018; Herbert et al., 2019; Basińska et al., 2020; Lamentowicz et al., 2020; Macumber et al., 2020, this issue; Zhang et al., 2020a,b
Trophic level	Species with a low test-aperture size over body size ratio are considered as having low trophic position (bacterivores, algivores), whereas species with high ratio as having a high trophic position (predators of other protists and micro-metazoans)	Reflects the complexity of the food web. Dominance of high trophic level species points to a more complex microbial food web in the peatland.	No	Jassey et al., 2012, 2013a,b, 2014, 2016; Lamentowicz et al., 2013a; Fournier et al., 2016; Payne et al., 2016; Creevy et al., 2018
Ecological preferences				
Preferred DWT (cm)	Wet vs. intermediate vs. dry indicators		Yes	Marcisz et al., 2016; Krashevska et al., 2020
Preferred pH	Species pH preferences (higher or lower pH values)		Yes	Marcisz et al., 2016; Krashevska et al., 2020
Other				
Gas vacuoles	Presence or absence	Structures used by testate amoebae to move vertically in the water column. They are used to float the organism from the bottom to the surface of the water in an inverted position.	No	Ogden, 1991; Schwind et al., 2016b

FIGURE 1 | An example of testate amoebae common in various types of peatlands along the bog-rich fen gradient: **(1)** *Archerella flavum* (Archer 1877) Loeblich et Tappan 1961, **(2)** *Arcella catinus* Penard 1890, **(3)** *Hyalosphenia papilio* Leidy 1874, **(4)** *Assulina muscorum* Greeff 1888, **(5)** *Euglypha strigosa* Ehrenberg 1848, **(6)** *Centropyxis aerophila* Deflandre 1929, **(7)** *Lesquereusia spiralis* Ehrenberg 1840, **(8)** *Cyphoderia* cf. *ampulla* Ehrenberg 1840, **(9)** *Difflugia bacillariarum* Perty 1849, **(10)** *Paraquadrula irregularis* Wallich 1863, **(11)** *Microchlamys patella* (Claparède et Lachmann 1859) Cockerell 1911, **(12)** *Pyxidicula patens* Claparède et Lachman, 1858. The distribution of species along the poor-rich gradient defines the bog-fen habitat that is mainly determined by hydrological dynamics, especially higher supplies of groundwater and nutrient input in the rich end of the gradient. Other variables influencing testate amoebae also vary between the peatland type, e.g., the poor end of the gradient is characterized by a low pH whereas the rich end of the gradient possesses a higher pH and high ground water Ca and Mg concentrations. SEM photos credit: **(1–11)**: Łukasz Lamentowicz and Mariusz Lamentowicz, **(12)**: Eckhard Völcker. White scale on each of the photos equals 10 μm.

Knowledge of the feeding preferences and the functional role of testate amoebae in relation to nutrient cycling and primary production is scarce [see Wilkinson and Mitchell (2010) for an overview]. Six distinct feeding groups were identified that encompassed freshwater protozoa: photosynthetic autotrophs, bacterivores/detritivores, saprotrophs, algivores, non-selective-omnivores and predators (Pratt and Cairns, 1985). These groups were also successfully applied to soil communities with the addition of the mycophagous group (Coûteaux and Darbyshire, 1998). However, these generalizations have not been formulated for testate amoebae due to a lack of important basic knowledge for most taxa. Most testate amoebae are predators with their primary diet being comprised of a wide range of food sources

including bacteria (Coûteaux and Pussard, 1983), other protists (Deflandre, 1936b; Gilbert et al., 2000), microalgae (Bles, 1929), fungi (Coûteaux and Dévaux, 1983) and small metazoa (i.e., rotifers, Mast and Root, 1916). Although prey size is often limited by the size of the aperture (Ogden and Hedley, 1980), testate amoebae are also able to feed on food sources much larger than themselves (e.g., filamentous algae, Stump, 1935). They also feed on prey such as significantly larger nematodes (Yeates and Foissner, 1995), which they have been observed to hunt in packs (Gilbert et al., 2000; Geisen et al., 2015). Schönborn et al. (1987) suggested that some species (i.e., *Schoenbornia humicola* Schönborn 1964) might also be saprophagic with different feeding phases. Bonnet (1958) and Heal (1964) found that light
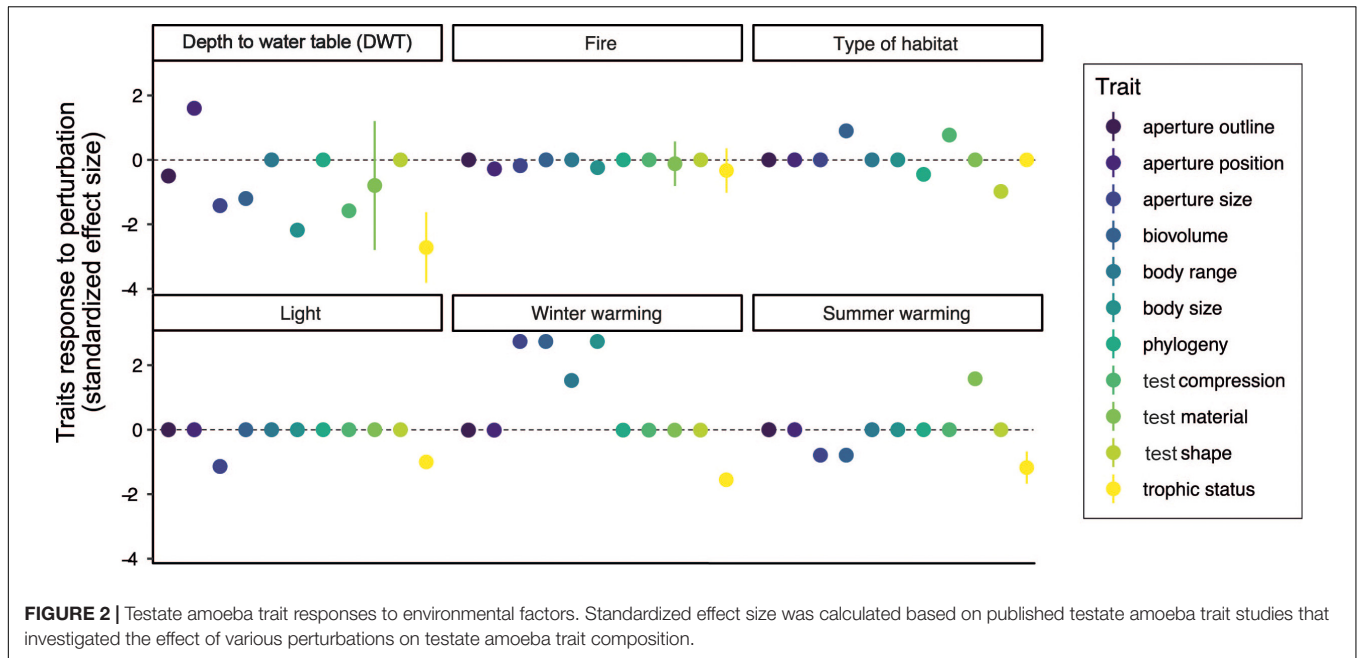
FIGURE 2 | Testate amoeba trait responses to environmental factors. Standardized effect size was calculated based on published testate amoeba trait studies that investigated the effect of various perturbations on testate amoeba trait composition.
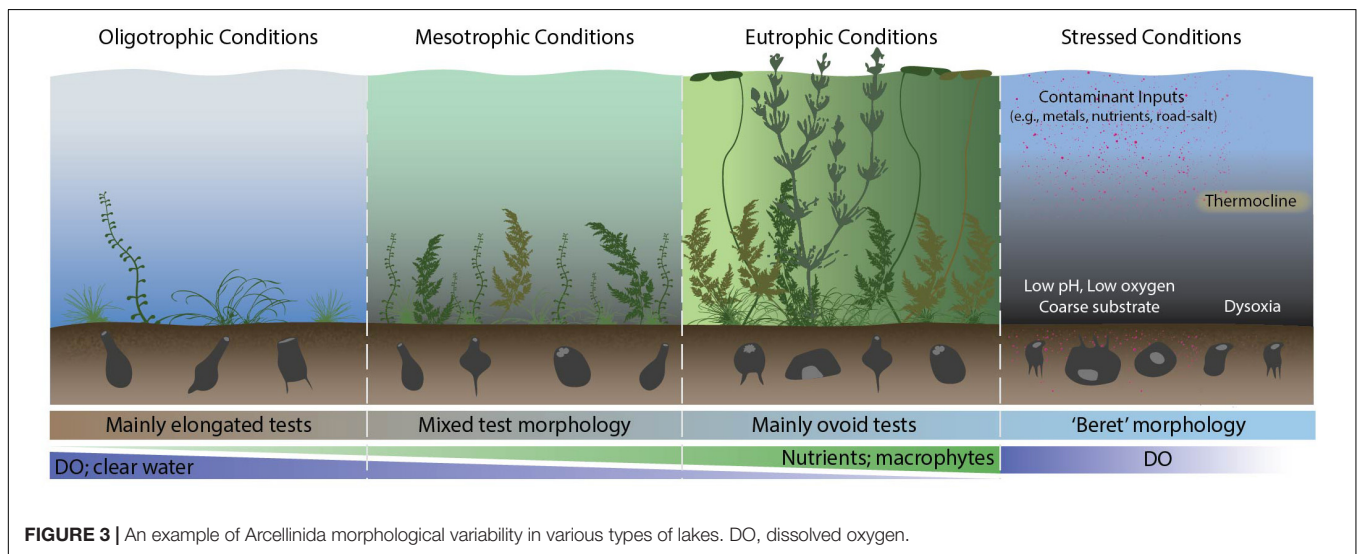

FIGURE 3 | An example of Arcellinida morphological variability in various types of lakes. DO, dissolved oxygen.

could determine the distribution of mixotrophic (zoochlorellae containing) species and Schönborn (1965) concluded that their occurrence was linked to the low nutrient content in *Sphagnum*-dominated bogs. However, a quantitative determination of the contribution of mixotrophic taxa to primary production in bogs was only recently demonstrated (Jassey et al., 2015).

Bonnet (1976b) suggested that filose testate amoebae (e.g., *Euglypha, Corythion, Trinema*) were assumed to be *r*-strategists (i.e., small test size, short generation times, etc.), whereas lobose testate amoebae (e.g., *Arcella, Nebela, Centropyxis, Difflugia*) are in contrast *K*-strategists (larger test size, longer generation times, etc.) and introduced the L/F index to estimate the developmental stage of testate amoebae communities (or ecosystems). The L/F index, which represents the relative proportion of lobose

vs. filose testate amoebae, has been applied in ecological and paleoecological studies to estimate ecosystem resilience and recovery after perturbation (see details in section "Soil and Other Wetland Habitats"). Unfortunately, only a few species have been cultured in laboratory settings (Wanner, 1999), and further research is thus required to validate the assumption concerning the life strategies of testate amoebae (Creevy, 2013). That said, unpublished research based on cultures of >100 taxa indicates that rather than there being a "filose-lobose" difference in growth rates, the rate of growth seems to depend primarily on biovolume, with smaller species reproducing faster than larger ones. Unfortunately, most of this research data has not been published (Ralf Meisterfeld, personal communication). The most consistent attempt to classify testate amoebae following

the concept of "vital attributes" (Noble and Slatyer, 1980) was undertaken by Jax (1992) in order to describe the succession and long-term dynamics within freshwater testate amoebae communities. In that work, testate amoebae were grouped according to their dispersion ability, the preference of particular successional phases and overall long-term ecosystem dominance. However, with only a few exceptions (e.g., Chardez, 1965; Raikov et al., 1989), there is a basic lack of information on the ability of most testate amoebae to, for example, form cysts, which is an important functional trait related to ecosystems resilience and recovery rate. Nevertheless, the available studies provide a considerable amount of data that can be used to infer the functional role of individual testate amoeba taxa, which can be considered within the frameworks of functional ecology to form the basis for future studies.

Evolution vs. Testate Amoeba Morphological Traits

Within the constraint of being unilocular, testate amoebae are characterized by a myriad of test morphologies that differ in general shape, size and composition, which are therefore useful for species identification. Additionally, Arcellinida testate amoebae have a very long fossil record that makes the group an important component of evolutionary studies on early eukaryotes (Schönborn et al., 1999; Porter and Knoll, 2000; Porter et al., 2003; Schmidt et al., 2006; Schmidt et al., 2010; Porter, 2011). Attempts to resolve the systematics and evolutionary relationships within the group began in the early 20th century (Deflandre, 1936a; Jung, 1942), and initially pseudopod morphology and test composition were used to classify testate amoebae into "filose" (euglyphids and amphitremids) and "lobose" (arcellinids), as well as the major suborders within these groups (Bovee, 1985; Meisterfeld, 2002).

Application of molecular methods changed the understanding of the deep evolutionary relationships within the testate amoebae resulting in several major taxonomic revisions. Studies based on single-gene phylogenetic reconstructions (i.e., SSU rRNA, mt COI) demonstrated that several genera (i.e., *Nebela*, *Quadrulella*, *Difflugia)* are paraphyletic, and that test morphology appeared to be one of the most consistent traits constraining deep phylogeny (Lara et al., 2008; Lahr et al., 2011; Gomaa et al., 2012). More recently, combined approaches using hundreds of genes as well as detailed morphological analyses have been used to more robustly reconstruct the major lineages within the Arcellinida (Lahr et al., 2019). In addition, reconstruction of ancient Tonian (Neoproterozoic, 730 million years ago) test morphologies of vase-shaped microfossils revealed that they display a remarkable similarity to modern arcellinidans (Lahr et al., 2019). These results, building on previous research, indicate that testate amoebae had already diversified before the beginning of the Sturtian glaciation, 717 million years ago (Porter and Knoll, 2000; Porter et al., 2003; Porter, 2011). The morphological diversity in place by the Neoproterozoic and apparent evolutionary conservatism since suggests that distinct functional types of testate amoebae related to ecological niches, feeding behaviors and distinct evolutionary strategies developed early in their evolutionary history (Lahr et al., 2019).

The recognition of arcellinidan cryptotaxa provides additional evidence of the important role of functional traits in constraining test morphology.

It can therefore be concluded that, at least in Arcellinida, test morphology has played a substantial role in shaping the evolution of testate amoebae. While the overall test outline is the most important trait defining deep phylogenetic groups, in some groups such as the Organoconcha, comprising genera *Pyxidicula* and *Microchlamys*, the characteristic very wide aperture may be of evolutionary significance. Furthermore, at the genus and species level other morphological traits can be equally important. For example, in the genus *Quadrulella,* the size and placement of siliceous test plates are species-specific (Kosakyan et al., 2016).

Testate Amoeba Molecular Variability vs. Trait Variability

Testate amoeba species identification based on test morphology has always been a challenge. Phenotypic plasticity is common among testate amoebae, making it difficult to determine valid morphological identification criteria (Medioli et al., 1987). Culturing studies by Jennings (1916) early on demonstrated the wide variation that could be observed within clonal lineages of *Difflugia*. Factors such as silicon availability (Wanner et al., 2016), food or temperature were shown experimentally to influence aperture shape and test size, both in the field (Wanner and Meisterfeld, 1994) and *in vitro* (Wanner, 1994). Given the importance of morphology-based taxonomic identification for applications such as paleoecology and biomonitoring (Mitchell et al., 2014), and the comparability of observations and experiments carried out within various research laboratories, taxonomic revisions, or the development of an alternative objective classification scheme is necessary. The existing testate amoeba classification schemes have been challenged by the results of molecular studies (see section "Evolution vs. Testate Amoeba Morphological Traits"). DNA barcoding of individual specimens based on variable mitochondrial markers has led to both the recognition of distinct new species within existing species complexes and the revision of phylogenetic relationships among taxa, which has further led to the description, or redefinition, of both genera and families (Singer et al., 2015; Kosakyan et al., 2016; Duckert et al., 2018). Of ecological relevance, some closely related and morphologically similar (pseudo-cryptic) species (e.g., *Nebela guttata* Kosakyan et Lara 2012 and *Nebela gimlii* Singer et Lara 2015) were shown to occupy different ecological niches (Singer et al., 2018). *Hyalosphenia papilio* Leidy, 1874, a common species in northern *Sphagnum* peatlands was found to be a species complex comprising at least 13 distinct genetic lineages with geographically limited distributions (Heger et al., 2013; Singer et al., 2019).

The unresolved state of testate amoeba taxonomy makes the use of morphology-based community descriptions particularly difficult, especially because closely-resembling species can occupy divergent niches and lumping them blurs taxon related ecological indication signals. In order to overcome these biases and to produce objective and comparable data, metabarcoding approaches are currently developed. Whole environmental DNA

is extracted on concentrated testate amoeba cells, and a group-specific PCR protocol is applied to obtain DNA sequences of the studied organisms (Kosakyan et al., 2015). These promising initiatives are however, at the moment, of limited applicability given the sparse molecular information available for most groups of testate amoebae; in the future, however, they could also be applied to fossil DNA. Likewise, in the future, tracking functional genes expressed by testate amoebae during identified and environmentally relevant processes within metatranscriptomes or ancient DNA metagenomes will probably increase the relevance of these protists as bioindicators (Kosakyan and Lara, 2019).

Trait analysis overcomes the biases linked to species identification, and importantly, can integrate any information derived from ecophenotypic plasticity. Likewise, a correspondence has been observed between measurable traits (such as test size and the number of pores) and climatic/environmental factors (Mulot et al., 2017). In addition, large test size has been reported as a trait related to humidity when considering the whole community in peatland settings (Koenig et al., 2018b), and climate variability in lacustrine Arctic studies (Dallimore et al., 2000). Paradoxically the largest species with the otherwise primarily wetland genus *Quadrulella* has been discovered in biocrusts from a Mexican tropical desert (albeit receiving substantial water through condensation; Pérez-Juárez et al., 2017).

These data are relevant for characterizing environmental change over time, but would be omitted in species only based studies, regardless of the level of taxonomic resolution analyzed. Studying the correspondence between observed traits, phylogenetic position and environmental factors is still a wide-open field of research. *Sphagnum*-associated species characterizing Palearctic peatlands are relatively well studied. However, many species may still be left to be described when taxonomists eventually take a closer look at individual species complexes (Kosakyan et al., 2016). Other biogeographic regions (e.g., the Neotropics), and other ecosystem types (e.g., rich fens) are still relatively less studied.

Testate Amoeba Trait-Environment Relations in Different Habitats
Sphagnum-Dominated Peatlands

Studies on testate amoeba-environment relationships in *Sphagnum*-dominated peatlands have been mainly carried out on raised ombrotrophic bogs (but see Opravilova and Hajek, 2006; Hajkova et al., 2011). Peatlands of this type are highly acidic (pH 3.5-5.5), have no contact with groundwater, and are supplied exclusively by rainwater (Rydin and Jeglum, 2006). Therefore, they only receive allochthonous material from precipitation (rain and dry deposition) but not from e.g., ground water from catchment, streams or rivers. Those ombrogenic conditions result in rather straightforward species-environment relationships that are relatively easy to explore in comparison with other peatland types (e.g., fens, spring-fed fens or landslide mountain fens; **Figures 1** and **2**). Early studies mostly focused on the diversity and community composition of testate amoebae

along ecological gradients (e.g., Heinis, 1910; Harnisch, 1927; Grospietsch, 1953; Warner, 1987), later leading to more quantitative and experimental studies (e.g., Tolonen et al., 1992; Warner and Chmielewski, 1992; Tolonen et al., 1994; Gilbert et al., 1998b; Mitchell et al., 1999). Most work on the ecology of peatland testate amoebae has focused on community patterns along the hydrological gradient (typically water table depth) and trophic gradients (typically pH). However, other factors such as peatland type, landscape openness, light intensity/shading, nutrient concentration and temperature changes have also been studied (**Figure 2**). Most research aimed at understanding testate amoebae morphological traits and their relationship to environmental gradients and changes, and the functional implications of these changes has in fact focused on peatlands (**Table 1**):

(1) **Trophic level and testate amoeba functional traits.** Testate amoeba community composition plays an important role in regulating the peatland microbial food web structure (Gilbert et al., 1998a, 2003; Jassey et al., 2012, 2013a,b; Lamentowicz et al., 2013a; Meyer et al., 2013), with mounting evidences that shifts in microbial food web structure may be linked to shifts in the functional trait composition of testate amoebae (Jassey et al., 2013b; Lamentowicz et al., 2013a; Hamard et al., 2019). For instance, it has been recently shown that the loss of mixotrophic testate amoebae (**Table 1**) destabilizes peatland microbial food webs by changing trophic interactions and decreasing connectivity within the microbial network (Hamard et al., 2019). Other research has further demonstrated that shifts in environmental conditions select for testate amoeba taxa with either a high or low trophic level based on their body size features (Lamentowicz et al., 2013a; Jassey et al., 2014; Fournier et al., 2016). Functional trait shifts toward either high and low trophic level testate amoebae species has often been the consequence of abrupt environmental changes connected with natural or anthropogenic influence (Jassey et al., 2013a, 2016; Lamentowicz et al., 2013a; Meyer et al., 2013; Krashevska et al., 2016; **Figure 2**). Other studies along open-to-forested bog transects have further shown that tree encroachment reduces the trophic level of testate amoeba communities leading to an increased abundance of smaller species (Payne et al., 2016; Creevy et al., 2018). Loss of testate amoeba functional diversity and a decrease in abundance of larger species have also been linked to extreme weather conditions; harder soil frosts (Jassey et al., 2016) as well as warming (Jassey et al., 2013a), suggesting that smaller species are more resistant to extreme climatic condition. In New Zealand peatlands, smaller species were found to be more closely correlated to water table depth and conductivity while larger species were correlated to pH, suggesting that these two components of the community may provide contrasting ecological signals (McKeown et al., 2019). Among direct anthropogenic impacts, atmospheric pollution has been shown to

negatively influence high trophic level testate amoeba species (Meyer et al., 2012, 2013), again emphasizing the generally higher sensitivity of larger testate amoeba taxa to environmental disturbances (**Table 1**).

(2) **Individual trait responses.** There has been an increase in research through the last decade on assessing the response of individual testate amoeba functional traits to environmental changes in peatlands. To identify general patterns in trait responses to environmental changes, we summarized the responses of individual testate amoeba traits to disturbances (DWT change, warming, light intensity and habitat change) by calculating standardized effect sizes. To do so, coefficients of correlations and/or F-values were extracted from tables, figures, the main text and/or supplementary materials available in the literature. Then, *F*-values and/or coefficient of correlations were converted into an effect size using the *compute.es* package in *R* (R Development Core Team, 2020); the results are presented in **Figure 2**. Overall, this analysis revealed that testate amoeba traits strongly respond to DWT and warming, while fire, light intensity and habitat shift had only weak and/or specific effects on individual testate amoeba traits. We also observed a strong, and primarily negative, response for most testate amoeba traits to water level changes (**Figure 2**). Most studies (Fournier et al., 2012; Jassey et al., 2013a; Marcisz et al., 2014b; Koenig et al., 2017, 2018a,b) have reported a decrease in test size (length, width, range) with decreasing water level, while mixotrophic species tended to disappear (**Figure 2**). Documented effects on test material and type have been more variable, with sometimes conflicting results (Fournier et al., 2016), suggesting that some postulated trait-hydrology relationships may be context-dependent, and might be more closely related to the initial water levels and peatland trophic status. Often confounded with hydrology, the most recent analyses reported that light intensity and habitat shifts had similar effects, and that both were more strongly correlated than hydrology to testate amoeba traits such as trophic status and test characteristics (Marcisz et al., 2014b; Payne et al., 2016; Ratcliffe et al., 2017; Creevy et al., 2018; Herbert et al., 2019; Lamentowicz et al., 2020; **Figure 2**). Overall, such findings show that not only testate amoeba community structure (Charman and Warner, 1992; Mitchell et al., 1999; Lamentowicz and Mitchell, 2005), but also the testate amoeba functional traits present can be directly correlated to peatland hydrology (Lamentowicz et al., 2020). These results further support recent attempts of using testate amoeba functional traits in transfer function models to quantitatively reconstruct past water table levels (van Bellen et al., 2017). Besides hydrology, studies focusing on the impact of climate change effects (e.g., precipitation, fire) have shown that testate amoeba body size, aperture size and trophic status can commonly be correlated to environmental changes (**Figure 2**), with related potentially important impacts on food webs and biogeochemical cycles (Jassey et al., 2015; Basińska et al.,

2020). It has also been observed that the trophic status (i.e., mixotrophy) of testate amoebae is a sensitive trait to most environmental disturbances. The importance of mixotrophs for peatland carbon cycling (Jassey et al., 2015) and microbial food web structure (Hamard et al., 2019) confirms that investigations of testate amoeba functional traits are as important to consider as species taxonomy and morphology. Identifying dominant testate amoeba traits that respond to environmental changes over long timescales (hundreds of years to millennia) can potentially serve as a sensitive paleoenvironmental indicator (e.g., documentation of shift of *Sphagnum* peatlands from a carbon sink to a carbon source; Zhang et al., 2020a,b).

Fens

In contrast to ombrotrophic bogs, fens are characterized by the influence of ground or surface water, and hence are typically more minerotrophic. The dominant environmental gradients in fens are water pH and Ca content (Bridgham et al., 1996; Hájek et al., 2006, 2014; Hájková et al., 2012). Fens cover a much wider range of habitats and abiotic conditions than ombrotrophic bogs, ranging from *Sphagnum*-dominated poor-fens to alkaline rich fens dominated by brown mosses (Gąbka and Lamentowicz, 2008) (**Figure 1**). This wider range of possible hydrological and hydrochemical conditions makes it more challenging to determine the testate amoeba species-environment relationships in fens than in ombrotrophic bogs. While testate amoeba community structure typically differs markedly between bogs and fens (Heal, 1961), some testate amoeba functional traits may be characteristic of both environments. For example, the abundance of mixotrophs and heterotrophs in peatlands differs along the poor-rich and wetness gradient, with higher abundances of mixotrophs in bogs and poor fens. Indeed, *H. papilio* and *Archerella flavum* (Archer 1877) tolerate slightly minerotrophic conditions such as existing in *Sphagnum*-dominated poor-fens where they can be very abundant, but they do not occur in calcium-rich fens dominated by brown mosses (Jassey et al., 2014).

Specific taxa restricted to extremely rich fens, such as *Pyxidicula* and *Microchlamys*, possess disk-like tests with a wide aperture (**Figure 1**). In *Microchlamys patella* (Claparède & Lachmann 1859) for example, the cell is enclosed within a membranous sac, which is fixed to the test at several points, but is lost in empty tests (Siemensma, 2019). These species are associated with high groundwater Ca and Mg concentrations, and they often occur at the base of peat deposits, indicating the past presence of calcium-rich or extremely calcium-rich fen stages in the early development of some peatlands (Lamentowicz et al., 2013b; Gałka et al., 2017). The enriched part of the gradient (Lamentowicz et al., 2011) is typically characterized by *Paraquadrula irregularis* Wallich 1863, a small species that builds its test from secreted quadratic or rectangular calcite plates, as well as *Quadrulella symmetrica* (Wallich 1863) which produces siliceous square plates, regularly arranged in rows (Siemensma, 2019).

Jassey et al. (2014) showed that small testate amoebae were more abundant in rich and extremely rich fens than in poor and moderately rich fens. This study also showed that species with a central aperture such as *Arcella discoides* Ehrenberg 1843 and *M. patella*, as well as idiosomic species such as *P. irregularis* and *Tracheleuglypha dentata* (Vejdovsky 1882), dominate communities extending toward the richer part of the gradient. In a study of subalpine peatlands covering the full bog to rich fen gradient, the species richness of testate amoebae was highest in calcium-rich and extremely calcium-rich fens when compared to calcium-poor fens and bogs (Lamentowicz et al., 2010). New Zealand peatlands in contrast, are characterized by higher relative abundances of small taxa in areas at the acidic end of the pH gradient (pH 4.0–4.5) as well as in wetter habitats (DWT −10 to 20 cm), as compared to higher pH (5.0–5.5) and drier habitats (DWT 25–50 cm; McKeown et al., 2019). These results clearly indicate the need for more detailed studies on determining the nature of testate amoeba-environment relationships in fens.

Tropical Peatlands

Tropical peatlands, which are mainly located in lowlands (Page and Baird, 2016), differ from temperate, boreal and montane peatlands in their hydrology, vegetation, nutrient distribution, oxygenation, as well as by these environments being characterized by generally higher temperatures (Lawson et al., 2014; University of Leeds Peat Club et al., 2017). Unfortunately, in comparison to high- and mid-latitude peatlands, there have been relatively few studies carried out on assessing the diversity and ecology of testate amoebae from tropical peatlands. Since the taxonomic composition in tropical peatlands may vary due to biogeographic limitations, there is a need to carry out additional studies on the communities composition, species richness, and functional traits for each region separately, in order to detect similarities or differences in the ecological constraints characterizing similar species, as well as for geographically restricted ones.

For example, in a study assessing the ecological influence of changes in hydrology in tropical montane rainforests along an elevation gradient, testate amoeba species richness did not respond to a 64% reduction of precipitation, but at the same times population density decreased by 91% (Krashevska et al., 2012). In contrast, in the subarctic it was observed that simulated extreme rainfall was correlated with a reduction in the mean abundance and species richness of testate amoebae (Tsyganov et al., 2013). Thus, although all testate amoebae need water to be active (i.e., to move, feed and reproduce), different taxa in different regions and ecosystems may have different tolerances related to soil water availability. It is therefore required that the environmental conditions influencing the morphological or functional traits characterizing the most representative taxa in the community should be emphasized.

Such traits as testate amoeba test size have been shown to be related to hydrology and temperature in temperate zones (Lousier, 1974; Bobrov et al., 1999; Mitchell et al., 2008a). This correlation is also true for the taxa frequently found in tropical systems (e.g., *Trigonopyxis arcula s.l.* Penard 1912, *Hyalosphenia*

subflava s.l. Cash and Hopkinson 1909). For instance, in both a tropical montane rainforest of Ecuador, and in lowland tropical rainforests and peatlands of Indonesia, over 40 different morphotypes of *T. arcula* were observed, with test size varying from 60 to 210 μm (Krashevska et al., 2007, 2010, 2016; Schulz et al., 2018). It was shown for *Trigonopyxis* that test size, increased on average by 20 μm, with decreasing temperature (from 19 to 9°C mean annual temperature) and increasing precipitation (from 2200 to 4500 mm year $^{-1}$; Schulz et al., 2018). Similarly, the test size of *H. subflava* in peatlands of Indonesia, Peru and Panama ranged from 35 to 140 μm, and different test sizes correlated differently with water table depth in both modern and paleo samples of peatlands (Swindles et al., 2014, 2016, 2018; Biagioni et al., 2015; Krashevska et al., 2020). Therefore, *H. subflava* test size changes from small to large can be considered as an indicator trait of frequent hydrological changes from drier to wetter conditions in tropical peatlands, whereas in high- and mid-latitude peatlands this species is considered as an unambiguous indicator of dry conditions (Charman et al., 2000).

Moreover, test composition has been shown to be a useful trait reflecting anthropogenic environmental changes in tropical lowlands. For example, the decrease in the abundance of testate amoebae with siliceous tests in oil palm plantations compared to that in rainforest environments has been hypothesized to indicate the influence of anthropogenic desilication on community structure. Further, species with siliceous tests showed a negative correlation with soil temperature and a positive correlation with water content and the amount of litter (Krashevska et al., 2016).

Similar to traits connected with the test, the trophic status (mixotrophy vs. heterotrophy) can be a potentially good indicator trait of habitat openness (Payne et al., 2016; Herbert et al., 2019), yet a less frequent studied one, especially in the tropics (Krashevska et al., 2012). A mixotroph, such as *H. papilio*, widespread in the Northern Hemisphere peatlands, is absent or very rarely found in tropical regions, underscoring the need for experimental studies to identify representative mixotrophs in the tropics. However, mixotrophic species within the genera *Placocista* and *Archerella,* as well as some species of the genus *Heleopera,* and heterotrophic species of *Assulina* and *Euglypha*, often found in the tropics, have been observed to respond to change in light intensity, making them potentially suitable indicators of plant habitat openness in tropical regions (Schönborn, 1965; Searles et al., 2001; Robson et al., 2005; Krashevska et al., 2012; Payne et al., 2016).

Lacustrine Environments

The principal testate amoebae studied in lacustrine environments are Arcellinida. Arcellinidans play a key role in aquatic ecosystems where they exert considerable predatory pressure on bacteria and smaller eukaryotic microbes and represent an important intermediary food web component (Beyens and Meisterfeld, 2001; Patterson and Kumar, 2002; Anderson, 2012). Tests typically range in size from 5 to 500 μm, and are comprised primarily of high-preservation potential agglutinated material (e.g., mineral grains and diatom frustules with autogenous cement), although species characterized by idiosomic tests are also observed (Medioli and Scott, 1988).

Arcellinidans are found in lacustrine environments from the equator to poles, although they are most abundant in temperate environments where they are often present in great abundances (500–3000 specimens per ml; Patterson and Kumar, 2002; Patterson et al., 2015).

Lakes are comprised of lentic ecosystems ranging in size from ponds to thousands of square kilometers that can be subdivided into a myriad of habitats influenced by numerous climatic and physio-chemical constraints (e.g., open water, shallow littoral habitats with macrophytes, varying trophic status, thermoclines, pH). Arcellinida are mostly restricted to benthic habitats, but species with at least a partial planktic habit have been documented (Schönborn, 1962; Medioli et al., 1987; Yu et al., 2014). A large body of research has been produced that has documented the complex community responses of Arcellinida in these subenvironments, and due to the large number of environmental variables typical of lacustrine systems considerable intra-lake and inter-lake assemblage variability has been observed (Patterson, 1996; Roe et al., 2010; Nasser et al., 2016, 2020a; Steele et al., 2018; Cockburn et al., 2020). There has been considerable taxonomic confusion within the Arcellinida due to a historical proliferation of new species as a result of the considerable morphological variability observed within some taxa, and the common practice of describing new species within a regional context with little consideration of research elsewhere, (e.g., Medioli et al., 1990; Wanner and Meisterfeld, 1994; Bobrov et al., 1999; Wanner, 1999; Charman et al., 2000). For Arcellinida found in lacustrine settings, Medioli and Scott (1983) proposed a possible solution by suggesting that species be considered as widely variable groups that collectively, for any given wild population, accommodate 75% or more of the morphological variability within the entire population. Through the late 1980s and 1990s this approach was refined with the establishment of an informal infrasubspecific nomenclature, which in the lacustrine research community became known as 'strains' (e.g., Medioli et al., 1987; Asioli et al., 1996). The 'strain' approach came out of the recognition that the morphology of certain specimen, not necessarily linked to specific taxa, could be associated with specific environmental stressors, which during multivariate statistical analysis permitted the recognition of more subtle environmental subdivision than would be otherwise possible (Patterson, 1996; Patterson and Kumar, 2002).

The increase in the number of functional taxonomic units afforded by deployment of the 'strain' concept has permitted lacustrine researchers to more effectively explore the spatio-temporal effects of various sedimentological, geochemical, and organic variables, as well as the influence of lacustrine parameters on community structure and dynamics (Collins et al., 1990; Patterson, 1996; Reinhardt et al., 1998; Kumar and Patterson, 2000; Escobar et al., 2008; Neville et al., 2010; Roe et al., 2010; Nasser et al., 2016; Gavel et al., 2018; Steele et al., 2018; Cockburn et al., 2020). For instance, many studies have confirmed the sensitivity of arcellinidan communities to variability in pH (e.g., Asioli et al., 1996; Kumar and Patterson, 2000; Escobar et al., 2008; Neville et al., 2010; Patterson et al., 2013). Changes in the trophic state of lakes have also been shown to profoundly impact arcellinidan distribution (e.g., Reinhardt

et al., 2005; Roe et al., 2010; Patterson et al., 2012; Gavel et al., 2018; Prentice et al., 2018). Several researchers have also linked community dynamics to changes in lake salinity (e.g., Roe et al., 2010; Roe and Patterson, 2014; Cockburn et al., 2020). The recognition that arcellinidan species and 'strains' are sensitive to industrial contamination has attracted particularly close attention. For example, studies from Italy (Asioli et al., 1996) and Canada (Patterson, 1996; Reinhardt et al., 1998) were amongst the first to demonstrate the sensitivity of Arcellinida populations to the impact of mine-induced metal contamination, albeit in a semi-quantitative manner. The advent of more sophisticated multivariate statistical techniques resulted in the quantification of the spatio-temporal relationship between Arcellinida assemblages and mine-derived contaminants (Kauppila et al., 2006; Kihlman and Kauppila, 2009, 2010, 2012; Patterson et al., 2013; Nasser et al., 2016; Gavel et al., 2018; Cockburn et al., 2020; Nasser et al., 2020a,b). The great diversity and variety in arcellinidan lacustrine research, coupled with the use of multivariate statistics, has not only permitted identification of the environmental controls on arcellinidan assemblage distribution, but also established better links between functional 'strain' traits and specific environments.

In spite of the significant advances in understanding species/'strain'-environment relationships, very few studies have focused on the characterization of specific traits in lake environments (e.g., Macumber et al., 2014, 2020; Steele et al., 2020). The lack of studies may be the result a number of factors, including:

(1) **Challenges associated with the counting medium**. In contrast to the analysis of peatland testate amoeba, which are counted under cover-slips using light microscopy, the size range of lake Arcellinida examined are typically in the 37–200 μm range and enumerated *in vitro* in Petri dishes using relatively low power stereomicroscopy, which hinders the measurement of some traits (e.g., process length and aperture size; Patterson and Kumar, 2002; Wall et al., 2010a,b). There are also complications relating to the 3D morphology of specimens examined in Petri dishes vs. the compressed 2D morphology of specimens observed under coverslips.

(2) **Taxonomic challenges**. As outlined above, phenotypic plasticity, especially within the difflugiids (Medioli and Scott, 1983; Wanner and Meisterfeld, 1994; Wanner, 1999), has led to challenges in determining the relationship between morphological characteristics and environmental drivers, or other factors (e.g., stochastic processes; cf. Medioli et al., 1987; Prentice et al., 2018; Macumber et al., 2020).

(3) **Taphonomic challenges**. Although the relative abundance of live vs. dead specimens are documented in applied lacustrine research, the emphasis is on providing an overview of average annual conditions so total specimen counts, which include both live and dead specimens, are analyzed, with little consideration of seasonal changes in standing crop and associated taphonomic processes (e.g., Nasser et al., 2020a,b). The

attraction of this approach is that average environmental conditions are measured, which would otherwise require multiple expensive geochemical analyses to replicate. Two studies, one carried out as part of a seasonal assessment of the effectiveness of an oil sands reclamation project in northern Alberta, Canada (Neville et al., 2010), and a second that looked at the impact of seasonality on a lake on the Ganga-Yamura Plains of North India (Farooqui et al., 2012), both demonstrated that there are significant seasonal changes in arcellinidan standing crop that can be directly related to taphonomic processes. These studies demonstrated the complexity of the response of Arcellinida to a range of environmental drivers, but also present the promise that the group can be used as a high temporal resolution biomonitoring tool.

Notwithstanding these issues, there has been a recognition of the significance of the role of test morphology between specific environments and across gradients. For example, Velho et al. (2003) and Lansac-Tôha et al. (2014) classified taxa according to dominant test morphology (e.g., hemispherial, flattened, spherical and elongated forms) in floodplain lakes in southern Brazil and linked this to habitat types and hydrological flow regimes. Macumber et al. (this issue) applied geometric morphometrics (Zelditch et al., 2012) to examine morphological responses across a temporal gradient of nutrient enrichment in a shallow Scottish lake (dominant test morphology, aperture size; biovolume) and compared this to species-based approaches. A further earlier study focused on an autecological approach to quantify taxonomic divisions between two strains of *Difflugia protaeiformis* LeClerc in Lamarck 1816, in relation to a wide array of environmental proxy data from urban lakes (Macumber et al., 2014). The more time-consuming characterization of traits in lake Arcellinida, in particular quantification of subtle changes in morphology (e.g., tapering of the neck, nature of complex basal processes, apertural characteristics), which are not readily captured by simple quantitative 2-dimensional metrics, has limited the application of traits-based analysis in lake Arcellinida. However, the introduction of new technologies may lead to a significant reduction in analytical time. A novel experiment carried out by Steele et al. (2020), demonstrated that a Flowcam flow cytometer used in conjunction with machine learning software could not only significantly decrease specimen enumeration time, but using a library of >40 morphometric properties, was able to group tests into morpho-groups that could be used to effectively identify distinct limnological habitats.

Soil and Other Wetland Habitats

Studies on the functional ecology of testate amoebae were first developed for soils with the test typology developed by Louis Bonnet (Bonnet, 1964, 1975). Bonnet developed a classification of testate amoebae communities based on a phytosociological hierarchical classification scheme and established correlations between soil and humus developmental stages and testate amoeba communities (Bonnet, 1961b). Based on this, he identified indicators for different soil types and also compiled extensive lists of ecological preferences for soil testate amoebae (Bonnet,

1976a, 1984, 1985, 1986, 1988, 1989, 1991a,b, 1992). The ecology of testate amoebae was also studied in agro-ecosystems and the impact of farming practices and pesticides on community structure was assessed (Foissner, 1987, 1997, 1999; Heger et al., 2012). These studies generally showed a negative impact of intensive farming on the diversity and abundance of testate amoebae. However, only a small number of studies have investigated functional traits of testate amoebae in soils, and these included terrestrial soils (Wanner and Xylander, 2005), various aquatic substrate types in the arctic tundra (Mattheeussen et al., 2005; Beyens et al., 2009), and floodplain soils (Fournier et al., 2012). All these studies included the phylogenetic grouping proposed by Bonnet (1976b) (i.e., the lobose vs. filose testate amoebae L/F index, see section "Testate Amoebae Traits and Ecological Roles Before "Functional Traits"").

Studies carried out in both high Arctic and sandy inland dune settings revealed similar recruitment patterns despite contrasting environmental conditions/filters (Mattheeussen et al., 2005; Wanner and Xylander, 2005; Beyens et al., 2009). In these habitats filose species typically fulfilled the role of rapid generalist colonizers, whereas lobose amoebae characterized more mature stable habitats. The lobose species that became part of these ecosystems during later successional stages did not outcompete and replace the earlier colonizers, but instead enlarged the existing microbial loop (Wanner and Xylander, 2005). The ready addition of lobose testate amoebae to these environments is in part related to these taxa being more resistant to warmer soil conditions, and associated desiccation that is better than filose species (Beyens et al., 2009). These findings confirmed previous assumptions that a high L/F index is characteristic of more stable and/or more developed habitats (Bonnet, 1976b).

The first ecological study of testate amoebae ever carried out in floodplain soils used not only functional traits, but also functional indices to characterize the testate amoebae communities, including: functional richness, divergence, dispersion, and evenness (Fournier et al., 2012). The results of this research revealed that although these environmental filters were significant in shaping the patterns of testate amoeba community structure, the main variable influencing amoeba diversity was soil moisture. Among functional traits analyzed, test-related traits, particularly compression and biovolume, were the most responsive to environmental changes.

The following studies that focused on the neotropical floodplains confirmed the significant role of environmental filters in the shaping of testate amoeba communities (Arrieira et al., 2015). Especially moisture was a variable to which testate amoebae species richness and abundance were significantly correlated (Arrieira et al., 2017). Among functional traits analyzed, morphological variability and test-related traits such as test composition, test height and breadth, and presence of gas vacuoles that support movement in the water column (Ogden, 1991), were the most responsive to environmental changes (Arrieira et al., 2016; Schwind et al., 2016a,b).

Marginal Marine Environments

Salt marsh testate amoebae are present both in brackish and intertidal zones next to diatoms and foraminifera (Riveiros et al.,

2007; Barnett et al., 2017b), and have been shown to be important sea-level indicators (Patterson et al., 1985; Charman et al., 1998; Roe et al., 2002; Barnett et al., 2016, 2017a,b). Testate amoebae are strongly correlated with elevation and flooding duration and frequency in salt marsh environments (Charman et al., 1998; Roe et al., 2002). When it comes to distribution of salt marsh testate amoebae, especially important factors are salinity, particle size and organic matter content that vary locally (Charman et al., 2002; Ooms et al., 2011). Idiosomic tests typically dominate in high saltmarsh habitats above the mean high water mark and in supra-tidal settings, while in mid marsh settings low diversity agglutinating assemblages are observed (Gehrels et al., 2001).

Another very diverse group of testate amoebae are the interstitial testate amoebae typical of sandy saline freshwater and marine habitats. Because of their relatively late discovery and scarce subsequent investigation, little is known about their adaptive strategies for inhabiting marine and psammal supralittoral marine environments (Golemansky, 1969, 1978, 1998; Chardez, 1971, 1980; Golemansky and Ogden, 1980). The most characteristic morphological feature characterizing many interstitial testate amoeba taxa is the presence of a collar, which can be either small (e.g., *Centropyxiella lucida* Golemansky 1971) or very large, having a similar diameter as the maximum breadth of the test [e.g., *Messemvriella filosa* Golemansky, 1973, *Pseudocorythion acutum* Wailes 1927, *Ogdeniella elegans* (Golemansky 1970), *O. maxima* (Golemansky 1970), *Chardezia caudata* Golemansky 1970, *Corythionella* sp., *Micramphora pontica* Valkanov 1970] (Golemansky and Todorov, 2004, 2006, 2007). The molecular variability within this group of species is unknown (Todorov et al., 2009; Heger et al., 2011). As a result, the inferred general taxonomic relationships between these species are primarily based on species morphology (Golemansky, 2008).

DESCRIPTION OF KEY TESTATE AMOEBA TRAITS FOR PALEOECOLOGY

Although testate amoeba traits have only recently been used in paleoecology, several functional traits have been found to be particularly useful for paleoecological reconstructions, while others have yet to be tested in long-term studies (**Table 1**).

Key Testate Amoeba Traits for Paleoecological Studies of Peatlands
Mixotrophy
In both observational and experimental studies mixotrophic testate amoebae (e.g., *H. papilio, A. flavum, Amphitrema wrightianum* Archer, 1869, *Heleopera sphagni* Leidy, 1874, *Placocista spinosa* Penard, 1899) have been found to be useful for analysis of both wet and open, highly acidic *Sphagnum*-dominated peatlands (i.e., high light intensity, landscape openness and high water table; Schönborn, 1965; Lamentowicz and Mitchell, 2005; Mazei and Tsyganov, 2006). In these studies the appearance of mixotrophic taxa in a peat sequence has been interpreted to be indicative of either development of an opening of the landscape due to forest decline or deforestation, especially in small sites surrounded by forest cover.

When peatlands develop over a siliceous impermeable bedrock following deforestation there is often a rise in the peatland water table due to increased surface runoff (Warner et al., 1989; Sillasoo et al., 2007). Such changes generally lead to higher abundances of mixotrophs due to both the higher water table changes, and an increase in solar radiation resulting from the disappearance of the forest canopy. The opposite case (i.e., the disappearance of mixotrophs in peat profiles) may indicate a lowering of the water table and/or tree encroachment and afforestation of the peatland. Such information is highly relevant for the interpretation of long-term changes in testate amoeba communities and has implications for land-use management (Davis and Wilkinson, 2004). In this way, testate amoebae provide not only water table depth changes information, but can also enhance our understanding of other paleoecological processes that took place in the studied site in the past.

Several previous paleoecological studies have examined long-term changes in the abundance of mixotrophic testate amoeba taxa in peat profiles, with the interpretation of the micropaleontological data being supported by multi-proxy biotic and abiotic evidence. This body of research includes research from Polish *Sphagnum*-dominated peatlands where it was determined that increased human peatland disturbance (e.g., deforestation, prescribed burns, peat extraction, establishment of drainage ditches) led to water table lowering; the effect on testate amoeba communities resulted in a rapid decline of mixotrophs (Lamentowicz et al., 2009b; Marcisz et al., 2015, 2016, 2019; Kołaczek et al., 2018). When no evidence of direct human peatland disturbance was observed, stratigraphic sections from an open bog were characterized by continuous *Sphagnum* growth and an associated stable hydrology, as indicated by the regular presence of mixotrophs within observed testate amoeba communities (Marcisz et al., 2020). As mixotrophs are the first functional group to respond to direct disturbances connected with either water table lowering or increased shading, it can be assumed that a loss of this trait from species in the testate amoeba community is an indicator of both water table lowering and peatland openness. A recent study by Zhang et al. (2020b) investigated peat cores from boreal bogs in Finland and compared paleoecological data with instrumental meteorological measurements. The authors confirmed that drying and associated lower carbon accumulation rates in the peatland were related to significant loss of mixotrophic testate amoebae (Zhang et al., 2020b). In another study, van Bellen et al. (2018) showed that the establishment of permafrost conditions in an ombrotrophic peatland in Canada coincided with the disappearance of mixotrophic testate amoebae. These researchers interpreted the of loss mixotrophs to be due to a significant reduction in peat accumulation, in conjunction with an input of dust on the surface of the peatland, which would impact food sources, giving heterotrophic testate amoebae a competitive advantage (van Bellen et al., 2018). These findings indicate that mixotrophs can easily outcompete heterotrophs under acidic peatland conditions by relying on photosynthetic symbionts for supplemental nutrition when prey abundance is scarce, whereas under nutrient-rich conditions heterotrophs have the competitive edge. The results of these

studies indicate that tallying changes in the abundance of mixotrophic testate amoebae alone, or by comparing the ratio between mixotrophs and heterotrophs over time, provides a simple index of environmental changes integrating hydrology, landscape openness and carbon accumulation potential. These results provide further confirmation of just how interconnected functional traits and environmental drivers are, highlighting their potential in paleoecological reconstructions.

Position of Test Aperture

Louis Bonnet first demonstrated the clear relationship between apertural position and soil moisture conditions (see section "Soil and Other Wetland Habitats"). Apertural position is believed to have evolved as an adaptation of testate amoebae to variable soil moisture conditions (Lahr et al., 2019), and has been strongly correlated to both modern-day and reconstructed water table depths (Lamentowicz et al., 2015; Marcisz et al., 2016). Hydrological instability and the drying of peatlands was shown to lead to an increase in the abundance of testate amoebae with small plagiostomic apertures, which during dry seasons may prevent desiccation, and a decline in taxa with axial or acrostomic apertures (Lamentowicz et al., 2015; Marcisz et al., 2016). Lamentowicz et al. (2007, 2009a) showed that increased soil erosion after deforestation caused a *Sphagnum* bog to shift to a fen; a process which led to an increase in the relative abundance of the plagiostomic species *Centropyxis aerophila* Deflandre 1929 highlighting its possible adaptation to disturbed sandy habitats (**Figure 1**). Furthermore, a study covering the whole bog-to-fen gradient shows that hidden apertures are not only linked to lower water tables, but are also associated to higher mineral matter input (Lamentowicz et al., 2009a). These promising results illustrate the need for more studies covering the entire rich fen to bog gradient (see section "Fens").

Test and Aperture Size

Several observations and experiments have shown that the size of testate amoeba tests may be controlled by hydrological conditions, which suggests that species with small tests are probably better adapted to survive under dry conditions (see McKeown et al., 2019). Therefore, in peat cores, an observed shift in the dominant test size of testate amoebae may indicate a change in hydrology (or other relevant environmental factor), as confirmed by two paleoecological studies. An analysis of four peat records from North America and Europe revealed the co-existence of small and large testate amoebae during high water tables phases, but the abundance of larger species decreased after the water table declined (Fournier et al., 2015). A similar pattern was observed in two Central European peatlands, where the communities were dominated by small testate amoebae following direct human-induced impacts (Marcisz et al., 2016). Smaller testate amoeba species are characterized by smaller apertures, which may reduce desiccation, but because the tests are smaller in general makes them more prone to drying out. In terms of a peatland trophic status, a shift to smaller species expressed by a decrease in aperture size, body length and biovolume has also been linked to decreasing pH in *Sphagnum*-dominated peatland (Gałka et al., 2017). These observations indicate that

interpreting the morphological adaptation of species to different microhabitats present on the surface of bogs can be complicated (i.e., hummock and hollows structure).

Test Type/Construction

Testate amoebae build their tests from various available material. The most commonly observed test types are those constructing: idiosomic tests produced using biosilica or calcite plates; organic-coated idiosomic tests; proteinaceous tests; and xenosomic (agglutinated) tests comprised of recycled organic or mineral material (Mitchell et al., 2008b). Several paleoecological studies have investigated whether changes in erosion processes or an increase in dust deposition translates into changes in the testate amoeba community structure. Increased input of mineral matter should stimulate the growth of species building idiosomic and xenosomic tests. Therefore, an increased abundance of these species in the stratigraphic record could indicate significant environmental change. Lamentowicz et al. (2009a) showed how vast deforestations led to increased catchment erosion, which increased the input of nutrients into the peatland, and led to a rapid increase in pH values from acidic to alkaline. This ecological shift caused a rapid decrease of testate amoebae possessing proteinaceous and organic-coated tests, and was directly linked to the subsequent appearance and dominance of *C. aerophila* and *Phryganella acropodia* (Hertwig et Lesser 1874), two species characterized by a xenosomic test (Lamentowicz et al., 2009a). A similar shift was described in another study based on a raised bog, where deforestation and severe disturbance by fire caused a temporal decrease in *Sphagnum* and an encroachment of vascular vegetation (Marcisz et al., 2019). In response to this environmental shift, testate amoebae with proteinaceous tests decreased in abundance in favor of those constructing tests utilizing xenosomes and organic-coated idiosomes (Marcisz et al., 2019).

Studies on dust deposition have significantly contributed to our understanding of testate amoeba trait variability over time. High levels of atmospheric dust deposition derived from southern Poland anthropogenic sources during the 1980s significantly impacted *Sphagnum* bog microbial communities (Fiałkiewicz-Kozieł et al., 2015). Testate amoebae with proteinaceous tests were observed to decrease and communities became dominated by xenosomic *C. aerophila* and *P. acropodia*. In addition, Al, Ti, Cr, Ni, and Cu concentrations were found to be highly correlated with aperture position/body size ratio and aperture position (Fiałkiewicz-Kozieł et al., 2015). In contrast, van Bellen et al. (2018) did not find any relationship between dust flux and the relative abundance of agglutinating testate amoebae. They hypothesized that the mineral particles typically being transported to mires were too large for testate amoeba to incorporate into their tests (van Bellen et al., 2018). In contrast, another study found that testate amoebae incorporated volcanic dust into their tests based solely on particle size with little or no selection by mineral type (Delaine et al., 2016). These results suggest that changes in test type and construction can therefore be used as an additional anthropogenic indicator, providing environmental information related to deforestation, human-induced changes in trophic status, dust deposition from

anthropogenic industrial sources, as well as influences related to natural events (e.g., volcanic eruptions). As generation times of testate amoebae are short, their response to external factors influencing grain size input is much faster than that of vegetation (be it local bryophytes and vascular plants, or the surrounding upland vegetation), adding to their value as indicators of both anthropogenic and natural grain-size related inputs.

Key Testate Amoeba Traits for Paleoecological Studies of Lakes

Test Type/Construction

Lake testate amoeba communities are overwhelmingly dominated by agglutinated species, although proteinaceous forms (notably *Arcella* species) are commonly observed. *Arcella vulgaris* Ehrenberg, 1830, for example, is a key component of 'stressed' assemblages associated with low oxygen and/or low pH conditions, and sediments strongly impacted by contaminants (e.g., heavy metals, winter de-icing salts; Dalby et al., 2000; Neville et al., 2011; Roe and Patterson, 2014; **Figure 3**). Idiosomic species, in contrast, typically form a minor assemblage constituent and are sometimes absent from paleolimnological records. This may partly reflect preparation techniques that result in the removal of smaller tests (notably the use of coarse sieve meshes to remove mineral content, but see Wall et al., 2010a,b), or preservation issues (Roe and Patterson, 2006). Some lake taxa exhibit a composite wall structure that may reflect changes in the availability of mineral material for test construction. *Cucurbitella tricuspis* (Carter, 1856), for example, displays complex changes in test wall composition related to life-cycle stage, switching from a dominance of xenosomic to idiosomic test construction between benthic and pelagic phases (Schönborn, 1962; Medioli et al., 1987; Meisterfeld, 1991). This transition is thought to be controlled by the ingestion of lipids from filamentous green algae, which aids buoyancy (Schönborn, 1962; Medioli et al., 1987). Given the significance of this species as an eutrophic indicator taxon, understanding the temporal controls on test composition (along with any associated changes in morphology) will continue to be important in paleolimnological studies (Prentice, 2019).

Test Morphology

Lake Arcellinida display enormous variability in test morphology, and there has been growing interest in assessing whether this is an adaptive response to aquatic conditions. Velho et al. (2003), for example, noted that in the floodplain environments of the Upper Paraná River, Brazil, species with a flattened (compressed) or an elongated test were most abundant in lotic (moving water) habitats associated with higher values of dissolved oxygen and pH, while spherical and hemispherical taxa were most abundant in lentic (still water) environments with greater concentrations of chlorophyll *a*. In this study and others, compressed morphologies, along with the presence of gas vacuoles (as observed, for example, in *Arcella* species) were hypothesized to minimize resistance to water, allowing floating and movement in the water column (Ogden, 1991; Velho et al., 2003; Arrieira et al., 2015, 2016).

Many shape-related observations have been made in macrophyte-enriched lakes. Lansac-Tôha et al. (2014) observed higher frequencies of spherical and elongated taxa in floodplain lakes rich in aquatic macrophytes, and a greater abundance of elongate species in sedimentary floodplain habitats. Macumber et al. (this issue) similarly noted that spherical and ovoid shape groups increased in sediments impacted by cultural eutrophication in a well-studied core from a large, shallow Scottish lake, while elongated taxa were dominant in sediments with oligo- to mesotrophic plant macrofossil assemblages (Salgado et al., 2010). Intra-species variations in morphology were also observed as the nutrient status of the lake changed. The functional diversity of floodplain testate amoeba communities in the Upper Paraná River, Brazil was also reported to be controlled by nutrient dynamics (Arrieira et al., 2015). These studies hold considerable promise, although it is likely that in macrophyte-dominated lake settings, testate amoeba communities are influenced by multiple drivers, including light and oxygen availability, substrate characteristics and the character of microbial food webs, as well as nutrient fluxes (Wiik et al., 2015; Prentice et al., 2018; Roe et al., unpublished data). Future work to elucidate traits in paleolimnological records must consider these complex, inter-related controls.

In addition to overall test morphology (i.e., test outline), the presence of basal processes (spines), or aperture-related features (e.g., serrated collars or teeth) have long been thought to play a functional role in lake Arcellinida (e.g., Penard, 1902). Spines may act to stabilize the organism during feeding or aid in the entrapment of prey (Han et al., 2008) and may provide protection against predation (Gomaa et al., 2015), while teeth may be used as a cutting tool to perforate algal membranes (Medioli et al., 1987).

Test and Aperture Size

Amongst the lake Arcellinida studies that have considered the significance of test size (or biovolume), a study of the assemblages characterizing thermokarst lakes on Richard's Island in the Canadian Arctic is noteworthy (Dallimore et al., 2000). They reported tests which were larger than those typically observed in other studies, including 'giant' specimens which were 2–3 times greater in size, and suggested that this might reflect low ambient temperatures and a short growing season. They hypothesized that the organisms might feed and grow for a period of time, reaching a large size, then wait for a few days to weeks to reproduce under optimal conditions, giving rise to exceptionally large test dimensions (Dallimore et al., 2000). Macumber et al. (this issue) also reported a decrease in centroid size (biovolume) and changes in aperture size in response to nutrient enrichment and lake level lowering in the core study in Scotland. As the aperture provides the organism's main interaction with the environment, variations in its size are likely to be adaptive (Schönborn, 1962; Medioli et al., 1987; Collins et al., 1990; Bobrov and Mazei, 2004), although further systematic analysis is required to assess this, and the relationship with other traits.

Mixotrophy

The significance of mixotrophy in lake testate amoeba communities is poorly understood. This partly reflects a lack of understanding of the distribution of algal symbionts

in limnological taxa. Feeding strategies/mixotrophy could nevertheless be important predictors in the structure of lake communities. Penard (1902) noted that mixotrophic testate amoebae can tolerate dysoxic conditions and lack of nutrition longer than non-mixotrophic specimens and hypothesized that it was due to the presence of zoochlorellae. Interestingly, Macumber et al. (2020) have recently demonstrated that mixotrophy and morphology are related within selected Difflugiidae clades, and this may also hold phylogenetic significance.

Trait-Based Transfer Function Model

In the past transfer function models have been typically based on testate amoeba species assemblage data, which are now routinely used to reconstruct past depth-to-water table (DWT) in long-term studies worldwide (Charman, 1997; Mitchell et al., 1999; Booth, 2002; Payne and Mitchell, 2007; Lamentowicz et al., 2008; Amesbury et al., 2016). A novel trait-based transfer function was recently developed by van Bellen et al. (2017) using a previously published training set (van Bellen et al., 2014), and including new measurements of several functional traits: test biovolume and compression, aperture size and position, mixotrophy, phylogenetic group, and mineral matter presence. This approach made it possible to include traits of all observed taxa, including rare ones, which is unusual in most species-based transfer function models, where rare taxa are excluded (van Bellen et al., 2017). Both the species-based and trait-based DWT reconstructions provided similar reconstructions, confirming the relevance of the trait-based approach in paleoecological reconstructions. In particular, trait-based transfer functions can be useful in regions where classical transfer function models are absent, or when an existing training set does not include a large number of taxa.

CONCLUSION, KNOWLEDGE GAPS AND PERSPECTIVES FOR THE USE OF TESTATE AMOEBA TRAITS IN PALEOECOLOGY

The development of testate amoeba functional traits as an area of active investigation has opened novel research avenues by providing a powerful tool for future ecological and paleoecological research. Their application can bridge long-term (paleoecological) and short-term (observational and experimental) studies addressing various aspects of not only testate amoebae ecology, but also microbial functionality and related ecosystem processes from all ecosystems where testate amoebae occur. Trait analysis can deliver important additional information that can be used to enhance that gleaned from species and community data, informing sounder paleoecological inferences.

Based on the current level of knowledge, testate amoeba morphological and functional traits can specifically provide important information on regime shifts and tipping points in ecosystem functioning caused by both natural and anthropogenic processes (Domínguez-García et al., 2019; Lamentowicz et al., 2019). Examples of systems where ecosystem functions and traits provide important monitoring data include:

- detection of forest decline, anthropogenic deforestation and landscape opening (mixotrophy);
- support for inferences of hydrological changes (i.e., dry shifts detection; mixotrophy, test size, aperture size and position);
- detection of increased nutrient deposition within a sedimentary basin (test type/construction);
- identification of autogenous environmental changes such as fen-to-bog transition (test and aperture size);
- identification of natural and anthropogenic dust deposition (test type/construction);
- assessment of carbon accumulation potential (mixotrophy);
- recognition of changes within microbial food web structures (proportion between mixotrophs and heterotrophs, L/F index).

Testate amoeba trait patterns observed in contrasting habitats show that functional traits can be a useful measure when comparing ecological shifts observed in different habitats and ecosystems where species composition may vary, but similar traits may be present.

Promising as this line of research has proven thus far, a trait-based approach applied to testate amoebae still requires substantial development in the research subdisciplines of paleoecology, as well as in observational and experimental ecology. The most significant knowledge gaps relate to the functional significance of specific traits related to testate amoeba communities, relevant biotic and abiotic characteristics in the environment, and ecosystem functioning. Many of these relationships can be inferred statistically (e.g., the correlation between peatland carbon accumulation rates and the relative abundance of mixotrophs; Zhang et al., 2020b).

Another important research question relates to the definition of response vs. effect traits. Distinguishing the two is not always obvious and in some cases, a trait can belong to both categories. An example of the latter is mixotrophy, which for example in peatlands, both responds to moisture and openness, and contributes to carbon sequestration.

In this review an outline of the current theoretical and empirical state of research of a functional traits approach applied to testate amoebae has been presented. Although this field of research is still in its infancy it presents great promise as an important tool in future ecological and paleoecological studies. We look forward to seeing its development in the near future!

AUTHOR CONTRIBUTIONS

KM led the study. All the authors contributed to the review with discussions, ideas, photos, diagrams, comments, and text.

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