Microbial diversity and biotechnological potential of terrestrial and aquatic environments from the remote South Atlantic Trindade Island, Brazil: Trends and Perspectives (#104995)

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Microbial diversity and biotechnological potential of terrestrial and aquatic environments from the remote South Atlantic Trindade Island, Brazil: Trends and Perspectives

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Trindade Island, located in the middle of the South Atlantic Ocean, faces environmental challenges such as the threat of pollution and reduced biodiversity. This study synthesizes knowledge of the microbial community (Archaea, Bacteria, and Fungi) on the island, highlighting their ecological roles and biotechnological potential. A series of studies using shotgun metagenomic sequencing, 16S and ITS amplicon techniques has been compiled, revealing a rich microbial diversity in soil, seawater, and coral tissue samples. Dominant soil genera such as *Acidothermus*, *Mycobacterium*, and *Conexibacter* play potential roles in cellulose degradation, hydrocarbon bioremediation, and soil ecosystem cycling. Water samples showed dominance of *Prochlorococcus* and *Pelagibacter*, which are important for marine carbon fixation. Coral-associated Bacteria such as *Streptomyces*, *Shewanella*, and *Mycobacterium* are involved in antibiotic production, metal reduction, and pathogenesis. Soil fungal diversity includes *Mortierella* and *Antarctomyces*, while water samples show *Aspergillus* species. Coral samples display a predominance of the genus *Aspergillus*, with unexpected discoveries such as *Paracoccidioides brasilienses* and *Scheffersomyces stipitis*, raising the possibility of artifactual results, as well as *Laccaria bicolor* in water samples, and *Antarctomyces psychrotrophyus* in soil samples. Isolated bacterial strains show remarkable abilities in hydrocarbon degradation and biosurfactant production, which are essential for bioremediation in oil-contaminated environments. Strains such as *Rhodococcus rhodochrous, Nocardia farcinica*, *Exiguobacterium*, and *Tistrella* stand out for

their biotechnological potential. This study highlights the importance of the microbial diversity of Trindade Island through molecular research to provide essential knowledge for biodiversity conservation and biotechnological applications, especially in petroleum-related sectors.

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Abstract

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Keywords: Trindade Island; Microbial composition; Metagenome; Bioprospection.

Introduction

Trindade Island, the largest one of the Trindade-Martim Vaz Archipelago, covers an area of approximately 10 km² in the South Atlantic Ocean and is located at the same latitude as the municipality of Vitória, Espírito Santo - Brazil, approximately 1,140 km from the coast (Camacho-Montealegre et al., 2019; Câmara et al., 2023). On Trindade Island, soils are generally fertile as a result of lithological, topographical, and biological activity influences, which are often closely linked (Clemente et al., 2009). The volcanic arc, to which Trindade Island belongs, is characterized by a high sodium content, providing a continuum of niche opportunities for salt-tolerant microorganisms (da Silva et al., 2015).

The island is home to a rich biota, including endemic and endangered species (Costa-Rezende et al., 2023). Nonetheless, the island faces several historical and recent environmental challenges that require immediate attention, as well as the implementation of effective strategies. Potential pollution from various sources threatens the integrity of this marine and insular ecosystem. These environmental threats include possible contamination with toxic metals resulting from fires, rock erosion, volcanic processes and sediment movement (Cariou et al., 2017; Santos-Silva et al., 2018), as well as the presence of plastic waste (Andrades et al., 2018; de Souza Petersen et al., 2016). Furthermore, the island is located close to the Campos Basin oil fields, which is an additional concern for the conservation of the marine environment and wildlife (Câmara et al., 2023; Rodrigues et al., 2018). In addition, human interventions, such as the introduction of goats from the years 1700s up to 2005, have led to a reduction in biodiversity due to their negative impact on the soil for pasturing and the consumption of native trees (Câmara et al., 2023; Costa-Rezende et al., 2023; Rodrigues et al., 2018; Silva & Alves, 2011).

In the environment, microorganisms are extremely important in ecological processes from the oceans to soils, such as biogeochemical cycles, climate regulation, carbon storage, disease propagation, and pollutant transformation, as well as can enhance functionality relationships among micro and macroorganisms (e.g. Ducklow, 2008; Escalas et al., 2019; Giller et al., 2004). Trindade Island has been the subject of studies on microbial diversity (eg. Câmara et al., 2023; Meirelles et al., 2015) and biotechnological potential (eg. da Silva et al., 2015; Rodrigues et al., 2015a; Rodrigues et al., 2018). Nevertheless, little is known about the relationship between the structural and functional diversity specific to Archaea, Bacteria, and Fungi on this Island (Costa-Rezende et al., 2023).

There is a consensus that microbial diversity is linked to ecosystem functioning, meaning that communities with higher microbial richness improve ecosystem performance (e.g. Delgado-Baquerizo et al., 2016; Jing et al., 2015; Maherali et al., 2007; Semchenko et al., 2018). Archaea, Bacteria, and Fungi can represent unique species that perform specific functions and play fundamental roles in biodiversity conservation (Olofintila & Noel, 2023). These microorganisms can act as highly sensitive indicators of environmental pollution and contamination (Korneykova et al., 2021), playing a very important role in the protection of ecosystems, especially considering the imminent threat of contamination by oil and other pollutants (Câmara et al.,

2023; Rodrigues et al., 2018). Moreover, they may also have a high biotechnological potential, including the ability to degrade pollutants through the production of specialized enzymes (Ghosh et al., 2020) and also the ability to degrade antibiotic substances (Lei et al., 2023), which can be harmful in natural environments.

Based on this scenario, the aim of this study was to synthesize and interpret, in a systematic way, the knowledge of the microbial communities (Archaea, Bacteria, and Fungi) of Trindade Island, highlighting, when possible, the ecological role and biotechnological potential of the most representative taxa.

Survey Methodology

Data collection

This systematic review was based on the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines (Page et al., 2021). Records were searched on 2 August 2024 in the Scopus, Web of Science, PubMed, PubMed Central, Dimensions, and Google Scholar databases using the Publish or Perish v8 tool (Harzing, 2007). The keywords used to search for records were: "trindade island" AND (metagenomics OR shotgun OR [amplicons AND (16S OR 18S OR ITS OR "internal transcribed spacer")]. There were no restrictions on document type, language or publication date to avoid excluding relevant records.

The results of the database searches were exported in CSV format. The scripts *format_input.py* (Jasper, 2023a) and *remove_duplicates.py* (Jasper, 2023b) were used to select unique documents. These scripts read the CSV files and filter out DOI-less and duplicate documents from the set of records (Dutra et al., 2023a,b; Gomes et al., 2023). The researchers García, G.J.Y. and Dutra, J.d.C.F. reviewed both the unique and DOI-less documents to select the scientific articles that met the selection criteria (Table 1). Disagreements in the selection of documents were resolved by the researcher Gomes, R.F.

After the initial review of titles and abstracts, only studies that addressed Trindade Island using shotgun metagenomics or amplicon sequencing were selected. These studies underwent a thorough evaluation, applying well-defined inclusion and exclusion criteria (Table 1), considering the collection area, sample type, methodologies used and the relevance of the results. The following data were extracted from the selected documents: taxonomic abundance of microorganisms (Archaea, Bacteria and Fungi) obtained by shotgun metagenomics and amplicon sequencing, type of substrate, samples or treatments, metagenomic approach, marker genes and sequencing platform used.

Extraction of taxonomic data

The set of selected documents was used to extract taxonomic information on Archaea, Bacteria, and Fungi, both in the main text and in the supplementary materials. Because of the use of different taxonomic databases or different versions of the same database between the studies analyzed, it was necessary to standardize the nomenclature of the taxa, identify synonyms, and

position in classification. This task was carried out using a local script written in Python v3.10.8, which consulted the Global Biodiversity Information Facility database (GBIF Secretariat, 2023) via its API. For taxa missing from the GBIF database, manual searches were performed in the NCBI Taxonomy database (Schoch et al., 2020).

Grouping samples

The sequences representing Archaea, Bacteria, and Fungi extracted from the papers assessed in this study were grouped to simplify data analysis. For grouping, we considered the types of substrates and the sequencing methods used. The analyzed samples were collected from various sources, such as soil, water, and coral tissue, and were obtained by both culture-dependent approaches (we attributed the suffix **_DCul**) and culture-independent methodologies (we attributed the suffix **_ICul**).

In order to facilitate comparative analyses, we organized the samples into five distinct categories: (i) culture-independent soil samples (Three samples named PD5, PD6, PF7, see Table 2) were named **Soil_ICul**; (ii) culture-independent water samples (Three samples named NOR_Island_W, PRI_Island_W, SAN_Island_W, see Table 2) were designated as **Water_ICul**; (iii) culture-independent coral tissue samples (Two samples named FAR_Island_C, NOR_Island_C, see Table 2) were named **Coral_ICul**; (iv) culture-dependent soil sample (One sample named Crude Oil, see Table 2) were identified as **Soil_DCul**; and, finally, (v) twelve treatments, from seawater samples (Named Oil, FLU, HEX, PHE, PHE+FLU, PHE+HEX, PHE+OIL, PHE+PYR, PYR, see Table 2) were grouped under the **Water_DCul** category. It is worth noting to highlight that taxonomic classification at the genus and species levels was only possible when cultivation-independent sequencing techniques were employed.

The other kingdoms described in our study were not analyzed because the information recovered was limited; however, these data were also extracted. For a better spatial understanding of the samples, a static map adapted from Witovisk et al. (2018) and an interactive map based on OSM (OpenStreetMap), and the Leaflet JavaScript library were generated.

Analysis of the communities of Archaea, Bacteria, and Fungi

A series of analyses were performed on the five sets (Soil_ICul, Water_ICul, Coral_ICul, Soil_DCul, and Water_DCul) using R v4.2.1. The relative abundances of all taxonomic categories were analyzed using bar graphs generated using the ggplot2 v3.4.3 package (Wickham, 2011). Shared (core) and unique (satellite) taxa were analyzed using Venn diagrams, generated using the venn v1.11 package (Dusa, 2018). The alpha and beta diversity analysis were performed with the abundances of the order category. Shannon indices were calculated with the vegan v2.6.4 package (Dixon, 2003) and plotted with the ggplot2 v3.4.3 package. Principal coordinates analysis were generated using the packages vegan v2.6.4, ggrepel v0.9.3 (Slowikowski et al., 2018), and ggplot2 v3.4.3.

Analyzes of strong association networks between groups and taxa were calculated using the package indicspecies v1.7.14 (de Caceres et al., 2016), using the *multipatt* function with the

point biserial correlation coefficient (r.g) to calculate the strength of association, which was considered statistically significant with a $p < 0.05$. Networks were constructed using Cytoscape v3.10.1 software (Shannon et al., 2003) with the edge-weighted sping-embedded layout. In the networks, the circles represent the taxa, the size of the circles represents the abundance of the taxa, the diamonds represent the sample groups, and the length of the edges represents the strength of the association; the smaller the edge, the stronger the sample-taxon association.

Non-parametric multivariate analyses were performed using the PERMANOVA test and the Bray-Curtis dissimilarity index with 9999 permutations in PAST v4.11 software (Hammer & Harper, 2001). The aim was to compare the community structure between the sample groups. In addition, the pairwise PERMANOVA model was used to assess statistically significant differences between pairs, with a significance level of $p < 0.05$.

Rodrigues et al. (2015) and Da Silva et al. (2015) identified a group of bacterial isolates from partial sequencing of the 16S rRNA gene using the MegaBACE 1000 DNA Analysis System (SANGER) platform (Table 2) but did not present abundance data; therefore, the abundance information was not included in the comparative analyses.

Additionally, to enrich the presentation of the profiles of the selected searches, a word cloud was generated using the wordcloud v1.9.1.1 (Mueller, 2023) and pillow v9.4.0 (Clark, 2023) libraries, based on the text of the selected articles.

Study selection

The database search protocol yielded a total of 274 studies [Scopus (n = 24), Web of Science (n = 1), PubMed (n = 2), PubMed Central (n = 13), Dimensions (n = 98), and Google Scholar (n = 136)], of which 67 were excluded because they were duplicates. Two hundred and one unique articles were included in the paired title analysis, of which eight studies were selected on methodology reading and included in our review (Fig. 1, Data S1, Data S2).

The researchers García, G.J.Y. and Dutra, J.d.C.F. agreed in their selection of documents, with only two cases of disagreement, which were resolved by the researcher Gomes, R.F., who accepted one of the documents and rejected the other because it did not meet the selection criteria (Table 1). Finally, the researchers selected eight documents that met the selection criteria (Fig. 1, Table 2). Câmara et al. (2022) and Câmara et al. (2023) worked with the same samples and presented equivalent results; thus, the study of Câmara et al. (2022) was not included in the discussion as it was redundant.

Profile of selected articles

After analyzing the selected articles, four of them focused on the study of bioremediation of hydrocarbon contamination (da Silva et al., 2015; Morais et al., 2016; Rodrigues et al., 2015b; Rodrigues et al., 2018) (Fig. 2). Most of the studies used sequencing of the 16S rRNA marker gene as the approach. Furthermore, most of the articles analyzed soil and seawater samples (Table 2, Fig. 3), with the exception of the study by Meirelles et al. (2015), which included

analyses of coral tissues (Table 2). For a more detailed visualization of the samples, an interactive map is available at: https://glenjasper.github.io/leaflet-trindade-island-review-map.

Recovered communities of Archaea, Bacteria, and Fungi

The focus of this review was to analyze the communities of Archaea, Bacteria, and Fungi, but the taxa of the other kingdoms, which are not part of this review, are included in Data S3. These tables contain standardized information according to the GBIF and NCBI Taxonomy databases.

The selected articles presented results in different taxonomic categories. Meirelles et al. (2015) and Câmara et al. (2023) reported up to the genus level, Rodrigues et al. (2018) displayed up to the family level, and Morais et al. (2016) exhibited up to the order level. Rodrigues et al. (2015) and da Silva et al. (2015) sequenced the 16S rRNA gene using the SANGER method and; therefore, identified a small community of bacterial species. Thus, their results were only considered in the discussion. Because of these differences in the presentation of taxonomic results, comparative analyses were mainly performed at the phylum, order, family, and genus level. Although the studies by Pylro et al. (2014) met our selection criteria, the authors did not show taxonomic data and limited themselves to comparing amplicon analyses approaches. Hence, this article could not be considered in our analyses.

Bacterial predominance, high rates of unclassified sequences in soil, and high abundance of satellite in water and coral samples

Regarding the analysis of Archaea and Bacteria, the vast majority of the community was identified as Bacteria, with Archaea being practically non-existent in the groups: they were only detected in the environmental samples, and the highest relative abundance was detected in coral samples, barely exceeding 3% (Data S4).

The amount of unclassified reads is remarkable, especially for the Soil_ICul group. Within the group, at the family level, 36.12% of the reads were unclassified. At the genus level, the percentage of unclassified reads reached almost 70%, and at the species level 99.7% of the reads were unclassified, with only one species of Bacteria identified (*Dinghuibacter silviterrae*). Interestingly, for Water_ICul and Coral_ICul groups, around 8% of the reads were unclassified at family and genera levels, and decreased to less than 1% at the species level (more details in the Data S4). Nonetheless, the percentage of reads found in low abundance (<1%, <2%, or <3%) and thus classified as Other, was remarkably high in Water_ICul and Coral_ICul groups at species (Fig. S1I), genus (Fig. 4B), family (Fig. S1G) and order (Fig. S1E) classification levels.

Distribution of Bacteria in sample groups

At the phylum level, the presence of Pseudomonadota was notable in all groups (Fig. 4A), except for Soil_DCul, in which the predominant phyla was Actinobacteriota (around 20%), followed by Pseudomonadota (17.3%), and Acidobacteriota (12%). In Soil_ICul, Actinobacteriota and Pseudomonadota were found in the same amount (around 26%), followed by Acidobacteriota (12.8%), Verrucomicrobiota (10.2%), and Chloroflexota (10.3%). In Water_DCul the dominance

of Pseudomonadota (81.7%) was remarkable. Besides, the phylum Bacteroidota (16.7%) was also identified. In Water_ICul Pseudomonadota (65.5%) was dominant, followed by Cyanobacteria (19.3%) and Bacteroidota (5.5%). Finally, for Coral_ICul group, Pseudomonadota prevailed (39.5%); however, many other phyla were detected in smaller amounts: Actinobacteriota (9.3%), Firmicutes (8.8%), Bacteroidota (8.2%), Cyanobacteria (6%), Chloroflexota (4.3%), Desulfobacterota (3.7%), Planctomycetota (3.6%), Myxococcota (2.5%), Acidobacteriota (2.4%), Poribacteria (2.3%), Verrucomicrobiota (2%), Thermoproteota (1.6%), and Deinococcota (1.1%).

In general, there was no predominant family of Bacteria in the groups, as the percentages were similar, with the exception of the Water_DCul group. In the latter, the dominance of Oceanospirillaceae (35.8%) was observed, followed by Alcanivoracaceae (16%), Flavobacteriaceae (13.4%), and Rhodobacteraceae (12.2%). Rhodobacteraceae was detected in water and coral samples. In Water_ICul, Cyanobiaceae (14.5%) is slightly increased compared to the others (Fig. S1G).

Acidothermus (around 10%) was the dominant genus in Soil_ICul group, followed by *Mycobacterium* (3%) and *Conexibacter* (2%). As mentioned, at the species level, only *Dinghuibacter silviterrae* was detected (0.3%). In Water_ICul group, the genera *Prochlorococcus* (around 15%), *Vibrio* (7%) and *Pelagibacter* (6.6%) predominated, as well as the species *Prochlorococcus marinus* (14.3%). In the Coral_ICul group, there were no dominant genera and a striking similarity of relative abundances between *Pseudomonas* (1.8%), *Streptomyces* (1.7%), *Mycobacterium* (1.5%), *Cyanothece* (1.5%), *Burkholderia* (1.3%), *Geobacter* (1.1%), *Bacillus* (1.1%), *Roseobacter* (1.1%), *Solibacter* (1.1%), *Roseiflexus* (1.1%), *Shewanella* (1%), and *Bacteroides* (1%) (Fig. 4B).

Distribution of Fungi in the samples

Similarly to the results found for Bacteria and Archaea, around 80% of the reads belonging to Fungi were unclassified at the species level and 50% at the genus level for the Soil_ICul group. For the Water_ICul and Coral_ICul groups, taxa with lower abundance (<1%) had high presence, varying between 12% and 17%, in the family, genus, and species levels (Fig. 4D, Fig. S1H, Fig. S1J).

Fungi belonging to the phylum Ascomycota predominated in all groups, except for Soil_DCul, where Mucoromycota was the most abundant. Basidiomycota was the second most common phylum found, except in Soil_DCul (Fig. 4C). *Aspergillus* was the predominant genus in Coral_ICul (34.7%) and Water_ICul (19%) groups; however, it was not found in Soil_ICul group. In Soil_ICul, the relative abundances of genera were similar, including *Mortierella* (7.4%), *Apiotrichum* (6.3%), *Antarctomyces* (6.1%), *Pseudogymnoascus* (5%), and *Coniochaeta* (4.5%). *Antarctomyces psychrotrophicus* (6.1%) and *Mortierella huminis* (4%) were the main species identified (Fig. 4D, Fig. S1J).

Many species of *Aspergillus* were found in the water samples, such as *A. nidulans* (4.8%), *A. fumigatus* (4.8%), *A. clavatus* (2.9%), *A. flavus* (2.9%), and *A. terreus* (2.9%), all of them with

similar relative abundance. Still, among the most abundant species were *Laccaria bicolor* (8.6%), *Cryptococcus neoformans* (6.6%), and *Candida albicans* (5.7%).
Aspergillus clavatus prevailed in coral samples (28.6%). Other species of *Aspergillus* identified were *A. ficheri* (2.3%), *A. flavus* (2%), and *A. nidulans* (1.3%). Still, *Paracoccidioides brasilienses* (14%), *Scheffersomyces stipitis* (7.5%), and *Talaromyces stipitatus* (5.2%) were found in relatively high amounts in coral samples.

Shared (core) and unique (satellite) taxa between sample groups

Venn diagram analyses highlighted the shared and unique taxa of representatives of the Archaea and Bacteria domains, as well as the Fungi kingdom, among the culture-independent (Soil_ICul, Water_ICul, and Coral_ICul) and culture-dependent (Soil_DCul and Water_DCul) groups for all the taxonomic categories (Fig. S2, Data S5).
Based on the data analyzed from the groups of non-cultured and cultured samples, 50 phyla of Bacteria were identified, followed by six phyla of Archaea, and seven phyla of Fungi (Fig. 5A). In addition, bacterial phyla were identified in all samples. In contrast, no archaeal or fungal phyla were detected in the Water_DCul group.
The groups of non-cultured and cultured samples shared six bacterial phyla (Actinobacteriota, Bacteroidata, Cyanobacteria, Planctomycetota, Pseudomonadota, and Verrucomicrobiota), while the groups Soil_ICul and Soil_DCul had uniqueness in six and 13 bacterial phyla, respectively (Fig. 5A).
The Water_ICul and Coral_ICul groups shared four phyla of Archaea (Halobacteriota, Methanobacteriota, Thermoplasmatota, and Thermoproteota) while the Soil_DCul group displayed uniqueness in two phyla of Archaea (Euryarchaeota and Parvarchaeota). The Soil_ICul, Soil_DCul, Water_ICul, and Coral_ICul groups shared two phyla of Fungi (Ascomycota and Basidiomycota). Only the Soil_ICul group exibited uniqueness in relation to two phyla of Fungi (Mucoromycota and Glomeromycota) (Fig. 5A).
Figure S8C shows that the five groups shared three orders of Bacteria (Burkholderiales, Rhizobiales, and Xanthomonadales). The Coral_ICul, Water_ICul, Water_DCul, Soil_ICul, and Soil_DCul groups have two, two, three, 19, and two exclusive bacterial families, respectively. The Coral_ICul, Water_ICul, and Soil_ICul groups have one, one, and 45 exclusive fungal families respectively. Only the Coral_ICul group had two unique archaeal families. It is worth noting that the Soil_DCul and Water_DCul groups only had Bacteria at the family level, with four families (Burkholderiales, Rhizobiales, Sphingomonadales, and Xanthomonadales) shared between these groups.
When analyzing genera, no results in this taxonomic category were presented by the studies using culture-dependent methods. Among the bacterial genera, the Water_ICul group stood out for its remarkable diversity, with 555 genera identified, followed by the Coral_ICul and Soil_ICul groups with 526 and 34 genera respectively (Fig. 5B, Data S5). These three groups shared 15 genera (*Acidothermus*, *Acinetobacter*, *Burkholderia*, *Chthoniobacter*, *Conexibacter*, *Flavobacterium*, *Haliangium*, *Legionella*, *Mucilaginibacter*, *Mycobacterium*, *Paraburkholderia*,

Pedosphaera, *Phenylobacterium*, *Pseudomonas,* and *Rhodomicrobium*) and 502 genera were shared between the Coral_ICul and Water_ICul groups. In addition, the Coral_ICul, Water_ICul, and Soil_ICul groups had 24, 53 and 19 exclusive bacterial genera, respectively.

For the archaeal genera, the Coral_ICul group presented 47 genera, 14 of which were unique. In contrast, the Water_ICul group showed 36 archaeal genera, of which three were exclusive (*Ignisphaera*, *Metallosphaera,* and *Methanolacinia*) (Fig. 5B). When analyzing the fungal genera, a total of 202 genera were observed. The Coral_ICul, Water_ICul, and Soil_ICul groups had six shared genera (*Aspergillus*, *Candida*, *Chaetomium*, *Malassezia*, *Saccharomyces,* and *Talaromyces*) and 12, seven, and 153 exclusive genera, respectively (Fig. 5B).

Analysis of alpha and beta diversity and correlation of sample groups

Alpha diversity analysis showed distinctive results for each group. The Water_DCul group exhibited an average Shannon index of 1.109, pointing to relatively low diversity in this particular environment. In contrast, the Sol_DCul group showed a Shannon index of 1.889, indicating moderate diversity. On the other hand, both the Sol_ICul and Water_ICul groups revealed average Shannon indices of 2.639 and 2.7 respectively, suggesting substantially higher diversity compared to the culture-dependent groups. Finally, the Coral_ICul group stood out with an average Shannon index of 4.094, underlining the presence of significantly rich biodiversity in culture-independent coral samples (Fig. 6A).

In the analysis of beta diversity in the taxonomic category of order, represented by the Principal Coordinates Analysis (PCoA) (Fig. 6B), one can observe the formation of groupings between samples based on the sample type. It is worth mentioning that the Water_ICul and Coral_ICul sample groups were close, not showing statistically significant differences according to the PERMANOVA analyses (Data S6) whereas only the Water_DCul group showed statistical differences from the Soil_ICul (p = 0.0051), Water_ICul (p = 0.0042), and Coral_ICul (p = 0.0186) groups.

In the network of strong associations by phylum, the Coral_ICul group had the highest number of associated phyla, as it showed no significant association with only five phyla. (Fig. 7A). As expected, coral samples exibited a greater number of shared associations with water samples (Water_ICul) than with soil samples (Soil_ICul and Soil_DCul), as well as with water samples (Water_ICul and Water_DCul), and these results are consistent with the PERMANOVA analyses. Unexpectedly, the Soil_ICul and Soil_DCul groups did not show much overlap in their associations, with the Soil_ICul group displaying more associations with coral samples (Coral_ICul).

The Water_DCul and Soil_DCul groups have a smaller number of associated phyla, with the soil phyla correlating with Ascomycota, Actinobacteriota, and Acidobacteriota, and the water phyla correlating only with Pseudomonadota. Usually, bacterial phyla dominated the associations with all substrates and methods while Fungi were represented by only two phyla (Ascomycota and Basidiomycota) associated with Soil_ICul and Soil_DCul samples, respectively. Methanobacteriota and Halobacteriota were the only phyla representing Archaea and are only

associated with the Coral_ICul group. Despite being more abundant (Fig. 7A), the phyla Ascomycota and Pseudomonadota did not display significant associations with all substrates and methods. Actinobacteriota, Chlamydiota, and Pseudomonadota were the phyla with the highest number of associations, being associated with three of the five types of substrates and methods.
The patterns of associations at order level are similar to those observed at phylum level, with the Coral_ICul group showing the highest number of associations. The culture-based samples show the same pattern of fewer associations with different orders. The Coral_ICul and Water_ICul groups showed a large number of common associations while the soil samples showed no overlap in associations (Fig. S3).
At the genus level, only the non-cultured samples identified communities of Archaea, Bacteria, and Fungi (Soil_ICul, Water_ICul, and Coral_ICul). The coral samples exhibited a greater number of significantly associated genera, including most of the archaeal genera present in the association network, followed by the water samples. The water and coral samples share a large number of associations, the majority of which are representatives of Bacteria, with a comparatively small number of associated genera representing Archaea and Fungi. Among the significantly associated genera only with the non-cultured water samples, the bacterial genera *Prochlorococcus*, *Pelagibacter*, *Pseudoalteromonas*, and *Alteromonas* were the most abundant while, for the coral samples, the most abundant bacterial genera were *Cyanothece*, *Streptomyces*, *Mycobacterium*, and *Geobacter* (Fig. 7B). Soil samples exhibited lower diversity compared to other substrates and few bacterial genera are significantly associated, but the most abundant bacterial genera were *Acidothermus* and *Mycobacterium*. On the other hand, more than half of the fungal genera recovered are significantly associated only with non-cultured soil samples, with *Mortierella* and *Lipomyces* displaying high abundance (Fig. 7B).

Biotechnological potential of bacterial isolates identified by partial sequencing of the 16S rRNA gene

Rodrigues et al. (2015) identified a number of bacterial strains and species capable of degrading different types of hydrocarbons. Using isolates from water samples, the species *Rhodococcus rhodochrous* and *Nocardia farcinica* were found to degrade a wide range of hydrocarbons, including aliphatic, aromatic and PAH compounds. These compounds included toluene, octane, xylene, naphthalene, phenanthrene, pyrene, hexadecane, anthracene, eicosane, tetracosane, triacontane, and pentacontane. The species *Cellulosimicrobium cellulans* and *Microbacterium lacticum* were able to degrade the hydrocarbons hexadecane and naphthalene respectively. In addition to these strains, strains belonging to the genera *Exiguobacterium*, *Microbacterium*, and *Tistrella* also showed the ability to selectively degrade some types of hydrocarbons (anthracene, hexadecane, naphthalene, tetracosane, octane, phenanthrene, pyrene, and xylene). Moreover, Da Silva et al. (2015) identified a group of strains belonging to the genus *Bacillus*, isolated from soil samples, which showed the ability to produce biosurfactants under high salinity conditions.

Idiosyncrasies of the selected studies

Despite the restricted molecular screening of the Trindade Island, this review focused specifically on six studies that had used DNA sequencing, either from culture-dependent or culture-independent methods, from environmental samples collected on Trindade Island. Amongst them, two investigations worked with culture-independent samples (Câmara et al., 2023; Meirelles et al., 2015) and four with culture-dependent samples (da Silva et al., 2015; Morais et al., 2016; Rodrigues et al., 2015b; Rodrigues et al., 2018). Five studies were based on marker gene sequencing (16S rRNA and/or ITS) (Câmara et al., 2023; da Silva et al., 2015; Morais et al., 2016; Rodrigues et al., 2015b; Rodrigues et al., 2018), and only one used shotgun metagenomic sequencing (Meirelles et al., 2015). The most commonly used platform was Illumina MiSeq, followed by Ion Torrent, and SANGER. Although the molecular data regarding the diversity of taxa at the Trindade Island is limited, Costa-Rezende et al. (2023) conducted an extensive bibliographic review of the last 100 years of studies on Trindade Island, identifying 312 references, mainly in the fields of biology, health sciences, and agriculture. Within this period, the first scientific record related to biology dates back to 1922 (Barreto 1922), but the first study based on DNA analysis was only published in 2014 (Pylro et al., 2014).

The only study with a shotgun metagenomic approach used pyrosequencing (454). There is an opportunity to improve metagenomic sequencing of environmental samples with newer technologies, such as short-read sequencing (Illumina platform) or long-read sequencers (ONT platform), which can provide more comprehensive and detailed insights in subsequent studies. Furthermore, only three genomic studies presented the draft genomes of the Bacteria *Rhodococcus rhodochrous* TRN7 (Rodrigues et al., 2016), *Nocardia farcinica* TRH1 (Rodrigues et al., 2017), and *Staphylococcus warneri* TRPF4 (Freitas et al., 2020).

The studies included in this review provide a comprehensive overview of the richness and complexity of microbial and eukaryotic communities, such as Fungi, on Trindade Island, and reveal the influence of environmental factors on the health of marine and terrestrial ecosystems. This research has important implications for understanding the natural mechanisms for managing and restoring natural niches on the island and in similar regions.

In the selected studies, it is clear that representatives of the Bacteria domain were the most extensively characterized. Nonetheless, many taxa could not be assigned to genus and species categories for Bacteria, Archaea, and Fungi, particularly in soil samples (Soil_ICul). This is an inherent limitation of studies on the molecular identification of microorganisms from environmental samples due to a number of reasons widely discussed in the literature, including the number of species of microorganisms that have not been formally described and scientifically characterized, and limitations inherent in the scope of the databases used for identification (Konstantinidis et al., 2017; Lu et al., 2017; Marcelino et al., 2020; Seol et al., 2019). Additionally, a significant correlation was observed between the water and coral samples, which was to be expected given that several samples were collected under the same conditions (location and depth).

In order to better understand the biotechnological potential of these communities, we considered discussing the most abundant and common microorganisms, and, thus, simplifying the analysis, highlighting the most abundant taxa and isolated bacterial strains.

Roles and characteristics of the main Bacteria and Fungi found in soil, water, and coral samples (culture-independent method)

The most abundant bacterial genera identified in the soil samples were *Acidothermus*, *Mycobacterium* e *Conexibacter*. *Acidothermus* has recently been described as a thermophilic Bacteria producing thermostable cellulolytic enzymes (Ghosh et al., 2020). This group of enzymes are capable of hydrolyzing plant biomass into its constituent monomers and; therefore, are promising alternatives for a wide variety of industrial applications following sustainability principles (Yeoman et al., 2010).

Mycobacteria constitute a diverse and well-studied group of Actinobacteria. They are virtually found in all environments; however, water and soil are considered their preferred habitats (Hruska & Kaevska, 2012, Walsh et al., 2019). Members of this group have been associated with human diseases of importance to public health worldwide. Nonetheless, most are non-pathogenic, and some mycobacteria are actually beneficial to human health (Fox et al., 2017). Still, strains of *Mycobacterium* have metabolic capabilities useful for the biodegradation of environmental pollutants (Hennessee et al., 2009) or as industrial biocatalysts (van Beilen et al., 2005). A recent study conducted by Gu et al. (2023) evaluated the capacity of indigenous microorganisms of soil to adapt and degrade phenanthrene (PHE). Among the bioaugmented genera, the authors found increased relative abundances of *Mycobacterium*. The native population of microorganisms in soils are considered the most efficient organisms for the biodegradation of contaminants since they are adapted to the local biotic and abiotic stresses.

The first representative of the genus *Conexibacter* (*C. woesei*) was isolated from temperate forest soil in Gerenzano (Italy), and was classified as a deep-rooting member of the class Actinobacteria. Besides its distinct phylogenetic position, *Conexibacter* showed unusual chemotaxonomic characteristics (Monciardini et al., 2003). *Conexibacter woesei* cells are small short rods, which motility is given by peritrichous flagella. They are obligate aerobes, and play roles in biogeochemical cycles, reducing nitrate to nitrite, and carbon cycling in soil ecosystems (Monciardini et al., 2003, Pukall et al., 2010; Seki et al., 2012). To date, only two species of the genera are known. The second, named *C. arvalis,* was described by Seki et al. (2012) and showed 98.6% similarity with *C. woesei.* Regarding biotechnological applications, a recent study (Lei et al., 2023) demonstrated the potential of the strain *Conexibacter* sp. LD01 to degrade lincomycin, an antibiotic highly resistant to degradation, and, thus, a serious environmental problem.

Regarding Fungi, the predominant species in the soil were *Mortierella humilis and Antarctomyces psychrotrophicus,* and, at the genus level, *Apiotrichum, Pseudogymnoascus,* and *Coniochaeta*.

New species of the filamentous Fungi *Mortierella* (Mucoromycotina) are continually being discovered. It is considered the most common soil-inhabiting Fungi but is not limited to this substrate, being widespread in various environments (Ozimek & Hanaka, 2020; Wagner et al., 2013). The omnipresence of such strains must be related to its broad biochemical repertory and the many roles they play in the different environments. The growing interest in *Mortierella* spp. is mainly because it acts as a plant growth-promoting Fungi by increasing plant nutrient uptake (Tamayo & Osorio, 2018). *M. humilis* produces a variety of enzymes acting in the degradation of complex carbon sources like cellulose, chitin, and xylans (Blanchette, 2000). Moreover, *M. humilis* has been reported as a producer of fatty acids useful in medicine, pharmacology, cosmetics, and food industry (Nguyen et al., 2019), as well as shows potential to be used in the biorecovery of metalloids, such as selenium and tellurium (Liang et al., 2019). In a recent study, Jiao et al. (2023) reported higher abundance of *M. humilis* in the rhizosphere of pine diseased hosts compared to healthy hosts. Since this species is known for its capacity to produce substances with antipathogenic activities, the reported microbiome change may be related with the activation of the plant's immune system to fight against the pathogen infection. In the soils of the giant fern forest (Desejado-Fazendinha), fungal sequences belonging to the species *M. humilis* were abundantly identified (Câmara et al., 2023). The presence of this species might suggest a contributory potential for the regeneration of dominant plant species, such as *Cyathea delgadii*.

The genus *Antarctomyces* includes only two species so far, *A. psychrotrophicus* and *A. pellizariae*, both isolated, for the first time, in Antarctica. Outside Antarctica, *A. psychrotrophicus* was identified in soil samples of the Brazilian Trindade Island (Câmara et al., 2023) and from fermentation cellars of a liquor manufacturer located in Luan city, China. The function of *A. psychrotrophicus* in the Chinese liquor is still unclear and needs further research (Pu & Yan, 2022). *A. psychrotrophicus* is one of the dominant species isolated from several different substrates in Antarctica, and the key determinant for its freeze tolerance is the secretion of antifreeze protein (AFP). Some studies have focused on the molecular characterization, physiological role, and intriguing evolutionary aspects of AFPs from *A. psychrotrophicus* (Arai et al., 2019; Xiao et al., 2010). More recently, the capacity of *A. psychrotrophicus* to produce antibacterial and antifungal compounds has also been shown (Nikitin et al., 2022). The presence of *Antarctomyces*, a typical psychrophilic Fungi, usually isolated in Antarctica is both curious and rather strange, and might be considered with caution since a contamination or artifactual result cannot be discarded.

The genus *Apiotrichum* (type species *A. porosum)* is an anamorphic basidiomycetous yeast closely related to the genera *Trichosporon* and *Hyalodendron.* The genus currently contains 20 species globally distributed, including a number of soil-associated species (Liu et al., 2015). Different ecological functions are attributed to the also globally distributed species of the genus *Pseudogymnoascus.* They can act as saprophytic, cellulolytic, and are well adapted to cold environments (Rice et al., 2006). Additionally, *Coniochaeta* is a genus of ascomycotan yeasts typically associated with soil, water, and wood (Weber, 2002). There is also evidence of

endophytic association with plants without causing damage to the host (Harrington et al., 2019), as well as species involved in clinical infections, which has increased the interest in the genus (Khan et al., 2013).

In water samples, the bacterial genera *Prochlorococcus* (*P. marinus*) and *Pelagibacter* dominated. *Prochlorococcus* is a genus of cyanobacteria very abundant in the sunlight zone of tropical oceans. The cells are very small (0.5 to 0.7 μm) and the nutritional requirement is minimal (Biller et al., 2015). Such physiological characteristics, associated to its capacity to use sulfolipides instead of phospholipids in their membranes confer adaptive advantages to this microorganism (Van Mooy et al., 2006). *Prochlorococcus* play an important role in oxygen production and carbon cycle. Along with *Synechococcus*, another genus of cyanobacteria, is responsible for approximately 50% of marine carbon fixation. Besides, *Prochlorococcus* is a fundamental primary supplier in the oceanic food webs. The only species described within the genus is *P. marinus* (Fu et al., 2007).

Candidatus pelagibacter ubique or SAR11 belongs to the phylum Pseudomonadota and was isolated in 2002 (Rappé et al., 2002). The term "*Candidatus*" is used for proposed species that are not validated according to the bacteriological code. *Pelagibacter,* along with *Prochlorococcus*, *and Synechococcus* are among the main representatives of the marine picoplankton, and share many characteristics with the genus *Prochlorococcus.* It also plays a major role in the Earth's carbon cycle and is one of the smallest self-replicating cells known (Giovannoni et al., 2005). The factors that regulate the metabolic requirements of SAR11 are still largely unknown. Tripp et al. (2008) reported a very unusual requirement for reduced sulfur compounds. It is hypothesized that species of the genus have been molded by evolution in a low nutrient ecosystem, such as the Sargasso Sea where it was first discovered in 1990.

Among the Fungi detected in water, many species of the ascomycotan genera *Aspergillus* were found, such as *A. clavatus, A. flavus, A. fumigatus, A. nidulans*, and *A. terreus*. *Aspergillus* is a very large genus containing around 250 species of wide geographic distribution. Its taxonomic classification is very complex and is constantly being revised. They are currently classified into seven subgenera that are subdivided into complexes of related species (Geiser et al., 2007). In general, *Aspergillus* are known as opportunistic pathogens of humans, animals and plants. They are commercially important for its capacity of producing enzymes and organic acids, and may also act as spoilage organisms. Several species produce mycotoxins, such as aflatoxins, and many other secondary metabolites (Varga et al., 2011). All the *Aspergillus* species identified in this study have been reported in the literature as pathogens of humans and animals and are commonly isolated from soil (Hedayati et al., 2007; Samson et al., 2011).

Besides *Aspergillum* species, *Laccaria bicolor, Candida albicans*, and *Cryptococcus neoformans* were identified in water. *Laccaria bicolor (Basidiomycota)* is an ectomycorrhizal fungus associated with a range of trees of the temperate and boreal forests of North America. It was the first ectomycorrhizal fungus to have its genome sequenced and is considered a model organism for symbiotic genetics studies (Martin & Selosse, 2008). The presence of typically terrestrial Fungi, such as *L. bicolor* in aquatic environments in environmental sampling has already been

reported (Hassett et al., 2019) at the genus level. Nevertheless, it might be an artifact of analytical procedures, especially in taxonomic annotation, possibly caused by the still limited knowledge we have of aquatic Fungi (Amend et al., 2019; Bärlocher & Boddy, 2016; Pagani et al., 2023). Both *Candida albicans* (Ascomycota) and *Cryptococcus neoformans* (Basidiomycota) are Fungi associated with opportunistic diseases, and are of particular concern in HIV-positive patients (Mora et al., 2012).

In coral samples, the bacterial genera *Streptomyces*, *Shewanella*, and *Mycobacterium* were the most dominant. *Streptomyces* are gram-positive filamentous actinomycete Bacteria. The genera comprise more than 700 species, commonly found in soil and decaying vegetation, and present very large genomes with high GC content (Nikolaidis et al., 2023). *Streptomyces* are known by a complex secondary metabolism, and produce the vast majority of the clinically useful antibiotics of natural origin, such as streptomycin, neomycin and chloramphenicol (Bibb, 2013). The presence of *Streptomyces* in coral samples is not a novelty, and new species have been described (Buangrab et al., 2022), as well as its potential to produce new antibiotics have been explored (Zhang et al., 2020).

Shewanella is an ubiquitous gram-negative bacterial genus of mostly aquatic Pseudomonadota. The physiological and respiratory versatility of *Shewanella* allows for its wide distribution along a range of ecological niches. *Shewanella* strains have the ability of degrading a wide variety of chemical pollutants (Fredrickson *et al.,* 2008) and may reduce a wide range of metals (Zou *et al.,* 2019). The impressive metabolic versatility of *Shewanella* species still includes the production of enzymes (Lemaire *et al.,* 2019), their use in bioenergy generation (Mukherjee *et al.,* 2020), and denitrifying activity (Deng *et al.,* 2014). Species of *Shewanella* have been previously isolated from the tropical coral genus *Favia* (Shnit-Orland et al., 2010) and deep-sea *Anthothela* coral species (Lawler et al., 2016). The aforementioned studies demonstrated that *Shewanella* plays an important role to the overall health of the host by its antibacterial properties, which provide protection from pathogenic or opportunistic Bacteria.

The metabolic capabilities displayed by the genus *Mycobacterium* in soil have already had previously described. Regarding coral, there is only one study reporting *Mycobacterium haemophilum* as the causal agent of human subcutaneous infection acquired from a coral injury in Thailand (Smith et al., 2003). Furthermore, in their review article about the emergence of mycobacteriosis in aquatic invertebrates, Davidovich et al. (2020) propose that global climate warming may be influencing microorganisms resistance and host susceptibility.

Aspergillus fungal species (mainly *A. clavatus*) prevailed in the samples of coral studied. This genus has frequently been isolated from coral, including samples from northeast Brazilian reefs (Paulino et al., 2020). Fungi are known as potential symbionts or pathogens of marine organisms, and the number of reports of fungal species associated with infections in corals have increased in frequency and severity (Góes-Neto et al., 2020). The most studied case is the aspergillosis caused by *Aspergillus sydowii.* Among the factors that may facilitate the emergence of this pathogen, increased temperatures stands out, which appears to increase the multiplication and

resistance of the microorganism and reduce host's resistance (Alker et al., 2001, Kim et al., 2006; Soler-Hurtado et al., 2016).

Paracoccidioides brasilienses represented around 16% of the Fungi sequences identified in the coral samples. *P. brasiliensis* is one of the etiologic agents of paracoccidioidomycosis (PCM), an endemic human mycosis that mainly affects Brazil (Stürme et al., 2011). On the other hand, the yeast *Scheffersomyces stipitis* (formerly *Pichia stipitis*) is commonly known for its capacity to ferment D-xylose to ethanol and has been extensively studied for its promising industrial applications (Santosh et al., 2017). To date, neither of the two Fungi, *P. brasiliensis and S. stipitis,* had been identified in association with corals, and as well as other aforementioned fungal taxa (e.g.: *Antarctomyces psychrotrophicus* and *Laccaria bicolor*), *P. brasiliensis* must be regarded as a contamination or artifactual result.

Roles and characteristics of the main Bacteria isolated of water and soil samples

Some bacterial strains isolated from water and soil samples have demonstrated the ability to degrade hydrocarbons or produce biosurfactants, which are highly relevant to bioremediation applications, especially given the island's proximity to oil basins in Brazil.

Rhodococcus rhodochrous is a Gram-positive bacterium with bioremediation potential, acting as a biodegradation agent for hydrocarbons such as toluene, octane, xylene, naphthalene, phenanthrene, pyrene, hexadecane, anthracene, eicosane, tetracosane, triacontane, and pentacontane. This species could be used in the pharmaceutical industry as a biocatalyst for pharmaceutical waste (Busch et al., 2019; Ivshina et al., 2022). Moreover, *R. rhodochrous* is able to inhibit the growth of the fungus *Pseudogymnoascus destructans*, which causes white-nose syndrome (WNS), a disease that affects bats (Lemieux-Labonté et al., 2017).

The *Nocardia farcinica* species was also able to degrade the same range of hydrocarbons biodegraded by the *R. rhodochrous* species (Rodrigues et al., 2015b). *N. farcinica* is a bacterium of great importance in causing infections in humans and, as well as other species of the genus *Nocardia*, can cause brain abscesses in immunocompromised (Galacho-Harriero et al., 2017) and non-immunocompromised patients (Song et al., 2021). In France, a significant increase in the occurrence of this species was observed between 2010 and 2014, particularly in patients who developed nocardiosis. This trend seems to correlate with the increasing use of solid organ transplantation (SOT) (Lebeaux et al., 2019).

The species *Cellulosimicrobium cellulans* has the potential to biodegrade the hydrocarbon hexadecane (Rodrigues et al., 2015b), as well as high molecular weight hydrocarbons from diesel oil (Nkem et al., 2019), including hydrocarbons from biodiesel (Bertel-Sevilla et al., 2020). Its biodegradation potential has also been demonstrated in rice cultivation experiments, showing its ability to degrade the highly selective, hormonal, and long-lasting low-toxicity herbicide known as quinclorac (QNC) while stimulating effective rice growth (Huang et al., 2021).

The species *Microbacterium lacticum* shows remarkable potential as a biodegrader of the hydrocarbon naphthalene (Rodrigues et al., 2015b). *M. lacticum* is also able to utilise

hydrocarbons (kerosene, petrol, motor oil, used oil, and crude oil) as a source of carbon and energy for the production of lysine (Ezemba, 2016), an essential amino acid that is very important for children and growing animals, as well as for the immune system. *M. lacticum* species, in combination with other species such as *Stenotrophomonas rhizophila*, *Bacillus licheniformis*, and *Calidifontibacter indicus*, are biofilm formers in the dairy industry, which is a major problem due to its spoilage potential and prevalence (Sadiq et al., 2023).

At least 17 species are known from the genus *Exiguobacterium* (Kasana & Pandey, 2018), each with the ability to grow in a variety of environments with different pH and temperature ranges. These characteristics mean that many isolates are targets for exploitation in various biotechnological and industrial applications, such as production of enzymes (protease, pullulanase, amylase, lipase), bioremediation (naphthalene, hexadecane, xylene), and biodegradation of toxic substances present in the environment, as well as stimulation of plant growth to increase agricultural productivity (Kasana & Pandey, 2018; Pandey, 2020; Rodrigues et al., 2015b).

The genus *Tistrella* is represented by only two species: *T. bauzanensis* and *T. mobilis*, which occur in high abundance in marine ecosystems. Rodrigues et al. (2015) demonstrated the biodegradation potential of *Tistrella* strains for the hydrocarbons phenanthrene, pyrene, tetracosane, naphthalene, hexadecane, and octane. *Tistrella* is known to be the only bacterium capable of producing didemnin, a cyclic depsipeptide compound with potential as an antitumour, and antiviral drug candidate. Recently, Tang et al. (2023) produced didemnin B using *Tistrella* strains and, subsequently, converted didemnin B to plitidepsin by chemical synthesis. Plitidepsin, besides being an anticancer drug, has also gained prominence as a potential agent in the treatment of COVID-19 with a Phase III clinical trial (Tang et al., 2023).

Da Silva et al. (2015) identified a group of strains of the genus *Bacillus*, including three subspecies *Bacillus subtilis* subsp. *subtilis* subgroup A, *Bacillus subtilis* subsp. *subtilis* subgroup D, and *Bacillus subtilis* subsp. *spizizenii*, with the ability to produce biosurfactants under high salinity conditions. These results have promising biosurfactant applications in saline environments, such as oil recovery, remediation of environments contaminated with oil and derivatives, cleaning of oil storage tanks, and in wastewater treatment processes. The use of Bacteria strains with a wide range of tolerance to abiotic factors, including a wide range of pH, salinity, and the presence of and petroleum compounds, is critical to the viability and productivity of strains in environmental applications, conditions that normally inactivate most synthetic surfactants (Krucon et al., 2023; Shavandi et al., 2011).

Furthermore, a comparative genetics study by Dunlap et al. (2020) suggests that the four subspecies *Bacillus subtilis* subsp. *subtilis*, *Bacillus subtilis* subsp. *spizizenii*, *Bacillus subtilis* subsp. *inaquosorum*, and *Bacillus subtilis* subsp. *estercoris* should possibly be classified as species due to the distinct production of bioactive secondary metabolites, highlighting the complexity and broad potential of this genus in biotechnology and environmental research.

Although research using DNA sequencing on environmental samples from Trindade island is still relatively scarce, there is a clear growth trend in the so-called "molecular era". Nonetheless,

to obtain deeper knowledge about the island's diverse habitats, which are unique environments, it is essential to direct more efforts towards developing projects in this direction. This information is extremely relevant, considering the uniqueness of this space, from which we still have a lot to learn.

Conclusion

In this study, we presented a comprehensive and detailed description of the main Bacteria, Archaea, and Fungi identified in soil, water, and coral samples from Trindade Island, as well as their potential biotechnological. We covered the most relevant literature and recent discoveries on those taxa. Overall, our results indicate a cryptic microbial diversity in several environments that can be influenced by anthropogenic impact, a great microbial diversity of isolates not yet identified at the species level, as well as, a promising potential use of this microbial diversity for oil bioremediation, hydrocarbon degradation, and production of biosurfactants.
Additionally, our review provide recommendations for: i) developing studies that expand our knowledge of diversity through advances in metagenomics from a spatial and temporal perspective, ii) investigating endemic taxonomic novelties, iii) identifying potential environmental threats and exploring biotechnological solutions that can contribute to the conservation of the island, and iv) studies that explore the biological potential of microbiota for biotechnological applications in various industries, including the oil industry.
As there still is a remarkable gap of our understanding of soil community ecology of Trindade island, our research group is currently conducting an integrative study of both taxonomical and functional diversity of soil microorganisms, using shotgun metagenomics, associated with highly characterized physicochemical analyses in distinct vegetational areas of this fascinating and isolated island of the South Atlantic.

Supplemental Information

- **Supplemental Figure S1**: Bar graph of Superkingdom/Kingdom (a, b), Class (c, d), Order (e, f), Family (g, h), and Species (i, j) taxonomic categories of Archaea, Bacteria, and Fungi by grouped samples.
- **Supplemental Figure S2**: Venn diagram of the categories of Phylum (a), Class (b), Order (c), Family (d), Genus (e) and Species (f) of Archaea, Bacteria and Fungi of the grouped samples.
- **Supplemental Figure S3**: Strong association network between Archaeal, Bacterial and Fungal orders and grouped samples.
- **Supplemental Data S1**: Records obtained from database searches: Scopus, Web of Science, PubMed, PubMed Central, Dimensions, and Google Scholar (PoP)
- **Supplemental Data S2**: Unique records, without DOI and duplicates
- **Supplemental Data S3**: Tables of absolute abundances by taxonomic category
- **Supplemental Data S4**: Tables of relative abundances by taxonomic category

- **Supplemental Data S5**: Absence and presence tables for Venn diagrams
- **Supplemental Data S6**: Results of PERMANOVA analyses

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Conflicts of Interest

The authors declare no conflict of interest

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1148

Figure 1

PRISMA flowchart of studies identified by database searches

This figure comprises the PRISMA flowchart of studies identified by database searches.

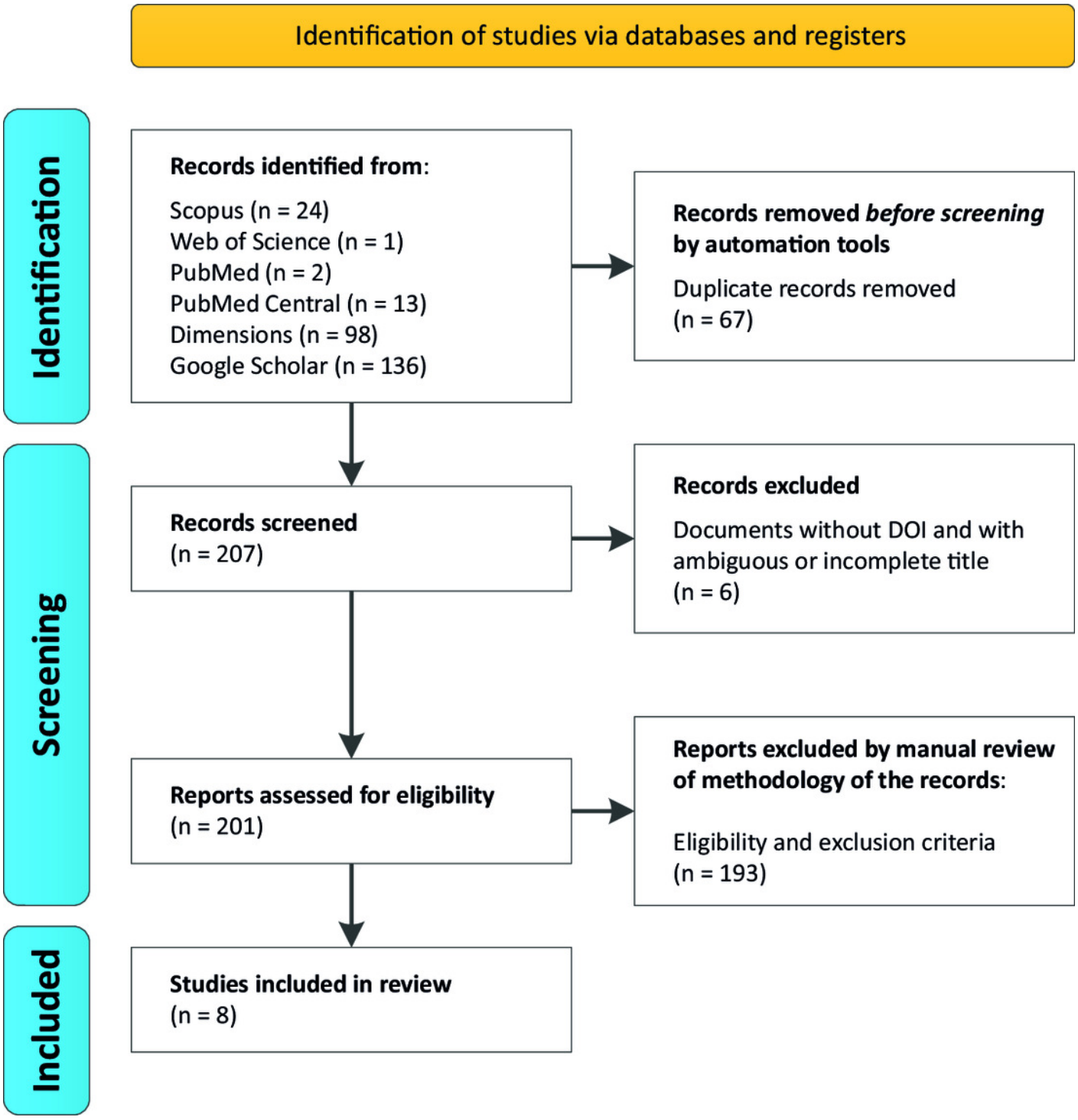
Identification of studies via databases and registers
Identification
Records identified from:
Scopus (n = 24)
Web of Science (n = 1)
PubMed (n = 2)
PubMed Central (n = 13)
Dimensions (n = 98)
Google Scholar (n = 136)
Records removed before screening by automation tools
Duplicate records removed
(n = 67)
Screening
Records screened
(n = 207)
Records excluded
Documents without DOI and with ambiguous or incomplete title
(n = 6)
Reports assessed for eligibility
(n = 201)
Reports excluded by manual review of methodology of the records:
Eligibility and exclusion criteria
(n = 193)
Included
Studies included in review
(n = 8)

Figure 2

Word cloud highlighting the profile of the articles included in the review.

This figure depicts a word cloud highlighting the profile of the articles included in the review.

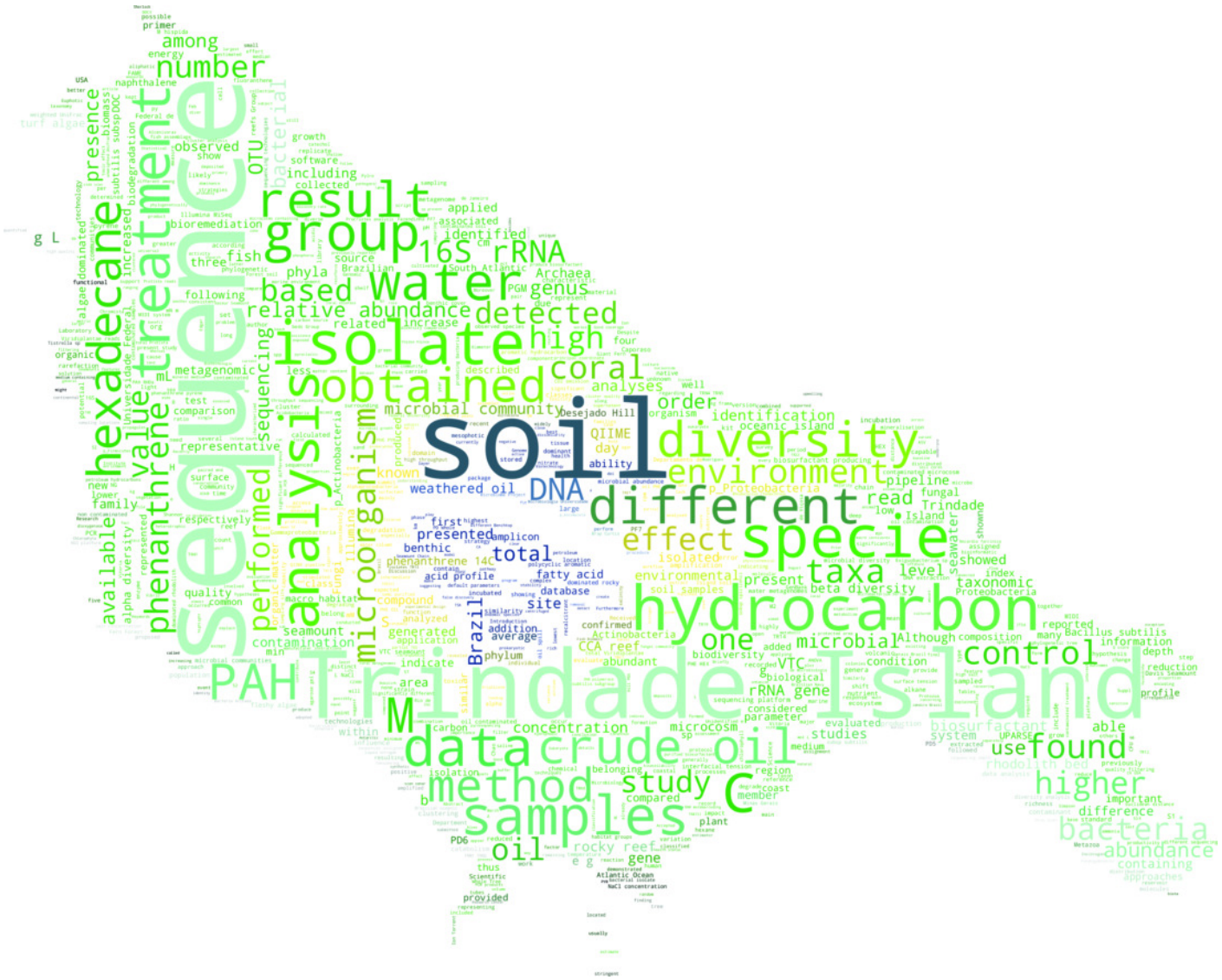

Figure 3

Map showing the locations of all types of samples analyzed in the selected articles.

This figure encompasses a map showing the locations of all types of samples analyzed in the selected articles. (1): Meirelles et al., 2015, (2): Câmara et al., 2023, (3): Rodrigues et al., 2018, (4): Morais et al., 2016, (5): Rodrigues et al., 2015b, (6): da Silva et al., 2015, (7): Pylro et al., 2014.

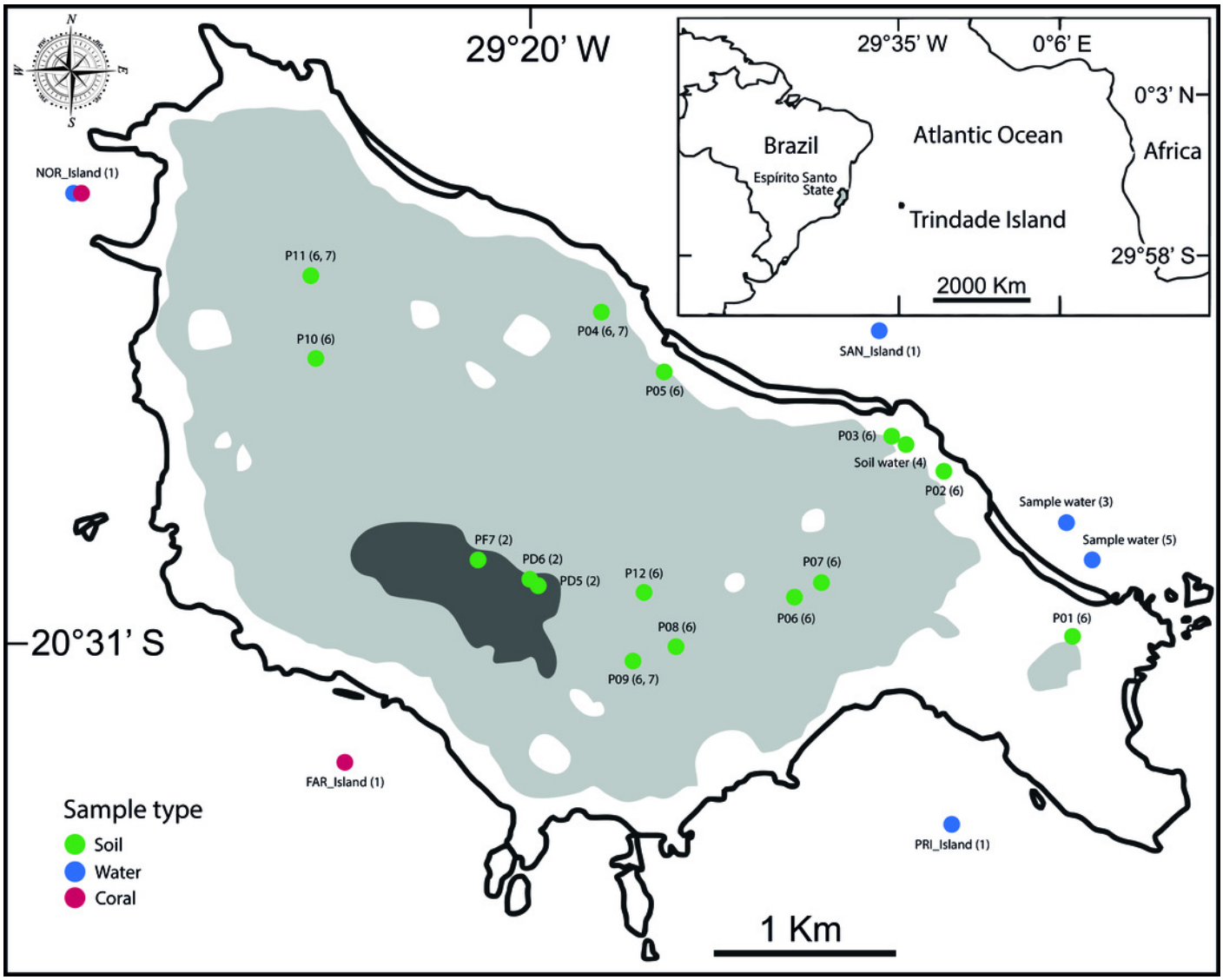

Figure 4

Taxonomic distribution of the Archaea, Bacteria, and Fungi identified and described in the samples of soil, water, and corals evaluated in the papers under analysis.

This figure shows the taxonomic distribution of the Archaea, Bacteria, and Fungi identified and described in the samples of soil, water, and corals evaluated in the papers under analysis. Phyla (a) and Genera (b) of Archaea and Bacteria, and Phyla (c) and Genera (d) of Fungi.

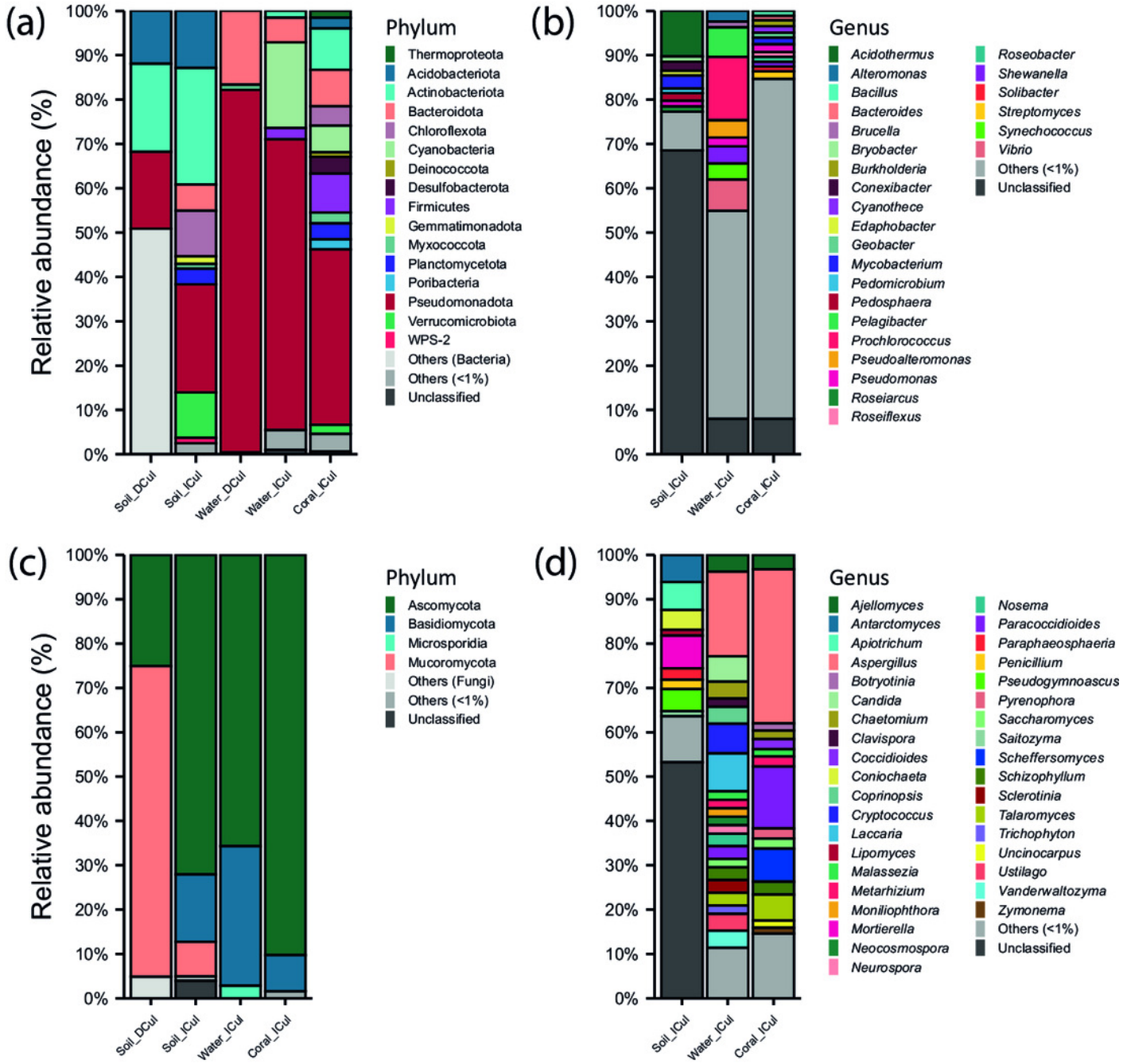
(a)
Relative abundance (%)
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
Soil_DCul
Soil_ICul
Water_DCul
Water_ICul
Coral_ICul
Phylum
Thermoproteota
Acidobacteriota
Actinobacteriota
Bacteroidota
Chloroflexota
Cyanobacteria
Deinococcota
Desulfobacterota
Firmicutes
Gemmatimonadota
Myxococcota
Planctomycetota
Poribacteria
Pseudomonadota
Verrucomicrobiota
WPS-2
Others (Bacteria)
Others (<1%)
Unclassified
(b)
Soil_ICul
Water_ICul
Coral_ICul
Genus
Acidothermus
Alteromonas
Bacillus
Bacteroides
Brucella
Bryobacter
Burkholderia
Conexibacter
Cyanothece
Edaphobacter
Geobacter
Mycobacterium
Pedomicrobium
Pedosphaera
Pelagibacter
Prochlorococcus
Pseudoalteromonas
Pseudomonas
Roseiarcus
Roseiflexus
Roseobacter
Shewanella
Solibacter
Streptomyces
Synechococcus
Vibrio
Others (<1%)
Unclassified
(c)
Relative abundance (%)
Soil_DCul
Soil_ICul
Water_ICul
Coral_ICul
Phylum
Ascomycota
Basidiomycota
Microsporidia
Mucoromycota
Others (Fungi)
Others (<1%)
Unclassified
(d)
Soil_ICul
Water_ICul
Coral_ICul
Genus
Ajellomyces
Antarctomyces
Apiotrichum
Aspergillus
Botryotinia
Candida
Chaetomium
Clavispora
Coccidioides
Coniochaeta
Coprinopsis
Cryptococcus
Laccaria
Lipomyces
Malassezia
Metarhizium
Moniliophthora
Mortierella
Neocosmospora
Neurospora
Nosema
Paracoccidioides
Paraphaeosphaeria
Penicillium
Pseudogymnoascus
Pyrenophora
Saccharomyces
Saitozyma
Scheffersomyces
Schizophyllum
Sclerotinia
Talaromyces
Trichophyton
Uncinocarpus
Ustilago
Vanderwaltozyma
Zymonema
Others (<1%)
Unclassified

Figure 5

Sharedness and uniqueness of phyla (left) and genera (right) of Archaea (a:), Bacteria (b:), and Fungi (f:) between groups of culture-independent and culture-dependent samples.

This figure presents the sharedness and uniqueness of phyla (left) and genera (right) of Archaea (a:), Bacteria (b:), and Fungi (f:) between groups of culture-independent and culture-dependent samples.

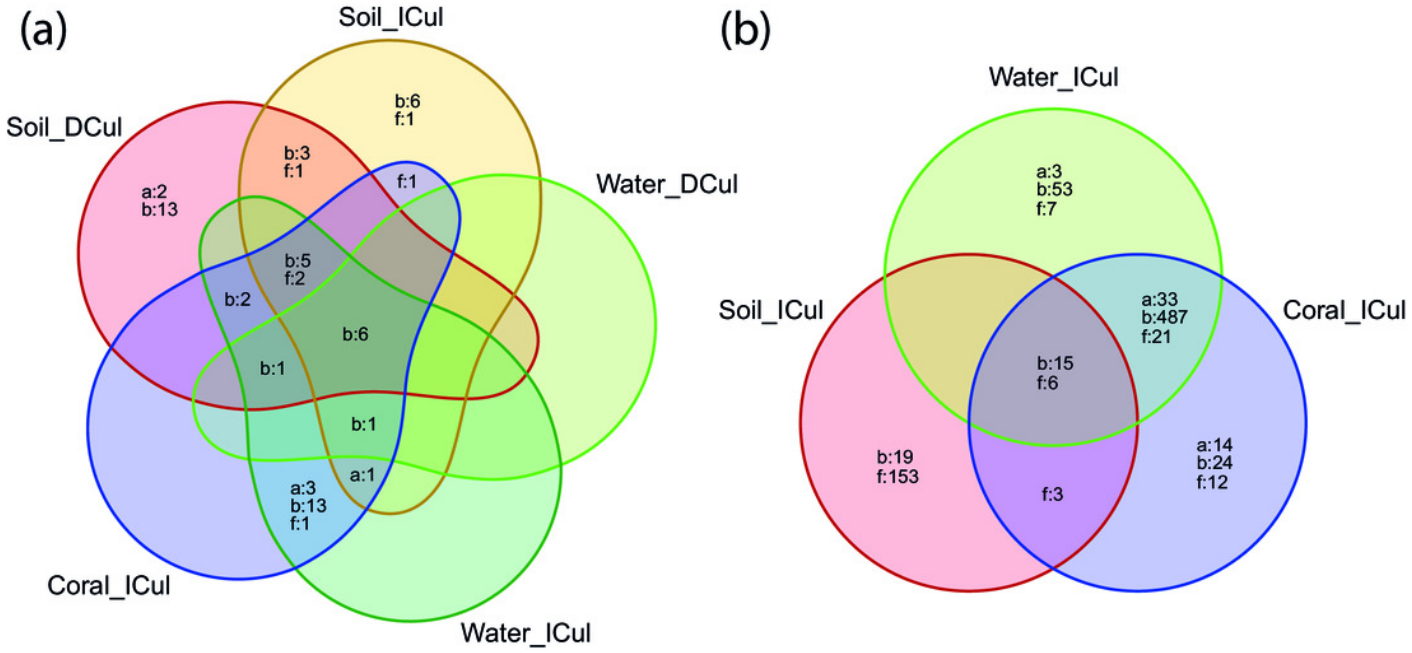

Figure 6

Alpha (a) and beta (b) diversity of culture-dependent and culture-independent samples.

This figure encompasses both alpha (a) and beta (b) diversity of culture-dependent and culture-independent samples.

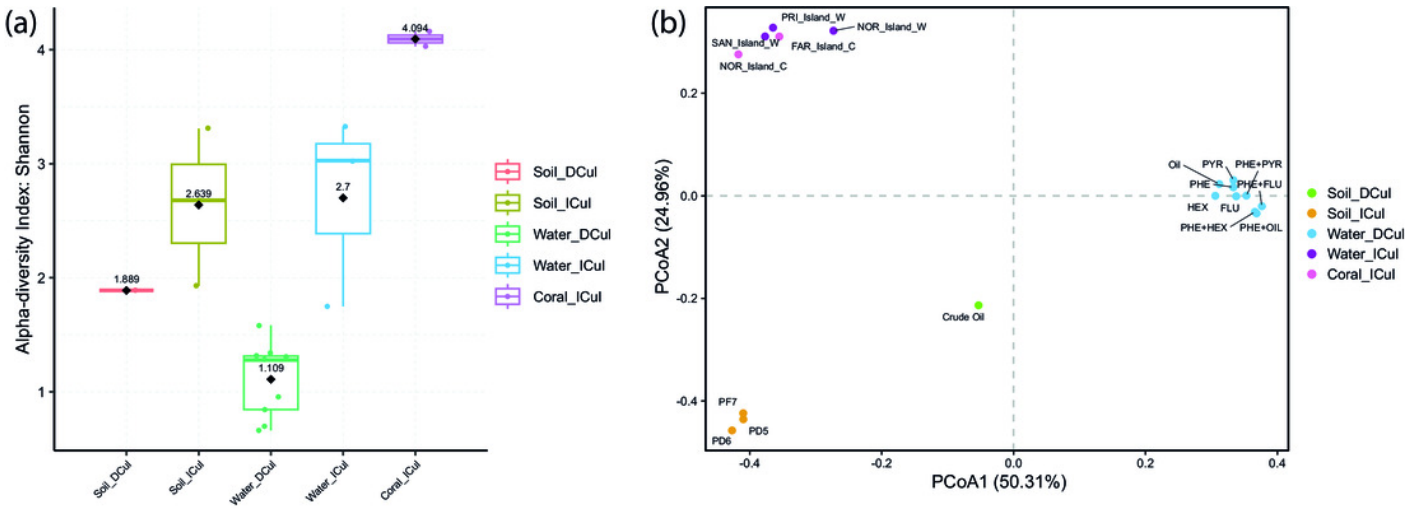

Figure 7

Network of strong associations between the phyla (a) and genera (b) of Archaea, Bacteria, and Fungi with the sample groups.

This figure depicts the network of strong associations between the phyla (a) and genera (b) of Archaea, Bacteria, and Fungi with the sample groups.

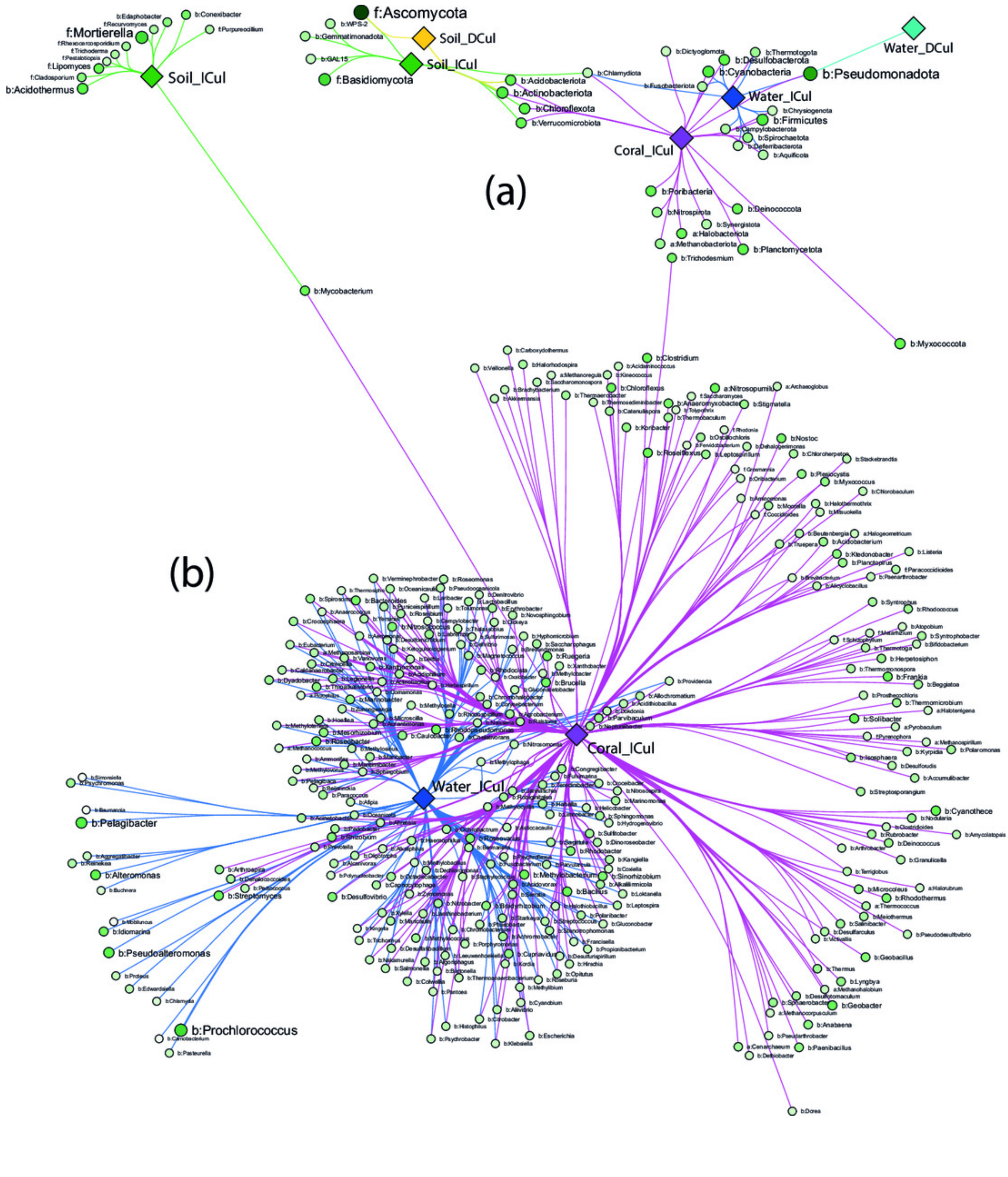
(a)
(b)
Soil_ICul
Soil_DCul
Water_DCul
Water_ICul
Coral_ICul
f:Ascomycota
f:Basidiomycota
f:Mortierella
f:Lipomyces
b:Acidothermus
b:Conexibacter
b:Gemmatimonadota
b:GAL15
b:WPS-2
b:Acidobacteriota
b:Actinobacteriota
b:Chloroflexota
b:Verrucomicrobiota
b:Chlamydiota
b:Dictyoglomota
b:Desulfobacterota
b:Thermotogota
b:Cyanobacteria
b:Pseudomonadota
b:Fusobacteriota
b:Firmicutes
b:Chrysiogenota
b:Campylobacterota
b:Spirochaetota
b:Deferribacterota
b:Aquificota
b:Poribacteria
b:Nitrospirota
b:Deinococcota
b:Synergistota
a:Halobacterota
a:Methanobacteriota
b:Planctomycetota
b:Trichodesmium
b:Mycobacterium
b:Myxococcota
b:Clostridium
b:Chloroflexus
a:Nitrosopumilus
b:Anaeromyxobacter
b:Stigmatella
b:Roseiflexus
b:Nostoc
b:Myxococcus
b:Acidobacterium
b:Bacteroides
b:Ruegeria
b:Brucella
b:Rhodopseudomonas
b:Caulobacter
b:Roseobacter
b:Mesorhizobium
b:Frankia
b:Solibacter
b:Providencia
b:Cyanothece
b:Pelagibacter
b:Alteromonas
b:Streptomyces
b:Idiomarina
b:Pseudoalteromonas
b:Prochlorococcus
b:Desulfovibrio
b:Methylobacterium
b:Bacillus
b:Sinorhizobium
b:Rhizobium
b:Lyngbya
b:Geobacter
b:Anabaena
b:Paenibacillus
b:Escherichia
b:Rhodothermus
b:Geobacillus
b:Dorea

Table 1(on next page)

Eligibility criteria for the inclusion of articles in the systematic review.

This table comprises the eligibility criteria for the inclusion of articles in the systematic review.

Table 1. Eligibility criteria for the inclusion of studies in the systematic review.

Eligibility criteria	
Sampling location	Trindade Island, Brazil
Sample type	Any substrate
Sequencing type	Shotgun metagenomics, amplicons 16S rRNA, 18S rRNA or ITS
Focus taxa	Studies must focus on the domains Bacteria, Archaea, or the kingdom Fungi
Study	Original
Exclusion criteria	
Sampling location	Studies not conducted on Trindade Island, Brazil
Sample type	Studies that do not involve substrate samples or focus on human hosts
Sequencing type	Studies not using shotgun metagenomics, or amplicons for 16S rRNA, 18S rRNA, or ITS
Focus taxa	Studies that do not focus on Bacteria, Archaea, or Fungi, or that focus on other domains/kingdoms
Study	Review articles, meta-analyses, editorials, or other non-original studies

Table 2(on next page)

Studies included in the systematic review.

This table shows the studies included in the systematic review.

1 **Table 2**. Studies included in the systematic review.

Article	Taxa studied	Substrate	Samples/Treatments	Study method	Approach	Marker gene	Sequencing platform
Meirelles et al., 2015	Archaea, Bacteria, Eukaryota (Fungi, Metazoa, Protozoa, Viridiplantae), Viruses	Water and Coral tissue	NOR_Island_W, PRI_Island_W, SAN_Island_W, FAR_Island_C, NOR_Island_C	Culture-independent (ICul)	WGS metagenomics	-	454 GS FLX Titanium
Câmara et al., 2023	Archaea, Bacteria, Eukaryota (Fungi, Metazoa, Protozoa, Chromista, Viridiplantae)	Soil	PD5, PD6, PF7	Culture-independent (ICul)	Amplicon	16S rRNA, ITS	Illumina MiSeq
Rodrigues et al., 2018	Archaea, Bacteria	Water	Water sample / Oil, FLU, HEX, PHE, PHE+FLU, PHE+HEX, PHE+OIL, PHE+PYR, PYR	Culture-dependent (DCul)	Amplicon	16S rRNA	Ion Torrent PGM
Morais et al., 2016	Archaea,	Soil	Crude Oil	Culture-	Amplicon	16S	Illumina

	Bacteria, Fungi			dependent (DCul)		rRNA, ITS	MiSeq
Rodrigues et al., 2015b	Bacteria	Water	Water sample / TRH1, TRH2, TRH3, TRH4, TRN1, TRN2, TRN3, TRN4, TRN5, TRN6, TRN7, TRN8, TRN9, TRN10, TRN11	Culture-dependent (DCul)	Amplicon	16S rRNA	MegaBACE 1000 DNA Analysis System
da Silva et al., 2015	Bacteria	Soil	P01, P02, P03, P04, P05, P06, P07, P08, P09, P10, P11, P12 / TR7, TR8, TR10, TR12, TR13, TR14, TR17, TR19, TR22, TR27, TR27II, TR35II, TR47II, TR59II	Culture-dependent (DCul)	Amplicon	16S rRNA	MegaBACE 1000 DNA Analysis System
Pylro et al., 2014	Archaea, Bacteria	Soil	P04, P09, P11	Culture-independent (ICul)	Amplicon	16S rRNA	Illumina MiSeq/Ion Torrent PGM
Câmara et al., 2022 [(a)]	Archaea, Bacteria, Eukaryota	Soil	PD5, PD6, PF7	Culture-independent (ICul)	Amplicon	16S rRNA, ITS	Illumina MiSeq

		(Fungi, Metazoa, Protozoa, Chromista, Viridiplantae)

[a] Article excluded from the discussion because it is equivalent to the research by Câmara et al. (2023).