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Experimental approach on the contribution of wind and animal vectors in the dispersal and colonization of testate amoebae (Protista, Amoebozoa) in freshwater ecosystems

Abordagem experimental sobre a contribuição do vento e de vetores animais na dispersão e colonização de amebas testáceas (Protista, Amoebozoa) em ecossistemas de água doce

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Abstract: Aim: We aimed to understand how testaceous amoebae spread in new sites, assessing their dispersal potential by wind and animals in freshwater ecosystems. **Methods:** We conducted a field experiment over 33 days between July and August 2018. The study included four different approaches: (i) a control group exposed exclusively to wind, (ii) the addition of propagules dispersed by Odonata (aquatic insects), (iii) the addition of propagules dispersed by amphibians, and (iv) the combined addition of propagules of both animals. **Results:** We detected a total of 13 species of testate amoebae. Regarding species richness, we observed a steady increase throughout the experimental period. In terms of abundance, a similar trend was observed, with differences in the treatment of all vectors combinated, when comparing the treatments with only wind, and the combination of wind and vectors alone, indicating a possible progressive colonization of these organisms in the new aquatic environment. Regarding the composition of testate amoebae, we did not detect significant differences between treatments within each period or between different treatments throughout the experiment. **Conclusions:** Our results demonstrate the importance of animal vectors in the transport of testate amoebae cysts.

Keywords: Amoebozoa; distribution; microcosm; ecological experiment; zoochory.

Resumo: Objetivo: Buscamos entender como as amebas testáceas se espalham em novos locais, avaliando seu potencial de dispersão pelo vento e por animais em ecossistemas de água doce. **Métodos:** Realizamos um experimento de campo durante 33 dias entre julho e agosto de 2018. O estudo incluiu quatro abordagens diferentes: (i) um grupo controle exposto exclusivamente ao vento, (ii) a adição de propágulos dispersos por Odonata (insetos aquáticos), (iii) a adição de propágulos dispersos por anfíbios, e (iv) a adição combinada de propágulos de ambos os animais. **Resultados:** Detectamos um total de 13 espécies de amebas testáceas. Em termos de riqueza de espécies, observamos um aumento constante ao longo do período experimental. Em termos de abundância, observou-se uma tendência semelhante, com diferenças no tratamento de todos os vectores combinados, quando comparados os tratamentos com somente vento, e da combinação do vento com os vetores de forma isolada, indicando uma possível colonização progressiva destes organismos no novo ambiente aquático. Relativamente à composição das amebas testadas, não foram detectadas diferenças significativas entre tratamentos dentro de cada período ou entre os diferentes tratamentos ao longo da experiência. **Conclusões:** Nossos resultados demonstram a importância dos vetores animais no transporte de cistos de amebas testáceas.

Palavras-chave: Amoebozoa; distribuição; microcosmos; experimento ecológico; zoocoria.

1. Introduction

The interest in studying the mechanisms that dictate the dispersal processes of biological communities has intensified with the need to understand how communities are structured (Cochak et al., 2021). Species can disperse through sites in an active and/or passive way (Bilton et al., 2001; Parry et al., 2024). Active dispersal involves the organisms' own movements (such as birds, amphibians and flying insects), while passive dispersal relies on external agents, known as vectors, to transport the organisms (Foissner et al., 2011).

Many physical and biological factors act as effective vectors in the passive dispersion of organisms, such as the flow of water in freshwater ecosystems (Padial et al., 2014), the action of the wind that efficiently disperses resistant forms of microorganisms between environments and the facilitated dispersion by animals transporting living organisms and forms of resistance (Incagnone et al., 2015; Cochak et al., 2021). These vectors assist in disseminating aquatic organisms by transporting them to new areas, extending their geographic distribution and promoting the colonization of new ecosystems. Understanding the role of these vectors is critical to understanding how aquatic microorganisms are dispersed and established in different environments.

To gain insights into the dispersion patterns of aquatic microorganisms within a novel ecosystem, it is crucial to examine their capacity for passive dispersal (Bohonak & Jenkins, 2003). Various organisms are recognized as agents facilitating the dispersal of freshwater organisms through a phenomenon referred to as "phoresy", where individuals from different species form an association wherein one carries the other (Foissner et al., 2011; Incagnone et al., 2015; Pilatti et al., 2024). Many organisms visit water bodies during their migrations or daily activities. Consequently, they can transport propagules of aquatic species, especially microorganisms, to new habitats (Bohonak & Whiteman, 1999). This is especially true when it comes to amphibians (Bohonak & Whiteman, 1999; Vanschoenwinkel et al., 2008) and aquatic insects, such as Odonata (Cochak et al., 2024). Amphibians and Odonata are important dispersers of microorganisms in freshwater environments, mainly due to their frequent contact with water, thus facilitating the transportation of propagules to different locations, making dispersal more effective (Weisse, 2008; Cochak et al., 2024). Although dispersal is critical for colonizing new habitats, the dispersion process becomes effective only after the propagules successfully establish themselves as active cells or resting stages (cysts) (Bohonak & Jenkins, 2003; Weisse, 2008; Weisse, 2024). In addition, adaptations to local environmental conditions also restrict the colonization of new habitats, as individuals from an established population may not adapt to habitats with different environmental conditions (Balkau & Feldman, 1973; Leturque & Rousset, 2002).

Dispersal strategies involve morphological, behavioral, and physiological aspects (Bowler & Benton, 2005). Microorganisms, due to their minimal sizes (Smith et al., 2008), can form resistance and dormancy cysts, which are dormant stages of the cell, showing no measurable metabolism, usually at low physiological activity, where they are enveloped by a highly protective covering (Dallimore, 2004). Dormancy allows microorganisms to survive in unfavourable environmental conditions and act as dispersal propagules, as described for many biological groups (Van Damme & Sinev, 2013;

Dumont & Negrea, 2002). It is their main strategy because they are easily transported by different physical and biological vectors over short and long distances, making dispersal more effective (Weisse, 2008; Heino, 2013). This encystment enables long-distance dispersal, requesting a capacity for passive transport and survival during the time needed for the transport, allowing the dispersion of microorganisms, such as those of the Phylum Rhizopoda (Bruni et al., 2024).

Microorganisms of the Phylum Rhizopoda, such as testate amoebae, are widely distributed in freshwater ecosystems. The testate amoebae are organisms characterized by the presence of a carapace (also called a shell) and short generation times, which allow rapid reproduction in response to environmental changes, facilitating the recovery of their communities from a disturbed state (Ndayishimiye et al., 2024). They play a relevant ecological role, participating in herbivory and detritivore chains (Gimenes et al., 2004; Zagumyonnaya et al., 2023). In freshwater ecosystems, they can colonize different compartments (such as the planktonic, benthic or periphytic) and habitats (such as rivers, lakes, wetlands, ponds) and may be associated with phytotelmata, such as some bromeliad species (Velho et al., 2003).

We evaluated the influence of physical (i.e., anemochory, by wind) and biological vectors (i.e., zoochory, defined in this study by Amphibians and Odonata) in the dispersal of testate amoebae. That said, this work represents an advance in the understanding of the dispersal process by different vectors in the testate amoebae community. More specifically, our objectives were: i) experimentally investigate the relative efficiency of wind and different animal vectors in the passive dispersal of the testate amoebae community; ii) investigate the attributes of richness, abundance, and species composition of testate amoebae according to each dispersal vector individually and together, evaluating how the community changes over time. We expected that: (i) the presence of propagules from biological vectors would lead to increased richness and abundance values as well as differences in species composition compared to dispersal mediated by wind, (ii) the composition of the testate amoebae community differs between wind and animal vectors, (iii) the greater the diversity of biological vectors (that is, considering the three vectors together), the greater and more efficient would be the change in abundance, richness and composition of the testate amoebae community over the time.

2. Materials and Methods

2.1. Experimental design

We conducted our experiment on the left bank of the Paraná River (PR, Brazil), at the Advanced Base of the Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura (Nupelia), in the Municipality of Porto Rico (PR, Brazil). Our experiment lasted over 33 days between July and August 2018.

We used a total of 128 artificial microcosms of polyethylene containers, with a capacity of one liter. The artificial microcosms were randomly placed on wooden pallets adapted for the experiment, approximately 30 cm from the ground and exposed to the open air (Figure 1). Each microcosm was filled with 800 ml of water collected from the Paraná River, previously filtered through GF/C (Whatman) fiberglass filters, which retain particles larger than 1.2 µm, so that no organism or form of resistance was present in the microcosms. The distance from the installed microcosms to the river was approximately 3 meters. With this, water filtration sought to remove all organisms and avoided the possibility of having testate amoebae alive before the experiment. Due to water filtration, sediments were not present in the microcosms.

We carried out eight samplings during 33 days: day zero (at the beginning of the experiment; T0), one (T1), three (T3), seven (T7), 12 (T12), 19 (T19), 26 (T26) and 33 (T33; last day of the experiment). We removed 4 replicates of the same treatment from each day sampled, totaling 16 microcosms per sampling day (4 replicates x 4 treatments = 16 microcosms). Because we employed an experiment with a destructive approach to microcosms, the number of microcosms decreased with each sampling event (from 128 to 16 artificial microcosms).

A square tent open on four sides was set up over the experimental units to prevent precipitation from causing dilution or even overflow of the microcosms. The side openings of the tent were open enough to allow wind action and the arrival of testate amoebae propagules carried by anemochory (wind) (Figure 2).

The microcosms were divided and randomized into four distinct treatments: i) Control (wind, or "W"); ii) Wind + Amphibian (abbreviated later as "W+A"), iii) Wind + Odonata ("W+O"); and

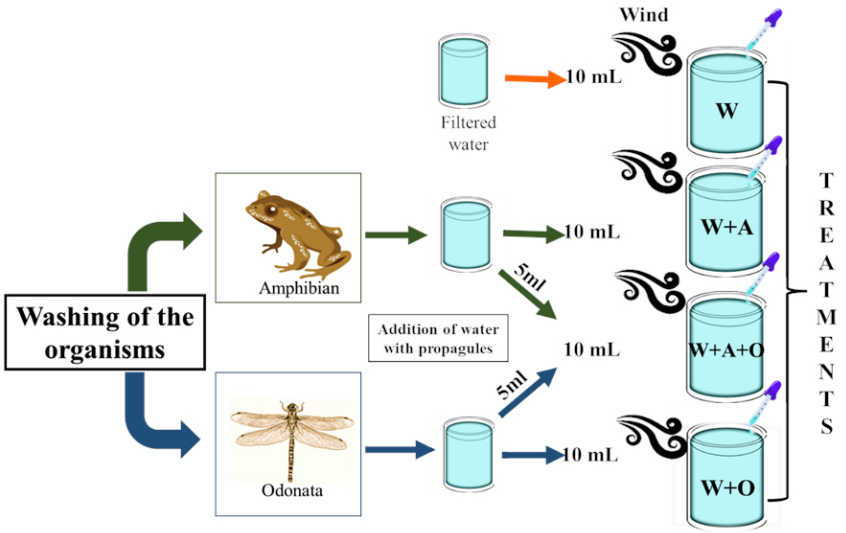

Figure 1. Schematic model of experimental design. W = Wind; W + A = Wind + Amphibian; W +A + O =Wind, Amphibian and Odonata; W + O = Wind + Odonata.

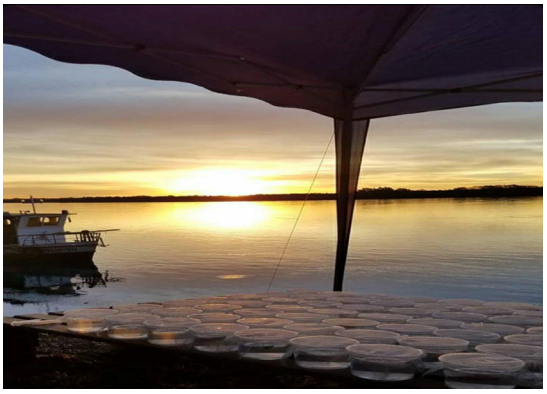

Figure 2. Disposition of the microcosms in a random way, being covered by a tent to avoid dilution and homogenization of the samples by possible rains.

iv) Wind + Amphibian + Odonata ("W+A+O"), which were covered with 500 µm netting to prevent contamination of any other insects during the experimental time. For the biological vector treatments, two vectors were used, one from the class Amphibia and one from the class Odonata. For the Amphibia class, individuals of the species *Scinax fuscovarius* (Lutz, 1925; Anura: Hylidae) were handled, and for the Odonata class vectors, individuals of *Pantala flavescens* (Fabricius, 1798). In the case of amphibians, we obtained a license from the National Council for Control of Animal Experimentation - CONCEA (CEUA No. 9995190118).

For the capture of animal vectors (Odonata and Amphibia), the collections were carried out based on an active search for individuals throughout the area adjacent to the Advanced Base in Porto Rico (PR, Brazil). Dragonflies were captured during the day using entomological nets. Due to the nocturnal behavior of amphibians, they were captured during the night and later isolated in sterilized plastic pots and adapted to keep them until the next morning, when the procedure for obtaining the propagules from both amphibians and dragonflies was carried out. The pots containing the amphibians were also washed to prevent propagules from sticking to their interior. All individuals collected, both Amphibians and Odonata, were washed separately in filtered water with the aid of cotton swabs, used to carefully scrape the animals' skin, in order to remove all possible propagules adhered to the animals' body surface. Considering that dispersal is a random phenomenon and that the number of individuals arriving in natural aquatic environments varies over time, the number of individuals captured for washing and subsequent addition of propagules in the experimental mesocosms ranged from a minimum of 1 individual to a maximum of 10 individuals of each vector, per day. Therefore, the maximum number captured during the experimental period was 10 individuals of each vector. After this procedure, the animals were returned to nature

To simulate the dispersal process, the water obtained from each vector was placed in their respective treatments with the aid of a graduated syringe, and this water was homogenized before addition. For the isolated treatments of each animal vector (W+A and W+O), 10 mL of water from vector washing were added while for the combination of the two biological vectors

(W+A+O), 5 mL of water of each vector were added to the treatment. In order to standardize the effect of adding water in the experiment, 10 mL of filtered water was added to the control treatment. This procedure occurred daily, from the beginning to the end of the experiment, based on the same method used by Cochak et al. (2021). The volume of water used (10mL) was standardized to avoid possible bias in the samples (Figure 1).

To ensure the availability of nutrients and food resources for the establishment and development of testate amoeba populations in the microcosm, 20 microliters of a mixture of Nitrogen (NO_3^-: 27500 mg/L) and Phosphorus (PO_4^{3-}: 5250 mg/L) were added every two days until the end of the experiment.

2.2. Laboratory analysis

On each sampling day, we homogenized all the water in each microcosm (800 mL) and concentrated in 100 mL through a plankton net with a 10µm mesh. Each sample was fixed with alkaline lugol, formaldehyde buffered with calcium borate and sodium thiosulphate (Sherr & Sherr, 1993), and stored in an appropriate place. Subsequently, we used a common optical microscope (model Olympus CX31) to count and identify the testate amoebae.

At each sampling, we used 9 mL to count the organisms, using a Sedgewick-Rafter slide (with a volume of 3 mL). The 9 mL were separated into 3 aliquots containing 3 mL each. Of these 3 aliquots, 2 of them were quantitative analyses, by homogenizing the sample and superficial collection of water. Finally, the last aliquot was used for qualitative analysis of the sample, using the water contained in the bottom of the sample, enabling the identification of species that were sedimented at the bottom of the container with the water. We identified the testate amoebae found at the lowest possible taxonomic levels (genus or species) using specialized literature (Gomes & Souza, 2008; Lansac-Tôha et al., 2000, 2001, 2007; Velho et al., 2003).

2.3. Statistical analysis

The difference in testate amoebae species richness and abundance was assessed: i) within each treatment over time, and ii) between each treatment at a given time using a Two-way ANOVA (Two-Way Analysis of Variance). The assumptions of normality and homoscedasticity were tested (considering as significance values of $p > 0.05$); with this, homoscedasticity and normality were achieved, allowing the analysis of variance to be carried out. When significant differences were found, we performed Tukey's post-hoc test (HSD).

To check for differences in species composition between treatments, we conducted the non-metric multidimensional scaling (NMDS) ordination method with the Bray-Curtis distance measure being applied to the species abundance data matrix. Then, we used a permutational multivariate analysis of variance (PERMANOVA; Anderson, 2005) to test for statistical differences in the observed compositional patterns, using sampling times and treatments as factors, compared to each other. Considering that at the beginning of the experiment many replicates of each treatment did not record any species of testate amoebae (which made analyses unfeasible), the difference in species composition was analyzed only from day 19 of the experiment (T19). We took this time as a basis because only from this time onwards were the results viable and significant. A species accumulation curve was made to observe the arrangement of species among the treatments.

All analyses were performed with the R 4.1.2 software (R Core Team, 2024) using the *vegan* (Oksanen et al., 2017) and *tidyverse* packages (Wickham et al., 2019). The *vegan* package assists in the description of ecological analyses such as diversity analysis, dissimilarity analysis, and community ordering (Oksanen et al., 2013), while the *tidyverse* package was used to handle the data and *ggplot2* was employed to perform the graphics (Wickham, 2016). All Two-Way ANOVA results with p-values < 0.05 were considered significant.

3. Results

We recorded thirteen species of testate amoebae, belonging to five different families, with the family Centropyxidae being the most species-rich, with five species (Table 1). Among all the species recorded, 10 of them occur in all the treatments analyzed. However, the species *Euglypha polylepis*, *Euglypha acantophora* and *Sphenoderia australis chardezi* were only observed in specific treatments (Table 1). Considering all treatments, it was observed through a species rarefaction a low stabilization of species richness from T19 (Figure 3).

We observed an increase in richness (Figure 4) and abundance (Figure 5) of the testate amoebae throughout the time, with more notable values starting at day 12. The accumulation of testate amoebae species over time, for the different vectors, was considerably consistent, since new species were recorded at each sampling time, and more species were added in treatments with biological vectors.

Table 1. List of testate amoebae species found in each treatment during the experiments.

Family	Species	TREATMENTS			
		W	W+ O	W+A	W+A+O
Difflugidae	*Netzelia gramen*	*	*	*	*
	Difflugia minuta	*	*	*	*
	Difflugia sp.	*	*	*	*
Centropyxidae	*Centropyxis ecornis*	*	*	*	*
	Centropyxis cassis	*	*	*	*
	Centropyxis platysoma	*	*	*	*
	Centropyxis minuta	*	*	*	*
	Cyclopyxis sp.	*	*	*	*
Euglyphidae	*Euglypha polylepis*		*	*	*
	Euglypha acantophora	*		*	*
Trinematidae	*Trinema lineare*	*	*	*	*
	Trinema enchelys	*	*	*	*
Sphenoderidae	*Sphenoderia australis chardezi*				*

W= Wind, W+O= Wind + Odonata, W+A= Wind + Amphibian, W+A+O= Wind, Amphibian and Odonata. The asterisk (*) represents the presence of the species in that experimental treatment.

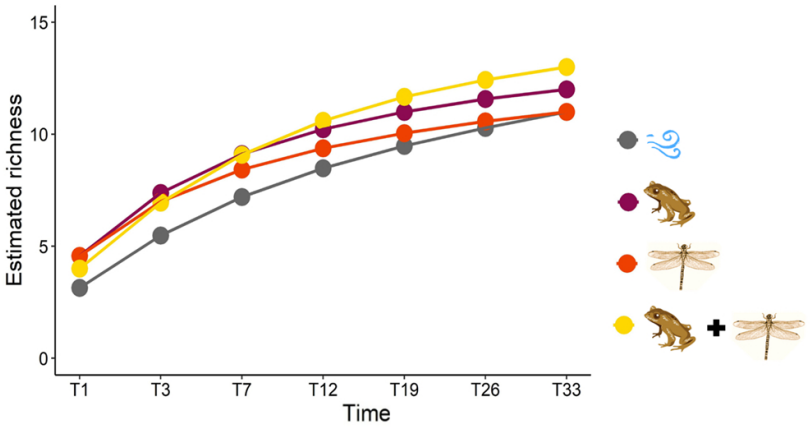

Figure 3. Rarefaction curve of estimated richness of testate amoebae species containing all treatments as a function of sampling time. Gray= Wind, Orange= Wind + Odonata, Purple= Wind + Amphibian, Yellow= Wind, Amphibian and Odonata.

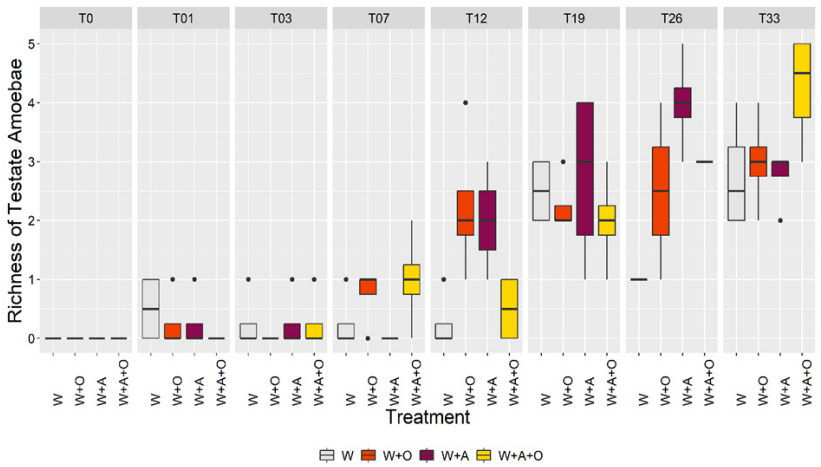

Figure 4. Variation of the richness of the testate amoebae community for each time of the experiment, where the central line denotes the mean values. W= Wind, W+O= Wind + Odonata, W+A= Wind + Amphibian, W+A+O= Wind, Amphibian and Odonata. The bars represent, respectively, the smallest and largest value within 1.5 times the interquartile range below the percentage limits and the points indicate outliers in treatments.

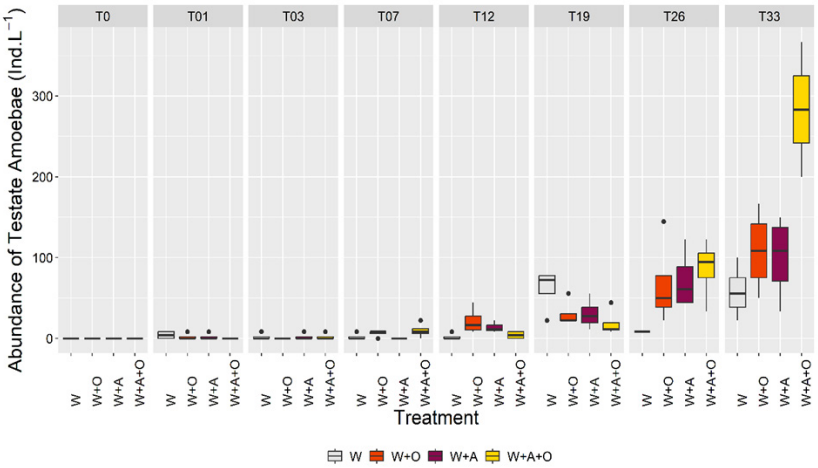

Figure 5. Variation of the abundance of the testate amoebae community for each time of the experiment, where the central line denotes the mean values. W= Wind, W+O= Wind + Odonata, W+A= Wind + Amphibian, W+A+O= Wind, Amphibian and Odonata. The bars represent, respectively, the smallest and largest value within 1.5 times the interquartile range below the percentage limits and the points indicate outliers in treatments. Abundance data were logarithmized.

We observed significant variations in species richness primarily attributed to time, further influenced by the specific treatment types (Table 2). Notably, the most pronounced differences were observed at T12 and T33. The Tukey HSD *post-hoc* test highlighted these differences across nearly all treatments. The largest significant variations were found between the 'Wind + Odonata' (highest values) and 'Wind ' only vector treatments, underscoring the temporal impact on species richness.

For the abundance of testate amoebae (Table 3), the patterns were very similar to those described for richness. Such variations in abundance became also more expressive after time T12, considering that in the first days of the experiment the values of this attribute were extremely low (Figure 5).

We observed significant differences in testate amoebae abundance between treatments only at T33 (p<0.05). The results of Tukey's *post-hoc* test (HSD) showed significant differences for the treatments of the Wind, Amphibian, and Odonata vectors over the dispersal performed by the respective vectors separately. The results of Tukey's *post-hoc* (HSD) test evidenced that these differences, as well as for richness, were significant, especially between the initial and final days of the experiment.

We found a similar species composition of testate amoebae among the vectors (Figure 6). Regarding sampling periods, we found a marginally significant difference at times T19 and T33 for the treatment of Wind, Amphibian, and Odonata vectors together (Table 4). Differently for the PERMANOVA analyses of the sampling days between treatments, no significance was obtained in the results of the differentiations of treatments between the final days of the experiment. Thus, the community attributes are repeated among the treatments, with no dominance among the biological vectors and with species similarities in the samples (Table 5).

4. Discussion

We found in our experiment 13 species already found in other studies in the Paraná River, its left bank, and its floodplain (Lansac-Tôha et al., 2000, 2001, 2007; Velho et al., 2003). The first testate amoebae observed at time 1 (T1) was the species *Netzelia gramen*, which symbiotically associates with Zoochlorella algae, providing energy produced by photosynthetic processes, which may influence the distribution of the group at lower levels of the food chain (Gimenes et al., 2004). Also, this species possesses a protective carapace. Its presence at the beginning of the experiment was not expected since the first experimental days were characterized only by the presence of bacteria in the microcosms. The algae-testate amoebae symbiosis may have facilitated the propagation and presence of this species in the experiment, which may suggest the presence of this species in the later sampling days. It was unexpected that a protist species would occur at T1 of the experiment in a treatment made to observe wind dispersion, since it has a low chance of occurrence. This may have been possible due to the great

Table 2. Two-Way Analysis of Variance (Two-Way ANOVA) for differences in species richness between treatments, at each time point. Variation in the richness of the Testate amoebae community for each time of the experiment.

Two-way ANOVA					
RICHNESS	**Df**	**SS**	**MS**	**F value**	**P**
Treatments	3	36.01	12.01	2.351	0.078
Time	6	726.3	121.06	23.69	**<0.001**
Treatments × Time	18	234.7	13.04	2.552	**0.002**
Residuals	81	413.9	5.11		

p values indicate significance at p<0.05, Df = degrees of freedom, SS = sum of squares, MS = mean square.

Table 3. Two-Way Analysis of Variance (Two-Way ANOVA) for differences in species abundance between treatments, at each time point. Variation of the abundance of the testate amoebae community for each time of the experiment.

Two-way ANOVA					
ABUNDANCE	**Df**	**SS**	**MS**	**F value**	**Pr(>F)**
Treatments	3	6632	2211	2.833	**0.043**
Time	6	161742	26957	34.542	**<0.001**
Treatments ×Time	18	71260	3959	5.073	**<0.001**
Residuals	79	61653	780		

p values indicate significance at p<0.05, Df = degrees of freedom, SS = sum of squares, MS = mean square, F value = ratio of mean squares, Pr = P value.

Table 4. Results of the permutational multivariate analysis of variance (PERMANOVA) performed with 999 permutations using the attributes of the testate amoebae community in relation to the times.

PERMANOVA BETWEEN TIMES								
	TREATMENTS							
Times	**W**		**W+O**		**W+A**		**W+A+O**	
	F	***p***	**F**	***p***	**F**	***p***	**F**	***p***
T19-T26	0.1679	0.427	0.1966	0.347	0.1524	0.464	0.1549	0.364
T19-T33	0.1482	0.517	0.1545	0.417	0.1294	0.635	0.2233	0.052
T26-T33	0.1402	0.551	0.0680	0.790	0.1282	0.577	0.207	0.640

W= Wind, W+O= Wind + Odonata, W+A= Wind + Amphibian, W+A+O= Wind, Amphibian and Odonata.

Table 5. Results of the permutational multivariate analysis of variance (PERMANOVA) performed with 999 permutations using the attributes of the testate amoebae community in relation to the treatments.

PERMANOVA BETWEEN TREATMENTS						
	TIMES					
Treatments	**T19**		**T26**		**T33**	
	F	***p***	**F**	***P***	**F**	***p***
W-W+A	-0.277	1	1.3086	0.226	0.1456	0.933
W-W+O	0.7889	0.556	1.0229	0.457	0.2834	0.804
W-W+A+O	1.1705	0.537	1.2309	0.371	1.1815	0.404
W+A-W+O	0.4705	0.926	1.495	0.26	-0.1979	0.968
W+A-W+A+O	0.8048	0.636	1.0415	0.464	0.7644	0.488
W+O-W+A+O	1.0257	0.486	0.2165	0.909	0.4697	0.779

W= Wind, W+O= Wind + Odonata, W+A= Wind + Amphibian, W+A+O= Wind, Amphibian and Odonata, F value = ratio of mean squares, Pr = P value.

randomness of dispersion by air current or by a sample contamination process through other entry routes. The high richness and abundance of individuals from the Centropyxidae may be related to its high dominance in lotic environments (Velho et al., 1999), such as the site of our experiment. The site of our experiment was very close to the Paraná River, allowing the entry of new propagules of testate amoebae from this environment.

Previous studies have shown that the colonization dynamics of microorganisms in different environments generally follow a predictable model, i.e. an ecological succession of species, the primary phase of which generally exhibits the following pattern: initially, bacteria colonize, followed by diatoms and flagellated autotrophic protists (usually within ten days), then ciliated protists and, finally, larger species with a broader feeding spectrum,

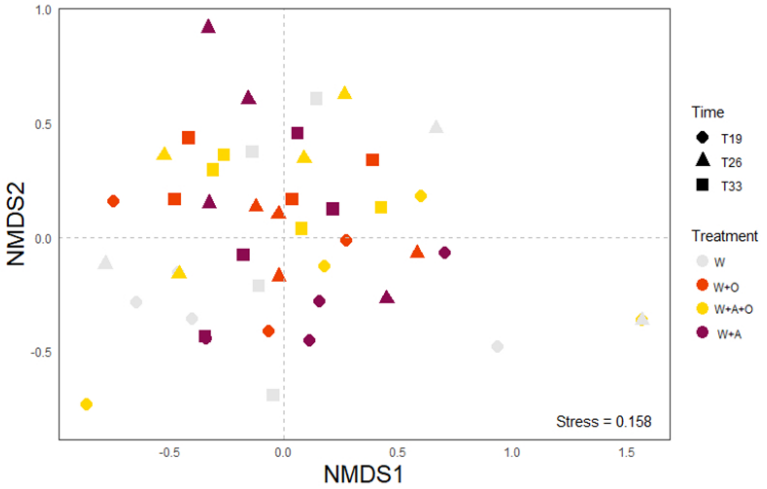

Figure 6. Sorting by the Non-Metric Multidimensional Scaling (NMDS) method based on the composition of the Testate amoebae community between different times and treatments. W= Wind, W+O= Wind + Odonata, W+A= Wind + Amphibian, W+A+O= Wind, Amphibian and Odonata.

such as testate amoebae (Zhang et al., 2012, 2013; Wang et al., 2016). This pattern, observed by the increase in testaceous amoeba species from the subsequent times of the experiment, may corroborate this, being caused by the colonization of the new environment and the success of dispersal mediated by different vectors between sites, which can occur via the passive dispersal of cysts in water (Padial et al., 2014) or the action of biological vectors, such as wind transport over long distances and between different aquatic ecosystems (Allen, 2007). The recorded presence of small omnivorous testate amoebae, such as those from the genera *Euglypha* and *Trinema*, suggests that feeding habits may influence smaller species to develop better, stabilizing in the environment over the course of the sampling times, assimilating available food. This was observed in the current study, where omnivorous species from the described genera established themselves in the microcosm from the midpoint of the experiment onwards. The presence of aquatic bacteria, algae, fungi, and rotifers can serve as food for testate amoebae, for instance, those from the genera *Centropyxis*, *Difflugia*, and *Euglypha* (Ndayishimiye et al., 2023), which were found in this study. Concurrently, testate amoebae from the genera *Trinema* and *Euglypha*, being of small size, can be carried by the wind, which is why they were present in all experimental treatments.

According to our findings, biological vectors represent an important route for the dispersal of testate amoebae. Several studies corroborate the importance of amphibians as dispersal vectors for freshwater invertebrates (Bohonak & Whiteman, 1999; Lopez et al., 2005; Vanschoenwinkel et al., 2008). Since amphibians have a large body area and mucous skin, providing some moisture, more species are able to support transport through this vector, due to their frequent contact with the aquatic environment, transporting the propagules to other habitats (Bohonak & Whiteman, 1999; Vanschoenwinkel et al., 2008).

Odonata also showed an important role in the dispersion of testate amoebae. This is due to the frequent contact of these organisms with different aquatic ecosystems, allowing the capture and/or deposition of propagules (Parsons et al., 1966). Thus, Odonata, which is a good flyer when adult, represents an important component of passive dispersal of freshwater microorganisms (Russo et al., 2006), making them a potential vector for determining the structure of these communities. The fact that they are flying organisms increases the possibility that propagules are dispersed over long distances (Rundle et al., 2007). Cochak et al. (2021) also showed in their study that Odonata played an important role in the transport of many species of ciliated protists, and some species were exclusively transported by this vector.

The fact that the species composition was relatively similar among the treatments ('Wind', 'Wind + Amphibian', 'Wind + Odonata' and 'Wind + Amphibian + Odonata'), especially after T26, suggests that the vectors are probably dispersing the same species at certain times in the succession. This repetition of species in the final stages may be due to the animal vectors coming into contact with different environments, taking the testate amoeba

species from one place to another; in addition, the wind alone can carry these species between sites (Wanner et al., 2015).

It is possible that the dispersal of testate amoebae species is facilitated by their high abundance in the various habitats of river-floodplain systems (Velho et al., 2013; Negreiros et al., 2017), which may serve as a source of propagules. In general, the observed patterns of species composition, abundance, and richness also support the hypothesis that community attributes vary temporally and across vectors (Cochak et al., 2021). The temporal pattern observed for species richness, with an increase in values at the end of the experiment, may be due to the greater effect of ecological succession, increasing the richness of species between treatments and showing the appearance of species as time increases. It can be assumed that there is an increase in the amount of food between the final treatments, which increases the abundance and richness of species.

The higher abundance and species richness values and differences in species composition for treatments containing the combination of all the vectors ('Wind + Amphibian + Odonata') may be related to the high dispersal rates, which ultimately facilitated the process of species colonization and establishment (Leibold et al., 2004). When propagule pressure is very intense, the chances of species colonizing an environment increase (Incagnone et al., 2015). Thus, the entry of new species can quantitatively impact community dynamics through a factor known as mass effects (Diniz et al., 2021). Although the spatial scale of vector sampling was limited, the high number of viable propagules suggests that the dispersal of testate amoebae mediated by biological vectors entails a dispersal of species into local habitats, and increased richness and abundance of organisms is possible if the experiment is continued by increasing the sampling time (and, if possible, increasing the presence of new vectors). In general, water bodies attract a significant number of vector organisms and play a significant role in the colonization of microorganisms through biological vectors.

In addition to dispersal as a determining factor in structuring the community, biotic factors, such as biotic interactions, can have a strong influence on group dynamics. Over time, especially in the final stages, the phenomenon of dispersal can be characterized by fewer new propagules arriving. This is due to since there is already an established community in the environment, together with occurrence of biotic processes, such as species interactions (Godsoe et al., 2015; Zhong et al., 2017). The water aging over the experimental period, may have influenced the change in the pattern of species distribution to wind-mediated dispersal treatments, with communities changing over time (Gonzalez et al., 2012). Ecological selection caused by abiotic and biotic factors can control microbial fitness through changes in community composition and relative species abundance (Ndayishimiye et al., 2023). Stochastic processes, species interactions, or priority effects may affect the diversity of testate amoebae, altering the number of individuals or species in the community (Wang et al., 2020). In natural ecosystems, each site can act as a distinct environmental filter due to its physical, chemical, and biological specificities. This can influence the responses of individuals arriving there and reduce the effect of dispersal, resulting in the selection of species adapted to these conditions (Diniz et al., 2021). This mechanism may explain our findings, especially towards the end of the experiment. The arrival of zooplanktonic organisms may be structuring the community differently in the final time treatments, being able to prey on protists or compete with them for the same food resource (Oliveira et al., 2019).

5. Conclusion

Our first prediction that the presence of biological vectors would lead to an increase in abundance and richness and a change in the species composition of testate amoebae compared to wind-mediated dispersal alone was partially accepted since we found higher values of community richness and abundance in treatments associated with vectors, in particular, with all associated vectors ('W+A+O'). In the study, local dispersal dynamics were intense when mediated by wind in combination with biological vectors such as amphibians and Odonata ('W+A+O'). This partially corroborates the second and third hypotheses, which predicted that in treatments that included both biological vectors, changes in the attributes of the testate amoebae community would be greater and more efficient, especially in the final days of the experiment. Functional characteristics of testate amoebae, such as forms of resistance, are efficiently dispersed to new environments by the vectors analysed in this study. Finally, it is worth mentioning that the wind, as a physical vector acting in the species dispersal, has a great influence on random dispersion, a

characteristic to be considered in future studies that address this topic.

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Data availability

Research data analyzed in this study is not publicly available by any mean.

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