ACTA
AMAZONICA

http://dx.doi.org/10.1590/1809-4392202403743

BIODIVERSITY AND CONSERVATION | ORIGINAL ARTICLE

Diversity hosted by moss carpets in the Amazonian forest of Amapá, new insights from DNA metabarcoding

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ABSTRACT

Bryophytes play an important role as habitats for many organisms, especially invertebrates, however, few studies have focused on understanding the cryptic ecosystems associated with them. The use of molecular tools allows for advances in diversity assessment of environmental samples. In particular, the use of DNA metabarcoding is an efficient method for detection of the DNA of rare and cryptic species, including resting stages typically undetected in morphological surveys. We used DNA metabarcoding to investigate the hidden diversity present in two moss carpets in the largest of the world's remaining rainforests, the Amazon. More specifically, our samples took place in the Brazilian state of Amapá, the least affected by anthropogenic pressures. Samples, 10 m apart, were collected under sterile conditions and eDNA was extracted. To maximize diversity coverage, three regions were sequenced (ITS2, COX1 and 16S). A total of 348 taxa were assigned from the sequences obtained, with 123 eukaryotic taxa representing five Kingdoms assigned from COX1, 64 representing four Kingdoms from ITS2 and 161 representing one prokaryotic Domain from the 16S region. A total of 38% of taxa were Fungi, 35% Bacteria and 27% non-fungal eukaryotes. The data obtained highlight the importance of moss carpets providing habitats that support diverse communities. Given the high number of unassigned sequences, the available sequence databases for Amazonian species require improvement. As the region faces multiple threats, there is an urgent need for improvements in collection, identification ability, sequencing and DNA curation. There were several assignments of disease-causing organisms, this highlights the need for monitoring changes in these under-researched habitats.

KEYWORDS: Bryophyte, High throughput sequencing, One Health, Cryptic diversity, environmental DNA, Tropical rainforest

Diversidade existente em tapetes de musgos na Floresta Amazônica do Amapá, novas abordagens com uso de DNA metabarcoding

RESUMO

Briófitas possuem um papel importante ao abrigar diversos organismos, em especial invertebrados. No entanto, poucos estudos têm focado no entendimento da diversidade críptica associada aos tapetes de musgos. O uso de ferramentas moleculares permitiu avanços nos estudos de levantamento da diversidade existente em amostras ambientais, especialmente o uso de DNA metabarcoding tem se revelado um método eficiente para detectar espécies raras ou crípticas, incluindo organismos em dormência ou encistados, geralmente ausentes em inventários morfológicos. Neste estudo utilizamos DNA metabarcoding para investigar a diversidade críptica abrigada em dois tapetes de musgos em uma comunidade localizada na maior floresta tropical do mundo – a Amazonia, no estado do Amapá. Amostras, localizadas 10 m aparte, foram coletados em condições estéreis e seu eDNA foi extraído. De forma a cobrir uma maior diversidade, três regiões foram sequenciadas (ITS2, COX1 e 16S). Um total de 348 taxa foram encontrados, sendo 123 taxa distribuídos em cinco reinos encentrados com uso de COX1, 64 taxa em quaro reinos com uso de ITS2 e 161 em um Domínio com uso de 16S. Um total de 38% dos taxa encontrados eram Fungos, 35% a Bacteria e 27% eucariotos não fúngicos. O uso de metabarcoding é uma ferramenta poderosa e mostra a importância dos musgos em prover abrigo a uma diversa comunidade. Por outro lado, o alto numero de sequencias desconhecidas sugerem que os bancos de dados para espécies amazônicas precisam de melhorias. Com a região continua sob intensas ameaças, esforços de coleta, identificação e sequenciamento de DNA precisam ser aumentados urgentemente. A alta ocorrência de organismos patogenicos demonstra a necessidade de monitoramento de mudanças que possam alterar o equilíbrio nesses ambientes ainda pouco estudados.

PALAVRAS CHAVE: Briófitas, Sequenciamento de Alto Desempenho, Saúde única, diversidade críptica, DNA ambiental, Floresta Tropical

CITE AS: Câmara, P.E.A.S.; Pujol-Luz, J.R.; Garrafoni, A.R.S.; Carvalho-Silva, M.; Alvarez, F.L.; Amorim, E.T. *et al*. 2025. Diversity hosted by moss carpets in the Amazonian forest of Amapá, new insights from DNA metabarcoding. *Acta Amazonica* 55: e55bc24374.

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INTRODUCTION

Bryophytes are the second largest group of land plants, second only to the angiosperms (Goffinet *et al.* 2009). However, they remain poorly investigated, especially in comparison with the flowering plants (Rousk & Villareal 2025). With an overall area of 8,500,000 km^2, Brazil is the largest country in South America and the fifth largest worldwide, hosting at least 892 moss species (Briofitas 2024), including 198 that are endemic to the country. Among the five phytogeographic domains in Brazil - Amazon, Cerrado, Atlantic Forest, Caatinga and Campos Sulinos (Fiaschi and Pirani (2009) the Amazon is the largest domain (~6,000,000 km^2) the most extensive of the world's remaining rainforests, and amongst the most biodiverse forests globally (Gentry 1988, Gradstein *et al.* 2001, Hopkins 2019). This phytogeographic domain houses in Brazil 182 genera and 598 species of bryophytes, second only to the Brazilian Atlantic Forest (Costa *et al.* 2011; Bryophytes 2025.

Bryophytes play important, although generally unappreciated, roles in habitat provision and shelter for many other organisms (Glime 2017, Dangar *et al.* 2024, Rousk & Villareal 2025), especially micro-invertebrates and micro-arthropods, algae, fungi, bacteria and protozoans (in turn, many of these groups are also poorly studied). Lindo and Gonzales (2010) coined the term 'bryosphere' to refer to the community that lives in association with mosses. Bryophytes are present in most terrestrial ecosystems on Earth, covering a significant proportion of available land area. They are relatively slow-growing with long lifespans, adapted to infertile areas, and have few direct consumers, parasites or pathogens (Lindo and Gonzales 2010). Commonly forming extensive ground cover, they capture organic debris and atmospheric nutrients at the surface while transforming the underlying soil microclimates and altering decomposition rates (Cornelissen *et al.* 2007).

The poikilohydric nature of bryophytes helps regulate water availability and, consequently, most physiological activities such as photosynthesis. Hydration is the most important factor influencing C balance, as well as favoring the growth of symbiotic cyanobacteria, the largest source of biological nitrogen fixation (Turetsky 2003), thereby contributing significantly to global nutrient cycles (DeLuca *et al.* 2008). Large amounts of dissolved organic carbon, nitrogen and phosphorus are released from bryophyte shoots, providing an important source of these nutrients for associated microbes (Davey and Currah 2006, Dangar *et al.* 2024). Other plants living within the bryosphere can affect C accumulation by affecting decomposition rates and soil respiration efflux (Anderson 2008). The bryosphere can account for more than 20% of the net primary productivity of the ground layer vegetation in boreal forests (Turetsky *et al.* 2012). It also contributes to soil C by producing recalcitrant litter, an important part of the upper humus layer (Jonsson *et al.* 2015) and controls decomposition by regulating temperature and moisture (Sun *et al.* 2017). The bryosphere is a major player in the global C cycle (Gornall *et al.* 2007), with its associated soil fauna playing a major role in carbon and nutrient cycles (van den Hoogen et a. 2019). Grau-Andrés (2021) considered the bryosphere to be a key driver of net primary production, nutrient cycling and decomposition. Its associated fauna influences these processes by impacting productivity through herbivory and stimulation of microbial decomposition (Schill *et al.* 2011).

The bryosphere forms an ecosystem that is usually supported by detritus or moss byproducts, containing a complex food-web involving functions ranging across herbivory, fungivory, detritivory, omnivory, coprophagy, necrophagy and opportunistic scavenging (Lindo & Gonzales 2010). The richness and abundance of its microarthropod community increases with humus produced or accumulated by the bryosphere (Lindo 2010). Approximately 300 species of ascomycetes are known to have an obligate relationship with mosses (Döbbeler 1997), while many other fungi often colonize dead and senescent portions of the moss (Davey and Currah 2006). Many invertebrates (e.g. nematodes, mites and springtails) inhabiting mosses have been associated with reducing soil nitrogen mineralization and carbon turnover (Delgado-Baquerizo *et al.* 2020). However, to date, very few studies have focused on understanding the cryptic ecosystems and diversity associated with the bryosphere, due to the fact that many of these groups are poorly understood taxonomically and their natural history and biology are often unknown. The high level of species richness and the small size of these cryptic organisms demand a high degree of taxonomic expertise, and until now, the few studies attempting to describe the bryosphere (e.g. Anderson 2006, Boeckner *et al.* 2006, Jönsson 2003) have been focused on specific groups and relied on the use of morphological approaches alone.

Elsewhere, in another poorly understood and very different environment, Câmara *et al.* (2021) illustrated the potential for the application of molecular tools in an attempt to survey the cryptic diversity associated with the Antarctic bryosphere, reporting DNA sequence assignments to 263 taxa representing five kingdoms and 33 phyla present in a single moss carpet in one of the most extreme environments on earth. There are presently no analogous studies from the much more diverse Brazilian Amazon. The use of newly available molecular biology tools is catalyzing considerable advances in the assessment of diversity in environmental samples. Amongst them, DNA metabarcoding represents an efficient method for the detection of environmental DNA (eDNA) from rare and cryptic species (Rippin *et al.* 2018; Ruppert *et al* 2019; Câmara *et al.* 2020, 2021), including organisms in resting stages that are typically not detected in traditional morphological surveys. The use of DNA metabarcoding has proved a very successful survey tool when applied to polar environments (e.g. Câmara *et al.* 2020, 2021, 2022a; Carvalho-Silva *et al.* 2021) and also in some other tropical regions (Câmara *et al.* 2022b). The approach has been successfully used in the Amazon region for monitoring fish (Vergueiro and Almeida-Val 2024), mammals (Sales *et al.* 2020; Marin *et al* 2024), air (Mota de Oliveira *et al.* 2022) and lakes (Bevilaqua *et al.* 2020). A review of the advances achieved using metabarcoding of neotropical protists was provided by Ritter *et al.* (2021). Mendes *et al.* (2024) highlight the relevance of and potential for using DNA metabarcoding for monitoring biodiversity in the Amazon. However, to date, this methodology has not been used to assess diversity associated with the bryosphere in tropical regions. In the current study, we provide a first descriptive report using DNA metabarcoding to investigate eDNA diversity present in Amazonian moss carpets.

MATERIALS AND METHODS

Study area

Seven states contribute to the Brazilian Amazon (Amazon, Pará, Acre, Roraima, Rondonia, Amapá and Tocantins), amongst which the state of Amapá hosts six major vegetation types included in the Amazon biome - shrub vegetation, mangroves, sandy coastal plains (known as restingas), lagoons and wetlands, palm forests and, predominantly, tropical rainforests (Drummond *et al.* 2008). Amapá is considered one of the least damaged or exploited of the Amazonian states, with more than 72% of its territory protected in conservation units (Drummond *et al.* 2008) and relatively low levels of anthropogenic change (CI-BRASIL 2007, 2009).

Collections were performed in Amapá municipality, at the community of Piquiá (1º52’17’’N; 50º54’21” W; Figure 1), located ca. 26 km from Amapá city. The community includes about 19 inhabitants that practice artisanal agriculture (https://www.amapa.ap.gov.br/municipio/dados-geograficos), located within the Amapá National Forest, a protected area designated for sustainable use. Collections were conducted on a primary *terra-firme* rainforest located in the conservation unit Floresta Estadual do Amapá (FLOTA/AP). Created by law on July 12th, 2006, the FLOTA/AP currently encompasses 10 municipalities (Amapá, Calçoene, Ferreira Gomes, Marzagão, Oiapoque, Pedra Branca do Amaparí, Porto Grande, Pracuúba, Serra do Navio, Tartarugalzinho). Comprising 23,694.0 km^2 of discontinuous forest (Figure 1), its management focuses on sustainable use involving the exploitation of renewable natural resources, ensuring the continuity of environmental resources and ecological processes, and maintaining biodiversity and other ecological attributes in an economically viable way.

Moss carpet sampling and species identification

Two carpets of the moss *Ectropothecium leptochaeton* (Schwägr.) W.R. Buck*,* referred to as AP1 and AP2, were chosen on the basis of being simple to locate and identify, and of forming carpets and clumps likely to provide microhabitats for other organisms. The carpets were growing on dead logs in the understory.

Identification was confirmed by mounting material on slides and examination under a compound microscope and using appropriate taxonomic literature. Two individual carpet samples of about 5 cm^2, separated by about 10 m, were collected under sterile conditions using sterilized gloves and immediately sealed in sterile plastic bags (Whirl Pack®/US). These were then kept frozen (-20 °C) until DNA extraction under sterile conditions at the Cryptogamic Botany Laboratory of the University of Brasilia.

DNA extraction and sequencing

Total DNA was extracted using the FastDNA Spin Kit for Soil (MPBIO, Ohio, USA), following the manufacturer’s instructions. DNA quality was analyzed by agarose gel electrophoresis (1% agarose in 1 x Tris Borate-EDTA) and

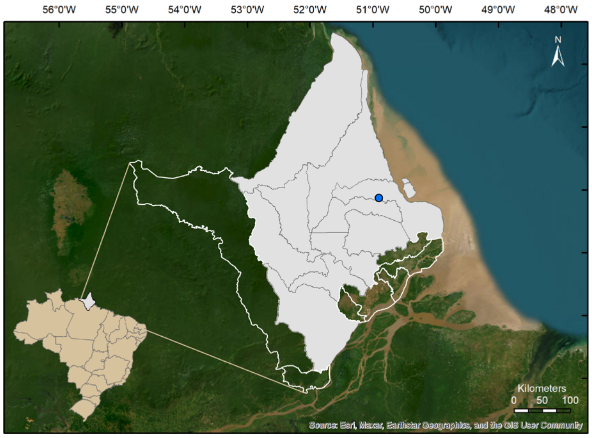

Figure 1. Map showing the collection location (blue dot) in Amapá state and in relation to the overall country of Brazil.

then quantified using the Quant-iT ™ PicoGreen dsDNA Assay (Invitrogen). We selected the internal transcribed spacer 2 (ITS2) of the nuclear ribosomal DNA (Chen *et al.* 2010; Richardson *et al.* 2015; Câmara *et al.* 2022) as a barcode, as it has been widely used to identify a diverse range of eukaryotic organisms including fungi, animals, protozoans, chromists and plants (Ruppert *et al.* 2009), has proved effective in recent studies of Antarctic samples (Câmara *et al.* 2020, 2022; Rosa *et al.* 2020; Ogaki *et al.* 2021; Carvalho-Silva *et al.* 2021) and has been applied in a tropical study (Camara *et al.* 2023). PCR-amplicons were generated using the primers ITS3 and ITS4 (White *et al.* 1990). For Bacteria and Archaea, we used the 16S rRNA gene V3-V4 region (Herlemann *et al.* 2001; Klindworth *et al.* 2013), and for Metazoa we selected the marker Cox1 marker using the primers described by Folmer *et al.* (1994). Sequencing was carried out commercially using high throughput sequencing by Macrogen Inc. (South Korea) on an Illumina MiSeq sequencer (3×300 bp).

Data analyses and taxon assignment

Quality analysis was carried out using BBDuk v. 38.87 in BBmap software (Bushnell 2014) with the following parameters: Illumina adapters removing (Illumina artefacts and the PhiX Control v3 Library); ktrim ¼ l; k ¼ 23; mink ¼ 11; hdist ¼ 1; minlen ¼ 50; tpe; tbo; qtrim ¼ rl; trimq ¼ 20; ftm ¼ 5; maq ¼ 20. The remaining sequences were imported to QIIME2 version 2021.4 (https:// qiime2.org/) for bioinformatics analyses (Bolyen *et al.*, 2019). The qiime2-dada2 plugin was used for filtering, dereplication, turn paired-end fastq files into merged, and remove chimeras, using default parameters (Callahan *et al.*, 2016).

For eukaryotes, taxonomic assignments of Amplicon Sequence Variants (ASVs) (Callahan *et al.* 2017), were determined using the qiime2-feature-classifier (Bokulich *et al.* 2018) classify-sklearn against different databases; with a sequence similarity threshold was 98%. We aimed to maximize resolution by obtaining data from specific and curated databases for the specific target groups For ITS2: in order to consult more than one database, ASVs were first classified against the curated PLANiTS2 database (Banchi *et al.* 2020). After this step, ASVs that remained unclassified were filtered and classify-sklearn classified against the curated UNITE Eukaryotes ITS database version 8.3 (Abarenkov *et al.* 2020). Finally, the remaining unclassified ASVs were filtered and aligned against the filtered NCBI non-redundant nucleotide sequences (nt) database (October 2021) using BLASTn (Camacho *et al.* 2009) with default parameters; the nt database was filtered with the following keywords: "ITS1", "ITS2", "Internal transcribed spacer", and "internal transcribed spacer". Taxonomic assignments were performed using MEGAN6 (Hudson *et al.* 2016). The same approach was used for COX1 but using only the MIDORI database (Leray *et al.* 2018).

Bacterial taxonomic assignments were determined for amplicon sequence variants (ASVs) of the 16S rRNA gene using the qiime2-feature-classifier (Bokulich *et al.* 2018) classify-sklearn against SILVA 138 Ref NR 99 (Quast *et al.* 2013). Only ASVs classified to taxa with current valid nomenclature according to the International Code of Nomenclature of Prokaryotes (ICNP) were accepted in the taxa table (Oren and Garrity, 2021, 2022; Oren *et al.* 2022; Göker and Oren, 2023). In instances of nomenclatural disagreements between the SILVA138 database and the ICNP, the latter nomenclature was used. It is generally accepted that the 16S rRNA gene can reliably assign sequences to the genus level, therefore no species names are reported in this study. ASVs classified as uncultured or numbers, for example, were grouped into higher taxonomic levels with recognized classification. The denomination "Candidatus" indicates a taxonomic status for uncultured bacteria according to the International Code of Nomenclature of Bacteria (Murray and Stackebrandt,1995; Oren and Göker, 2023).

It is important to note that assignment of an ASV does not confirm the actual presence of a taxon, but rather its associated DNA sequences available in the databases consulted (i.e., we refer to ASVs by their database-matched taxonomic assignments, though these do not confirm organismal presence). However, for simplicity, we henceforth refer to the assigned ASVs as "taxa" (Rippin *et al.* 2018, Câmara *et al.* 2022, 2024). Many factors, including extraction, PCR and primer bias, can affect the number of reads obtained (Medinger *et al.*, 2010), and may lead to misinterpretation of absolute abundances (Weber *et al.*, 2013). However, Giner *et al.* (2016) concluded that such biases did not affect the proportionality between reads and cell abundance, implying that more reads are linked with higher abundance (see also Deiner *et al.*, 2017; Hering *et al.*, 2018). Consequently, for comparative purposes, we consider reads as a proxy for relative abundance (Deiner *et al.* 2017, Hering *et al.* 2018; Câmara *et al.* 2021a, b, 2022, 2024; Rosa *et al.* 2021; Carvalho-Silva *et al.* 2021). Rarefaction curves were generated using the software PAST 3.26 (Hammer *et al.* 2001).

All descriptions of geographical distributions were based on information obtained from available databases such as GBIF (www.gbif.org), Catalogue of Life (https:// www.catalogueoflife.org/), Tropicos (www.tropicos.org), AlgaeBase (www.algaebase.org) and the relevant literature cited. Classification and systematic ranks for kingdoms and phyla followed Ruggiero *et al.* (2015).

RESULTS

We assigned 348 ASVs in this study. For the COX1 region, a total of 354,672 sequences were generated, of which 140,016 remained after quality control. These were assigned to 123 taxa representing five Kingdoms (Chromista, Fungi, Metazoa, Protozoa and Viridiplantae), with 8,389 sequences (about 6%)

remaining unknown (Figure 2, Table 1). The ITS2 region generated a total of 252,645 sequences, of which 188,062 remained after quality control, which were assigned to 64 ASVs representing four Kingdoms (Chromista, Fungi, Metazoa and Viridiplantae). The 16S region generated a total of 142,078 sequences of which 95,443 remained after quality control. These were assigned to 200 ASVs, all representing the Domain Bacteria. Overall, the assigned ASVs represented 161 taxa (Table 1).

Overall, a total of 348 ASVs were assigned for all markers, with Bacteria being the most diverse, followed by Fungi (Figure 3). For more details on specific groups, see supplemental material.

Rarefaction curves for all samples and markers reached a plateau, suggesting that our sampling represented the local diversity based on the collections made (Figure 2).

Fungi

Representing 38% of all DNA reads, a total of 70 fungal ASVs were detected using both markers (ITS and COI), representing *Ascomycota*, *Basidiomycota*, *Chytridiomycota* and *Rozellomycota*, in rank abundance. The most abundant taxa (>1,000 DNA reads) were, in rank order, *Xylaria* sp., *Endomelanconiopsis* sp., *Arthrocladium fulminans*, *Verticillium nonalfalfae*, *Penicillium* sp., *Leohumicola verrucosa* and *Sporothrix schenckii*, all representatives of *Ascomycota*. Members of *Xylaria* are widely distributed across temperate, subtropical and tropical regions worldwide. The genus includes species that are typically associated with wood, fallen fruit or seeds, fallen leaves or petioles, and termite nests (Pan *et al.* 2022), consistent with its high abundance in this study. *Endomelanconiopsis* is a genus recently erected by Rojas *et al.* (2008), which is related to endophytic species present in the leaves of tropical plants such as *Theobroma cacao* and *Heisteria concinna* in Panama, although it has also been isolated from soil in Europe. The genus *Arthrocladium* includes nonsporulating dematiaceous (black) fungi, which are commonly rotten wood saprophytes (Diallo *et al.* 2017). However, *A. fulminans*, the third most abundant fungal taxon detected in the moss carpet, has been reported as the only species of the genus considered an opportunistic fungus able to infect humans, and has been involved in the fatal infection of an immunocompromised patient (Egenlauf *et al.* 2015). Diallo *et al.* (2017) also reported *A. fulminans* as the cause of septic arthritis and osteomyelitis in an immunosupressed patient. *Sporothrix schenckii* is the agent of opportunistic mycosis sporotrichosis, which is regarded as an environmentally acquired or zoonotically transmitted disease (Sharma *et al.* 2022; Chieosilapatham *et al.* 2023). The largest public health impact of *S. schenckii* infections in humans to date has been in outbreaks in workers involved in farming activities (CDC 1984, CDC 1988, Dixon *et al.* 1991). Currently, in a context of disease emergence at the interface between environmental, human and animal health - One Health - the genus member *Sporotrix brasiliensis* is associated with major epidemics of skin infections in felines, acquired

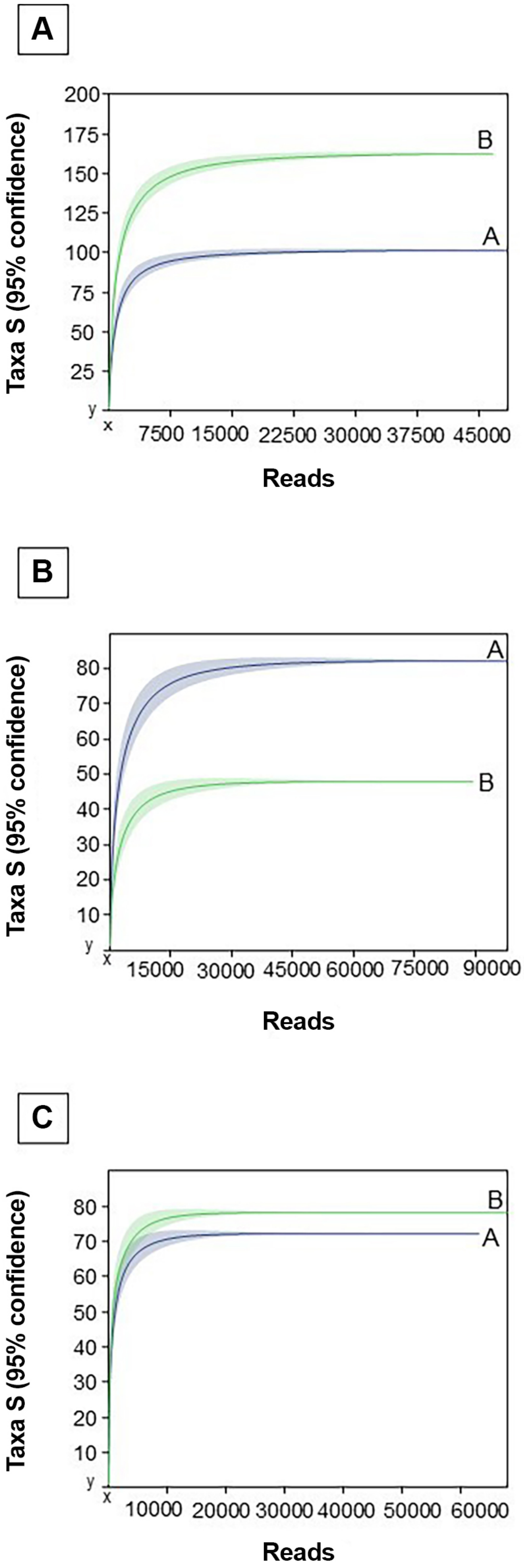

Figure 2. Rarefaction curves obtained from all samples: **A**) COI, **B**) ITS and **C**) 16S. Line A represent sample AP01 and B represent AP02. Parallel lines represent 95% confidence intervals.

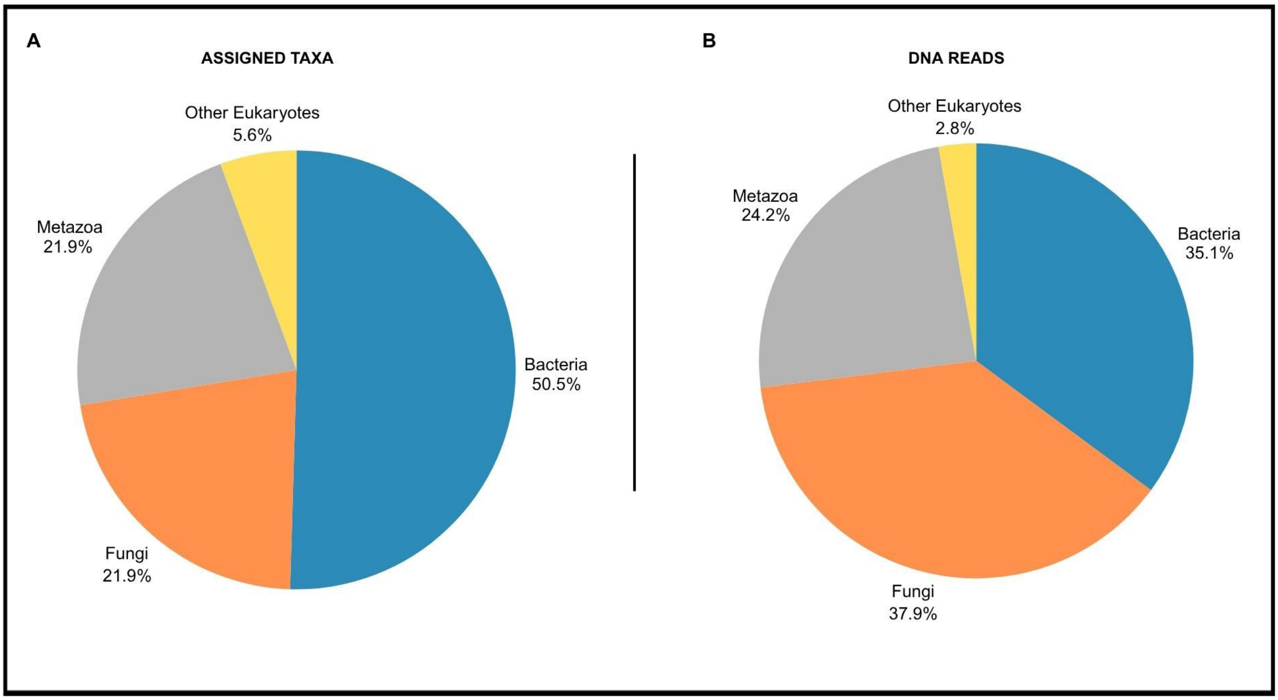

Figure 3. Diversity of assigned taxa and abundance based on sum DNA reads for both markers and both localities. **A**) Diversity (assigned taxa) and **B**) Abundance (DNA reads). Other Eukaryotes includes Chromista, Protozoa and Viridiplantae.

Table 1. DNA reads and associated ASV taxa from two moss carpets sampled in Floresta Estadual do Amapá, Brazil. Hab/Distr. indicates the habitat and distribution according to the following categories: C = Cosmopolitan, F = Freshwater, M = Marine, T = terrestrial, B = Brackish. As = Asia, Au = Australia, Eu = Europe, NA = North America, NZ = New Zealand, In = India. Al = Atlantic Islands, Ac = Arctic, Neo = Neotropical, PA = Palearctic, Pa = Pacific, Oc = Oceania, SAfr = South Africa, Nea = Nearctic, Hol = Holarctic, Af = Africa, Sat = South Atlantic, Inv = Invasive, IP = Indo Pacific. AP01 and AP02 indicate the sampled sites, * indicates a taxon not previously recorded from Brazil.

ASV associated taxa	Hab/ Distr.	Marker	AP01	AP02	TOTAL
KINGDOM CHROMISTA					
Phyllum Bacillariophyta	C/W	ITS2	774	93	867
Eunotia bilunaris	F/W	COI	429	1,468	1,897
Gomphonema clevei	F/W	COI	09	0	09
Phylum Ciliophora	C/W	ITS2	179	19	198
Class Spirotrichea	C/W	ITS2	0	07	07
Fam Oxytrichidae	C/W	ITS2	226	110	336
Apocarchesium sp.*	C/As, Eu	ITS2	23	15	38
Vorticella sp.	C/W	ITS2	100	64	164
Phylum Ochrophyta					
*Spumella lacusvadosi**	F/NZ	COI	0	936	936
*Schizocladia ischiensis**	M/Eu	COI	0	51	51
Phylum Oomycota					
Globisporangium iwayamae	C/W	COI	0	84	84
Globisporangium spinosum	C/W	COI	116	0	116
Pythium aphanidermatum	C/W	COI	58	550	608
Pythium viniferum	C/W	COI	0	119	119
KINGDOM FUNGI		ITS2	533	193	746
Phyllum Ascomycota					
Class Leotiomycetes	C/W	ITS2	81	25	106
Class Sordariomycetes	C/W	ITS2	203	316	519
Order Capnodiales	C/W	ITS2	04	29	33
Order Chaetothyriales	C/W	ITS2	544	53	597
Order Pleosporales	C/W	ITS2	106	101	207
Order Saccharomycetales	C/W	ITS2	13	0	13
Order Xylariales	C/W	ITS2	24	0	24
Fam. Chaetosphaeriaceae	C/W	ITS2	103	0	103
Fam. Nectriaceae	C/W	ITS2	22	0	22
Absconditella rubra	C/W	ITS2	03	0	03
Acremoniopsis suttoniae	C/W	ITS2	23	0	23
Annulohypoxylon atroroseum	C/W	ITS2	73	229	302
Annulohypoxylon sp.	C/W	ITS2	334	0	334
Arthrocladium fulminans	C/W	COI	2,038	3,418	5,456
Ascosphaera celerrima	C/W	ITS2	20	0	20
Aspergillus puulaauensis	C/W	COI	0	488	488
Cercospora nicotianae	C/W	COI	0	30	30
Cladophialophora bantiana	C/W	COI	100	113	213
Cladophialophora sp.	C/W	ITS2	47	0	47
Cladosporium cladosporioides	C/W	COI	67	0	67
Cladosporium sphaerospermum	C/W	COI	148	10	158
Clonostachys sp.	C/W	ITS2	05	0	5
Colletotrichum tamarilloi	C/W	COI	180	0	180
Cyphellophora sp.	C/W	ITS2	75	0	75
Endomelanconiopsis sp.	C/W	ITS2	3,430	49,633	53,063
Fusarium decemcellulare	C/W	COI	09	10	19
Leohumicola verrucosa	C/W	COI	1,344	0	1,344

Table 1. Continued

ASV associated taxa	Hab/ Distr.	Marker	AP01	AP02	TOTAL
Madurella mycetomatis	C/W	COI	459	0	459
Mycoleptodiscus sp	C/W	ITS2	0	20	20
Myxotrichum deflexum	C/W	COI	0	25	25
Neopestalotiopsis clavispora	C/W	ITS2	0	20	20
Ophiostoma himal-ulmi	C/W	COI	315	0	315
Penicillium sp.	C/W	ITS2	1,408	2,744	4,152
Phyllopsora corallina	C/W	COI	25	0	25
Plectosphaerella sp.	C/W	ITS2	39	0	39
Pyrenochaetopsis leptospora	C/W	ITS2	40	0	40
Rhinocladiella sp.	C/W	ITS2	45	0	45
Scytalidium sp	C/W	ITS2	101	26	127
Sporothrix schenckii	C/W	COI	1,095	230	1,325
Sydowia polyspora	C/W	COI	20	0	20
Veronaea sp.	C/W	ITS2	40	0	40
Verticillium nonalfalfae	C/W	COI	981	3,170	4,151
Xenoroussoella triseptata	C/W	ITS2	03	0	03
Xylaria sp.	C/W	ITS2	86,566	30,103	116,669
Phyllum Basidiomycota					
Class Agaricomycetes	C/W	ITS2	35	0	35
Order Agaricales	C/W	ITS2	51	0	51
Order Polyporales	C/W	ITS2	16	05	21
Order Sebacinales	C/W	ITS2	0	22	22
Order Tremellales	C/W	ITS2	20	08	28
Order Unilacrymales	C/W	ITS2	11	08	19
Fam. Auriculariaceae	C/W	ITS2	134	0	134
Fam. Polyporaceae	C/W	ITS2	318	163	481
Amanita thiersii	C/W	COI	243	458	701
Basidiodendron alni	C/W	ITS2	68	40	108
Basidiodendron sp.	C/W	ITS2	310	0	310
Bjerkandera sp.	C/W	ITS2	13	0	13
Coprinellus disseminatus	C/W	ITS2	26	07	33
Coprinellus micaceus	C/W	COI	14	0	14
Ganoderma ecuadorense	C/W	ITS2	139	66	205
Ganoderma sp.	C/W	ITS2	309	110	419
Lactarius deliciosus	C/W	COI	36	0	36
Tremella fuciformis	C/W	COI	0	71	71
Xylodon flaviporus	C/W	ITS2	12	0	12
Xylodon sp.	C/W	ITS2	15	0	15
Phyllum Chytridiomycota					
Order Chytridiales	C/W	ITS2	14	0	14
Order Rhizophydiales	C/W	ITS2	0	07	07
Dendrochytridium crassum	C/W	ITS2	10	0	10
Terramyces sp.	C/W	ITS2	39	46	85
Phylum Rozellomycota	C/W	ITS2	148	219	367
Class Rozellomycotina	C/W	ITS2	0	20	20
KINGDOM METAZOA					
Phylum Arthopoda					
Class Arachnida					
*Argiope macrochoera**	T/In	COI	40	0	40
Draconarius sublutulentus	T/Pa	COI	0	205	205
Loxosceles sp. *CRBA-LX2003*	T/W	COI	0	39	39
Cheiracanthium uncinatum	T/Pa	COI	0	16	16
Oppiella nova	T/W	COI	107	0	107
Leptonetela hangzhouensis	T/As	COI	39	233	272
Class Copepoda					
Cletocamptus sp.	C/W	ITS2	0	55	55
Class Insecta					
Azteca chartifex	T/Neo	COI	69	0	69
*Brachyusa concolor**	T/Pa	COI	09	0	09
*Chimarra butmasensis**	T/Oc	COI	930	6,007	6,937
*Culicoides subschultzei**	T/SAf	COI	0	521	521
*Drosophila pseudoobscura**	T/Oc, As, Nea	COI	15	0	15
*Epiophlebia superstes**	T/As	COI	0	17	17
*Hydaticus continentalis**	T/Hol	COI	28	25	53
*Hypaurotis mushaellus**	T/Pa	COI	48	0	48
Liriomyza sativae	T/W	COI	207	117	324
*Larentioides cacothemon**	T/SAfr	COI	17	0	17
Lutzomyia castanea	T/Neo	COI	0	202	202
Lutzomyia robusta	T/Neo	COI	3,639	8,129	11,768
*Mycalesis visala**	T/Pa	COI	0	22	22
Notozulia entreriana	T/Neo	COI	17	0	17
*Oeneis uhleri**	T/Nea	COI	700	1,411	2,111
*Paratonkinacris vittifemoralis**	T/Pa	COI	111	351	462
*Praon volucre**	T/Pa	COI	25,426	0	25,426
*Sergentomyia inermis**	T/Af	COI	0	14,657	14,657
*Therophilus festivus**	T/Pa	COI	2842	0	2842
*Trechosiella laetula**	T/Af	COI	220	0	220
Class Malacostraca					
*Portunus trituberculatus**	M/As	COI	0	118	118
*Scopelocheirus schellenbergi**	M/As, SAt	COI	0	67	67
Class Thecostraca					
Amphibalanus eburneus	M/Inv	COI	223	0	223
Phylum Annelida					
Allonais inaequalis	F, T/W	COI	680	0	680
Hemienchytraeus sp.	T/W	ITS2	274	0	274
*Hydroides ezoensis**	M/IP	COI	44	0	44
Phylum Cnidaria					
Amphicaryon peltifera	M/Neo	COI	59	427	486
Craterastrea levis	M/In, PA	COI	144	355	499
Cyclocanna producta	M/Hol, Neo	COI	71	676	747
Zanclea sessilis	M/PA	COI	53	0	53
Phylum Chordata					
*Kantaka brevidorsalis**	F/In	COI	0	115	115
*Strix aluco**	T/Hol, Af	COI	0	27	27
Phylum Echinodermata					
Tropiometra carinata	M/Neo, SAfr	COI	12	0	12
Phylum Gastrotricha					
Chaetonotus jaceki	F/PA	COI	0	118	118
Chaetonotus persimilis	F/PA	COI	331	0	331
Turbanella ambronensis	M/Hol	COI	0	242	242
Turbanella hyalina	M/Hol	COI	25	0	25
Turbanella mustela	M/PA	COI	09	469	478

Table 1. Continued

ASV associated taxa	Hab/ Distr.	Marker	AP01	AP02	TOTAL
Phylum Ichthyosporea	C/W	ITS2	07	0	07
Phylum Mollusca					
Class Bivalvia					
Mactra antiquata	M/As	COI	561	1,188	1,749
Mactra chinensis	M/As	COI	0	91	91
Mytilus edulis	M, B/Eu	COI	0	22	22
Periglypta puerpera	M/Af, As	COI	0	73	73
Class Gastropoda					
Conus acutangulus	M/In, Pa	COI	65	0	65
Conus obscurus	M/In, Pa	COI	151	194	345
Conus moluccensis	M/In, Pa	COI	0	196	196
*Deroceras laeve**	T/NA, Eu	COI	0	14,657	14,657
Geomalacus anguiformis	T/Eu	COI	0	43	43
Helminthoglypta talmadgei	T/NA	COI	48	216	264
Lophiotoma brevicaudata	M/In, Pa	COI	26	240	266
Lottia argrantesta	M/NA	COI	0	342	342
Nipponacmea nigrans	M/PA, As	COI	17	95	112
Mysticarion hyalinus	T/PA, As, Au	COI	50	0	50
Turris cristata	M/As	COI	81	0	81
Phylum Platyhelminthes					
Caenoplana coerulea	T/Nea, PA, Oc	COI	14	24	38
Stenostomum leucops	F/PA, Neo	COI	0	2,162	2,162
Stenostomum sp.	F/PA, Neo	ITS2	11	31	42
Phylum Porifera					
Haliclona pigmentifera	M/In, Au	COI	0	22	22
Phylum Rotifera					
Adineta vaga	F/Nea, Neo PA, Af	COI	149	0	149
Brachionus calyciflorus	F/C	COI	0	12	12
Macrotrachela quadricornifera	F/Nea, PA, Af,	COI	82	52	134
Synchaeta stylata	F/Nea, Neo, PA, Af,	COI	10,261	6,064	16,325
Synchaeta tremula	F/Nea, Neo, PA, Af,	COI	6,382	9,061	15,443
KINGDOM PROTOZOA					
Phyllum Choanoflagellata					
*Monosiga brevicollis**	M/Eu, NA	COI	1,159	320	1,479
Phylum Discosea					
*Cochliopodium marrii**	F/NA	COI	300	258	558
*Cochliopodium pentatrifurcatum**	F/NA	COI	227	0	227
KINGDOM VIRIDIPLANTAE			144	53	197
Phyllum Chlorophyta					
Auxenochlorella protothecoides	F/Eu, NA, Al	COI	0	186	186
Dictyochloropsis sp	F, T/W	ITS2	118	27	145
*Jaagichlorella roystonensis**	F/As, Eu	COI	0	48	48
Phyllum Bryophyta					
Callicostella sp.	T/Neo	ITS2	45	822	867
Ectropothecium leptochaeton	T/Neo	ITS2	684	4,205	4,889
Phylum Magnoliophyta					
*Plantago maxima**	T/As, Eu	COI	0	145	145
Phylum Rodophyta					
Gloiopeltis compressa	M/As	COI	0	80	80
UNKOWN EUKARYA		ITS2	89	34	123
UNKOWN EUKARYA		COI	1,633	6,756	8,389
Total			**98,276**	**89,773**	**188,049**
DOMAIN BACTERIA					
Phylum Abditibacteriota					
Abditibacterium	A	16S	1,460	3,294	4,754
Phylum Acidobacteriota	C	16S	178	674	852
Paludibaculum	C	16S	125	150	275
Blastocatella	C	16S	11	92	103
Geothrix	C	16S	9	14	23
Candidatus_Solibacter	C	16S	0	15	15
Fam. Vicinamibacteraceae	C	16S	0	10	10
Fam. Pyrinomonadaceae	C	16S	21	134	155
Order Blastocatellia	C	16S	0	3	3
Order Acidobacteriales	C	16S	12	0	12
Order Vicinamibacterales	C	16S	0	67	67
Class Holophagae	C	16S	0	49	49
ClassVicinamibacteria	C	16S	0	93	93
Phylum Actinomycetota (Actinobacteriota)	C	16S	357	1,260	1,617
Iamia	C	16S	43	19	62
Ilumatobacter	C	16S	0	78	78
Acidothermus	C	16S	20	28	48
Blastococcus	C	16S	0	6	6
Geodermatophilus	C	16S	32	0	32
Angustibacter	C	16S	46	0	46
Virgisporangium	C	16S	0	10	10
Pseudonocardia	C	16S	0	233	233
Fam. Lamiaceae	C	16S	14	27	41
Fam. Sporichthyaceae	C	16S	2	0	2
Fam. Nitriliruptoraceae	C	16S	27	0	27
Fam. Microbacteriaceae	C	16S	0	7	7
Fam. Nitriliruptoraceae	C	16S	20	0	20
Fam. Propionibacteriaceae	C	16S	0	6	6
Fam. Pseudonocardiaceae	C	16S	0	6	6
Fam. Streptomycetaceae	C	16S	5	0	5
Fam. Bacteroidia	C	16S	0	41	41
Fam. Chitinophagaceae	C	16S	44	48	92
Fam. Saprospiraceae	C	16S	22	21	43
Order Actinomarinales	C	16S	0	153	153
Order Gaiellales	C	16S	82	575	657
Phylum Armatimonadota	C	16S	0	194	194
Chthonomonas	C	16S	0	43	43
Fam. Fimbriimonadaceae	C	16S	0	58	58
Order Armatimonadales	C	16S	0	93	93

Table 1. Continued

ASV associated taxa	Hab/ Distr.	Marker	AP01	AP02	TOTAL
Phylum Bacteroidota	C	16S	423	866	1,289
Aurantisolimonas	C	16S	0	45	45
Ferruginibacter	C	16S	0	17	17
Parasediminibacterium	C	16S	0	11	11
Phaeodactylibacter	C	16S	0	8	8
Rubidimonas	C	16S	0	86	86
Siphonobacter	C	16S	241	189	430
Dyadobacter	C	16S	0	35	35
Fluviicola	C	16S	93	212	305
Antarcticibacterium	C	16S	0	63	63
Sphingobacterium	C	16S	21	29	50
Fam. Hymenobacteraceae	C	16S	0	8	8
Order Chitinophagales	C	16S	0	12	12
Order Flavobacteriales	C	16S	0	15	15
Order Sphingobacteriales	C	16S	65	56	121
Order Sphingobacteriales	C	16S	0	57	57
Order Sphingobacteriales	C	16S	0	23	23
Class Bacteroidia	C	16S	3	0	3
Phylum Bdellovibrionota	C	16S	134	181	315
Peredibacter	C	16S	129	152	281
Bdellovibrio	C	16S	5	29	34
Phylum Chloroflexota (Chloroflexi)	C	16S	689	1,039	1,728
Litorilinea	C	16S	38	79	117
Chloronema	C	16S	215	359	574
Chloroflexia	C	16S	0	3	3
Fam. Roseiflexaceae	C	16S	12	0	12
Fam. Ktedonobacteraceae	C	16S	44	61	105
Order Thermomicrobiales	C	16S	82	162	244
Class Anaerolineae	C	16S	51	60	111
Class Dehalococcoidia	C	16S	59	91	150
Class Ktedonobacteria	C	16S	15	64	79
Phylum Cyanobacteriota (Cyanobacteria)	C	16S	105	479	584
Microseira	C	16S	25	0	25
*Oscillatoria*_PCC-6304	C	16S	8	14	22
*Kamptonema*_PCC-6407	C	16S	0	12	12
*Scytolyngbya*_XSP1	C	16S	0	2	2
Phylum Cyanobacteriota (Cyanobacteria)	C	16S	105	479	584
*Phormidium*_SAG_37.90	C	16S	18	0	18
*Phormidesmis*_ANT.LACV5.1	C	16S	0	16	16
*Pseudanabaena*_PCC-7429	C	16S	0	8	8
Sericytochromatia	C	16S	0	48	48
Fam. Leptolyngbyaceae	C	16S	0	227	227
Order Oxyphotobacteria	C	16S	0	5	5
Chloroplast	C	16S	54	147	201
Phylum Candidatus Dependentiae	C	16S	691	945	1636
Fam. Vermiphilaceae	C	16S	322	363	685
Order Babeliales	C	16S	369	582	951
Phylum Desulfobacterota	C	16S	102	84	186
Citrifermentans	C	16S	58	61	119
Class Desulfuromonadia	C	16S	44	23	67
Phylum Elusimicrobiota	C	16S	48	83	131
Class Elusimicrobia	C	16S	48	55	103
Phylum Bacillota (Firmicutes)	C	16S	163	303	466
Lysinibacillus	C	16S	36	43	79
Tyzzerella	C	16S	0	9	9
Veillonella	C	16S	0	15	15
Fam. Hungateiclostridiaceae	C	16S	0	8	8
Order Oscillospirales	C	16S	127	228	355
Phylum Gemmatimonadota	C	16S	31	99	130
Gemmatimonas	C	16S	17	62	79
Roseisolibacter	C	16S	0	18	18
Fam. Gemmatimonadaceae	C	16S	14	19	33
Phylum Candidatus Latescibacterota	C	16S	103	100	203
Phylum Myxococcota	C	16S	357	263	620
Myxococcus	C	16S	96	0	96
Sandaracinus	C	16S	116	75	191
Fam. Myxococcaceae	C	16S	64	90	154
Fam. Myxococcaceae	C	16S	0	13	13
Class Polyangia	C	16S	17	20	37
Order Polyangiales	C	16S	64	65	129
Phylum Planctomycetota	C	16S	613	954	1567
Fimbriiglobus	C	16S	0	27	27
Gemmata	C	16S	29	0	29
Pirellula	C	16S	341	344	685
Schlesneria	C	16S	22	179	201
Candidatus_Nostocoida	C	16S	0	72	72
Fam. Phycisphaeraceae	C	16S	22	0	22
Fam. Gemmataceae	C	16S	61	98	159
Fam. Pirellulaceae	C	16S	76	73	149
Fam. Pirellulaceae	C	16S	0	65	65
Order Tepidisphaerales	C	16S	0	10	10
Class Planctomycetes	C	16S	62	86	148
Phylum Pseudomonadota (Proteobacteria)	C	16S	41,474	33,237	74,711
Roseomonas	C	16S	0	9	9
Asticcacaulis	C	16S	45	36	81
Brevundimonas	C	16S	2	2	4
Caulobacter	C	16S	27	39	66
Reyranella	C	16S	0	19	19
Psychroglaciecola	C	16S	15	0	15
Labrys	C	16S	0	45	45
Methylopilaceae	C	16S	7	0	7
Allorhizobium-Neorhizobium-Pararhizobium-Rhizobium	C	16S	40,313	31,734	72,047
Pseudolabrys	C	16S	0	20	20
Variibacter	C	16S	0	53	53

Table 1. Continued

ASV associated taxa	Hab/ Distr.	Marker	AP01	AP02	TOTAL
Amaricoccus	C	16S	0	5	5
Flavimaricola	C	16S	32	55	87
Altererythrobacter	C	16S	0	47	47
Sphingomonas	C	16S	0	16	16
Sphingopyxis	C	16S	0	16	16
Cellvibrio	C	16S	78	114	192
Escherichia-Shigella	C	16S	34	0	34
Acidibacter	C	16S	9	29	38
Pseudohongiella	C	16S	23	0	23
Agitococcus_lubricus_group	C	16S	0	69	69
Pseudomonas	C	16S	0	20	20
Steroidobacteraceae	C	16S	5	0	5
Ahniella	C	16S	155	78	233
Arenimonas	C	16S	166	147	313
Candidatus_Captivus	C	16S	100	150	250
Candidatus_Ovatusbacter	C	16S	39	0	39
Fam. Hyphomonadaceae	C	16S	130	15	145
Fam. Rhodanobacteraceae	C	16S	0	19	19
Fam. Acidiferrobacteraceae	C	16S	150	242	392
Fam. Neisseriaceae	C	16S	0	13	13
Order Micavibrionales	C	16S	43	0	43
Order Rhizobiales	C	16S	76	158	234
Order Rickettsiales	C	16S	4	0	4
Class Alphaproteobacteria	C	16S	21	43	64
Class Gammaproteobacteria	C	16S	0	39	39
Class Gammaproteobacteria	C	16S	0	5	5
Phylum Verrucomicrobiota	C	16S	1,046	2,113	3,159
Chthoniobacter	C	16S	45	75	120
Prosthecobacter	C	16S	310	707	1017
Roseimicrobium	C	16S	18	0	18
Candidatus_ Xiphinematobacter	C	16S	0	6	6
Fam. Parachlamydiaceae	C	16S	0	8	8
Fam. Chthoniobacteraceae	C	16S	466	924	1,390
Fam. Methylacidiphilaceae	C	16S	0	33	33
Fam. Opitutaceae	C	16S	7	13	20
Fam. Pedosphaeraceae	C	16S	0	36	36
Fam. Pedosphaeraceae	C	16S	200	309	509
Class Verrucomicrobiae	C	16S	0	2	2
Phylum Candidatus Eremiobacterota (WPS-2)	C	16S	272	148	420
Phylum Patescibacteria (not valid for ICNP)	C	16S	309	572	881
Parcubacteria	C	16S	0	21	21
Candidatus_Azambacteria	C	16S	47	0	47
Candidatus_Kaiserbacteria	C	16S	0	47	47
Candidatus_Moranbacteria	C	16S	0	41	41
Candidatus_Yanofskybacteria	C	16S	12	0	12
Phylum Patescibacteria (not valid for ICNP)	C	16S	309	572	881
Candidatus_ Zambryskibacteria	C	16S	0	30	30
Order Saccharimonadales	C	16S	153	387	540
TOTAL			93,454	84,096	177,641

in the environment or in contact with other animals, with repercussions in hundreds of human cases of zoonotic origin in South America (Rossow *et al.* 2020). The species found in this study in Amapá has already been associated with zoonotic transmission in Belém, Pará (Silva *et al.* 2022), which should raise an alert element for public health in this northern region of Brazil. *Verticillium nonalfalfae* is a phytopathogenic species and one of the most problematic hop (*Humulus lupulus*) diseases due to its high virulence and ability to cause severe annual yield losses by infecting entire hop fields (Jeseničnik *et al.* 2022). Members of the genus *Penicillium* occur globally in many different environments, ecosystems and habitats, including soil and plant surfaces and tissues, and are known to play an important ecological role as decomposers (Kirk *et al.* 2011). *Penicillium* has been reported as an abundant taxon associated with the moss species *Campylopus introflexus* (Repečkienė *et al.* 2015). *Leohumicola verrucosa* was first reported in soils from lowbush blueberry fields in Canada; however, this fungus appears to have a broad distribution, including in soil from Puerto Rico and Panama (Hambleton *et al.* 2005).

Bacteria

With ca. 35% of all assigned taxa, the bacterial phyla representatives assigned in the present study are similar to those in other reports of moss-associated microbiota (Bragina *et al.*, 2012; Ishak el al., 2023, Câmara *et al.* 2023). However, the samples from Amapá contained a low diversity with high dominance of the phylum Pseudomonadata. A single taxon contributed 75.5 % of all ASVs, belonging to the *Allorhizobium-Neorhizobium-Pararhizobium-Rhizobium* group, which are closely related nitrogen-fixing bacteria. This group has previously been observed in association with mosses, although cyanobacteria are generally regarded as the primary nitrogen-fixing microbe in moss-associated microbiota (Chen and Nelson, 2022). Cyanobacteriota represented only 0.61% of all reads and, amongst the classic genera of nitrogen-fixing cyanobacteria, only the genus *Oscillatoria* was detected. The second most abundant taxon was *Abditibacterium*, a heterotrophic and oligotrophic bacterium originally isolated from Antarctic soils (Tahon *et al.* 2018). However, sequences belonging to this genus are commonly detected in samples from extreme environments. All reads assigned to this ASV belonged to this taxon in the phylum Abdibacteriota, a phylum not previously reported in association with mosses.

The low diversity of the assigned bacterial community suggests that the host moss is inhabiting or providing a harsh environment. The predominance of nitrogen-fixing bacteria and the presence of the uncommon phylum Abditibacteriota suggests an environment with low nutrient availability, which may be a feature of epiphytic ecosystems.

Chromista, Metazoa, Protozoa and Viridiplantae

The four Kingdoms together contributed 27% of all DNA reads (individualy, 90% Metazoa; 5% Viridiplantae; 4% Chromista; 1% Protozoa). The majority of assigned sequences represent widespread taxa and some are poorly known organisms, (see Suppl. Mat.). Pathogens such as *Globisporangiun* and *Pythium* (water mold), are parasitic organisms which attack a wide range of economically important plants including soybeans, cucurbits, cotton, papaya, peanuts, tomato, tobacco, cabbage, maize and can also infect humans (Calvano *et al*. 2011). Also, Ichthyosporea are pathogens of fish, amphibians, birds and mammals (Glockling *et al*. 2013). *Lutzomyia* and *Sergentomyia* (both abundant) can potentially transmit diseases such as leishmaniosis.

The host moss species

Ectropothecium leptochaeton is not listed as occurring in the state of Amapá by Moura *et al*. (2024), although they do list it as occurring in the neighboring state of Pará. However, Oliveira-da-Silva *et al*. (2020) included this species in their checklist for Amapá state. Species identification was done by the main author with the use of proper literature and confirmed by the DNA data obtained.

DISCUSSION

Ou study aimed to use DNA metabarcoding for asking hidden diversity associated with moss carpets in a fragment of Amazon Rainforest. A total of 348 taxa were assigned from the sequences obtained, with 123 eukaryotic taxa representing five Kingdoms assigned from COX1 marker, 64 representing four Kingdoms from ITS2 marker and 161 representing one prokaryotic Domain from the 16S region. Our results suggested a highly diverse community associated with the sampled moss carpets, including exotic and potentially dangerous taxa.

In studies such as this one is important to keep in mind that the assignment of eDNA does not confirm the actual presence of viable organisms or propagules. Furthermore, the use of different DNA markers yields different diversity outcomes, while assignments are strongly dependent on the quality and completeness of consulted databases. In particular, the presence of apparently exotic taxa may simply mean that the local species is not present in the database consulted, while records based on very low numbers of DNA reads could represent false positives (Ficetola 2016). However, we cannot fully rule out the possibility that some taxa may have a much wider distribution than previously thought. The presence of DNA assigned to marine species may be a result of the relatively close proximity of the sampling site to the ocean (ca. 35 km), as wind can move aerosols, small droplets and particles inland. It could also, again, be a result of freshwater relatives not being present in the consulted databases, with assignments then inevitably being to the closest available species. Notably, Brazil hosts most of the freshwater species of Porifera globally, about 260 (Batista *et al*. 2007), but the large majority of these are not represented in DNA databases. It is also important to note in studies like ours, is that other confounding sources of contaminant DNA can result from human activity, such as food and waste from settlements that may originate far from the study location. Unassigned taxa may represent species absent from the consulted databases, including those that have yet to be sequenced, or currently undescribed species.

Unfortunately, few studies focusing on communities associated with moss carpets using DNA metabarcoding are available, hampering more meaningful comparisons. The only two studies we are aware of have found several thousands of OTUs, although they have used different markers and sampled different habitats. Ritter *et al*. (2018) obtained 6,625 OTUs for prokaryotes - fungi and bacteria (16S) and 15,840 OTUs for eukaryotes (18S) from Amazon soil and litter communities. Mota de Oliveira *et al*. (2022) got 4,209 OTUs, mostly of Fungi, from air samples collected 300m high, above the Amazon forest canopy, using only the ITS marker. Although they sampled air and not moss carpets, we expect that a percentage of what is found associated with the bryosphere reaches the carpets by air, the so-called diaspore rain (Sundberg 2013), however how organisms actually circulate in Amazonian air and mosses are still poorly understood.

The abundance of assignments to certain disease-causing organisms like the fungi *Arthrocladium fulminans*, associated with fatal infections in immunosupressed humans, *Sporothrix schenckii*, responsible for causing human and animal sporotrichosis and the plant pathogenic group Oomycota (e.g. *Globisporangium* and *Pythium*) is notable. This highlights the importance of further investigating that the role that moss carpets may play in providing natural microhabitats for some potentially dangerous microorganisms.

CONCLUSIONS

eDNA metabarcoding has proven to be a powerful tool to determine the diversity contained on moss carpets. The use of different markers in future studies could give further insights on various groups of organisms poorly represented in our study. Our data also indicate that available databases for Amazonian species remain poor and inadequate for diversity studies. More extensive sampling and expansion across different regions within the Amazon are also required. Clearly, with the multiple threats currently facing the Amazon region, urgent improvements are required in collecting, identification ability and expertise, sequencing and DNA curating.

ACKNOWLEDGEMENTS

We thank Dr. Luciano Pereira from Universidade Estadual do Amapá for his splendid support. The authors acknowledge funds provided by CNPq. Peter Convey is funded by NERC core funding to the British Antarctic Survey 'Biodiversity, Evolution and Adaptation' Team.

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RECEIVED: 27/10/2024
ACCEPTED: 25/07/2025
ASSOCIATE EDITOR: Thaise Emilio

DATA AVAILABILITY: The data that support the findings of this study are available, upon request, from the corresponding author.

AUTHOR CONTRIBUTIONS:
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ALVAREZ, F.L.: Formal Analysis.
AMORIM, E.T.: Investigation.
BARRETO, C.C.: Investigation.
ANDRADE LIMA, J.R.P.: Investigation.
CONVEY, P.: Investigation, Writing – original draft, Writing – review & editing.
ROSA, L.H.: Investigation, Formal analysis.

SUPPLEMENTARY MATERIAL

Câmara *et al.* Diversity hosted by moss carpets in the Amazonian forest of Amapá, new insights from DNA metabarcoding

TAXONOMIC AND GEOGRAPHICAL DISCUSSION

Chromista: The majority of assigned sequences are widespread taxa but, among the new records it is notable that *Spumella lacusvadosi* is a New Zealand species, while other members of the genus are widespread and include species already reported from Brazil such as *S. dinobryonis* (Bicudo *et al.* 2003). The peritrich genus *Vorticella* contains 82 widespread species (Su *et al.* 2011), whereas the closely related *Vorticella* segregate, *Apocarchesium*, includes only two species, *A. rosettum* from Japan and *A. arndti* from Europe (Norf and Foissner 2010). These are extremely difficult to differentiate without the analysis of DNA, so it is highly plausible that more species exist (Su *et al.* 2011).

Amongst the Oomycota, pathogens such as *Globisporangiun* (a segregate of *Phytium*) can attack a range of important food plants. *Pythium* (water mold), is also a parasitic organism that attacks a wide range of economically important plants including soybeans, cucurbits, cotton, papaya, peanuts, tomato, tobacco, cabbage, maize and can also infect humans (Calvano *et al.* 2011).

Metazoa:

Phylum Arthopoda

Within the Class Arachnida, the species *Argiope macrochoera* originates from India, but representatives of the genus are widespread globally with more than 88 species described (Platnick 2012). The genus *Draconarius* currently comprises 271 species distributed from Central Asia to Japan in the east and Thailand in south, with their highest diversity in China (Xu *et al.* 2008). *Loxosceles* is a widespread genus, with more than 100 species, 30 reported from South America (Vetter, 2008). *Cheiracanthium uncinatum* is an endemic species from Korea, but the genus is widespread with more than 200 species. *Leptonetela hangzhouensis* is a member of a genus is restricted do China, and is an endemic species from Shanghai (Gloor *et al* 2019). *Oppiella nova* is a mite representing a cosmopolitan genus with more than 50 described species (Seniczak 1975) and has been recorded extensively in Brazil (Oliveira *et al.* 2017).

The only copepod representative assigned (*Cletocamptus*) is widespread and common in Brazil (Gómez 2007).

Within the Class Insecta, *Azteca chartifex* is a neotropical ant, representing a genus that is endemic to tropical America (Longino 2007). The beetle genus *Brachyusa* includes eight species and has a Holarctic distribution. The species assigned here occurs exclusively in Europe, but was represented by <10 reads. The caddisfly species *Chimarra butmasensis* occur in the Vanuatu Islands in the South Pacific Ocean (Oceania), but the genus *Chimarra* is the most speciose amongst the Trichoptera with around 950 species known globally (Blahnik & Andersen 2022). In an analogous fashion, the hematophagous biting midge *Culicoides subschultzei* occurs in the Afrotropical region but the genus itself is cosmopolitan and widely distributed globally, and is the most diverse in the Ceratopogonidae (Diptera) with 1,368 known species (Mendez-Andrade & Ibánez-Bernal, 2023). The family Drosophilidae currently includes around 4,400 species globally and the genus *Drosophila*, with more than 1,600 species, is also cosmopolitan. Around 900 species of drosophilids are recorded in the Neotropical region (Valadão *et al.*, 2019), the species *D. pseudoobscura* has been recorded only in the USA and China (O'Grady & De Salle, 2018). The dragonfly *Epiophlebia superster* is endemic to Japan. There are only three described species in this genus, all of which are distributed in the Eastern Palearctic Region (Buthan, China and Japan). Bybee *et al.* (2021) in a study of the phylogeny and classification of Odonata using targeted genomics, note that the family Aeshnidae, with several species common in Brazil, is closely related to the Epiophlebiidae. The dytiscid diving beetle *Hydaticus continentalis* has a Holarctic distribution (North America to Russia) but, again, the genus itself (156 species) is cosmopolitan, with many species recorded in South America, mainly in the northern parts of the continent. Currently, the butterfly *Chrysozephyrus mushaellus* (Matsumura, 1938) includes two subspecies in China and Taipei. This genus includes around 56 species found in the west of the Palearctic region and in the Oriental region, however the wider family Lycaenidae is cosmopolitan and there are more than 420 species in Brazil alone (Duarte *et al.*, 2021). The cosmopolitan leaf-mining fly genus *Liriomyza* (Diptera: Agromyzidae) currently contains more than 400 species worldwide. In Brazil, *Liriomyza sativae* is an important pest in agriculture and is widely distributed and economically important, as it causes damage to at least 14 plant families, especially Solanaceae, Cucurbitaceae, Asteraceae and Fabaceae (Ferreira *et al.*, 2017). The geometrid moth genus *Larentioides* is monotypic and *L. cacothemon* (another example of a species with a low number of – 17 – reads in this study) is endemic to South Africa. However, the Geometridae is a cosmopolitan family with representatives abundant worldwide and it is one of the most speciose families in the Lepidoptera, with around 24,000 known species. The Neotropical region hosts the highest species richness with ca 6,595 recorded species (Rajaei *et al.*, 2022). The phlebotomine sand fly genus *Lutzomyia* is characteristic of the New World, comprising around 400 species, 122 of which have been recorded in the Amazon region of Brazil (Gil *et al.*, 2009). *Lutzomyia castanea* occurs in Peru and Venezuela and *Lutzomyia robusta* can be found in the inter-Andean valleys in Peru and Ecuador (Galatti *et al.*, 1995). The genus *Sergentomyia* is cosmopolitan and there are records of its occurrence in northern Brazil, but *S. inermis* is restricted to the south of the Afrotropical region. The brush-footed butterfly genus *Mycalesis* (201 species) has distribution records in the Palearctic, Oriental, Afrotropical and Australian regions, but *Mycalesis visala* occurs exclusively in the Oriental region. The genus *Oeneis* (58 species) has a wide distribution in the Holarctic region (Nearctic+Palearctic). *Oeneis uhleri* occurs exclusively in the Nearctic region. The Nymphalidae are the largest family of butterflies, with more than 6,000 described species, widely distributed globally and around 850 species of nymphalids are known in Brazil (Shirai *et al.* 2019). The monotypic spittlebug genus *Notozulia* occurs in the Neotropical Region and *N. entreriana* reaches the extreme north of Brazil (Fidelis *et al.*, 2021). The grasshopper genus *Paratonkinacris* (5 species) is restricted to China, however, the Acrididae are cosmopolitan and in South America there are about 1,620 species representing 436 genera. In Brazil alone there are 567 species of 196 genera (Costa *et al.*, 2015). Braconid wasps of the genus *Praon* (circa 70 species) have a predominantly Holarctic distribution, with a few records of tropical species. There are some records of the genus from south-eastern Brazil. However, *P. volucre* has distribution records only in the Nearctic and Palearctic regions. The genus *Therophilus* (around 56 species) is cosmopolitan and there are records of species in south-eastern Brazil, but *T. festivus* is endemic from India. *Trechosiella laetula* is endemic from South Africa. The ground beetles (carabid beetles), with more than 40,000 species, can be found in practically every habitat in the world other than the high polar regions (Jasmim *et al.*, 2024), and many species occur in Brazil.

Within the Class *Malacostraca, Portunus trituberculatus* (gazami crab) is a Asian species widely used as food, however the genus includes about 13 species, ranging from New Jersey (USA) to Rio Grande do Sul in southern Brazil (Branco *et al.* 2002) and five species (*P. anceps, P. ordwayi*, *P. rufiremus, P. spinicarpus* and *P. spinimanus*) have been reported from Brazil, including from the state of Amapá (Cintra *et al.* 2003). *Scopelocheirus schellenbergi* has been reported from Puerto Rico and (Kilgallen & Lowry 2015). Within the Class *Thecostraca, Amphibalanus eburneus* (ivory barnacle) is originally from North America and the Caribbean but has been recorded from Brazil. It is an invasive species easily transported on ship hulls and in ballast water (Farrapeira *et al.* 2010).

Phylum Annelida

Allonais inaequalis tropical freshwater annelid associated with macrophytes and reported from the Brazilian states of São Paulo, Mato Grosso and Rondonia (Gomes *et al.* 2017). *Hemienchytraeus* is a widespread terrestrial genus with 23 species, *H. stephensoni* being recorded from Brazilian Atlantic rainforest (Christoffersen 1979, Schmelz & Collado 2012). *Hydroides ezoensis* is a marine annelid originally from Asia but considered as invasive species (Faasse *et al.* 2020); in Brazilian waters four species of this genus have been reported (*H. diramphus, H. plateni, H. brachyacanthus* and *H. gairacensis*) from the south to the north-east of the country (de Assis *et al.* 2009, Schwan *et al.* 2016).

Phylum Cnidaria

All cnidarians assigned here are marine species and only two of them - *Amphicaryon peltifera* and *Cyclocanna producta* - have been reported from the Neotropical Region previously (Martell-Hernández *et al.* 2014), few species of *Zanclea* are found in Brazil (Migotto, 1996; Boero *et al.* 2000).

Phylum Chordata

Strix aluco (tawny owl) is a Eurasian species but other members of the genus are common in Brazil, including the motted owl (*S. virgata*) and the black-banded owl (*S. hulula*), which are both commonly found in Amazon forest and Amapá (Konig *et al.* 2009). The freshwater fish assigned is a member of Cyprinidae originating in India, but this is the largest family of freshwater fishes and includes some widely used as food (e.g. carp) that are cultivated in aquaculture. Garcia *et al.* (2004) demonstrated that, during floods, exotic Cyprinidae can easily spread from tanks to local rivers.

Phylum Echinodermata

The marine species *Tropiometra carinata* (elegant feather star) is commonly found throughout the Brazilian coast (Messing 2019).

Phylum Gastrotricha

The freshwater species *Chaetonotus jaceki* and *C. persimilis* are only reported from the Palaeartic region, but the genus is the most speciose amongst gastrotrichs and many representatives are found in Brazil (Kisielewski, 1991, Garraffoni & Araújo, 2020, Salgado *et al*, 2022). The three *Turbanella* species assigned are marine species and distributed in the Northern Hemisphere, but there is one species of the genus reported from Uruguay - *Turbanella corderoi* Dioni, 1960 - and other members of the family are found in Brazil (Campos & Garraffoni, 2019)

Phylum Ichthyosporea

This is a basal animal lineage of fungus-like aquatic organisms comprising ca. 40 species, which are mostly pathogens of fish, amphibians, birds and mammals (Glockling *et al.* 2013). Formerly a poorly recorded group, recent environmental sampling has revealed a high diversity of Ichthyosporea in various marine, freshwater and terrestrial environments

(Takishita *et al.* 2005, 2006), including from Brazil (Borteiro *et al.* 2018)

Phylum Mollusca

Amongst the Bivalvia, both species of *Mactra* assigned are Asian, but the genus is well represented in Brazil and *M. petiti* found as far north as the shores of Maranhão state (Kempf & Matthews 1968) the family Mactridae is present with 12 species ranging from the shores of Guiana south to Uruguay (Machado *et al.* 2023). *Mytilus edulis* (blue mussel), a Mediterranean species, is widely used as food and is has been reported as invasive species in Brazil (Santos *et al.* 2019), its finding here is likely associated with human activity. On the other hand, *Periglypta puerpera* (youthful venus), is an Indo-pacific species representing a genus of about 10 species, all from Asia (Palomares & Pauly 2024). Amongst the Gastropoda, *Conus acutangulus*, *C. obscurus* and *C. moluccensis* all originate in the Indian and Pacific Oceans. The genus *Conus* has about 761 valid species (Puillandre *et al.*, 2014) and is cosmopolitan, , especially in the tropics, where they are one of the richest groups of marine molluscs. The slug *Deroceras laeve* is cosmopolitan with distribution records in southeastern and central-western Brazil. The genus *Deroceras* (120 species) is cosmopolitan, but there are no records of it in northern Brazil. Most of the known distribution records are concentrated in North America and Europe. Some of the species are invasive and harmful to biodiversity, reducing the richness of native species and, in agriculture, causing infestation in different crops (Zając & Stec., 2020). The slug *Geomalacus anguiformis* has a distribution restricted to the Iberian Peninsula. The other three species of *Geomalacus* are also endemic to this region and one of them reaches Ireland (Patrão *et al.*, 2015). The land snail *Helminthoglypta talmadgei* occurs exclusively in the USA. The genus *Helminthoglypta*, with around 120 species, is distributed from northern Baja California (Mexico) through California and southern Oregon (USA) (Cordero *et al.* 2021). The snail *Lophiotoma brevicaudata* occurs in Australian and Oriental regions. The genus *Lophiotoma* (about 25 species) is distributed mainly in the Indian and Pacific Oceans, but there are records of species in the Southern Ocean. Only two species have been recorded off the coasts of Mexico, Panama and the USA. *Lottia argrantesta* is a limpet endemic to the Gulf of California (USA). The genus *Lottia* (more than 80 species) can be found on the coast, from the tropics to the North Pole. On the shores of Brazil, the most common species found is *Lottia subrugosa* (Nakayama *et al.*, 2017). The limpet *Nipponacmea nigrans* is endemic to Japan, but the genus (with 12 species) is Palearctic and widely distributed in East Asia. Some species have been recorded from the Sea of Japan to the South China Sea, in Thailand and Vietnam (Teruya *et al.*, 2022). *Mysticarion* (4 species) is a genus of arboreal pulmonate land snails found only in Australia. This genus belongs to the Helicarionidae, found in the eastern Palearctic, Malagasy, India, southeast Asia, Hawaii and Australia. Only the invasive species *Ovachlamys fulgens* has been recorded in Brazil (Hyman *et al.*, 2017, Marchi et al., 2021). *Turris cristata* is a species of marine snail endemic to the Philippines (GBIF.org, 2024). The genus *Turris*, with more than 20 species (Vera-Pelaez *et al*, 2000; Fedosov *et al.*, 2011), is widely distributed throughout the world, and there are records of its presence in the South American Pacific and on the shores of Brazil.

Phylum Platyhelminthes

The terrestrial *Caenoplana coerulea* is native to Eastern Australia, but it has been introduced in many countries around the world (Suárez *et al.* 2018*).* The freshwater microturbellarian *Stenostomum leucops* is a cosmopolitan species that is present in Brazil), but a recent study has questioned its distribution and suggested it is a species complex (Rosa *et al.* 2015).

Phylum Porifera

The genus *Haliclona* with more than 428 species is represented by nine species widely distributed in Brazilian waters (Hadju *et al.* 2011). *Haliclona pigmentifera* however is from the Indian ocean.

Phylum Rotifera

The five Rotifera species found here are widespread in inland waters globally and may include complexes of cryptic species (Walczyńska *et al.* 2024). *Brachionus calyciflorus* and *Synchaeta stylata* are well represented in Brazilian freshwater environments, while *S. tremula* and *Adineta vaga* are known from a smaller number of locations (Garraffoni & Lourenço, 2012). *Macrotrachela quadricornifera* is known from the Northern Hemisphere, but at least six species of the genus are found in Brazil (Garraffoni & Lourenço, 2012).

Protozoa: members of the genus *Cochliopodium*, with 23 species worldwide, are free living organisms (Tekle *et al.* 2014). According to Melton Jr. *et al* (2019) species of this genus are hard to identify due to the plasticity of their taxonomic features and can only be reliably identified with the use of molecular data. Both species assigned here were described from the USA and are known only by the original references (Tekle *et al.* 2013; Melton Jr. *et al.* 2019), *C. pentatrifurcatum* in now a synonym of *C. minus*. *Monosiga brevicollis* is a marine Choanoflagellate, a group with more than 100 species including some in freshwater.

Viridiplantae: All sequences classified as chloroplast DNA represented Microthamnion kuetzingianum, a representative of the phylum Chlorophyta. This taxon was not itself assigned from the COI or ITS2 markers, likely a consequence of the different levels of completeness of each database. The Phylum Chlorophyta was represented only by 3 taxa: *Auxenochlorella protothecoides* (Krüger) Kalina & Puncochárová is a green alga widely used as source for biofuel, in wastewater treatment and as food (Xu *et al.* 2006, Zhou *et al.* 2012, Caporgno *et al.* 2020). The genus is found naturally growing on sap from trees in Germany and has only three species, and is now widespread in the Northern Hemisphere, Australia and South-east Asia (Guiry and Guiry 2024). *Dictyochloropsis* is a genus comprising only two species commonly found in the Northern Hemisphere and South-east Asia (Guiry and Guiry 2024) and is an important lichen-forming photobiont and is also used as biofuel producer (Junaid *et al.* 2019). *Jaagichlorella* is a genus with only nine species, widely distributed and as occurs as close to Brazil as Cuba (Guiry and Guiry 2024). The Phylum Bryophyta is here represented by two taxa: the host *Ectropothecium leptochaeton* and *Callicostella*, both widely distributed in Brazil. The Phylum Rodhophyta is represented solely by the marine *Gloiopeltis*, a genus with about five species from Asia and North America. Amongst the flowering plants, *P. maxima* is as Eurasian species but the genus *Plantago* has 22 species in Brazil, including in Acre state.

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