

Geographical, environmental, and biotic constraints define the spatial distribution of *Diaphanosoma* species (Cladocera)

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ABSTRACT

Species distribution is a combination of ecological, historical, stochastic, and evolutionary mechanisms, and is a process that has been severely impacted by anthropogenic activities. Freshwater zooplankton is adequate to assess that combination because it groups cosmopolitan and endemic species. We hypothesized that the spatial distribution of *Diaphanosoma* species is defined by a complex interaction between factors such as spatial limitation, limitation of environmental conditions, and ecological conditions. We georeferenced the occurrence of

Diaphanosoma in Brazil to study the potential distribution of the species, preference of ecoregions, environmental features associated with *Diaphanosoma*, and their co-occurring patterns. Five species of *Diaphanosoma* are widely distributed in Brazil. *D. spinulosum* and *D. birgei* were widely distributed while *D. fluviatile* and *D. polypspina* had a more restricted distribution. The occurrences of *Diaphanosoma* species were shown to have an association with factors such as the total concentrations of nitrogen and phosphorus, pH and, temperature, except in the case of the *D. brevireme*. Our results show that geographic, environmental, and biotic filters can drive the spatial distribution of species of the genus *Diaphanosoma*. Therefore, the distribution and spatial occurrence of these species depend on dispersal capacity and spatial restrictions, suitability of the abiotic environment, and ecological interactions.

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Key words: environmental filters, competition, ecoregions, congeneric species, biogeography.

Authors' contributions: all the authors made a substantive intellectual contribution. All the authors have read and approved the final version of the manuscript and agreed to be held accountable for all aspects of the work.

Conflict of interest: the authors declare no potential conflict of interest.

Funding: none.

Availability of data and materials: all data generated or analyzed during this study are included in this published article.

Acknowledgements: we thank Tatiane Mantovano by suggestions in the manuscript and Universidade Federal do Sul da Bahia. This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Received: 7 September 2022.

Accepted: 19 January 2023.

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Advances in Oceanography and Limnology, 2023; 14:10848

DOI: 10.4081/aio.2023.10848

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Introduction

The distribution of wild life species on Earth is heterogeneous and requires ecologists and biogeographers to formulate hypotheses to explain their patterns. Understanding the spatial and temporal distribution of species as well as identifying the factors that restrict their area of occurrence is fundamental to biogeography, ecology, conservation, and ecosystem management (Brambilla *et al.*, 2009; Thuiller *et al.*, 2009; Heino *et al.*, 2015). However, elucidating the mechanisms that organize the species of a taxonomic group in space and time is complex (Pither, 2007). Species distribution is often described as a combination of several ecological (*i.e.*, resource availability, environmental heterogeneity, and biological interactions), historical (*i.e.*, climatic variations), stochastic, and evolutionary (*i.e.*, evolutionary time and diversification) mechanisms (Willig *et al.*, 2003).

Theoretical models have shown that the success of a population in a region depends on its dispersion skills to surpass geographical barriers, the environmental, and physical and chemical conditions that provide physiological support for survival, and their performance with respect to inter-specific interactions (Krebs, 2009). Time is fundamental in the establishment of a species, regardless of scale. On a macroscale, intercontinental biogeographic patterns have historically been

defined by the movement of continents, glaciation events, and speciation rates (Whittaker *et al.*, 2001). At the mesoscale, geomorphology is responsible for barriers and environmental conditions in areas of survival (Poff, 1997), which prevent gene flow between populations. Lastly, on a microscale, communities of organisms are outlined as a result of both interspecific (*i.e.*, predation, parasitism, and competition) and abiotic interactions within local habitat patches (Cohen & Shurin, 2003).

Some researchers have argued that anthropogenic changes over the last 500 years (Anthropocene) have reshaped global communities (Ellis, 2019) and modified the biogeography of taxonomic groups (Dirzo *et al.*, 2014). This effect is particularly severe in aquatic ecosystems as the potential for organism distribution is determined by hydrological connectivity, the degree of isolation of these environments (Torrente-Vilara *et al.*, 2011; Fletcher *et al.*, 2018), and environmental conditions, which have been severely impacted by human activities during this period (Best, 2019). This has promoted ecological barriers that filter species and prevent gene flow between populations.

Some mechanisms associated with the spatial distribution of aquatic microorganisms include: dispersal ability and species sorting (Finlay, 2002), historical factors and body size (Martiny *et al.*, 2006), historical events and contemporary environment (Wang *et al.*, 2019), monopolization of resources resulting from the priority effect (De Meester *et al.*, 2002), neutral dynamics based on the ecological equivalence of species (Hubbel, 2001), and trophic interactions in the aquatic food web (St-Gelais *et al.*, 2021). No exclusive hypothesis explains the distribution of aquatic invertebrates because of the evolutionary complexity of distinct groups, leading to a variety of behavioral responses to environmental stresses. The zooplankton community in inland waters, for example, is primarily composed of three large groups (Rotifera, Cladocera, and Copepoda), which, despite sharing the same habitat and being subject to similar environmental pressures, have different evolutionary histories. In this context, discriminating the mechanisms responsible for the spatial distribution of species and/or zooplankton groups is pivotal to better understand their ecology and biogeography.

Freshwater zooplankton represent a group that was historically considered as dominated by cosmopolitan species (Xu *et al.*, 2009), following the assumption of ‘everything is everywhere’ (Baas-Becking, 1934). According to Martiny *et al.* (2006), microorganisms have enormous dispersal capabilities that rapidly erase the effects of past evolutionary and ecological events. However, cosmopolitanism has been replaced by continental/regional endemism (Xu *et al.*, 2009), which believes that ‘everything is everywhere: but the environment selects’ (Finlay, 2002). Recently, several studies have demonstrated the importance of environmental selection on zooplankton at the meso and macroscales (Viana *et al.*, 2014; Perbiche-Neves *et al.*, 2019; Sodr e *et al.*, 2020). However, studies on the importance of biotic interactions to represent patterns of zooplankton species distribution are rare.

To understand the processes related to the distribution of zooplankton species, we analyzed the spatial distribution of species of the genus *Diaphanosoma* (Sididae/Diplostraca/Branchiopoda/Arthropoda), a representative genus of plankton found in tropical regions, to unveil the factors that organize the distribution and define characteristics of the niche of the

Diaphanosoma species. Species of this genus have traits that permit easy identification at the intermediate level in the Cladocera taxonomy, thereby reducing identification errors and improving the quality of a biogeographic survey. *Diaphanosoma* is characterized by the absence of a rostrum, fornicis, or ocellus. The first antennae are small, truncated, with terminal olfactory arrows and with a thin flagellum. Their second antennae have a bisegmented dorsal branch and a ventral section with three segments, and basal spine are absent in the post-abdomen region (Elmoor-Loureiro, 1997). Although the *Diaphanosoma* species are mostly limnetic, some species have been found in vegetation zones and bromeliads (Korovchinsky, 1992; Fuentes-Reines *et al.*, 2012).

Despite the wide distribution of *Diaphanosoma*, local co-existence between three or more congeneric species is rare. Thus, we hypothesized that the spatial distribution of *Diaphanosoma* species is defined by a complex interaction between spatial limitation, environmental conditions, and ecological interactions. We predicted that: i) a spatial difference is present in the distributions of *Diaphanosoma* species; ii) some species show regional distribution limited by space; iii) some species have a spatial distribution limited by environmental characteristics; and iv) a few species are excluded from the environment because of competitive interactions with species of the same genus.

Materials and Methods

Database

Diaphanosoma were mapped using a georeferenced database to verify their distribution. We used data from studies conducted in the Brazil, a continental scale country with high variability in aquatic habitats. The Brazilian Government has divided the main hydrographic landscape into twelve hydrographic regions in accordance with the 32/2003 resolution of the National Council of Hydric Resources (Conselho Nacional de Recursos Hídricos, CNRH); the highest hydrographic region (Amazonas and Parana ) are among the major rivers of the Earth.

The occurrence of the species was located by referencing papers published in national and international journals whose study on Cladocera was confined to Brazil. The papers were extracted from databases, such as Scielo (<http://www.scielo.br/>) and Web of Science (portal.isiknowledge.com). The last record was a paper published in June 2020 (*Supplementary Material A*).

A total of 779 occurrence records were found (geographic coordinates), with at least one *Diaphanosoma* species in Brazil, which is referred to as the Total Base (TB) data. In addition to the georeferencing of occurrences, we also recorded limnological variables, such as water temperature, pH, dissolved oxygen, total nitrogen, and total phosphorus, from various studies.

After georeferencing, we identified clusters of records with similar spatial information or studies from the same area of occurrence, but from different years that often overestimate the occurrences in that region. This sampling bias was resolved by dividing the map of Brazil into a $0.5^\circ \times 0.5^\circ$ grid (hereafter termed Base of Distribution, BD), and only one record was marked in each cell. The spatial range of the species was analyzed using the latitudinal and longitudinal amplitudes

estimated using the BD. To estimate the potential distribution of *Diaphanosoma*, we created a geospatial model containing data on its presence and absence. We also modelled the distribution of each species using the kriging method, with an interpolation of the inverse distance power, as defined by Gräler *et al.* (2016). The extrapolation of spatial data allows biologists to use statistical models and simulations, such as Species Distribution Modelling (SDM), which correlates the occurrence of species due to spatial autocorrelation or climatic-environmental data to identify favorable environmental conditions for target populations (Pearson *et al.*, 2007; Franklin, 2010).

We also used the Bioclim model (Nix, 1986; Booth *et al.*, 2014; Dou *et al.*, 2022) to analyse the potential distribution using the bioclimatic data such as variables for temperature and precipitation (Table 1). However, this procedure was not efficient for our data, as it does not reflect the current distribution of *Diaphanosoma*. Potential distribution maps were generated using R Software version 4.1.0 (R Core Team, 2021) with the gstat package and its 'predict' function (Gräler *et al.*, 2016).

Data analysis

First, the potential distribution of *Diaphanosoma* species in Brazil (hypothesis i) was compared through a visual analysis of the maps, based on BD. The frequency of occurrence of each species in a hydrographic region (hypothesis ii) was calculated by overlying the BD of all species with the BD of each species. Hydrographic regions were used as surrogate ecoregions. This procedure provided the percentage presence of each species in a hydrographic region with respect to the total occurrence of the species. The occurrence frequency was categorized into the following groups: $\leq 20\%$, $\leq 40\%$, $\leq 60\%$, $\leq 80\%$, and $\leq 100\%$.

Generalized additive models (Hastie & Tibshirani, 1990) were used to define whether the distribution of some

Diaphanosoma species responds to environmental characteristics (hypothesis iii). In all models, the presence and absence of the species was considered as a response variable using a logit link function. Water temperature, pH, dissolved oxygen, total nitrogen, and total phosphorus were used as predictor variables in the model. To find the best fit, we examined the significance test and plot between environmental characteristics and occurrence probability.

Finally, the effect of competition on the distribution of *Diaphanosoma* species (hypothesis iv) was assessed using the C-scores Index (Stone & Roberts, 1990), which represents the average number of checkerboard units for each unique species pair (Gotelli & Rohde, 2002). The higher the C-score value, the lower is the number of species co-occurring in an assembly. To check if the distribution pattern was different from a random distribution, a null model was constructed with a non-sequential algorithm for binary matrices that preserved the site (row) frequencies, but used column marginal frequencies as probabilities of selecting species (Gotelli & Rohde, 2002). We applied the probabilistic model of species co-occurrence that uses an algorithm to calculate the observed and expected frequencies of co-occurrence between each pair of species (Veech, 2013), using the R package cooccur (Griffith *et al.*, 2016).

Results

Five species of *Diaphanosoma* were recorded in Brazil: *Diaphanosoma birgei* (Korineck 1981), *Diaphanosoma brevireme* (Sars 1901), *Diaphanosoma fluviatile* (Hansen 1899), *Diaphanosoma polyspina* (Korovchinsky 1982), and *Diaphanosoma spinulosum* (Herbest, 1967). *D. spinulosum* and *D. birgei* were widely distributed in Brazil, ranging from -1° to -32.5° S latitude and -35° to -68.5° W longitude (Figure 1a and 1b). *D. fluviatile* and *D. polyspina* were limited from -42.5° to -63.5° W (Figure 1d and 1e).

D. fluviatile and *D. brevireme* occurred in eight hydrographic regions, whereas *D. polyspina* occurred in four of the twelve hydrographic regions in Brazil (Figure 2). In general, *D. fluviatile*, *D. brevireme*, and *D. polyspina* showed limited occurrences in the hydrographic regions.

The frequencies of occurrence of *D. spinulosum*, *D. birgei*, *D. fluviatile*, and *D. polyspina* (Figure 3) were associated with environmental variables (Table 2, *Supplementary Material A*). An increase in pH favored the occurrence of *D. spinulosum* (positive coefficient), but did not favor the occurrence of *D. polyspina*. The frequencies of occurrence of *D. birgei* and *D. fluviatile* decreased with an increase in the concentration of total phosphorus. The frequency of occurrence of *D. fluviatile* was negatively associated with water temperature. Lastly, the frequency of occurrence of *D. brevireme* showed a low fit with environmental variables (*Supplementary Material A*).

The co-occurrence analysis identified that the checkerboard patterns were higher than that expected at random (observed $C_s=0.85$; simulated $C_s=0.60$; $p<0.001$). Pairwise analysis between species identified negative relationships between the five species that occur in Brazil (Figure 4) except for *D. brevireme* and *D. fluviatile*. In addition, no positive relationships were observed.

Table 1. Bioclimatic variables used in Bioclim model.

Code	Variables
BIO1	Annual Mean Temperature
BIO2	Mean Diurnal Range (Mean of monthly)
BIO3	Isothermality
BIO4	Temperature Seasonality
BIO5	Max Temperature of Warmest Month
BIO6	Min Temperature of Coldest Month
BIO7	Temperature Annual Range
BIO8	Mean Temperature of Wettest Quarter
BIO9	Mean Temperature of Driest Quarter
BIO10	Mean Temperature of Warmest Quarter
BIO11	Mean Temperature of Coldest Quarter
BIO12	Annual Precipitation
BIO13	Precipitation of Wettest Month
BIO14	Precipitation of Driest Month
BIO15	Precipitation Seasonality
BIO16	Precipitation of Wettest Quarter
BIO17	Precipitation of Driest Quarter
BIO18	Precipitation of Warmest Quarter
BIO19	Precipitation of Coldest Quarter

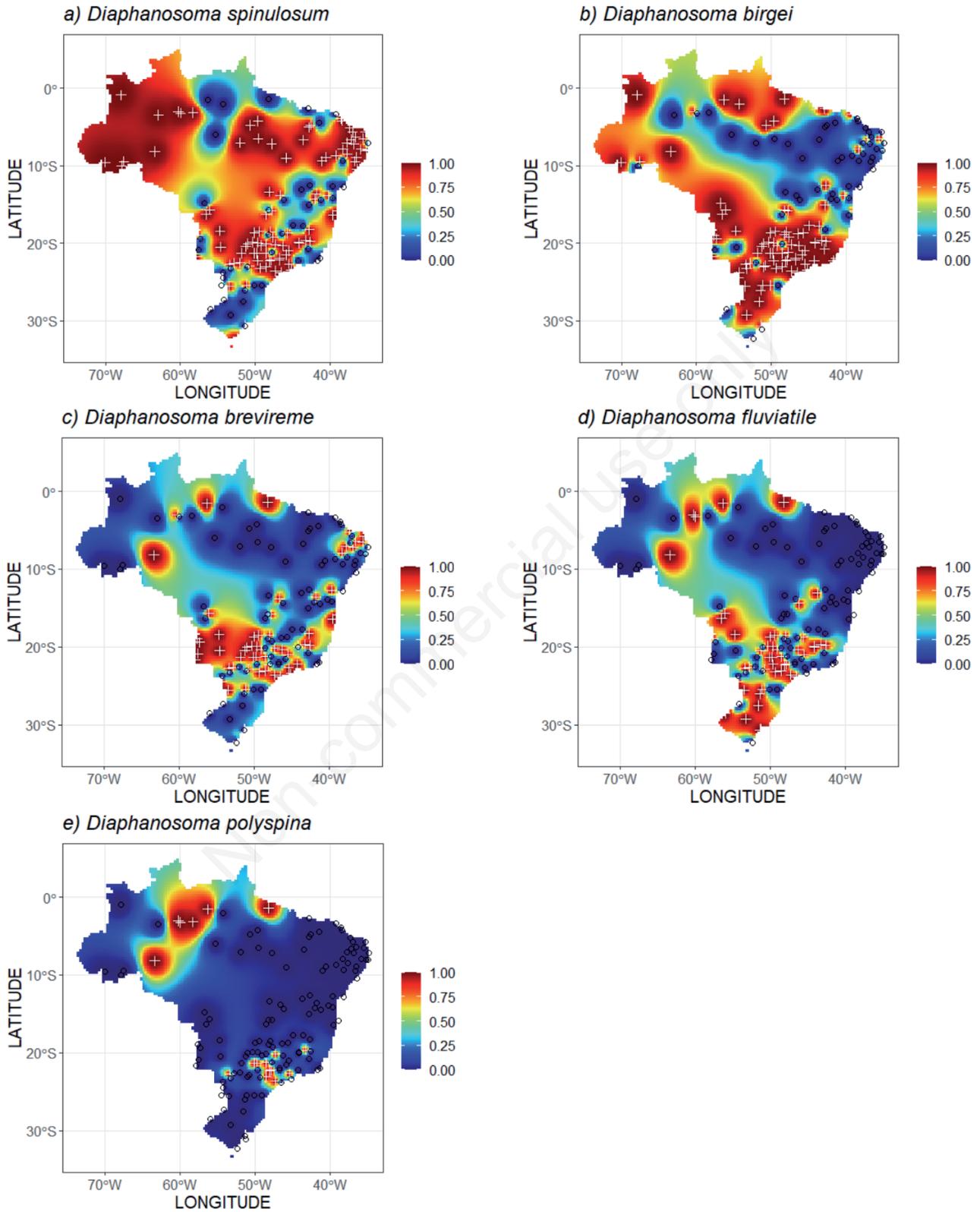


Figure 1. Distribution of species of the *Diaphanosoma* genus as recorded in Brazil: presence (+) and absence (o); heat map based on the spatial autocorrelation of the species.

Discussion

Our results showed that geographic, environmental, and biotic filters determine the spatial distribution of the *Diaphanosoma* species. This indicates that the distribution and spatial occurrence of these species depend on dispersal capacity, spatial restrictions, suitability of the abiotic environment, and ecological interactions (St-Gelais *et al.*, 2021), corroborating previous heuristic models that frame assemblage rules and species pools (Poff, 1997; Rahel, 2002).

In this study, *D. spinulosum* and *D. birgei* displayed a wide spatial distribution, corroborating the hypothesis of the high dispersal capacity of zooplankton and that some species are extremely widespread, probably because of the plasticity of these species to environmental variation. This phenomenon can be associated with genetic diversity as the population variability of *Diaphanosoma* is associated with environmental gradients (Liu *et al.*, 2021). *D. fluviatile* and *D. polyspina* showed a narrower spatial distribution, suggesting that their distribution is a consequence of the joint influence of spatial limitation, preference for hydrographic regions, and ecological interactions. Brazil has a large continental extension (latitudinal range varying from ca. 5° in the north to ca. 33° in the south) and a high diversity of aquatic ecosystems, each with varying environmental conditions, which may have resulted in this distribution pattern.

These aquatic environments are subject to different averages and temperature variations: sites close to the equator are subject to higher temperatures that are stable over time, while those further south fall under a sub-tropical climate, and are subject to lower, but more variable temperatures. Under this spatial and environmental range, *Diaphanosoma* have been recorded in

several aquatic environments: reservoirs, lakes, and perennial and intermittent rivers. Some *Diaphanosoma* species prefer small tropical water bodies with intermittent regimes, including

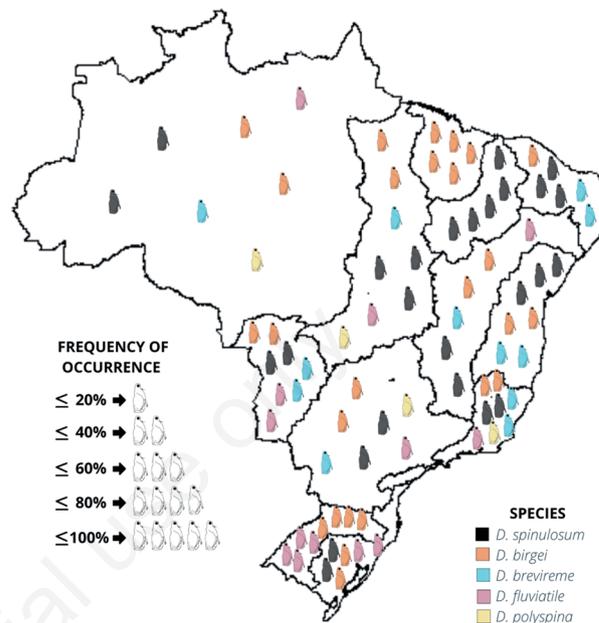


Figure 2. Graphic representation of the occurrence frequencies of *Diaphanosoma* species as recorded in Brazilian hydrographic regions. The frequency of occurrence was categorized as: $\leq 20\%$, $\leq 40\%$, $\leq 60\%$, $\leq 80\%$, and $\leq 100\%$.

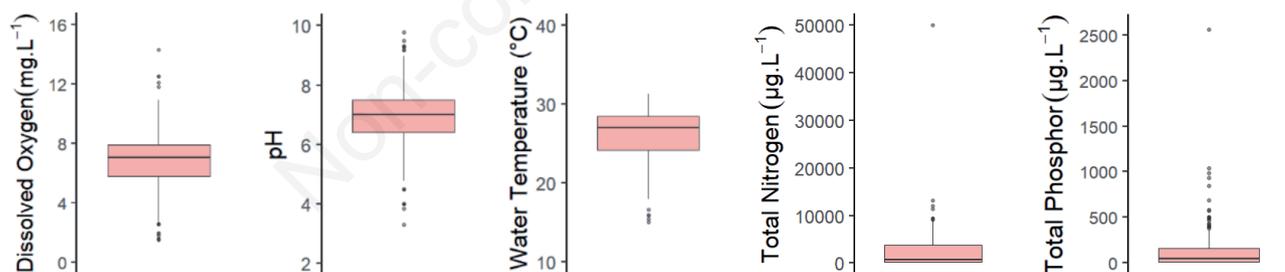


Figure 3. Statistical summary of the limnological variables associated with *Diaphanosoma* distribution in the Brazil.

Table 2. Relation between environmental variables and the frequency of occurrence of species of the genus *Diaphanosoma*, as recorded in Brazil. The models are a result of the smoothed logistic regression.

	Dissolved oxygen		pH		Temperature		Total nitrogen		Total phosphorus	
	b	R ²	b	R ²	b	R ²	b	R ²	b	R ²
<i>D. spinulosum</i>			0.56	0.05						
<i>D. birgei</i>									-0.70	0.17
<i>D. brevireme</i>										
<i>D. fluviatile</i>					-0.19	0.07			-0.47	0.09
<i>D. polyspina</i>	-0.51	0.09	-0.77	0.09						

b, angular coefficient; R², coefficient of determination only significant coefficients (p<0.001) were shown.

temporary ones (Korovchinsky, 2016), and inhabit warm and food-rich water. This adaptation may confer a decisive advantage to life in tropical waters (Han *et al.*, 2011). *D. spinulosum* is a good representation of this adaptive capacity as it is widely distributed and is characteristic of plankton in tropical regions (Dumont *et al.*, 2021). This species is common in northeastern Brazil, which is composed of many intermittent rivers subject to high temperatures and ecological restrictions (Nobre *et al.*, 2020).

Environmental conditions were also important in determining the spatial distributions of *D. spinulosum*, *D. birgei*, *D. fluviatile*, and *D. polyspina*. Ecological barriers were significant for Cladocera distribution (Korovchinsky, 2006) as the species have tolerance limits (minimum and maximum values) with respect to environmental conditions and resources (Shelford's Law of tolerance), which limits their occurrence and establishment. Water temperature, dissolved oxygen, pH, and total phosphorus were all associated with species distribution, showing that aquatic conditions and/or eutrophication are also important drivers for the spatial distribution of *Diaphanosoma* species.

D. spinulosum occurs in areas with higher pH values, primarily in northeastern Brazil where aquatic environments are naturally subject to reduced inlet water-to-evaporation ratios, which increases lake eutrophication (Menezes *et al.*, 2019). However, these circumstances decreased the occurrence frequencies of *D. fluviatile* and *D. polyspina*, which were recorded in less eutrophic environments with lower water temperatures. The frequencies of *D. birgei* and *D. fluviatile* also decreased with increasing eutrophication. In general, *Diaphanosoma* prefers warm regions (Matveev & Gabriel, 1994), but recent surveys have also suggested suitability for a subtropical climate with warm waters and cold winters (Dumont *et al.*, 2021). Moreover, they have high energetic requirements (Sarma *et al.*, 2005) and high bacteria-feeding efficiency, and in some situations prefer smaller food particles (Brendelberger, 1991).

Our records suggest that the preference for temperature ranges is species-specific: *D. spinulosum*, *D. polyspina*, and *D. brevireme* prefer the tropics, whereas *D. fluviatile* and *D. birgei* prefer the subtropics. These results also have important implications with

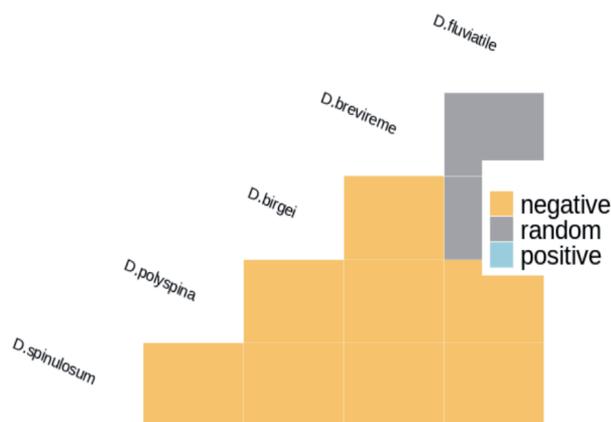


Figure 4. Pairwise species co-occurrence matrix of the *Diaphanosoma* species in Brasil.

respect to preparing for the ongoing global warming, as an increase in eutrophication is expected with an increase in temperature, which may favor the distribution of *D. spinulosum* in Brazil, but restrict the distribution of other species.

Interspecific interactions can also determine the spatial distribution of species; the exclusive competition might have contributed to the spatial distribution of some species of *Diaphanosoma* in Brazil. In the co-occurrence analysis, the checkboard pattern was higher than that expected at random, suggesting that the presence of one species, on an average, is associated with a low probability of others occurring in the same region at the same time. This corroborates our prediction of the low probability of three or more species of *Diaphanosoma* occurring together under the same conditions. Under our experimental conditions: i) species of the genus *Diaphanosoma* were competitively excluded by *Ceriodaphnia* because of direct competition for resources (exploratory competition), leading to adult individuals perishing because of limited resources (Matveev & Gabriel, 1994); ii) *D. excisum* showed competitive superiority over *D. dubium* in monopolizing available resources (Liu *et al.*, 2021). These results suggest that zooplankton species that can better exploit resources dominate the environment and exclude other species from it.

Thus, two mechanisms can explain the checkboard pattern of the various species of *Diaphanosoma*. i) Response to environmental conditions: due to the spatial extent of this study as well as the variety of environmental conditions intrinsic to the region studied, species may respond antagonistically to the effects of the environment. For example, *D. spinulosum* reacted positively to changes in pH, whereas *D. polyspina* responded negatively. ii) Competitive exclusion: some species may have the ability to exclude other species that could potentially occupy the same ecological niche. The pairwise co-occurrence analysis identified that a negative relationship existed between *D. spinulosum* and *D. birgei* and with other *Diaphanosoma* species.

The competition between species of *Diaphanosoma* can be justified by behavioral, morphological, or physiological features, which improve fitness and offer competitive advantages in the exploration of the environment, and consequently, lead to niche differentiation. The main morphological differentiation between these species is the presence of duplication, thorn patterns on the edges of the carapace, and the number of arrows in the P6 endopodite (Elmoor-Loureiro, 1997; Dumont *et al.*, 2021). However, the morphological conservatism through time (Jurassic–Cretaceous) suggests that natural selection cannot further refine the structural adaptation of these animals to their environments (Dumont *et al.*, 2021). Thus, behavioral and/or physiological adaptations to explore specific conditions may be important in defining which species of *Diaphanosoma* inhabits a region at a specific time. In addition, *D. brevireme* was limited by interaction only due to competition, as it occurs in several hydrographic regions (although at a low frequency) and does not respond significantly to environmental variations.

Phylogeographic estimates with cladocerans and rotifers indicated that the strong priority effect and local selective regime can structure populations with independent evolutionary trajectories (Xiang *et al.*, 2011; Liu *et al.*, 2021), owing to the rapid growth and local adaptation in new habitats (De Meester *et al.*, 2002). Additionally, deeper phylogenetic patterns are known to be consistent with vicariance scenarios linked to continental

(Adamowicz *et al.*, 2009) and intracontinental (Xu *et al.*, 2009) fragmentation. Hydrographic basins and ecoregions also have a selective role on the distribution of aquatic species (Poff, 1997), including zooplankton (Sodré *et al.*, 2020). In South America, several fish species are endemic to watersheds (Albert & Reis, 2001), and biogeographical patterns in multiple species are frequent in large-scale analyses (Lansac-Tôha *et al.*, 2020). This indicates that allopatric divergence is also likely an important mechanism of diversification for invertebrates inhabiting continental waters (Adamowicz *et al.*, 2009; Xu *et al.*, 2009).

Limitations of this study include: i) different databases were used to test the hypotheses owing to the absence of standardized information; ii) therefore, we did not partition the sources of variation in this study; iii) there are no identified confounding effects among filters; iv) the absence of information related to top-down control that can affect the cladoceran distribution; and v) the lack of information about competition with other cladocerans. However, these limitations do not invalidate the results and discussions presented in this study, but present a challenge for future perspectives.

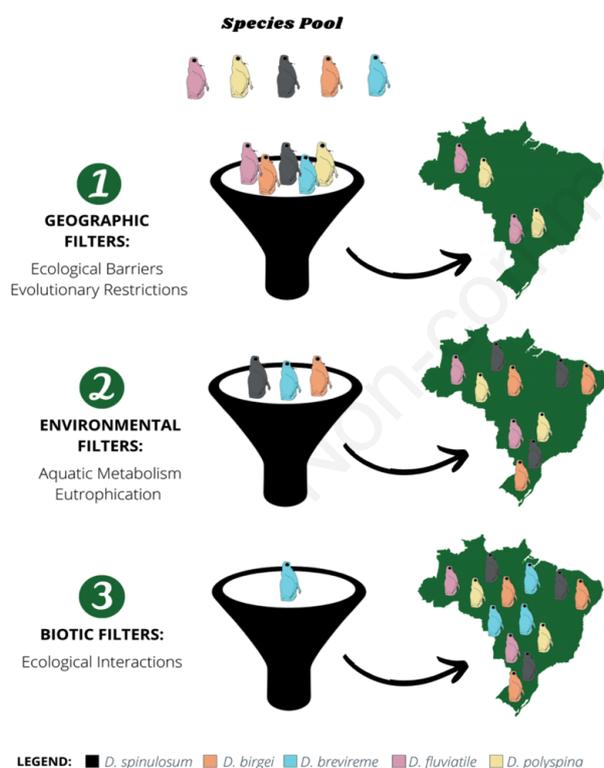


Figure 5. Spatial distribution of *Diaphanosoma* species recorded in Brazil and their associations with different geographical and ecological filters. Spatial filters (geographical and evolutionary constraints) define the spatial distribution of *D. fluviatile* and *D. polypina*. Environmental conditions define the spatial distribution of *D. spinulosum* and *D. birgei* species. Ecological interactions were important to define the spatial distribution of the *D. brevireme* specie.

Conclusions

In this study, we showed that spatial and ecological filters are crucial for the spatial distribution of species of the genus *Diaphanosoma* (Figure 5). Spatial filters (geographic constraints) defined the spatial distribution of *D. fluviatile* and *D. polypina*. Environmental conditions were important for *D. spinulosum* and *D. birgei*, whereas ecological interactions were significant for *D. brevireme*. Thus, the distribution of *Diaphanosoma* species in Brazil may be a combination of founding historical events responsible for the colonization of habitats, historical adaptations that allowed species to survive in a variety of situations (such as tolerance to a wide temperature range and production of resistant eggs), ecological unpredictability defined by the randomness of dispersion but resulting in the priority effect and the monopolization of resources, and ecological responses to environmental variations underlying the quality of the environment (*e.g.*, metabolism and eutrophication). This combination of factors suggests that the fitness of aquatic invertebrates is a function of their morpho-physiological and behavioral traits that allow their populations to be dynamic, opportunistic, resilient, and resistant to the variability of environmental conditions. Studies describing the spatial distribution mechanisms of zooplanktonic species at macroscales although rare in literature, are fundamental for understanding biogeographic patterns and the behavior of species under the various anthropic impacts that natural systems have suffered and will continue to suffer in the future.

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