

Testate amoebae: a review on their multiple uses as bioindicators

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Abstract: Testate amoebae (TA) are unicellular protozoans enclosed in a test capable of indicating a wide variety of environmental conditions. Among others, characteristics such as short life cycle, great sensitivity and worldwide distribution makes them adequate bioindicators. As a complement to physical and chemical measurements, biomonitoring can be a cheaper and fastest way of environmental monitoring. This research sought to evaluate the extent of TA use in biomonitoring and the responses given by them to environmental features. The research was conducted in Scielo, Science Direct, Online Library, Google Scholar and Capes Journal Portal and yielded 211 papers. TA bioindication is able to provide information on metal, trace element and atmospheric pollution, and to point out different trophic states, pH, and evidence on characteristics of hydrology. Further, TA can be used in paleoenvironmental reconstruction as they reflect climate, volcanic and even sea level change phenomena. Sometimes, together with other organisms in environmental analysis, they have shown to be an important complement to biomonitoring. Additionally, a functional traits approach has been recently included as a promising tool. Methodological adjustments that have been conducted throughout the years are allowing TA use to be more reliable and precise. This review provides insight on the many possible functions of TA in bioindication studies, highlighting their wide use as bioindicators.

Keywords: biomonitor, thecamoebian, bioindication, protozoan, hydrology, restoration

1. INTRODUCTION

In a biomonitoring study, an organism, a part of it, or a community is used as bioindicators pointing out environmental changes in a specific moment and habitat,

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offering qualitative information about the quality of the ecosystem (Markert et al. 2003, Sumudumali and Jayawardana 2021). Bioindicator species may show changes in their population dynamics and stability when responding to environmental modifications, which can be measured through variations in abundance, distribution, age structure, reproductive effort and success, and growth (Burger and Gochfeld 2001). The biomonitoring approach is an important complement to physical and chemical measurements as it's a fast, efficient and

cost-effective method (Dale and Beyeler 2001), providing a more continuous data, sometimes including extreme events that have not been detected by standard methods (Nguyen-Viet *et al.* 2007).

The testate amoebae (TA) are a polyphyletic group that comprises ameboid protozoans enclosed in a test, common in freshwater (sediments, plankton), and terrestrial habitats (Kosakyan *et al.* 2020). In order to feed and locomote, thecamoebians protrude filose or lobose pseudopodia through the test's aperture, the pseudostome (Cavalier-Smith 2004, Adl *et al.* 2019). TA present key characteristics to act as reliable bioindicators, such as: 1) short life cycle that allows fast response to ecological change (Foissner 1999); 2) persistent test, that can resist fossilizing processes (Charman 2001, Patterson and Kumar 2002); 3) sensitivity to a wide range of environmental variables (Nasser *et al.* 2020); 4) great abundance and diversity in different environments (Foissner 1999, Lansac-Tôha *et al.* 2007, Alves *et al.* 2010, Miranda *et al.* 2020); 5) worldwide distribution and established as bioindicators throughout different biotopes (Nasser *et al.*, 2020). These organisms have been studied and used as bioindicators, answering to past and present conditions (Payne 2013, Roe and Patterson 2014, Amesbury *et al.* 2016) in the many biotopes in which those species inhabit.

In freshwater ecosystems, TA inhabit rivers (Costa *et al.* 2015), lakes (Nasser *et al.* 2020), reservoirs (Misailidis *et al.* 2018) and phytotelm (Kratina *et al.* 2017); but they can be also found in brackish environments, such as estuaries (Eichler *et al.* 2006), salt-marshes (Barnett *et al.* 2017) and marine sand supralittoral (Golemansky 2007). In terrestrial habitats, TA inhabit soils (Wanner *et al.* 2020), *Sphagnum* and mosses (Basińska *et al.* 2020), phytotelm (Kratina *et al.* 2017), and are also present in wastewater treatment systems (Hu *et al.* 2013). Thecamoebians occupy key roles in the trophic webs, varying in feeding types and trophic positions (Gilbert *et al.* 1998a, b; Lamentowicz *et al.* 2013a). They feed on bacteria, cyanobacteria, microalgae, fungi, humus, or even small thecamoebians, ciliates, rotifers and nematodes (Schroeter 2001, Gilbert *et al.* 2003, Han *et al.* 2008, Jassey *et al.* 2012). TA can be directly affected by environmental changes such as moisture fluctuation, and indirectly by water chemistry, via the impact on the organism's TA prey on (Mitchell *et al.* 2000a). Thecamoebians also participate in chemical and nutrient cycling such as carbon, nitrogen and silicon cycles (Puppe 2020). All above highlight the-

camoebians role in both ecological health functioning and structure (Burger and Gochfeld 2001).

Anthropogenic impacts throughout the globe affect Earth system's resilience by processes like land-system changes, freshwater uses, changes in biosphere integrity and in biogeochemical flows, such as carbon, nitrogen and phosphorus (Steffen *et al.* 2015). Considering this, bioindicators can offer an early warning of environmental changes, in a way to spotlight specific damages and trends in the habitat's conditions (Paoletti 1999, Burger and Gochfeld 2001). Thus, allowing restoration and conservation management tools to be intelligently associated with the environment condition, and by providing an assessment on ecological health, bioindication will keep track of goods and services provided by it contributing to human health (Paoletti 1999, Burger and Gochfeld 2001).

The present study aimed to review the current available scientific literature on testate amoeba's use as bioindicators throughout different habitats and purposes, focusing on the knowledge gathered about the responses given by these protozoans to environmental changes.

2. MATERIALS AND METHODS

The search has been conducted in the following scientific databases: Scielo, Science Direct, Online Library, Google Scholar and Capes Journal Portal. The keywords used were ("testate amoebae" OR "testate amoeba" OR "thecamoebian") AND ("bioindicator" OR "biomonitoring" OR "bioindication" OR "paleoecology" OR "transfer function"), paired with Boolean Operators. Papers published until 2020 were gathered, with no inferior limit, in order to access a greatest number of papers. During the article's survey, an evaluation of the title and abstract were carried out, in order to select the papers that utilized thecamoebians as a tool in biomonitoring research, those being the focus or used as support with other organisms. Were also selected articles taken from previous gathered paper's references. Afterwards, a full text assessment was made, in order to detail what responses the thecamoebians gave in each environment and to different variables.

3. RESULTS AND DISCUSSION

The database search encountered a total of 3.481 results. There were selected 211 papers that present testate amoebae as eligible or potentially indicators in environmental monitoring and paleoenvironmental reconstructions at peatlands, bogs, lakes, soil, wet-

lands, rivers, streams, saltmarsh and paleocryosols. A total of 70 under genera taxa, with specific bioindication properties including several environmental and paleoenvironmental features (Figure 1), were cited in this paper. The specific tolerance and/or indicator property to some environmental variables are presented in Table 1. These protozoans are further used to develop transfer functions in order to reconstruct palaeohydrology, paleoclimate and sea-level changes. Another use is in sewage treatment, where, amongst other microorganisms, thecamoebians indicate the health of activated sludge plants and water quality of wastewater treatment systems.

3.1. Organic matter, pH and nutrients

Environmental impacts, especially those caused by human activities, have been causing a series of losses in water quality (Cardoso and Novaes 2013). In lakes, rivers, reservoirs and streams, TA have their communities affected by the pollution caused by high concentration of nutrients (McCarthy et al. 1995, Qin et al. 2009, Neville et al. 2010, Qin et al. 2016, Schwind et al. 2019), minerals (Casper and Schonborn 1985), thaw salts (Qin et al. 2013), acidification of streams (Costan and Planas 1986) and industrial and domestic untreated effluents (Costa et al. 2015).

Acidification in streams can decrease thecamoebians density, which can be explained by environment modification (e.g., potassium liberation from the sediments) and by the disturbance caused on the mechanical osmotic regulators of TA (Costan and Planas 1986). The pollution of lakes by thaw salts, especially sodium chloride (NaCl), is another impact that water resources may suffer, causing lower diversity of TA (Roe and Patterson 2014). In these places, the increase of brackish tolerant species as *Arcella vulgaris*, *Centropyxis constricta spinosa* and *Centropyxis aculeata aculeata* is reported, being those recommended for tracking salt increase in healthy lakes (Roe and Patterson 2014). On the other hand, a higher diversity of TA was registered in alkaline lakes, pointing out strong correlations of the community with water pH. *Pontigulasia elisa*, *Pontigulasia compressa* and *Lesquereusia modesta* were the most abundant taxa, making them indicators of higher pH (Qin et al. 2013).

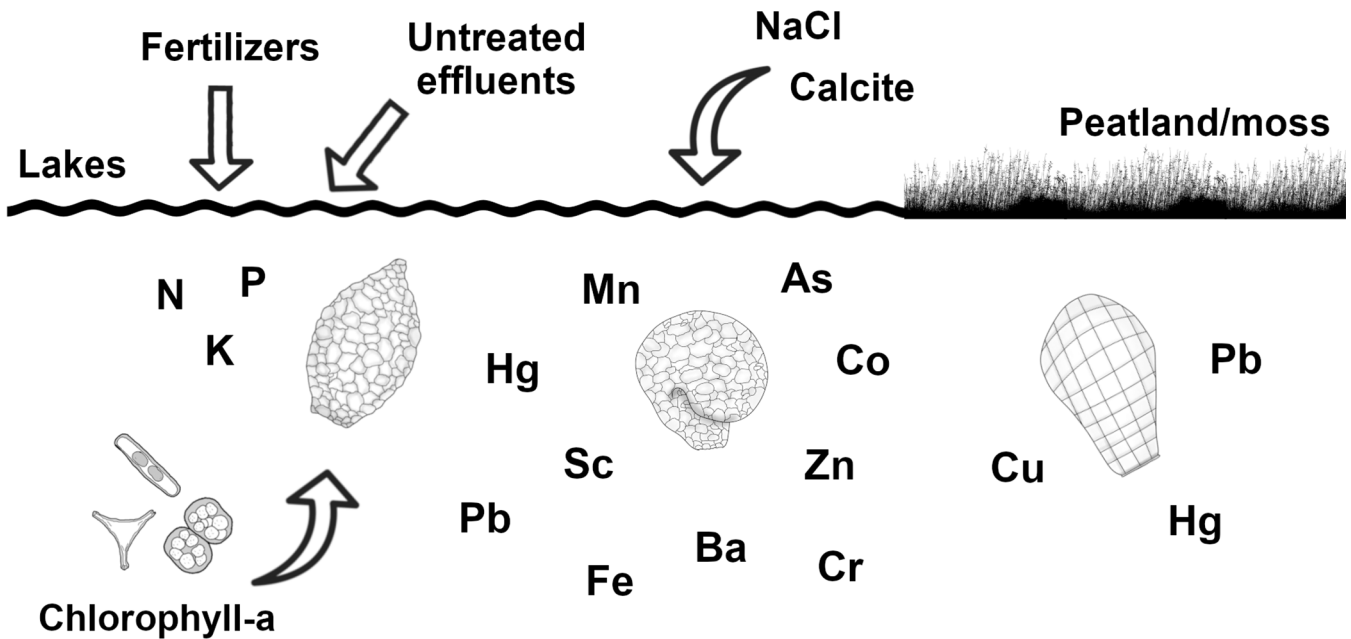
Suspended matter can be considered an influence to TA communities in aquatic environments, since it is mostly composed of minerals used in the test construction (Pereira et al. 2006, Du Châtelet et al. 2010, Schwind et al. 2019). In a lake with high levels of calcite, the species *Diffflugia limnetica* replaced the sand

grains on its carapace for calcite grains (Casper and Schonborn 1985), being considered a good indicator of calcite precipitation in lakes (Casper and Schonborn 1985). In particular, the exogenous species respond significantly to the suspended matter in the water column, which can reflect in the abundance and occurrence of individuals (Schwind et al. 2019). Positive responses to higher concentrations of suspended inorganic matter were reported for *Diffflugia pseudogramen*, *Diffflugia lobostoma* and *Centropyxis eornis*. Conversely, *Protocucurbitella coroniformes*, *Cucurbitella crateriformis* and *Cucurbitella dentata f. quinquelobata* responded negatively to increases of suspended inorganic matter (Schwind et al. 2019).

Anthropic impacts increase and speed up processes that lead to high concentrations of suspended matter in water resources (Souza and Knoppers 2003), being eutrophication one of the problems that strikes the water environments the most, being able to limit heterotrophic microorganism's metabolic activities (Smith and Schindler 2009). In rivers contaminated by industrial and domestic untreated effluents, the low abundance of *Diffflugia distenda* was considered an indicative of impact at the water quality (Costa et al. 2015). *Heleopera sphagni* and *Nebela collaris* were conspicuous in lakes with high concentrations of organic matter (McCarthy et al. 1995). In comparison, a more diverse community was observed in hypereutrophic and mesotrophic grassland regions lakes, with *Diffflugia oblonga* and *Cucurbitella tricuspis* being dominant (Neville et al. 2010). However, the greatest diversity was reported for the boreal forest, where most of the lakes are eutrophic (Neville et al. 2010). In lakes with high concentrations of nutrients and heavy metals, the community of TA had its richness reduced, being the genera *Centropyxis* and *Diffflugia* the most tolerant to high nutrient's concentrations, and dominant in all the pollution gradients (Qin et al. 2016). *Cucurbitella tricuspis* was also pointed out as commonly associated with high levels of solid waste (Escobar et al. 2005). However, there is still a lack of studies about the ecology of the group in polluted lakes, which makes it hard to explain the dominance of certain taxa in a specific condition (Qin et al. 2016).

In lakes and rivers, there have been recorded correlations between TA and ammonia, nitrate, phosphate and chlorophyll-*a* content (Arrieira et al. 2015, Arrieira et al. 2016, Schwind et al. 2017); interfering in their size and morphometry (Arrieira et al. 2016) and frequency and abundance (Schwind et al. 2017). Those nutrients are linked to the environment's productivity, impact-

(a) Variables liable to be identified by testate amoebae



(b) Paleoenvironmental variables recorded by testate amoebae

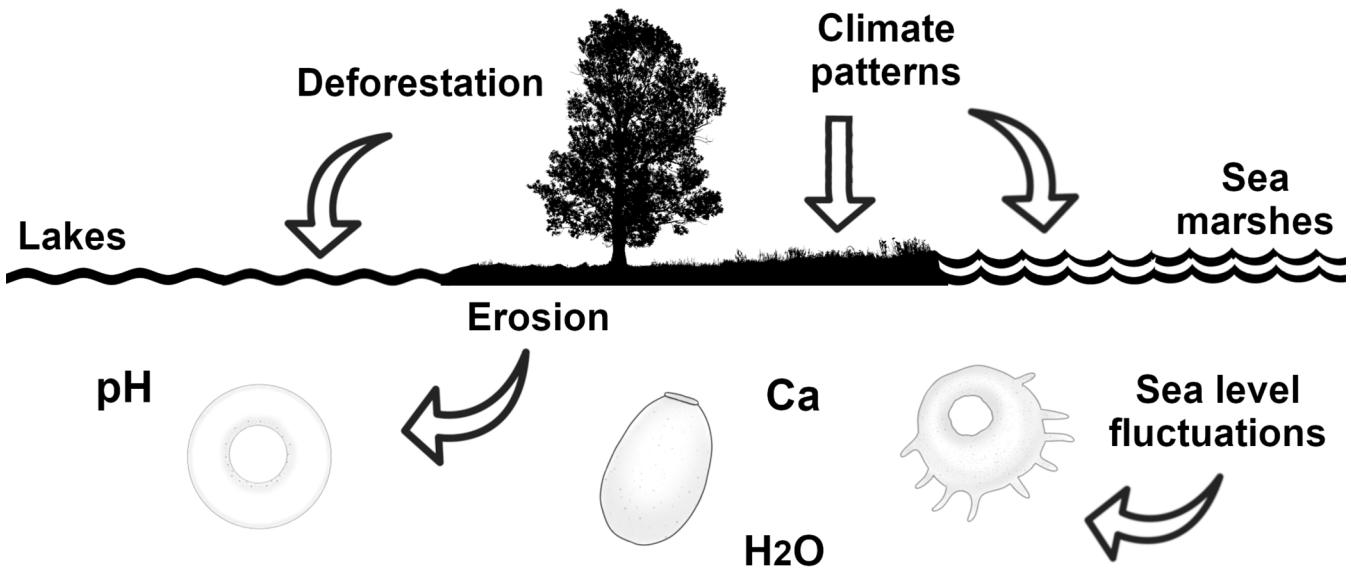


Fig. 1. Diverse bioindication properties shown by testate amoebae in lakes, peatlands, soil and sea marshes. (a) Variables liable to be identified by testate amoebae. (b) Paleoenvironmental variables recorded by testate amoebae. N: nitrogen, P: phosphorus, K: potassium, Mn: magnesium, Hg: mercury, Sc: scandium, Pb: lead, Fe: iron, Ba: barium, Cr: chromium, Zn: zinc, Co: cobalt, As: arsenic, Cu: copper, Ca: calcium.

Table 1. Testate amoebae specific tolerance and/or indicator property to some environmental variables.

Testate Amoebae	Brackish tolerant	Acidic pH	Alkaline pH	Temperature	Calcite precipitation in lakes	Concentration of heavy metals and/or semimetals	Concentration of organic matter	High concentrations of suspended inorganic matter	Chlorophyll-a	Good water quality	Very high water content in peatlands	High-water content	Low-water content	Burning indicator	Non-shaded habitats	Atmospheric pollution and NO ₂
1 <i>Alabasta militaris</i>		*				*							*			
2 <i>Amphitrema wrightianum</i>		*					*					*			*	
3 <i>Arcella</i>		*										*				
4 <i>Arcella catinus</i>						*										
5 <i>Arcella discoides</i>		*	*			*						*				
6 <i>Arcella hemisphaerica</i>							*									
7 <i>Arcella megastoma</i>						*										
8 <i>Arcella vulgaris</i>	*					*	*					*				
9 <i>Archerella flavum</i>		*					*		*		*	*			*	
10 <i>Assulina</i>													*			
11 <i>Assulina muscorum</i>		*					*						*			
12 <i>Bullinularia indica</i>		*					*						*			
13 <i>Centropyxis</i>						*	*									
14 <i>Centropyxis aculeata</i>		*	*	*		*	*					*				
15 <i>Centropyxis aculeata 'aculeata'</i>	*															
16 <i>Centropyxis cassis</i>			*			*										
17 <i>Centropyxis constricta</i>				*		*										
18 <i>Centropyxis constricta 'spinosa'</i>	*															
19 <i>Centropyxis discoides</i>						*										
20 <i>Centropyxis ecornis</i>		*	*					*					*			
21 <i>Corythion</i>		*											*			
22 <i>Corythion dubium</i>		*				*	*						*			
23 <i>Cucurbitella crateriformis</i>								*								
24 <i>Cucurbitella dentata f. quinquilobata</i>								*								
25 <i>Cucurbitella tricuspis</i>						*	*									
26 <i>Cyclopyxis arcelloides</i>		*				*							*			
27 <i>Diffugia</i>						*	*					*				
28 <i>Diffugia acuminata</i>			*			*	*	*								
29 <i>Diffugia amphoralis</i>			*					*								
30 <i>Diffugia bacillifera</i>												*				
31 <i>Diffugia bicornis</i>			*			*										
32 <i>Diffugia biwae</i>			*													
33 <i>Diffugia distenda</i>									*							
34 <i>Diffugia elegans</i>		*	*			*	*									
35 <i>Diffugia gramen</i>						*										
36 <i>Diffugia helvetica</i>							*	*	*							
37 <i>Diffugia kempnyi</i>								*	*							

Kukuryk 2017; Lamentowicz et al. 2020; 10 – Song et al. 2014; Payne et al. 2016; 11 – Warner and Chmielewski 1992; Mitchell et al. 1999; Laggoun-Défarge et al. 2008; Mieczan and Tarkowska-Kukuryk 2013; Lamentowicz and Mitchell 2005; Niedzwiecki et al. 2016; Mieczan and Tarkowska-Kukuryk 2017; Lamentowicz et al. 2020; 12 – Tolonen et al. 1992; Mitchell and Gilbert 2004; Mieczan 2009; Lamentowicz and Mitchell 2005; 13 – Qin et al. 2016; Nasser et al. 2020; Asada and Warner 2009; 14 – McCarthy et al. 1995; Patterson et al. 1996; Mitchell et al. 1999; Nguyen-Viet et al. 2008; Yang et al. 2011; Qin et al. 2013; Song et al. 2014; Qin et al. 2016; Lamentowicz and Mitchell 2005; Mieczan and Tarkowska-Kukuryk 2017; 15 – Roe and Patterson 2014; 16 – Asada and Warner 2009; Qin et al. 2013; Qin et al. 2016; 17 – Patterson et al. 1996; McCarthy et al. 1995; 18 – Roe and Patterson 2014; 19 – Yang et al. 2011; 20 – Lamentowicz and Mitchell 2005; Qin et al. 2013; Qin et al. 2016; Amesbury et al. 2016; Schwind et al. 2019; 21 – Mieczan 2009; Song et al. 2014; 22 – Mitchell et al. 1999; Laggoun-Défarge et al. 2008; Nguyen-Viet et al. 2008; Lamentowicz and Mitchell 2005; Payne et al. 2012; Mieczan and Tarkowska-Kukuryk 2017; 23 – Schwind et al. 2019; 24 – Schwind et al. 2019; 25 – Escobar et al. 2005; Qin et al. 2016; Nasser et al. 2020; 26 – Mitchell et al. 1999; Booth 2002; Lamentowicz and Mitchell 2005; Asada and Warner 2009; Yang et al. 2011; Turner et al. 2013; Heinemeyer and Swindles 2018; 27 – Qin et al. 2016; Song et al. 2014; Nasser et al. 2020; 28 – Qin et al. 2013; Schwind et al. 2017; Qin et al. 2016; 29 – Qin et al. 2016; Schwind et al. 2017; 30 – Charman and Warner 1997; 31 – Qin et al. 2016; 32 – Qin et al. 2016; 33 – Costa et al. 2015; 34 – Lamentowicz and Mitchell 2005; Qin et al. 2013; Niedzwiecki et al. 2016; Mieczan and Tarkowska-Kukuryk 2017; Nasser et al. 2020; 35 – Misailidis et al. 2018; 36 – Schwind et al. 2017; 37 – Schwind et al. 2017; 38 – Casper and Schonborn 1985; 39 – Schwind et al. 2019; Schwind et al. 2017; 40 – Qin et al. 2016; Misailidis et al. 2018; McCarthy et al. 1995; 41 – Schwind et al. 2017; 42 – Patterson et al. 1996; 43 – Schwind et al. 2019; 44 – Schwind et al. 2017; 45 – McCarthy et al. 1995; Qin et al. 2016; 46 – Schwind et al. 2017; 47 – Nguyen-Viet et al. 2007; 48 – Mitchell et al. 1999; Yang et al. 2011; 49 – Mitchell et al. 1999; Mieczan 2009; Mieczan and Tarkowska-Kukuryk 2013; Wanner et al. 2020; 50 – Mitchell et al. 1999; Lamentowicz and Mitchell 2005; Meyer et al. 2012; Nguyen-Viet et al. 2008; 51 – Madoni 1994; Lamentowicz and Mitchell 2005; Mieczan 2009; Hu et al. 2013; 52 – Mitchell et al. 1999; Lamentowicz and Mitchell 2005; Niedzwiecki et al. 2016; Heinemeyer and Swindles 2018; 53 – McCarthy et al. 1995; Lamentowicz and Mitchell 2005; Nguyen-Viet et al. 2008; Marcisz et al. 2014a; Marcisz et al. 2016; Niedzwiecki et al. 2016; Lamentowicz et al. 2020; 54 – Charman and Warner 1992; Tolonen et al. 1994; Mitchell et al. 1999; Lamentowicz and Mitchell 2005; Charman et al. 2007; Warner et al. 2007; Mieczan 2009; Niedzwiecki et al. 2016; Ratcliffe et al. 2017; Creevy et al. 2018; 55 – Charman and Warner 1992; Tolonen et al. 1994; Mitchell et al. 1999; Lamentowicz and Mitchell 2005; Charman et al. 2007; Warner et al. 2007; Marcisz et al. 2014a; Niedzwiecki et al. 2016; Payne et al. 2016; Marcisz et al. 2016; Niedzwiecki et al. 2016; Ratcliffe et al. 2017; Creevy et al. 2018; Lamentowicz et al. 2020; Basińska et al. 2020; 56 – Charman and Warner 1992; Booth 2002; Turner and Swindles 2012; Turner et al. 2013; Niedzwiecki et al. 2016; 57 – Misailidis et al. 2018; 58 – Qin et al. 2013; Qin et al. 2016; 59 – Schwind et al. 2017; 60 – McCarthy et al. 1995; Misailidis et al. 2018; Qin et al. 2013; Qin et al. 2016; 61 – Charman and Warner 1997; Mitchell et al. 1999; Lamentowicz and Mitchell 2005; Nguyen-Viet et al. 2008; Mieczan 2009; Mieczan and Tarkowska-Kukuryk 2017; 62 – McCarthy et al. 1995; Mitchell et al. 1999; Lamentowicz and Mitchell 2005; 63 – Mitchell et al. 1999; Booth 2002; Lamentowicz and Mitchell 2005; Laggoun-Défarge et al. 2008; Mieczan 2009; Meyer et al. 2012; 64 – Niedzwiecki et al. 2016; Misailidis et al. 2018; 65 – Nguyen-Viet et al. 2004; 66 – Mitchell et al. 1999; Mitchell 2004; Heinemeyer and Swindles 2018; 67 – Mitchell et al. 1999; Warner et al. 2007; 68 – Qin et al. 2013; Qin et al. 2016; 69 – Qin et al. 2013; 70 – Schwind et al. 2019; 71 – Mitchell et al. 1999; Lamentowicz and Mitchell 2005; Nguyen-Viet et al. 2007; 72 – Mitchell et al. 1999; Charman et al. 2000; Lamentowicz and Mitchell 2005; Turner and Swindles 2012; Meyer et al. 2012; Turner et al. 2013; Swindles et al. 2015; Mieczan and Tarkowska-Kukuryk 2017; Heinemeyer and Swindles 2018; 73 – Song et al. 2014; 74 – Wanner et al. 2020; 75 – Wanner et al. 2020; Nguyen-Viet et al. 2008.

ing TA by the food web (Arrieira et al. 2015, Arrieira et al. 2016). *Diffugia parva*, *D. acuminata*, *Lesquereusia ovalis*, *Diffugia schuurmani* and *Diffugia Helvetica* were positively correlated with chlorophyll-*a* (Schwind et al. 2017). *D. parva*, *D. acuminata* and *D. ventricosa* are indicator organisms that are positively associated with phosphorus concentrations, unlike *D. lobostoma* (Schwind et al. 2017). Regarding nitrogen, *D. helvetica* and *D. schuurmani* are positively associated with high concentrations, while *D. lobostoma*, negatively (Schwind et al. 2017). The bioindicator species that expressed positive associations with chlorophyll-*a*, phosphorus and nitrogen, responded preferentially to higher concentrations of them commonly found in eutrophic conditions (Schwind et al. 2017).

3.2. The influence of hydrology

Moisture/humidity is the main factor influencing thecamoebians composition at bogs. In addition, microtopography, water chemistry and seasonality have some impact on testate amoeba's distribution (Warner et al. 2007).

Capable of causing more than one third of variance in testate amoeba communities (Song et al. 2018), water-table depth has been pointed out as the main factor influencing these communities at peatlands (Lamentowicz and Mitchell 2005, Mitchell et al. 2008, Li et al. 2015, Payne et al. 2016, Zhang et al. 2017, Song et al. 2018). Seasonality plays an important role in those environments, as it changes water availability to TA (Heal 1964, Gilbert et al. 2003, Warner et al. 2007). Thus, TA

communities can suggest water table fluctuation, or its stability over prolonged time scales (van Bellen *et al.* 2018, Lamentowicz *et al.* 2019, Marcisz *et al.* 2020). Also, seasonality can have an impact on TA communities through changes in temperature (Lamentowicz *et al.* 2013a), light abundance (Marcisz *et al.* 2014a) and even in combination with nutritional conditions (Mitchell 2004, Payne and Mitchell 2007, Mieczan 2007, Mieczan 2010, Elliott *et al.* 2012, Jassey *et al.* 2013, Song *et al.* 2018). The last combination could be inferred also when correlating TA with *Sphagnum* species, due to chemical compounds released by the plants (Jassey *et al.* 2013, Jassey *et al.* 2014, Marcisz *et al.* 2014b).

The above cited variables can be related to testate amoebae size structure, as smaller species have been more abundant at drier periods of the year (Warner *et al.* 2007, Jassey *et al.* 2014, Fournier *et al.* 2015, Marcisz *et al.* 2016), while the biggest ones were more common at the wettest seasons (Lamentowicz *et al.* 2013a).

In a wet open bog, *Argyria vitraea*, *D. oblonga*, *Nebela carinata* were characteristic species, while *Sphenoderia lenta*, *Cryptodiffugia oviformis*, and *Nebela lageniformis* inhabited a drier forested swamp (Warner *et al.* 2007). During the season with wetter conditions, *Hyalosphenia papilio*, *Hyalosphenia elegans*, *Arcella discoides*, and *Placocista spinosa* were found, reinforcing their relation to high soil water content (Warner *et al.* 2007). In relation to spatial patterns, microtopography of the *Sphagnum* have affected testate amoebae's assemblages, reflecting ecological gradients that, otherwise, wouldn't be visible macroscopically. Albeit, ecological variables cannot be inferred precisely by it (Mitchell *et al.* 2000b). The taxa *Archerella flavum*, *H. papilio*, and *H. elegans* were pointed out as good high paleo-moisture indicators, while *Hyalosphenia subflava*, was related to the drier sampling points (Charman and Warner 1992, Tolonen *et al.* 1994, Warner and Charman 1994). Species of narrow ecological amplitude are *A. discoides*, *Diffugia bacillifera*, *N. carinata*, *Nebela griseola*, *Nebela marginata*, *Cryptodiffugia sacculus*, *Quadrullella symmetrica*, *Amphitrema stenostoma*, and *S. lenta* (Charman and Warner 1997). In a Chile peatland, *Centropyxis* was the only dominant genera during all the four seasons of the year, being pointed out as generalist and opportunist (Fernández and Zapata 2011).

The community of testate amoebae is affected by a hydroseral gradient, changing according to the stage, from open water to fen and pioneer raised mire to ombrotrophic bog (Elliott *et al.* 2012). It was also suggested that thecamoebians could be used alongside plant

macrofossils with the potential for delimiting salinity changes, as they responded more quickly and were more sensitive to nutrient gradients than the plant communities (Elliott *et al.* 2012). In Moorlands, subject to a lot of changes and degradations over the past centuries, hydrology was the strongest environmental factor controlling the communities of TA, allowing their use as monitors of this ecosystem. (Turner and Swindles 2012).

Characteristic taxa of wet *Sphagnum* habitats are *Amphitrema wrightianum*, *Nebela carinata*, *Archerella flavum* and *Hyalosphenia papilio*, *Assulina species* (Charman *et al.* 2000, Booth 2002, Lamentowicz and Mitchell 2005, Mazei and Tsyganov 2006). Characteristic taxa of dry *Sphagnum* habitats are *Trigonopyxis arcula*, *Bullinularia indica*, *Nebela tincta*, *Alabasta militaris* (Charman *et al.* 2000, Booth 2002, Lamentowicz and Mitchell 2005, Mazei and Tsyganov 2006). Other abundant and notable taxa from the wetter end of the water table were *Pseudodiffugia fulva* type, and *Diffugia pulex* type, *H. papilio*, *Assulina seminulum* type, *Arcella catinus* type and *H. elegans* for the dryer end (Charman *et al.* 2007). Studies in mosses indicate that the species *A. wrightianum*, *A. vulgaris* and *Archerella flavum* were indicative of a more humid environment (Turner *et al.* 2013, Swindles *et al.* 2015, Amesbury *et al.* 2016, Heinemeyer and Swindles 2018). On the other hand, *C. arcelloides* and *Heleopera petricola* indicate intermediate humidity (Amesbury *et al.* 2016). Conversely, *B. indica*, *A. militaris*, *C. ecornis*, *C. arcelloides*, *H. petricola*, *Phryganella acropodia* and *Trigonopyxis arcula* were indicative of drier locations (Turner *et al.* 2013, Swindles *et al.* 2015, Amesbury *et al.* 2016, Heinemeyer and Swindles 2018). Species with spines, such as *Centropyxis aculeata*, species from the *Arcella* genus and belonging to the genus *Diffugia*, are also useful for indicating higher humidity (Song *et al.* 2014). In contrast to the genus *Trinema*, *Assulina* and *Corythion*, linked to the drier places (Song *et al.* 2014).

3.3. Ecosystem restoration

Testate amoebae indicate changes in regenerating peatlands and floodplains. Afforestation, drainage and harvest at peatlands are concerns in these ecosystems, as they cause ecological damage and carbon loss to the atmosphere (Lachance *et al.* 2005). Efforts have been made to restore such environments, allowing the peat to re-growth (Parry *et al.* 2014). Simultaneously, in floodplains, anthropic impacts have created the necessity to apply restoration projects (Sudduth *et al.* 2007), and strategies for tracking recovery are welcome.

At different levels of succession, peatlands can be inhabited by different assemblages of TA that respond to physical and chemical properties of the peat (Butler et al. 1996). As the peatland becomes drier and more acidic, species richness and abundance increased, while density, biomass and average thecamoebian size decreased (Laggoun-Défarge et al. 2008). *N. tinctoria*, *Assulina muscorum* and *Corythion dubium* were characteristic species of the advanced stage environment, being indicators of dry and acidic conditions (Mitchell et al. 1999, Laggoun-Défarge et al. 2008). *A. muscorum* and *C. dubium* have already increased in abundance after one and a half to two years from drainage in a forested mire, showing their capability to monitor soil microenvironmental effects (Warner and Chmielewski 1992). Thecamoebian communities were able to show impacts from harvest, even when secondary succession surface vegetation appeared to be similar to the natural site's vegetation. These protists are an alternative to continuous measurement in the field, in order to indicate water table depth and pH (Laggoun-Défarge et al. 2008). Also, in a restoring peatland, management have partially caused the TA community changes, but besides it, the weather has also contributed (Swindles et al. 2016). With the management intervention, wet indicator species appeared, such as *Amphitrema stenostoma*, *Archerella flavum*, *Arcella discoidea* type, *Diffugia bacillifera* and *D. bacillarum* (Swindles et al. 2016).

TA can further be used as bioindicators in peatlands undergoing forest-to-bog restoration (Creevy et al. 2018). By comparing the community inhabiting open, forested and forest-to-bog sites, significant differences in relative abundance between them were observed. Although diversity was lower in the open sites (a factor that was influenced by peatland microtopography), the richness was higher than at forested and forest-to-bog ones (Creevy et al. 2018). Commercial forestry practices have caused the loss of mixotrophic taxa in the forested sites. This result was related especially with the light condition, as mixotrophic taxa persisted in undisturbed open bog because of their need for light to survive. *A. discoidea* was considered a potential indicator in forested sites and it was recommended that future sampling designs encompass microtopography (Creevy et al. 2018).

Thecamoebians functional traits (FT) related to their carapace were indicated as candidates for bioindication of woody debris impact on shaping the community at a restored floodplain in Switzerland (Fournier et al. 2012). Taking into consideration the multiple environ-

mental pressures selecting testate amoeba's FT, and the potential of FT to complement classical indices, further research regarding TA FT has been encouraged (Fournier et al. 2015).

3.4. Agricultural practices

Soil quality is essential in the sustainable performance of agricultural practices (Carter 2002); however, the increased use of pesticides, herbicides and fertilizers have side effects on the environment (Nesbitt and Adl 2014). Many protists are sensitive to pesticides and other components commonly used in agricultural practices, and insecticides are more harmful to these organisms than herbicides (Foissner 1994, 1997). *A. vulgaris*, in presence of the fungicide Fundasol had the growth stimulated, but some hours later all species in the study were dead (Todorov and Golemansky 1992).

Testate amoebae in an Arctic Tundra had abundance and biomass reduced by 77 and 84% with long-term nitrogen (N) and phosphorus (P) fertilization. Some species vanished from the fertilized plots, while *P. acropodia* increased (Mitchell 2004). These results were probably related to the deterioration of the mosses caused by fertilization and the availability of preys (Mitchell 2004). Furthermore, when inhabiting moss fertilized with N, *Bullinaria indica* showed greater abundance (Mitchell and Gilbert 2004), but this response needs further investigation, as the species has already been related to the lowest preferences of N at peat (Tolonen et al. 1992). In a *Sphagnum* peatland N and P fertilization experiment, testate amoeba's richness and density decreased (Mieczan et al. 2015), which could be related to a decrease in oxygen concentration. The testacean *C. dubium* presented lower abundance in a heathland when the sites were treated with huge concentrations of nitrogen for 20 years (Payne et al. 2012). Although it may highlight the species as a N bioindicator, it is discussed that the response may have been indirect, more related to plant community changes (Payne et al. 2012).

3.5. Fire events and volcanic activities

Fire events have already shown to impact testate amoebae communities in moorlands, where, after charcoal deposition, water infiltration may be reduced and drought and erosion increased (Turner and Swindles 2012). *Hyalosphenia subflava* and *T. arcuata* have already been pointed out as potential burning indicators, being related to the driest sites (Turner and Swindles 2012, Turner et al. 2013). Although Qin et al (2017) registered a growth at thecamoebians with xenosomes af-

ter a wildfire episode, in a multi-proxy study, TA with idiosomes with organic coating became more abundant after fire (Marcisz et al. 2019). Also, fire events caused a selection of smaller TA species (Marcisz et al. 2016) and a substantial decrease of mixotrophs (Marcisz et al. 2016, Marcisz et al. 2019). The last, may be caused by the water table depth lowering after the fire, alongside changes at the site's vegetation and ash fallout shade, that diminished the photosynthetic capacity of the mixotrophs (Fournier et al. 2015, Lamentowicz et al. 2015a, Marcisz et al. 2016). On the other hand, when fire occurs on the peatland's surrounding vegetation, it may increase water table depth, as the plants cease to absorb water from the soil. These events can contribute to a change in TA assemblages to wet indicator species (Lamentowicz et al. 2007, Marcisz et al. 2015).

Deposition of sulphuric acid by anthropogenic or volcanogenic activities have presented an impact to TA communities (Payne 2010), such as deposition of sodium sulphate (Payne et al. 2010). Although it is not clear by which mechanisms these protozoans were affected, they can be related to changes in the ecosystem's trophic web, with a sulphate-reducing bacteria (SRB) and methanogenic archaea (MA) shift (Payne 2010, Payne et al. 2010).

Thecamoebians are indicators of past and current volcanic activity, in a way that could be used as proxies of both frequency and extent of eruptions, dating and correlating paleoenvironmental data. This is possible by the ability of TA to be one of the first protists in the succession to inhabit volcanic ash fallout (Smith 1985), incorporating particles with less than 125µm, called cryptotephra, into their tests. This characteristic facilitates the extraction and counting of these minerals (Delaine et al. 2016). Moreover, the construction of thecamoebian's carapace using foreign material can turn them into indicators of microplastic pollution. Thecamoebians from order Arcellinida were capable of incorporating 4µm polystyrene spheres into their tests under laboratory conditions (Bian et al. 2019). With microplastics being accumulated year after year in freshwater ecosystems to hundreds or thousands of particles per litre (Li et al. 2020), its bioavailability may impact the test construction.

3.6. Metal and semimetal contamination

In areas previously impacted by mining, protozoa were the first eukaryotic organisms to colonize the environment (Wanner and Dunger 2001). This way, TA are affected and responsive to metals and semimetals,

pointing out contamination. When reclaiming an open-cast coal mining in Germany, different assemblages of testate amoebae demonstrated sensitivity to different stages of soil recovery, relating to characteristics that alter the quality of the substrate (Wanner and Dunger 2001). In lake's sediments and water columns affected by gold mining, the techniques implemented for measuring arsenic are not efficient to point out ecological impacts (Nasser et al. 2020). Notwithstanding, strong correlations between thecamoebians and arsenic (As) have already been pointed out (Nasser et al. 2016), with this group being considered a good indicator of contamination by As. When related to that, the least tolerant group was mainly represented by the genus *Diffflugia* and by the species *Cucurbitella tricuspis*; and the greater tolerance, represented by some species of *Centropyxis* and *Diffflugia elegans* (Nasser et al. 2020). In addition, these protists were also correlated with phosphorus (P), barium (Ba), carbon (C) and calcium (Ca) (Nasser et al. 2016).

The concentration of heavy metals in lakes were positively correlated with the taxa *Mediolus corona*, *Diffflugia bicornis*, *C. tricuspis* and *P. compressa*, and negatively with *Diffflugia acuminata* and *L. modesta*. However, the research only points to the influence of heavy metals under the structure of the community (Qin et al. 2016). The specie *A. vulgaris* was registered in great abundance in lakes with high heavy metals concentrations and low pH, which shows that this specie was tolerant to stressing conditions, being able to present different alterations in tropical environments (Patterson et al. 2013, Kumar and Patterson 2000, Escobar et al. 2005). The species *Centropyxis aculeata*, *C. constricta* and *A. vulgaris* were shown to be tolerant in a lake heavily polluted by mercury and arsenic (Patterson et al. 1996). Although the genus *Centropyxis* and *A. vulgaris* showed affinity with metals, only *A. vulgaris* was considered a good indicator, as it was not being favoured by the trophic state and salinity of the lake. Moreover, a relationship between mercury and arsenic levels with the distribution of *Diffflugia proteiformis* is notorious, being present at highly contaminated sites (Patterson et al. 1996).

The presence of potentially toxic trace elements in a reservoir substrate (As, Cr, Cu, Fe, Mn, Ni, Pb, Sc and Zn) affected the abundance and diversity of the community of thecamoebians (Misailidis et al. 2018). Places with low rates of contamination presented a higher number of species, and regions with aggregations of roots and low concentrations of pollutants are dominated by *Diffflugia corona*, *D. oblonga* and *D. gramen*. As the

concentration increases, species that were more tolerant remain and dominate. They were: *Arcella megastoma* and *D. corona*, in contrast with the most sensitive ones: *D. gramen*, *Lesquereusia globulosa* and *Netzelia tuberculata* (Misailidis et al. 2018). The identification to the lowest taxonomic resolution leads to a conclusion less uncertain and more clear of the biomonitoring properties of testaceans, especially in dynamic habitats as reservoirs, besides contributing with ecological information regarding genera and species (Vieira et al. 2017).

In a floodplain contaminated by heavy metals (Cu, Pb, Zn, Co) in Japan, the diversity of TA was lower in the most polluted places, where the concentrations of Cu, Pb and Zn were higher (Wanner et al. 2020). Their results showed in areas contaminated by heavy metals, species such as *Euglypha rotunda*, *Trinema enchelys* and *Trinema lineare* as indicators of the impact on the biogeochemical cycle in proterozoic silicon wells due to the self-secrete composition of their test (Wanner et al. 2020).

C. arcelloides and *Centropyxis cassis* were abundant in peatlands areas where copper (Cu) concentration was high, suggesting that the genera could be tolerant to high concentrations of this metal. However, the diversity of TA in general was lower, pointing out *Centropyxis* species's tolerance as an exception. It is believed that the high concentrations of metals, such as Cu, might reduce the abundance of prey (e.g., algae and bacteria) and only species tolerant to food shortage would survive (Asada and Warner 2009). In stream mosses, *C. aculeata*, *C. discoides*, *C. arcelloides*, and *Euglypha laevis* can be potentially used to measure Cu pollution in water, while mercury (Hg) causes community's abundance to decline (Yang et al. 2011). *Euglypha strigosa* was also pointed out as sensitive to Cu (Meyer et al. 2012). When the moss retains such pollutants, a different picture was found at 63 Canadian lakes, where low concentration of Hg didn't have an impact on TA (Yang et al. 2011, Neville et al. 2013).

Increasing concentration of lead (Pb) accumulated in *Barbula indica* moss diminished thecamoebians species richness, abundance and Shannon index. Pb significantly decreased abundance of some *Euglypha*, *Trinema*, *Centropyxis* and *Tracheleuglypha* species, while *Quadrullella symmetrica* and *Euglypha diliociformis* have suggested resistance to lead (Nguyen-Viet et al. 2007). TA had their richness, total density and total biomass decreased as Pb concentration and time of exposition increased in a controlled environment. *N. carinata*, *E. strigosa*, and *H. sphagni* were the most sensitive taxa, while *A. catinus*,

A. discoides, *A. militaris*, *C. dubium*, *T. lineare*, and *C. aculeata* are the most resistant (Nguyen-Viet et al. 2008).

3.7. Atmospheric influence and its pollution

Moss with inhabiting testate amoebas are good bioindicators for atmospheric pollution since they are in subaerial environments, directly exposed to atmospheric pollutants (Nguyen-Viet et al. 2007). Parameters as appearance/extinction of species or decrease in biomass/abundance can be used to identify the atmospheric condition (Meyer et al. 2012). The contamination with nitrogen dioxide (NO₂) can impact the richness, abundance and biomass of the testate amoebae community (Meyer et al. 2009, Meyer et al. 2012), with the species richness being significantly correlated with NO₂ concentration (Nguyen-Viet et al. 2004). Changes in interactions at microbial level, especially predation, enhanced this effect (Meyer et al. 2009). *Paraquadrula irregularis* was pointed out as an indicator of atmospheric pollution caused by this gas, what could be related to acidification of the environment, and calcium leaching of its calcareous test (Nguyen-Viet et al. 2004). *N. tincta* and *Trygonopyxis arculla* were also sensitive to NO₂, and the community that lives in *Pseudoscleropodium purum* moss can be used to differentiate sources of pollution (industrial or urban ones) (Meyer et al. 2012). In an experiment with atmospheric carbon dioxide (CO₂) increase, *Sphagnum* TA decreased in biomass (Mitchell et al. 2003). Moreover, road traffic pollution was able to cause a decrease in abundance and diversity of soil TA (Balik 1991). The locations with the greatest impact, also had a different composition. From a total of 42 recorded TA species, 16 were restricted to less polluted locations (Balik 1991), showing their relationship with atmospheric pollution (Nguyen-Viet et al. 2004). Testate amoeba assemblages from a brown coal combustion polluted peatland were impacted by it, with Al and Cu being indicated as the most toxic elements to them (Fiałkiewicz-Kozieł et al. 2015). The pollution decreased mixotrophic and larger TA species, but an increase in *Centropyxis aerophila* and *Phryganella acropodia* species (Fiałkiewicz-Kozieł et al. 2015).

Environmental variations caused by climate change such as increase in temperature and precipitation alterations have an impact on peatland microbiota, and TA are pointed out as candidates to monitor them (Jassey et al. 2011b). At the *Sphagnum* upper segments, thecamoebians biomass and density increased together with temperature. Although more studies in this subject are necessary, in this condition they fed on an ex-

pressive range of prey and react to their changes (e.g., bacteria) (Jassey et al. 2011b). Temperature increase altered the trophic web, as it has the Sphagnum polyphenols selecting differently the microbial community and shortening the food web. This led to a faster carbon and nutrient recycling by decreasing predators and omnivores (including larger TA, with bigger pseudostome) while increasing autotrophs and decomposers (Jassey et al. 2013). *H. papilio* was an indicator of temperature increase, and could be an important tool in monitoring during the reconstruction of *Sphagnum* peatlands, since it's a mixotrophic thecamoebian inhabiting the top layers of *Sphagnum* (Basińska et al. 2020).

The species *C. constricta*, *C. aculeata*, *Diffugia urceolata*, *D. oblonga* and *D. corona*, presented high density in core studies from three lakes in Atlantic Canada as a result of an increase of the temperature (McCarthy et al. 1995). In lakes of rocky mountain regions with low temperatures, a low diversity of TA was registered, with dominance of the taxa *C. aculeata* and *C. constricta* (Neville et al. 2010).

3.8. Paleoenvironmental reconstruction

Fossil thecamoebian shells are very often well preserved and abundant in peatlands, making them special as bioindicators when compared to conventional fossil indicators (Warner and Charman 1994). Modern and fossil assemblages of testate amoeba paired with depth to water table analysis and radiocarbon-dating were used to construct transfer functions, which provides palaeohydrological data when applied to the corresponding site (Warner and Charman 1994, Charman et al. 2007). Those have been applied to infer centennial scale climate patterns (Charman and Hendon 2000, Hendon et al. 2001, Booth 2002), anthropic impacts (Patterson et al. 2002, Ndayishimiye et al. 2020) and sea level change (Barnett et al. 2017). Regional transfer functions have already been developed throughout Europe (Tolonen et al. 1992, 1994; Schnitchen et al. 2006; Swindles et al. 2015; Lamentowicz et al. 2020), to Russia (Willis et al. 2015, Lamentowicz et al. 2015b, Kurina and Li 2019), China (Qin et al. 2013, Li et al. 2015), New Zealand (Charman 1997), United States and Canada (Booth 2001, 2008; Amesbury et al. 2013; Lamarre et al. 2013), Peru (Swindles et al. 2014) and Panama (Swindles et al. 2018).

Functional trait-based reconstructions have been increasing recently, being conducted over several landscapes (Marcisz et al. 2020), and provide reliable analysis when there is no transfer function and inde-

pendently from taxonomic identification (Lamentowicz et al. 2015a, van Bellen et al. 2017, Krashevskaya et al. 2020). By constructing statistical models based on functional traits, identification errors and taxonomic change inaccuracies are diminished, while there is a bigger chance of comprehending community dynamics and functional processes over long time-scales (Marcisz et al. 2020). Also, a multi-proxy approach involving functional-traits could benefit paleoenvironmental reconstructions by correlating ecological processes to functional roles (Lamentowicz et al. 2015a, van Bellen et al. 2017, Galka et al. 2017, Marcisz et al. 2020, Krashevskaya et al. 2020).

Water table depth (WTD) was the main variable to which thecamoebians responded, along with pointing out microtopography differentiation in peatlands (Warner and Charman 1994, Krashevskaya et al. 2020). TA species could indicate increase, instability, and lowering of the water table (even when it happens by sharp declines of the WTD) (Galka et al. 2014, Galka et al. 2015). In these environments, moisture content has been primarily taken into consideration (Booth 2002), but, as it changes more often, even during a day, WTD is the main variable observed (Charman and Warner 1997, Warner et al. 2007). More reliable reconstructions can be carried out during wetter conditions phases, as taxa with dry optima can be wider distributed than those with wet optima. During dry conditions phases, the absence of a wet indicator becomes more reliable than the encounter of a dry one (Charman et al. 2007).

On the other hand, WTD influence becomes secondary when most of the sample is collected from minerotrophic mires, and not ombrotrophic ones. In those cases, the trophic state of a mire, that can be reflected by pH (Payne et al. 2006, Markel et al. 2010), conductivity and calcium content, will have a bigger impact on the thecamoebians assemblages (Lamentowicz et al. 2013b). This way, when applied to WTD reconstruction through transfer functions, assemblages from ombrotrophic and minerotrophic mires should be regarded to the construction of different transfer functions to different peatland development stages (Kurina et al. 2020). When constructing a transfer function to an ombrotrophic peatland, the bog stage of its development should be reconstructed with an ombrotrophic model, and a minerotrophic model should fit the earlier fen-bog and fen transition stages (Kurina et al. 2020).

Thecamoebian's assemblages are pointed out as paleolimnological and paleoecological indicators at lakes, being able to reflect climate changes (McCa-

rthy et al. 1995). During the late glacial and Holocene, five assemblages identified the beginning of the epoch, alongside with climate phenomena that palynology alone could not indicate (McCarthy et al. 1995). These protists could also indicate lake depth (Tsyganov et al. 2019), sedimentation rates and pH changes throughout the Holocene (Ellison 1995). In a multi-proxy approach study, a thecamoebians based WTD reconstruction paired peaks in the bog surface water with periods with lower sunspot activity (Turner et al. 2013). In an East Siberian Arctic permafrost study, thecamoebians species composition from the Late Pleistocene-Holocene were used to identify differences between both periods and between their temperatures (Bobrov et al. 2004).

Regarding the difficulty of separating climate change from human impact; when testate amoebae are integrated with micro and macrofossils, such as pollen, microcharcoal, local plant community, spores and dendroecological analysis, in a multi-proxy approach, it can be possible to separate these two factors in peatlands and lakes (Patterson et al. 2002, Lamentowicz et al. 2008, Lamentowicz et al. 2015a, Galka et al. 2017, Lamentowicz et al. 2019, Lamentowicz et al. 2020). Moreover, TA showed to be very responsive to hydrological fluctuations, while macrofossils may be delayed (Lamentowicz et al. 2008). At peatlands, TA assemblages structure differentiated after land use change, caused by deforestation and implementation of agriculture (Marcisz et al. 2020). Because of changes in water absorption, a bigger availability of water may increase WTD. In this case, testate amoeba size and biovolume (Marcisz et al. 2020), pseudostome size and position are affected by WTD (Lamentowicz et al. 2015a), and may there will be an increase in mixotrophs, if light becomes more available (Galka et al. 2017, Marcisz et al. 2020). Deforestation may also lead to terrestrialization, as it increases dust deposition and nutrient flow to the peatland (Ireland and Booth 2012, Lamentowicz et al. 2020); this way, a shift in the plant community can also impact TA assemblages (Ireland and Booth 2012). Furthermore, in a scenario of WTD lowering, after peat extraction, TA size and mixotrophs decreased (Marcisz et al. 2016). Further, TA with smaller (Krashevskaya et al. 2020) and more hidden pseudostome increased with dryness (Marcisz et al. 2016). Thecamoebians core assemblages from Swan Lake (Canada), have been able to show the different uses of the land around it (Patterson et al. 2002). The different communities were compared to palynological data, and reflected the great impact of deforestation for agriculture and human set-

tlement, even in underwater life. The Deforestation Assemblage, presented dominance of stress indicator taxa, such as *C. aculeata* and *A. vulgaris* (Patterson et al. 2002). *C. tricuspis*, in contrast, appeared in the Eutrophication Assemblages, a period after World War II with high use of chemical fertilizers (Patterson et al. 2002). Although erosion was also present in the latter study, its combination with nutrient input at Lake Erie (Canada) inferred a bigger impact in the community, being indicated by *Diffugia biddens* presence (Scott and Medioli 1983). Soil erosion also played a key role modelling thecamoebians assemblages in lake Lugu (China) where three characteristic assemblages were identified through 2500 years (Ndayishimiye et al. 2020). Assemblages also shifted by change in nutrient input, by forest growth and eutrophication influenced by human activities (Ndayishimiye et al. 2020). All those papers point out that these protozoans are proxies for land use changes.

A salt-marsh is a wet biotope located next to the coast regions, flooded by salt waters by the high tide (Viswanathan et al. 2020). Despite the known importance of these organisms, there is a scarcity of studies that use this group as an indicator in the salt marsh biotope (Barnett et al. 2017). A few species inhabit these regions with strong zonation, from the high salt-marsh environments transitioning into the supratidal zone (Barnett et al. 2013, Barnett et al. 2017). In salt-marshes, the TA were paleoenvironmental indicators related to the reconstruction of the sea level and being used to construct tendencies of it in the current geological period (Barnett et al. 2015), being more precise in its indication when compared to foraminifera (Gehrels 2000, Gehrels et al. 2006). Throughout the North Atlantic, a thecamoebian's assemblages-based transfer-function could indicate, with great precision, sea level fluctuations, revealing information when other proxies are missing. Moreover, when paired with foraminifera-based data, the reconstruction capability extends back in time (Barnett et al. 2017).

3.9. Sewage Treatment

The biological sewage treatment process is based on the formation of suspended bacterial flakes, which have a diverse microfauna associated, being segregated from the effluent in the sedimentation tanks (Zhou et al. 2006). The microbiota is sensitive to environmental variations, so changes in the community are responsible for disassembling the trophic web, affecting the biological performance of the treatment station (Madoni

2003). The microfauna protists perform a vital function, mainly controlling microbial population density through predation, assuring by that the quality of the effluent (Curds and Cockburn 1970).

Testate Amoebae of the genera *Arcella*, *Diffugia* and *Euglypha* were bioindicators (Madoni 1994, Nicolau et al. 2005, Pérez-Uz et al. 2010, Hu et al. 2013) found in greater abundance in older sludge plants, as their growth was favoured (Madoni et al. 2000). In addition, specific system characteristics, such as low loading, long retention time and high aeration rate of the tank influence their abundances. These variables indicate the effluent quality and the high biological activity of sludge plants (Chierici and Madoni 1991). Therefore, TA can be indicators of the functioning quality of a sewage treatment system. In treatment places, TA with less than 20µm that were associated with flocs helping to improve productivity of nitrifying bacteria that lives inside those, since those little thecamoebians are bacteria predators (Pérez-Uz et al. 2010). Furthermore, this group of organisms responds to nitrification in the treatment system, once its occurrence decreases with the decrease of the removal of nitrogen, mostly in species of the genera *Arcella* (Pérez-Uz et al. 2010). Species that stood out in this biotope were *Arcella hemisphaerica* and *Euglypha tuberculata*, that respond to the system nitrification (Madoni 1994, Hu et al. 2013). However, in an activated sludge plant, it was shown that the first one was related to good settlement of sludge plants and should be used as an indicator of the effectiveness of the plant, because its abundance decreased when the effluent's quality dropped (Zhou et al. 2006). Nowadays, the ecological importance that TA play in these systems is known, and according to the advance of the decades, studies have emphasized these organisms and their bioindicator potential. However, studies on this issue are still scarce.

3.10. Taxonomic and methodology issues

Biomonitoring using zooplankton has indicated that it's identification and analysis, including TA, can be done to genera level (Machado et al. 2015, Souza et al. 2019). Identification to the genera level has been an economic strategy to overcome the lack of specific taxonomists to certain groups. However, TA studies did not obtain a high agreement between the data provided by the level of genera and of species, which excludes them from that strategy (Alarcão et al. 2014, Gomes et al. 2015). The lack of specialists can be explained as a result of a certain negligence with testate amoebae in

comparison to other members of zooplankton, mainly regarding its lack of a specific methodology for data collection and analysis (Leipnitz et al. 2006), as well as a recognized relevance to biodiversity in biosystems (Corliss 2002, Han et al. 2011).

Some concerns regarding methodology include sampling. For instance, significant differences between upper and lower *Sphagnum* thecamoebians, raise concern about how deep the samplings should occur. As it would change community composition, diversity and dominance, providing an incomplete answer of the site's thecamoebians if not taken into consideration (Booth 2002, Jassey et al. 2011a, Ireland and Booth 2012). Upper and lower portions shelter restricted taxa, and lower assemblages have shown to have bigger richness than shallower ones, as it accumulates tests of thecamoebians from upper portions and from previous years (Booth 2002). Mixotrophs are dominant in surface layers, while heterotrophic species are more abundant in deeper layers, but the use of xenosomes to build the carapace also plays a part in the vertical distribution, as *Amphitrema wrightianum* where more abundant in intermediate segments of the *Sphagnum* rather than in the top layers (Jassey et al. 2011a). Upper layers of *Sphagnum* are more exposed to water table fluctuations, and may indicate it differently than deeper layers (Basińska et al. 2020). Although upper taxa would be more representative of environmental variables at the sample time, collecting all the vertical extension of testate amoeba distribution could be the best way to characterize its relations with environment variables (Booth 2002, Ireland and Booth 2012).

4. CONCLUSION

Testate amoebae are reliable indicators when applied to different uses in a diversity of biotopes. They can be an important tool as biological indicators in various conditions ranging from water, soil and atmospheric pollution, to sea level fluctuations, land use change and paleoclimate reconstruction. A multi-proxy approach and inclusion of functional trait-based analysis more recently developed for the testaceans should contribute to a crescent importance and extension of their use. It is clear that, although testate amoebae's use as indicators has gained space through different fields, in all the areas where applied, there is still room for growth.

Acknowledgments. The authors would like to thank the Undergraduate Program in Biological Sciences of the Federal University of the State of Rio de Janeiro – UNIRIO, (Brazil) for laboratory facilities. The authors Beatriz Ramos, Gabriela Sampaio and Yemna Silva were supported by UNIRIO scholarships.

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Received on 23rd March, 2021; revised on 21st September, 2021; accepted on 5th March, 2022

