Oecologia Australis
29(1):1–17, 2025
http://doi.org/10.4257/oeco.2025.2901.01

A GLOBAL REVIEW ON THE KNOWLEDGE GAPS OF BENTHIC FORAMINIFERA OF COASTAL LAGOONS

Pierre Belart[1], *Fabíola Keesen*[2], *Lazaro Laut*[1], *Carla Bonetti*[3], *Marcos S. L. Figueiredo*[1] & *Maria Lucia Lorini*[1]

[1]Universidade Federal do Estado do Rio de Janeiro, Av. Pasteur, 458, Urca, CEP 22290-240, Urca, Rio de Janeiro, RJ, Brasil.

[2]Universidade Federal do Rio de Janeiro, Av. Carlos Chagas Filho, 373, Cidade Universitária - Ilha do Fundão, CEP: 21941-971, Rio de Janeiro, RJ, Brasil.

[3]Universidade Federal de Santa Catarina, *Campus* Universitário Reitor João David Ferreira Lima, s/nº, CEP: 88040-900, Trindade, Florianópolis, SC, Brasil.

Emails: pbelart@gmail.com (*corresponding author); fbkeesen@gmail.com; lazaro.laut@gmail.com; cbonetti@gmail.com; mslfigueiredo@gmail.com; mluc.lorini@gmail.com

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Abstract: In order to obtain a perspective of the distribution of benthic foraminifera across the globe, we present the first comprehensive data compilation on living foraminifera from coastal lagoons. Benthic foraminifera are an important bioindicator of water and sediment conditions group, but there is a relative scarcity of studies in coastal lagoons about this group. Our literature search (following the PRISMA methodology) retrieved 1,380 peer-review publications, of which 902 came from the Web of Science database and 478 from Scopus. We removed the duplicates (n = 469) and with the remaining 911 manuscripts we applied the exclusion criteria filters to get our final database composed of 49 studies used for this review. We recorded a total of 458 benthic species distributed in 17 countries. Our results reveal the existence of studies not homogeneously distributed in coastal lagoons around the globe (Wallacean shortfall) that limit in-depth understanding of the biogeography of this important bioindicator group, directly reflecting on another's knowledge gaps: the Linnean Shortfall (gap of species), Hutchinsonian shortfall (gap of abiotic tolerances) and Prestonian Shortfall (gap of populations dynamics).

Keywords: Benthic community, Biogeography, Coastal environments, Community ecology, Shortfalls in ecology, Species Distribution.

INTRODUCTION

Over the last decades, the biodiversity of marine and coastal systems has been experiencing unprecedented changes, mainly due to overexploitation, climate change and pollution (Herbert-Read *et al.*, 2022). This is worrisome since they are among the most important systems on Earth in terms of ecosystem services (Barbier, 2017; Ramírez *et al.*, 2022). Therefore, assessing the state of marine and coastal system resources, and predicting how these resources will change over time, space and levels of biological organization are tasks of increasing relevance (Benson *et al.*, 2021). Biodiversity indicator methods and knowledge integration become urgently required to evaluate and monitor marine and coastal ecosystems health, and to support suitable responses to underpin a sustainable future (Ramírez *et al.*, 2022).

Although the understanding of temporal biodiversity and spatial distribution on our planet represents one of the most important topics in biogeographic studies (Guisan & Rahbek, 2011; Whittaker *et al.*, 2013), there are several gaps for many biodiversity groups, especially for marine invertebrate organisms (Chen, 2021). Even though the knowledge gaps are continually filled by advancing studies in the most remote places on the world, and with the help of technology in improving methods to sample and quantify biodiversity, our knowledge is still incomplete in terms of how many species are there, and in how they are distributed on the planet (Pelletier *et al.*, 2022). Identifying and quantifying the shortfalls in our knowledge of biodiversity can help defining priorities for future ecological and evolutionary research, as well as for designing effective biodiversity monitoring, management, and conservation strategies (Freitas *et al.*, 2021). In the last years, the incompleteness of biodiversity knowledge has been formalized through the proposition of seven knowledge shortfalls, aiming to account for the lack of knowledge on the species richness (Linnean); the geographic distribution of species (Wallacean); species abundance and population dynamics (Prestonian); the evolution and phylogenetic relationships of species or lineages (Darwinian); species tolerances to abiotic factors (Hutchinsonian); species traits and functions (Raunkiæran); and biotic interactions (Eltonian) (Hortal *et al.*, 2015).

Occupying approximately 13% of the world's coasts (Barnes, 1980), coastal lagoons are landscape mosaics that are important for many biogeochemical processes and have high productivity, as well as a variety of habitats and rich biodiversity (Watson *et al.*, 2018). However, coastal lagoons are among the most threatened and stressed aquatic habitats due to different pressures such as uncontrolled urbanization, unconscious tourism, agriculture and aquaculture, pollution, eutrophication, as well as climate change, to which they are especially sensitive. These threats will impact the ecological integrity of these iconic and valuable systems in the future, and, for example, by destabilizing the trophic webs (Pérez-Ruzafa *et al.*, 2019b).

In the last decades, an important group has been widely used as a proxy to describe the quality of coastal environments: the Benthic Foraminifera (BF) (Frontalini *et al.*, 2011; Alves Martins *et al.*, 2013; 2015; Belart *et al.*, 2019; Laut *et al.*, 2021). To be easily and reliably applied, ecological indicators should be based on sensitive, diverse, worldwide widespread, abundant organisms, and BF have all these characteristics (Romano *et al.*, 2022). In addition, their tests preserved in the sediments allow past reconstruction of the marine environment and in-situ ground-reference conditions of environmental health changes over time (Dolven *et al.*, 2013; Romano *et al.*, 2022). Inhabiting all marine environments from shallow water intertidal regions to deep trenches (Mackensen & Douglas, 1989; Gooday, 2003), BF has been commonly used as descriptors of marine environments (Schönfeld *et al.*, 2012). BF distribution is controlled by many factors such as temperature, salinity, dissolved oxygen, sediment grain size or substrate (Murray, 1991, 2001, 2006; Belart *et al.*, 2019; Laut *et al.*, 2021, 2022), and changes in the nutrient amount (Gooday, 2003; Murray, 2006). Some species colonize the oxygen sediment interface, but others tolerate very depressed levels of oxygen and episodes of anoxic conditions (Bernhard & Gupta, 1999), having its distribution determined, above all, by the conditions of the sediment (Murray, 2006).

Although there has been a growing interest in BF, there are still many knowledge gaps, such as taxonomic and geographic inconsistencies (Murray, 2007), creating generalities and uncertainties with direct implications on topics such as biodiversity monitoring, management and conservation (Hortal *et al.*, 2015). This is particularly concerning for coastal lagoons because despite their ecological and socioeconomic importance, the scientific knowledge about BF (organisms at the base of the trophic chain) in these environments is scattered along the literature. Although Frontalini *et al.* (2011) have organized defined patterns of distributions of BF species from the coastal lagoons, no other study has been published with emphasis on identifying the main knowledge deficits for this group of organisms. A global review of such studies is currently lacking, which reinforces the need to improve our knowledge and research effort on this topic.

Therefore, our main goal was to assess the current state of knowledge on living BF in coastal lagoons all over the world. We present a systematic review of published peer-reviewed scientific literature on the topic to investigate global trends in terms of publication rate, research biases and knowledge gaps. Our database is the first comprehensive global compilation of detailed, voucher-based, occurrence records of BF from coastal lagoons. With this review we aim to contribute towards a better understanding of this important microfauna group and shed light on what we know and do not know about the distribution of BF from coastal lagoons. The present study also aims to complement the database of the existing Global Biodiversity Information Facility - GBIF and Ocean Biodiversity Information System - OBIS platforms, since these are not completely updated, especially in tropical environments.

MATERIALS AND METHODS

Literature review and data collection

We conducted a global systematic review of the available scientific literature on living benthic foraminifera in coastal lagoons, following the guideline of the Preferred Reporting Items for Systematic reviews and Meta-Analyses (PRISMA) statement (Page *et al.*, 2020) (Fig. 1). This method is designed to help systematic reviewers report transparently why the review was carried out, what the authors did and what they found. A literature search was performed in two databases, Web of Science' and Scopus to increase our research coverage. We performed searches by topic (article title, abstract, and keywords) for the strings foraminifer* and coastal lagoon* in both databases. The terminology "coastal lagoon" is widely used to define the shallow coastal body of water separated from the ocean by barrier islands, spits, or sandbars and are typically connected to the ocean through narrow inlets (Kjerfve, 1994). We searched for studies published until May 10, 2023, restricting our survey to articles published in indexed journals. First, we combined the search results from both platforms into a single database and removed duplicated studies, which reduced the results to 911 studies. To consolidate our database on living BF in coastal lagoons, we established the following criteria to exclude studies that: 1) were not conducted in coastal lagoons, 2) deal exclusively with fossil organisms, 3) were not conducted with benthic foraminifera, 4) deal with BF total assemblage (dead + living BF combined). Through the above steps, we identified 49 relevant studies (Fig. 1). From each of them we extracted the following information: full publication reference, publication year, study area, country, geographic coordinates of sampling sites, abiotic parameters associated with the species (such as temperature, dissolved oxygen, pH, etc), and the species list. All species names were standardized following the World Register of Marine Species (WoRMS), and the respective description year and authors were assigned to each species.

Data analysis

All geographic coordinates (sampling sites, lagoons and species occurrences) were converted to decimal degrees in WGS 84 Datum. To investigate geographical biases and gaps, the distribution of studies, lagoons and species occurrences data were analyzed through spatial overlay operations with the limits of the oceans, the marine biogeographic provinces and the ecoregions (Spalding *et al.*, 2007). We also estimated the frequency of occurrence (FO) based on the species distribution in each lagoon using the following equation: $FO = p \times 100/P$, where: (p) number of lagoons where the species occurs; (P) total number of lagoons sampled. We assigned species to the following six FO classes: rare, occurs in one site; very infrequent (>1 site - 10%); infrequent (>10 - 25%); frequent (>25 - 50%); very frequent (>50%); occurs in all sites (100%). To assess and visualize possible patterns of species composition among the biogeographic provinces, we performed Non-metric Multidimensional Scaling (NMDS) using the Jaccard similarity index calculated from the species presence–absence matrix. Data processing and statistical analyses were conducted in Microsoft Excel, PAST 4.03 *software*, and in the R Studio version 2022.07.00 with the vegan package. Spatial processing and analyses were undertaken using ArcGIS 10.6.

RESULTS

Our literature searches retrieved 1,380 peer-review publications, of which 902 came from the WoS database and 478 from Scopus. We removed the duplicates (n = 469) and with the remaining 911 manuscripts we applied the exclusion criteria filters to get our final database composed of 49 studies that were used for this review (Appendix 1, Studies).

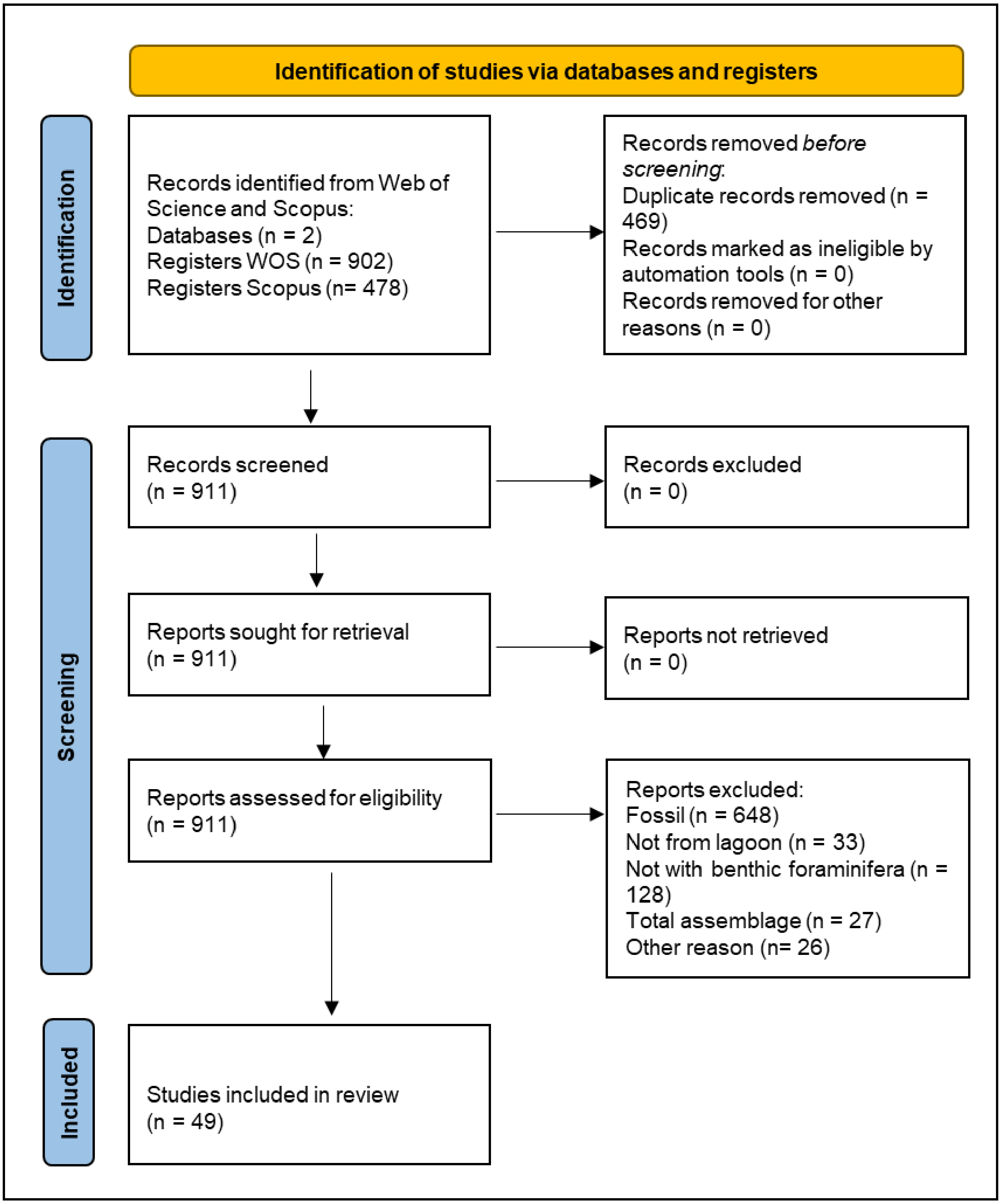

Figure 1. Flow diagram of the methodology and selection processes used in this systematic review, following the rules and templates of PRISMA (Preferred Reporting Items for Systematic Review) statement. Adapted from Page *et al.*, 2020.

Regarding the temporal publication trend on BF in coastal lagoons, we found that the first study was published in 1970 on the Abu Dhabi Lagoon (United Arab Emirates). From the next five decades (1970 – 2008) the scientific production remained restricted to a maximum of one publication per year (Fig. 2). In the last decade (2010 - 2022) an uneven increase in the scientific production can be observed. More

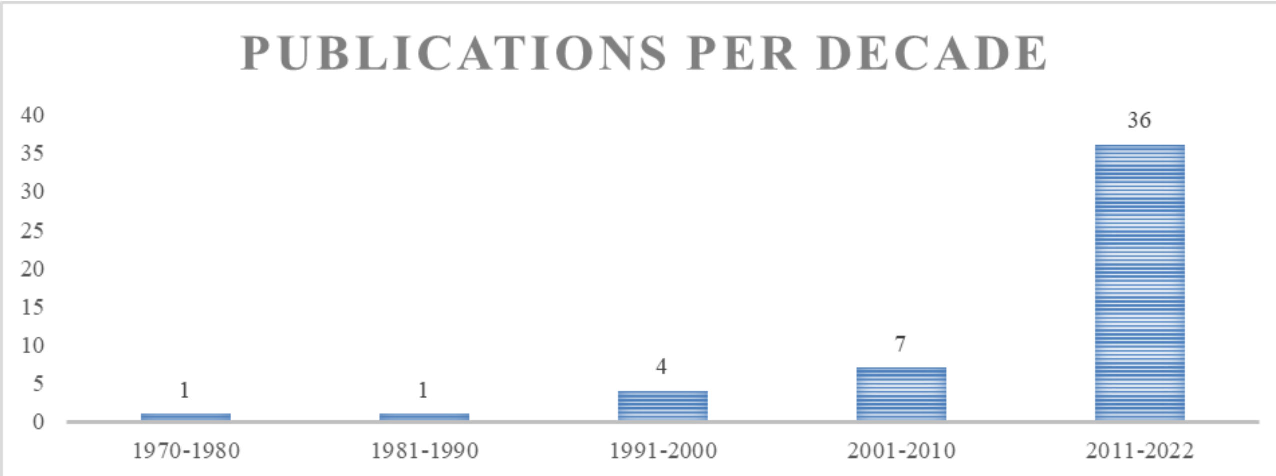

Figure 2. Number of publications on benthic foraminifera from coastal lagoons per decade.

than 70% of the studies on BF in coastal lagoons were published in this last decade (Fig. 2).

The 49 studies included in this review encompassed 48 coastal lagoons, distributed among 17 countries. Italy had the highest number of studies in lagoons (10) followed by Brazil (7) and Portugal (6) (Fig. 3). Some lagoons such as Venice Lagoon in Italy (6 published studies) concentrated the most studies in the country (Appendix 1, Studies).

The publications on coastal lagoons included in our review were distributed from tropical to temperate regions, along 8 from the 10 major oceanic regions (Baltic Sea, Indian Ocean, Mediterranean Region, North Atlantic Ocean, South Atlantic Ocean, North Pacific Ocean, South Pacific Ocean, and South China and Easter Archipelagic Seas) (Fig. 4). It was possible to identify studies carried out in 18 from the 232 ecoregions described by Spalding *et al.* (2007), and in 13 from the 62 provinces (Bay of Bengal, Cold Temperate Northwest Atlantic, Cold Temperate Northwest Pacific, East Central Australian Shelf, Lusitanian, Mediterranean Sea, Northern European Seas, Red Sea and Gulf of Aden, Somali/Arabian, Sunda Shelf, Tropical Northwestern Atlantic, Warm Temperate Northwest Atlantic and Warm Temperate Southwestern Atlantic). Half of the coastal lagoons studied in the present review was distributed in Mediterranean Sea province (50%) (Fig. 4).

In terms of abiotic parameters measured in the 49 studies included in this review, we found a low coverage of environmental variables. Only temperature, salinity and dissolved oxygen were the most frequently measured variables (Appendix 1, Complete).

Our literature review documented a total of 458 BF species in coastal lagoons, belonging to 12 different orders, of which the most common were Rotaliida, Miloliolida, and Lituolida (Fig. 5). Regarding the composition of the foraminifera test, 71% of them were of calcareous, being 44% hyaline and 27% with porcelaneous test (Fig. 6).

The analysis of the discovery trend for all the 458 BF species recorded in coastal lagoons showed that these species started to be described by the second half of the 18th century (1758) (Fig. 7). The discovery rate increased in two different periods, the first peak was identified between the interval of 1826 – 1850 in the 19th century, with 97 species described from which 91 were described by d'Orbigny. The second peak corresponded to the first half of the 20th century (1926 - 1950), with 87 species described from which 71 were described by Cushman. The discovery rate was stabilized by the end of the 20th century (1976 - 2000), and after that only one species was described during the two decades of the 21st century (*Resigella laevis*) (Fig. 7).

The estimated Frequency of Occurrence (FO) showed that more than half of BF species in coastal lagoons occurred in only 1 site (n = 252). About a third of species (n = 157) occurred in more than 10% of the sites, assigned as very infrequent (Appendix 1). Infrequent species occurring in 10-25% of the sites, totalized 38 species, while frequent species occurring in 25 - 50% of the sites, summed 9 species. Only *Ammonia tepida* and *Quinqueloculina seminulum* were the most frequent species along the coastal lagoons, classified as very frequent (Appendix 1). No species occurred at all sites (Appendix 1).

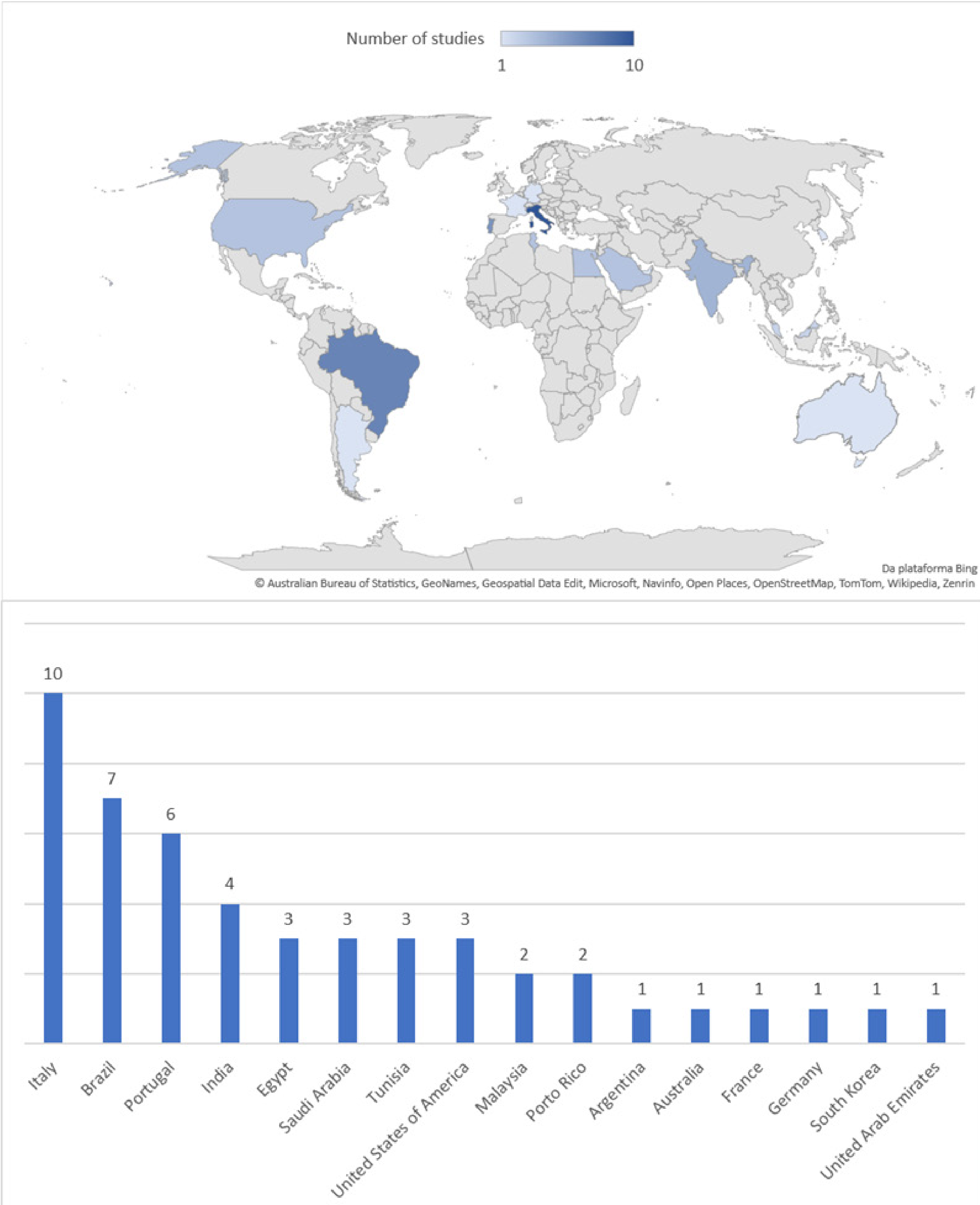

Figure 3. Number of studies on benthic foraminifera from coastal lagoons per country.

Regarding the distribution of the 458 BF species, we found that more than half occurred in only one province (62%) or one major oceanic region (63.5%) (Appendix 1). Almost a quarter of species occurred in only two provinces (n = 105; 23%) or major oceanic regions (n = 107; ~23%). About 7.5 % of species occurred in 3 provinces or 3 oceans at the same time, while 3% and 3.5% occurred in 4 provinces and 4 major oceanic regions, respectively. Less than 2% of species occurred at the same time

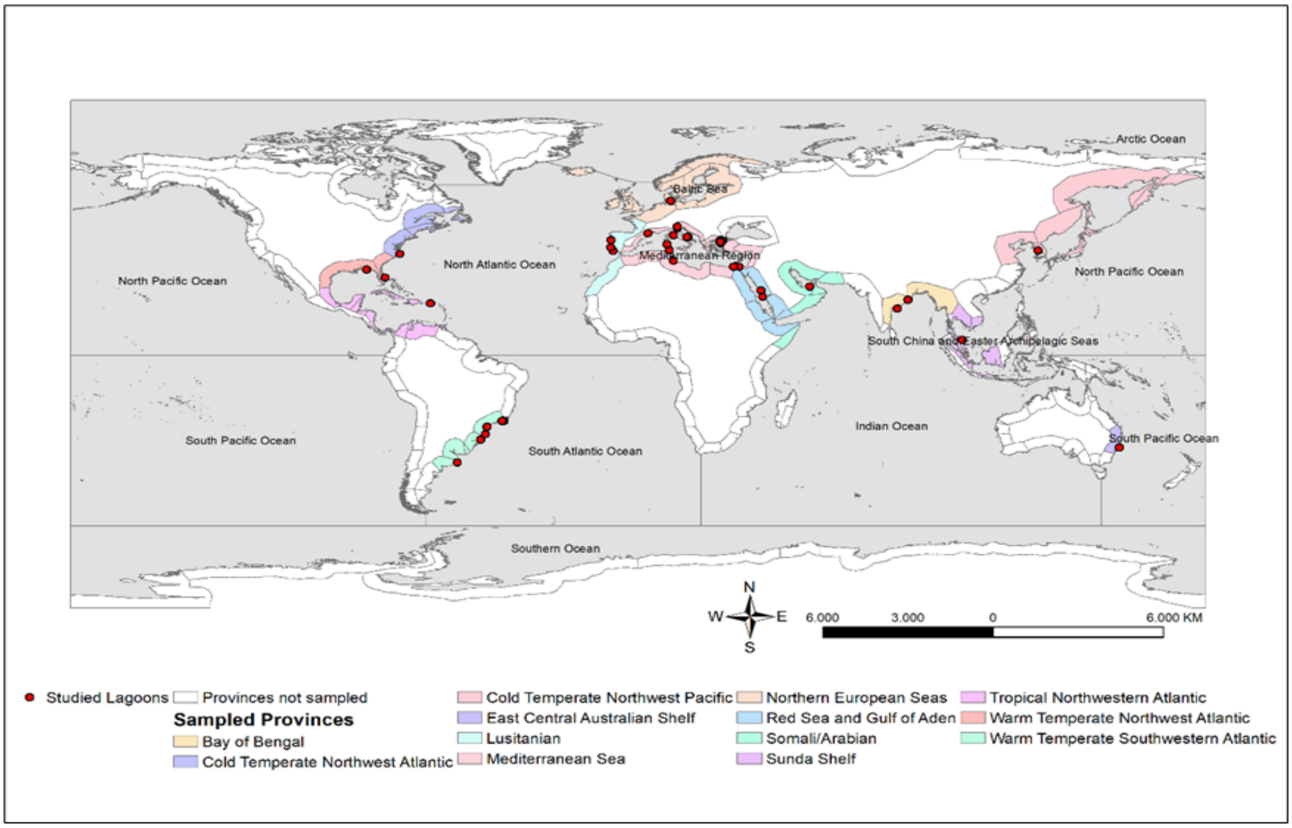

Figure 4. Distribution of the coastal lagoons included in the publications on benthic foraminifera from coastal lagoons. Marine biogeographic provinces according to Spalding *et al.* (2007) and world oceans are also represented.

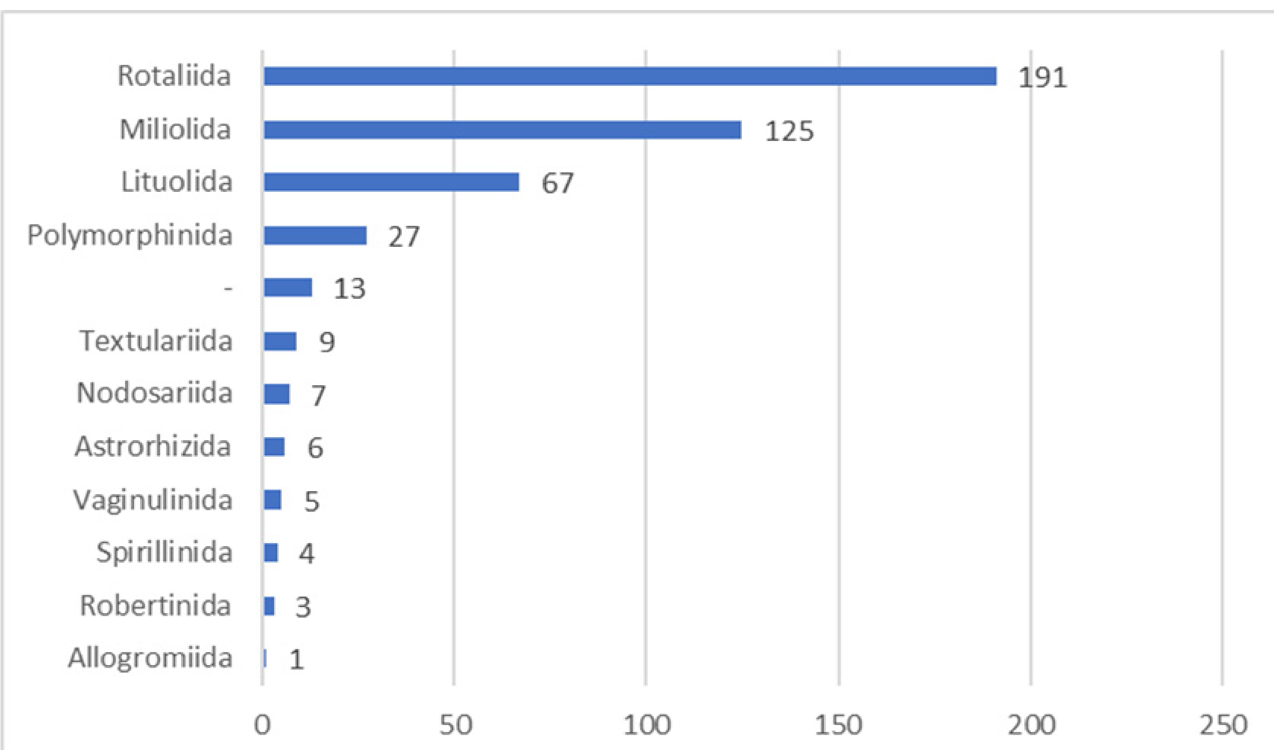

Figure 5. Number of species included in the publications on benthic foraminifera from coastal lagoons arranged by order.

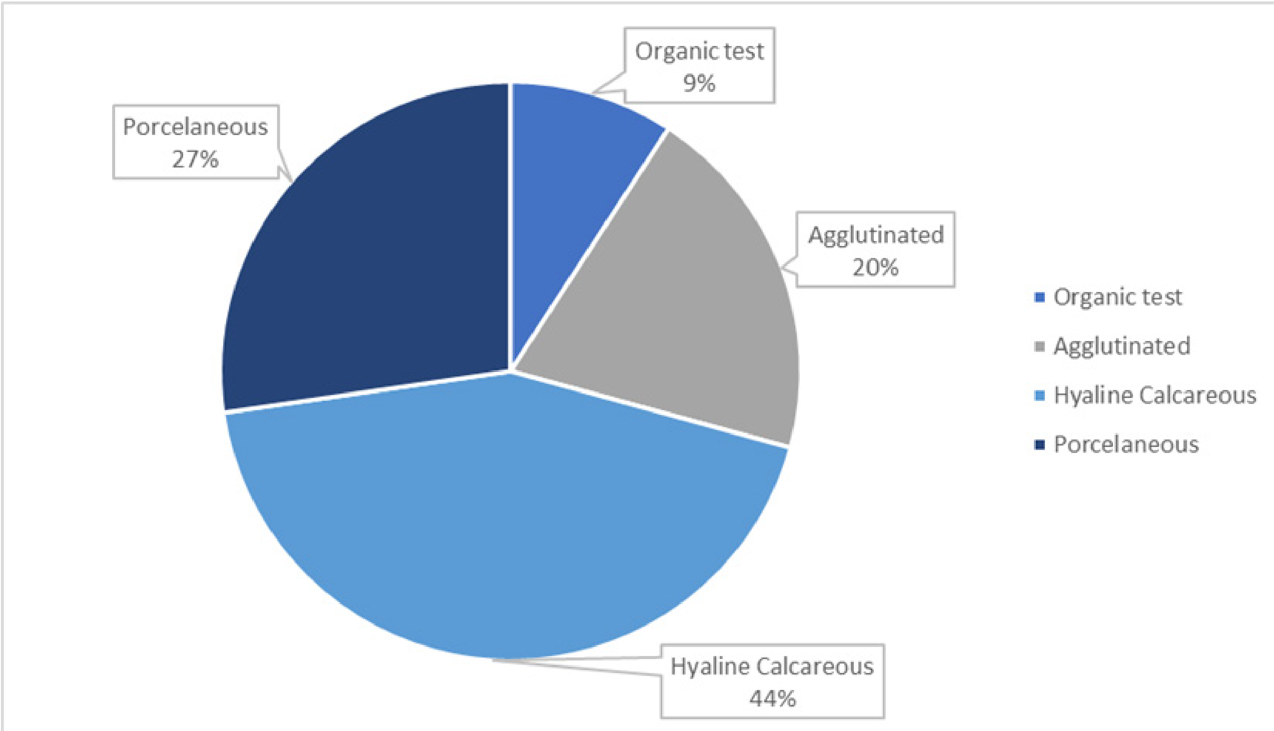

Figure 6. Species included in the publications on benthic foraminifera from coastal lagoons arranged by shell composition.

in 5 to 8 provinces or oceans. (Appendix 1). No species was found in all provinces and oceans, but *Elphidium excavatum*, *Miliammina fusca* and *Trochammina hadai* were founded in 6 of 8 major oceanic regions and *Miliammina fusca* was found in 8 of 12 provinces. *Ammonia tepida* was found in five major oceanic regions and seven provinces.

Benthic foraminifera species richness varied notably among coastal lagoons (mean 23.6, maximum 191 species). Considering the species richness per lagoon, our results show that the highest richness were found in the Ria de Aveiro (Portugal, with 191 living species) followed by Venice Lagoon (Italy, with 80 living species) and Bizerte Lagoon (Tunisia, with 69 living species). The lowest richness values were in the lagoons of Diremin and Enez Gala in Saudi Arabia (ranging from 1 to only 4 living species) (Appendix 1, Richness).

The NMDS using the data located within the "Provinces" tab in the Appendix 1 (stress = 0.22) showed that the southern Atlantic lagoons (Argentina and Brazil) formed a cohesive group with great similarity in species composition. Conversely, this pattern was not found in the Mediterranean region, where the stations were heterogeneously organised even within the same biogeographical province, this pattern was repeated in the Bay of Bengal province (Fig. 8). Lagoons in the provinces of East Central Australian Shelf, Cold Temperate Northwest Atlantic, Northern European Seas, Cold Temperate Northwest Pacific, Somali/Arabian, and Sunda Shelf were not organized in groups (Fig. 8).

DISCUSSION

Our results showed that, although foraminifera were considered one of the best-studied groups of marine meiofauna (Holzmann *et al.*, 2021), only 49 studies were carried out with living BF in coastal lagoons until to date. Hortal *et al.* (2015) suggest that deficiencies in biodiversity data can be grouped into seven main categories corresponding to the knowledge domains of systematics, biogeography, population biology, evolution, functional (trait-based) ecology, abiotic tolerances, and ecological interactions. Of the group of seven shortfalls, in the present study, it was possible to identify that BF from coastal lagoons are related to at least four of these shortfalls.

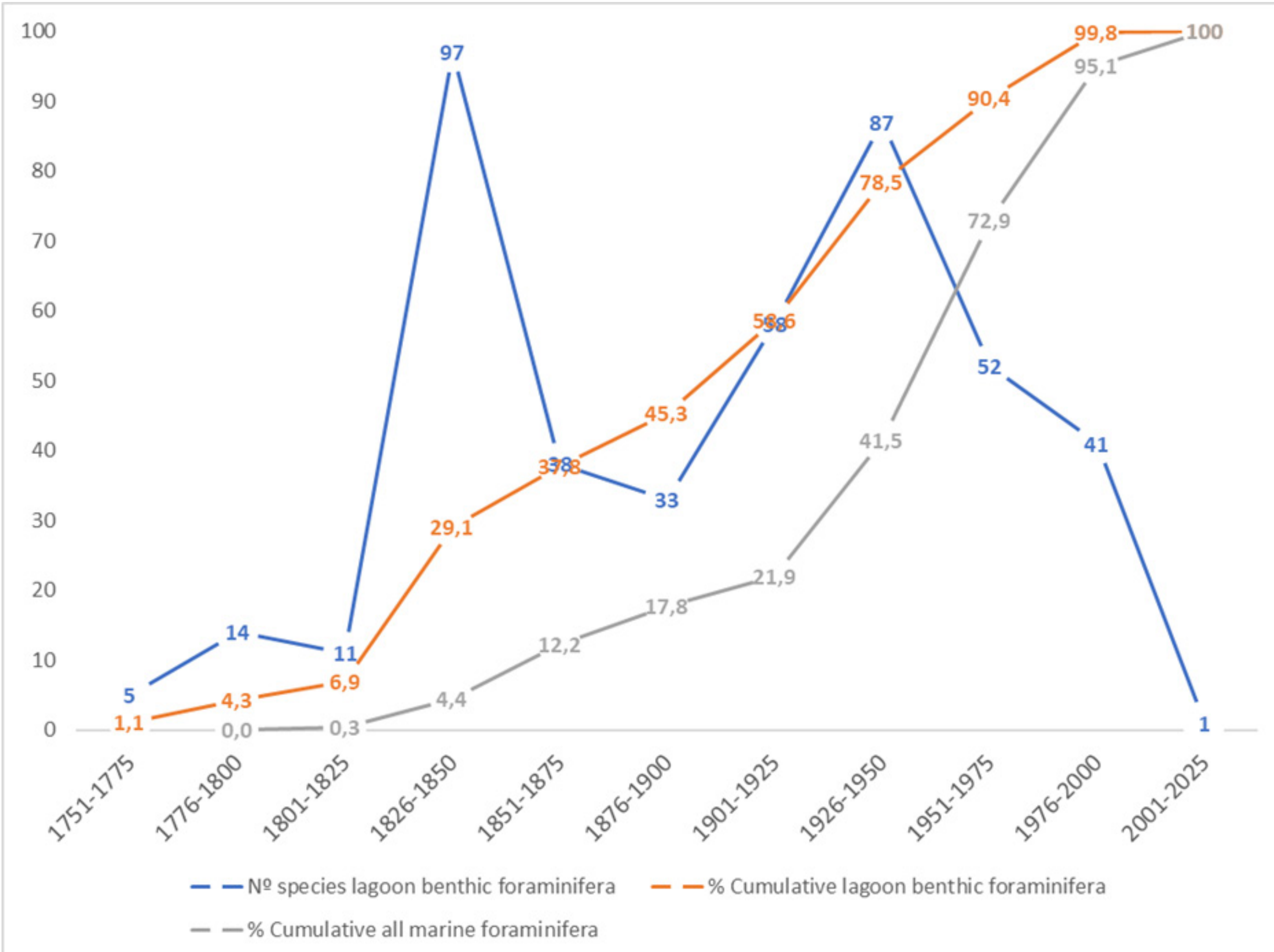

Figure 7. Number of coastal benthic foraminifera species described per 25 years interval. Cumulative number of all marine foraminifera are also represented, based on data from The World Foraminifera Database (https://www.marinespecies.org/foraminifera).

Linnean shortfall

The first problem that we found in the recorded data was that despite being frequently revised, there were only two major species description booms. The first peak being in the early 19th century is associated with the early naturalist phase and the beginning of optical microscopy, with emphasis on the important work of d'Orbigny. The second peak in the early 20th century is associated with the phylogenetic and geologic history – oil exploration phase, with highlight to the important work of Cushman, and the use of foraminifera by the petroleum industry as bioindicator of geological eras. In both periods, the foraminifera were observed under low-power magnification stereomicroscopes and species identified based only on their morphological characteristics including the shape, chamber arrangement, wall texture, presence of apertures, and other diagnostic features (Boltovskoy, 1981). Nowadays, advances on microscopic techniques (such as scanning electron microscopy, transmission electron microscopy, confocal laser scanning microscopy, and x-ray micro-computed tomography), as well as the use of Next-Generation Sequencing (NGS) techniques such as DNA metabarcoding, provide important insights into species identification, genetic diversity, and phylogenetic relationships (Pawlowski *et al.*, 2014). Genetic analyses are a powerful tool for revealing the evolutionary history and taxonomic position of species that cannot be detected by other means (Pawlowski *et al*, 2014). Some Rotalidae species like *Ammonia tepida*, *Ammonia parkinsoniana*, and *Elphidium excavatum* were found all over the world from tropical lagoons such as the Brazilian and Indian ones to the Mediterranean and Iberian lagoons such as Italian, Tunisian, and Portuguese ones (see Appendix 1). That brings us to the question, is it really the same species in such distant places for single-celled organisms? Pawlowski *et al.* (1995) investigated morphotypes of *Ammonia beccarii* from different locations and concluded that at least three of these belong to different species, possibly Ammonia tepida, *Ammonia parkinsoniana* and *Ammonia beccarii*. They suggest that the postulate that ecophenotypic adaptation is the only explanation for morphological variability in *Ammonia beccarii* is difficult to accept. However, environmental influence on morphological variations in foraminifera species should never be completely excluded. So, following Pawlowski *et al.* (1995), we also assume that any foraminiferal species can develop morphological characteristics which will resemble those of other closely related species and that can lead to a biased taxonomic identification. Frontalini *et al.* (2020) analyzed the foraminiferal diversity using the traditional morphology-based approach and 18S rDNA-based metabarcoding and said that the two methods give congruent results once taxonomic composition of the morphological and metabarcoding datasets are very different. This is another study that reinforces our questions: Was it the same species? Do the morphological similarities lead researchers to erroneously identify as the same species? Only with more effort in applying the new approaches will be able to solve these questions.

Riddle *et al.* (2011) suggest that the Linnean shortfall is more severe for organisms that are smaller in size, niche width, or distributional range and which are less complex or phenotypically conspicuous, with this pattern holding both between and within taxonomic groups. Murray (2006) states

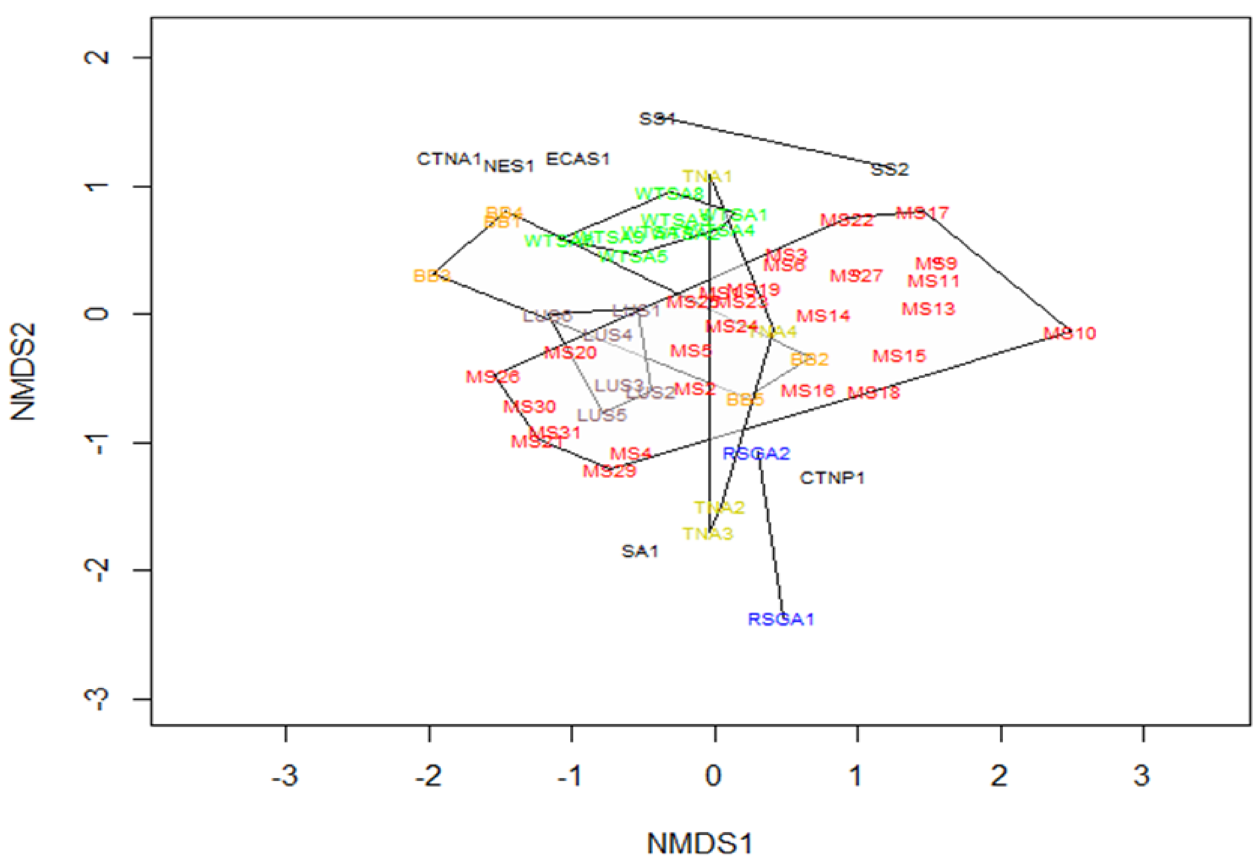

Figure 8. Non-metric multidimensional scaling (NMDS), using species composition among coastal lagoons sampled in Biogeographic Provinces (BP). The coastal lagoons sampled are indicated in the NMDS as: BB - Bay of Bengal; CNTP - Cold Temperate Northwest Pacific; CTNA - Cold Temperate Northwest Atlantic; ECAS - East Central Australian Shelf; LUS - Lusitanian; MS - Mediterranean Sea; NES - Northern European Seas; SA - Somali/Arabian; SS - Sunda Shelf; TNA - Tropical Northwestern Atlantic; WTNA - Warm Temperate Northwest Atlantic; WTSA - Warm Temperate Southwestern Atlantic and RSGA - Red Sea and Gulf of Aden.

that ~2140 species of benthic foraminifera have been recorded being 701 species living in marginal marine environments, 989 in the shelf and 831 species in the deep sea, and 381 species occur in more than one major environment. Of these total of 2140 species, 602 species are agglutinated, 341 porcelaneous and 1197 hyaline. However, Murray (2006) also estimates the number of species that have not yet been described, raising the total number of benthic foraminifera species to somewhere between 3210 and 4280 species. In the present study, we only found 458 living species (92 agglutinated, 125 porcelaneous, 199 hyaline and 42 with organic shell) which represents approximately 65% of the number of species described for marine marginal environments, showing that the present study, although covering only 48 lagoons, was very representative. Thus, based on the data obtained in the present study, we can suggest that the BF are directly related to the Linnean shortfall, since at least 35% of marine marginal species seems to not be described yet. Another problem founded is that the knowledge about benthic foraminiferal biodiversity was mainly based on total assemblages (living + dead organisms) (Debenay *et al.*, 1998, 2001; Vilela *et al.*, 2004; Duleba, 2004), without little or no emphasis on seasonal approach. The absence of seasonal data on benthic foraminiferal distribution can limit their application for environmental biomonitoring, particularly as after death, foraminiferal tests are exposed to taphonomic processes, such as transport, breaking, and dissolving of carbonates (Belart *et al*, 2019). Most BF species were described in the 19 and 20 centuries, without further genetic revisions, making a high number of species that co-occur between coastal lagoons with completely different environmental characteristics (*e.g.*, temperature, salinities, pH). For a group considered as bioindicator of environmental characteristics (Belart *et al.*, 2019; Raposo *et al.*, 2018, 2022; Laut *et al.*, 2021), this does not seem to be a reasonably expected pattern in a global perspective, even though generalist and highly plasticized species may occupy different environments (Holt & Miller, 2010).

Wallacean shortfall

The results presented here clearly show the existence of a Wallacean shortfall for this group of organisms, with a bias toward the most studied Mediterranean region. Each sampled coastal lagoon was considered as an independent location, having by definition a functional physical boundary - shallow water bodies parallel to the coast, with some type of barrier preventing direct contact with the ocean, but connected to the ocean by one or more inlets (Phleger, 1969). We observed a huge difference of record along the globe, possibly influenced by the definition of sampling unit and the presentation of these data on consulted studies. In some studies, only one geographic coordinate of the sampled coastal lagoon was presented, while other studies presented the coordinates of each sample unit, considering them as independent records. Thus, the same species can present different records in the same study and in the same coastal lagoon. The definition of sample independence for a coastal lagoon proved to be subjective for most studies, which may have generated a biased and overestimated result for some countries. However, it was possible to notice that in recent years, a standardization of sampling and analysis methods have started to emerge, possibly due to the Foraminiferal Bio-Monitoring Initiative, which took place during an expert workshop held in June 2011 in Fribourg, Switzerland, bringing together 37 scientists from 24 research groups and 13 countries, aimed to draw up a set of standard methods to use foraminifera in biomonitoring studies (Schönfeld *et al.*, 2012). Based on the heterogeneity of the data obtained in the present study, we suggest that the protocols defined in FOBIMO be used as a standard for studies with live benthic foraminifera from transitional environments. In addition, we suggest that temperature, salinity, dissolved oxygen, pH and, if possible, total organic carbon and total sulfur data should always be collected together with foraminifera.

The NMDS analysis showed that there is a distribution pattern of benthic foraminifera communities around the globe. In fact, these data favor the use of these organisms as bioindicators of major regional environmental conditions, since some species were only found in lagoons with specific conditions such as the Red Sea lagoons, the Mediterranean and also the Brazilian ones. Based on our outcomes, we suggest that the regional characteristics of the lagoons could be the main factors that influenced community composition of these environments. That is, nearby lagoons can have similar abiotic and geochemical characteristics, such as temperature, salinity, dissolved oxygen and organic matter compounds, which tend to harbor a similar species composition. When we consider the marine ecoregions, the scenario found is of a heterogeneous species composition, reflecting the breadth of studies carried out in only 18 of the 232 ecoregions of the entire world. The investigation of patterns and areas of special interest to the biomonitoring, management and conservation based on this group is only possible with the expansion of sampling areas and regions.

The small number of studies on living foraminifera in coastal lagoons can be associated with a lot of factors, one of them is that BF initially were used by the Petroleum Industry, because some species are associated with oil formation environments (Galloway *et al.*, 1991; Schoder-Adams, 2014). The use of living BF as a tool to describe coastal environments such as coastal lagoons began in the 70s with Murray (1970), but only in the early 2000s they started to be used more frequently. Although there are several studies before that date, such as Closs & Madeira (1965) in Lagoa dos Patos (south of Brazil), they gave less importance to the ecological question and also used total assemblage to describe these environments. Of the 193 countries recognized by the UN, we only found studies in 17 of them, showing, for example, the lack of surveys developed on the Atlantic coast of Africa that have several coastal lagoons, mostly in Angola and the Ivory Coast. The same occurs in Brazil where the studies were concentrated in the Southeast coast, mostly in Rio de Janeiro State, and this can be explained by the large number of universities enabling greater structure for the samplings (Rodrigues *et al.*, 2010).

Prestonian shortfall

Hortal *et al.* (2008) and Boakes *et al.* (2010) explain that the knowledge of species distributions is intimately connected with temporal and spatial variation in surveying effort, which not occur with BF studies from coastal lagoons, that mostly do not have temporal and spatial variation emphasis. Some regions are better sampled than others and it is inevitable given the stark differences in scientific capacity and accessibility between countries and regions (Rodrigues *et al.*, 2010) such as in the Atlantic coast of the African continent. Although there are studies that compile several data on the spatial distribution of benthic foraminifera species, especially Murray (2013), one of the best ever done on the subject, most of the compiled data refer to studies carried out with a total assemblage, which does not necessarily reflect the characteristics and variability of the populations in the context of the temporal resolution necessary for studies of environmental quality diagnosis and biomonitoring. Since after death these organisms are subject to several taphonomic processes, the total assemblage may lead to wrong conclusions about the real time distribution of the species (Raposo *et al.*, 2018; Laut *et al.*, 2021). Once again, we suggest that this problem will only be solved with the standardization of sampling and treatment methods.

Hutchinsonian shortfall

With the lack of standardization in the study methods of BF from coastal lagoons, in which not all of them present the environmental parameters associated with the species identified, it was difficult to identify which species could be bioindicators of physicochemical and/or sedimentary characteristics and even how is the range of tolerance of the species to the common parameters founded in the water or sediment. This problem specifically is the definition of Hutchinsonian shortfall described by Cardoso *et al.* (2011) as the lack of knowledge about the responses and tolerances of species to abiotic conditions. In the present study, however, we can state that the following species have the potential to be classified as cosmopolitan, that is, with eurytopic behavior, and because of that characteristic they can be classified as bioindicator species of lagoonal environments, especially in paleoecology studies: *Ammonia beccarii*, *Ammonia parkinsoniana*, *Ammonia tepida*, *Ammotium morenoi*, *Cribroelphidium gunteri*, *Elphidium excavatum*, *Haynesina depressula*, *Haynesina germanica*, *Miliolinella subrotunda*, *Miliammina fusca* and *Quinqueloculina seminulum*. We suggest that new approaches be used in the study of these organisms, in order to describe which species can be indeed considered bioindicators. Analysis such as metacommunity approaches (Presley *et al.*, 2010) or other statistical analyses that also consider the spatial distribution of the BF communities, such as Generalized Linear Models (GLMs) or Generalized

Least Squares (GLS) (Burnham & Anderson, 2002) can provide great contributions to the knowledge of this group of organisms.

Ways to mitigate the Shortfalls

We strongly recommend that new studies be developed in areas not yet sampled, such as the Atlantic and Indian coasts of the African continent and that these samplings be carried out following the methodology proposed by Schönfeld *et al.* (2012), developed for biomonitoring studies, but which in the absence of another, can and should be used in benthic foraminifera community characterization studies. In addition, studies using genetic analysis should be focused on species that have a wide geographic distribution, such as those described here as frequent and very frequent, in order to address the Wallacean deficit and mitigate the Linnean one. As for the lack of knowledge about the tolerance limits of species to environmental parameters, we run into two challenges, once again the lack of standardized sampling methods and/or absence of metadata in older studies does not allow us to make environmental inferences with great efficiency. In addition, we suggest the development of more bioassay studies in laboratory and mesocosm covering as many environmental parameters as possible, primarily focusing on basic parameters such as pH, salinity, temperature, and dissolved oxygen.

CONCLUSION

Our study was efficient in gathering most published data from scientific peer-review production that deal exclusively with living benthic foraminifera from coastal lagoons. The results presented here show the four main gaps existing for benthic foraminifera group, in the geographic scale, data scarcest (absence of parameters in a great number of studies) and in the taxonomic uncertainties and absences. The lack of studies homogeneously distributed in coastal lagoons around the globe limits in-depth discussions about the importance of this bioindicator group, making even the basic framework of species structure and composition impossible.

In order to solve or minimize these gaps, we strongly recommend that new studies follow some standardized sampling and analysis protocols and carried out preferentially from a seasonal approach. Furthermore, more studies should be conductede in remote spots and more efforts should be given on studies that investigate taxonomically similar species, but which may be genetically different. Here we suggest the use of FOBIMO protocols as standard for living BF from transitional environments.

On the other hand, the bibliometric analysis allowed us to observe an overview of the studies of foraminifera in coastal lagoons and, thus, it was efficient in pointing a direction for new studies that aim to reduce the amount of data gaps founded and, in this way, mitigate all the shortfalls for benthic foraminifera studies. Finally, it was possible to infer that regional characteristics directly influence the composition of lagoon species. Thus, according to our analysis, Brazilian lagoons form a cohesive group because they have a very similar species composition, which is not the case with the Mediterranean lagoons, which are very heterogeneous. The results presented here strongly indicate the lack of homogeneity of benthic foraminifera species along the studied coastal lagoons. Most of the BF species presented distribution restricted to few lagoons, provinces and major oceanic region. Therefore, biotic indexes should consider species composition on a regional scale. Therefore, expanding knowledge of these organisms, especially focusing more efforts on filling knowledge gaps, can strengthen arguments for using these organisms as bioindicators.

CONFLICT OF INTERESTS

The contact author has declared that none of the authors has any competing interests.

ACKNOWLEDGMENTS

The authors would like to thank Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil CAPES (Finance Code 001) for the PhD Fellowship of Pierre Belart and the Brazilian National Council for Scientific and Technological Development - CNPq for the PHD fellowship of Fabíola Keesen and for the research grants of Carla Bonetti (Grant 307796/2022-1), Pierre Belart (Grant 152314/2022-9) and Lazaro Laut (Grant 302582/2019-3). This paper is a contribution of the National Institutes for Science and Technology in Ecology, Evolution and Conservation of Biodiversity (INCTEECBio) and the Brazilian Network on Global Climate Change Research (Rede CLIMA).

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SUPPLEMENTARY MATERIAL

Appendix 1.

Submitted: 07 December 2023
Accepted: 11 April 2024
Published online : 15 April 2024
Associate Editor: Gabriel Massaine Moulatlet