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Research Article

Diversity and bioactivity of sediment-associated fungi from a mangrove forest in Mexico with different conservation conditions

Irene Lagunes[1,3], Homero Lumbreras-Martínez[2], César Espinoza[1], José M. Padrón[3] Jorge López-Portillo[4] & Ángel Trigos[1]

[1]Centro de Investigación en Micología Aplicada, Universidad Veracruzana, Xalapa-Veracruz, Mexico
[2]Doctorado en Ciencias en Ecología y Biotecnología, Instituto de Biotecnología y Ecología Aplicada (INBIOTECA), Universidad Veracruzana. Xalapa, Veracruz, Mexico
[3]Instituto Universitario de Bio-Orgánica "Antonio González" (IUBO-AG) Universidad de La Laguna, Tenerife, Spain
[4]Red de Ecología Funcional, Instituto de Ecología, AC (INECOL), Xalapa-Veracruz, Mexico
Corresponding author: Ángel Trigos (atrigos@uv.mx)

ABSTRACT. The biological importance of rhizosphere sediment-associated fungi in mangroves is poorly understood, especially when they are affected by high salinity and anaerobiosis in disturbed areas. This study evaluated the fungal diversity in the rhizosphere sediments of three mangrove species associated with three conservation conditions of mangrove forests in preserved, semi-preserved, and deteriorated areas. In addition, fungal bioactivity was correlated to the fungal diversity found in mangrove species from each area. We isolated 50 fungal strains belonging to three phyla, seven classes, and 10 orders. The fungal diversity was higher in the preserved area (H' = 2.22) than in the semi-preserved (H' = 1.73) and deteriorated areas (H' = 1.68); the redundancy analysis showed a tendency of fungal accumulation towards the rhizosphere of *Rhizophora mangle* and *Avicennia germinans* in the preserved and semi-preserved areas. In addition, the redundancy analysis showed that 10 bioactive fungi genera tended to accumulate on the rhizosphere of *R. mangle* and *A. germinans* in the preserved and semi-preserved areas. The preserved area is related to the semi-preserved area, with a 28% Jaccard similarity coefficient. The diversity and bioactivity of the isolated fungi encourage the need to conserve and restore mangrove ecosystems considering their current and potential services, such as bioprospecting new pharmacological compounds.

Keywords: fungal diversity; fungal bioactivity; sediment-associated fungi; mangrove species; mangrove forest

INTRODUCTION

Mangrove forests are highly productive coastal ecosystems that host a vast diversity of bacteria, algae, protozoa, and fungi. The latter, called manglicolous fungi (Sahoo & Dhal 2009), fulfill various essential functions such as the decomposition of organic matter, phosphate solubilization, and carbon flux (Mahanti et al. 2021). They are potential sources of enzymes, antibiotics, antifungals, pesticides, and antitumor agents discovered in bioprospecting studies (Jia et al. 2020, Zucconi et al. 2020, Peraza-Jiménez et al. 2021, Raimi & Adeleke 2021). The distribution of manglicolous fungi seems to be associated with mangrove individuals and their substrate. However, there is much to learn about the effect of hypersaline environments on fungi, especially those associated with the mangrove rhizosphere (Vittal & Sarma 2006, Chung et al. 2019, Sen et al. 2022).

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Substrate salinity may decrease during the rainy season and increase during the dry season (Méndez-Alonzo et al. 2012). Still, human activities such as the disruption of water flow can increase salinity concentrations and affect mangroves chronically, causing even massive mortality (Vovides et al. 2011, Chowdhury et al. 2023). These changes could lead to the displacement of native fungi or changes in the metabolism that allow a few of them to survive and reproduce.

Hyde & Lee (1995) found that relatively young forests (<50 years old) are poor in fungi species when compared to older forests, which is probably related to a higher tree species diversity that provides substrate fungi. However, only some studies compare fungal diversity in the rhizosphere of different mangrove species and environments. Fewer still include their antiproliferative activity as an indicator of change in fungal metabolism. Here, we report the first study in Mexico considering fungal diversity in the rhizosphere of three mangrove species of preserved, semi-preserved, and deteriorated sites. Also, we explored the biotechnological potential of these fungi based on their antiproliferative activity against three cancer cell lines.

MATERIALS AND METHODS

Study area

Sediment samples from the rhizosphere were collected in the mangrove forest of the Tampamachoco Lagoon, Tuxpan, Veracruz, Mexico. Vovides et al. (2011) previously characterized the sampling sites as follows: preserved area with 35-45 salinity, a semi-preserved area with 65 salinity, and a deteriorated area with up to 140 salinity. This mangrove forest presents different degrees of disturbance due to human activities.

Biological material

In February 2013, five samples of sediments from the rhizospheres were collected from *Avicennia germinans* (black mangrove), *Rhizophora mangle* (red mangrove), and *Laguncularia racemosa* (white mangrove). *L. racemosa* was not present in the deteriorated area. The sediments were collected at 10-15 cm depth around the roots, at 30 m intervals between samples of each species. Each undrained sample was placed in a sterilized polyethylene bag, sealed, and transported to the laboratory in ice, where the bags were kept at 4°C.

Isolation of fungal strains and preparation of fungal extracts

Rhizosphere sediments were diluted (1:10) in a sterile solution of peptone-NaCl (0.1-0.4% w/v), and serial dilutions were made until a 10^{-3} concentration was reached. Fungi isolation was made in solid culture mediums (marine agar and malt extract agar) supplemented with antibiotic (chloramphenicol 0.2 g L^{-1}) and incubated in darkness for seven days at 25 ± 2°C. After purification, 120 isolates were obtained (5 samples × 3 mangrove species × 3 mangrove areas × 3 replicates). From the pure strains, liquid fermentation was developed in 500 mL of Wicherham's culture medium for 14 days (shake/static) incubated at 25 ± 2°C in darkness (Kjer et al. 2010). Fungal extracts were obtained from the freeze biomass and culture medium (Labconco Freeze Dry 5-85°C, and 5 µm Hg vacuum), using an organic solvent mixture chloroform: methanol (1:1).

Fungal strain identification

The morphological identification was made by observation of reproductive fungi structures dyed with a lactophenol blue solution under a compound microscope (Carl Zeiss Microscopy GmbH, Jena, Germany), following the taxonomic keys developed by Barnett & Hunter (1998) and Watanabe (2002).

Bioactivity of fungal extracts

The antiproliferative activity of the fungal extracts was tested against three human solid tumor cell lines: HBL-100 (breast), HeLa (cervix), and SW1573 (lung), according to the methodology described by Lumbreras-Martínez et al. (2018). The results were interpreted in the Redundancy Analysis (RDA) as level A: strains with GI_{50} values ranging from 101 to 250 µg mL^{-1}; and level AA: strains with GI_{50} values ≤100 µg mL^{-1}.

Data analysis

The colonization rate was calculated as the total number of Petri dishes colonized by one or more fungi divided by the total number of inoculated Petri dishes. The isolation rate per genus was calculated as the number of Petri dishes colonized by a specific genus divided by the total number of inoculated Petri dishes. The relative abundance (RA) of each taxon was the number of isolates of each taxon divided by the total number of isolates obtained. The Shannon diversity index (*H'*), species accumulation curves, and the Jaccard species similarity coefficient were obtained with EstimateS ver. 9.1.0 (Colwell 2013), Past 3.24 (Hammer et al. 2001), and Microsoft Excel® software. Differences in colonization rates of fungi between plant species and disturbance conditions were evaluated with one-way analyses of variance (one-way ANOVA) using SigmaPlot 11 and InfoStat ver. 2019 (Di Rienzo

et al. 2019). We used the RDA (Legendre & Legendre 1998) to evaluate the relationship between bioactivity and relative abundance of fungi genera *vs*. mangrove plant species and site degradation. The significance was tested within the forward selection procedure using a Monte Carlo random permutation test (499 permutations, $P \leq 0.05$). The analysis used Canoco 4.5 (Ter Braak & Smilauer 2002).

RESULTS

Fungal strains

The analysis of the 15 Petri dishes inoculated with rhizosphere samples of each mangrove species per site resulted in 20 to 40% colonization rates (Table 1). The colonization rate was similar among mangrove species and areas (one-way ANOVA, $P < 0.05$). From a total of 50 fungal strains isolated, 10 orders, seven classes, and three phyla were identified. Ascomycota strains isolated corresponded to 70%, Oomycota 2%, Zygomycota 2%, and the remaining 26% were non-identified strains (Table 2). The identified 16 genera of rhizosphere fungi were *Aspergillus*, *Penicillium*, *Fusarium*, *Phomopsis*, *Acremonium*, *Alternaria*, *Trichoderma*, *Phytophthora*, *Geotrichum*, *Sepedonium*, *Mucor*, *Nectria*, *Monacrosporium*, *Humicola*, *Blastomyces*, and *Talaromyces*. The species accumulation curves in the semi-preserved and deteriorated areas reached the asymptote, suggesting a good sampling effort (Fig. 1). In all species accumulation curves, genera were observed only once (singletons); the curves did not reach the asymptote.

Fungi diversity

The fungal diversity of the 50 strains isolated from mangrove corresponded mainly to Ascomycota phylum. Relative abundance analysis in the preserved area showed that the fungal distribution of 23 isolated strains corresponded to three classes: Sordariomycetes (30.4%), Eurotiomycetes (39.2%) and Dothideomycetes (4.3%). From the semi-preserved area, 18 fungal strains corresponded mainly to the classes Sordariomycetes and Eurotiomycetes, with 33.3 and 28% of the strains, respectively. Only nine fungal strains were isolated from the deteriorated area, mainly belonging to Sordariomycetes (33.3%). Even so, the efforts in identification work were impossible to identify six, four, and three strains isolated from preserved, semi-preserved, and deteriorated areas, respectively, due to the lack of reproductive structures in the isolates (Table 2).

Shannon diversity index (H') of fungal strains related to mangrove areas showed $H' = 2.22$ for the preserved area, $H' = 1.73$, and $H' = 1.68$ for semi-preserved and deteriorated areas, respectively. The fungal diversity related to mangrove tree species where H' were 2.04, 2.1, and 1.56 for *R. mangle*, *A. germinans*, and *L. racemosa*, respectively, were also analyzed. In the preserved and semi-preserved areas, *Fusarium* and *Aspergillus* were seen to be the most abundant fungi genera isolated (Fig. 2).

When comparing fungal clusters by mangrove areas through the Jaccard index, we found a 28% similarity between the preserved and semi-preserved areas shared by *Aspergillus*, *Fusarium* and *Penicillium* and a 21% similarity coefficient between the preserved and deteriorated areas, shared by *Penicillium* and *Acremonium.* When comparing semi-preserved and deteriorated areas, an 18% similarity was shared only by *Penicillium*. Fungal clusters of mangrove species from the Jaccard index showed a 50% similarity between *A. germinans* and *L. racemosa*, which decreased to 30% when comparing *R. mangle* with *L. racemosa* and 25% when comparing *A. germinans* with *R. mangle*. There were significant differences in the fungal assembly when comparing semi-preserved and deteriorated areas (one-way ANOVA, $P < 0.05$). However, no significant differences between mangrove species in the niches per collection site were found. In the RDA, fungal strains accumulated from the semi-preserved to the deteriorated areas in *A. germinans* and *R. mangle* (Fig. 3).

Fungal community and bioactivity level

The antiproliferative activity of 50 fungal extracts was evaluated, from which 17 were active against at least one cancer cell line tested. Ten active fungal extracts exhibited bioactivity ≤ 100 µg mL^{-1} and were classified at level AA; the remaining seven were classified up to level A because their bioactivity was >101 µg mL^{-1} (Table 3). The distribution analysis of bioactive strains related to mangrove areas showed no significant differences (preserved 34%, semi-preserved 33%, and deteriorated 33%). However, in the RDA, a tendency of association between bioactive fungal extracts towards *R. mangle* and *L. racemosa* species was observed relating to the preserved and semi-preserved areas (Fig. 4).

DISCUSSION

Fifty fungal strains were isolated from sediments at the rhizospheres of *Avicennia germinans*, *Rhizophora mangle*, and *Laguncularia racemosa* in the mangrove forest. The isolated fungal strains corresponded to

Table 1. Isolation and colonization rates of fungi sampled from rhizosphere sediments from mangrove species in different areas. Rm: *Rhizophora mangle*, Ag: *Avicennia germinans*, Lr: *Laguncularia racemosa*.

Mangrove area	Mangrove species	Petri dishes inoculated	Petri dishes colonized	Colonization rate (%)	Isolated strains
Preserved	Rm	15	5	33.3	11
	Ag	15	6	40.0	6
	Lr	15	4	26.7	6
	Total	45	15	33.3	23
Semi-preserved	Rm	15	5	33.3	8
	Ag	15	4	26.6	4
	Lr	15	4	26.6	6
	Total	45	13	28.8	18
Deteriorated	Rm	15	4	26.6	6
	Ag	15	3	20.0	3
	Total	30	7	23.3	9

Table 2. Taxonomic classification of the fungal strains isolated from rhizosphere sediments by mangrove area at the Tampamachoco Mangrove. RA: relative abundance.

Phylum	Class	Order	Preserved		Semi-preserved		Deteriorated		Phylum Total
			Strains	RA (%)	Strains	RA (%)	Strains	RA (%)	
Ascomycota	Sordariomycetes	Hypocreales	6	26.1	6	33.3	1	11.1	35
		Diaporthales	-	-	-	-	2	22.2	
		Sordariales	1	4.3	-	-	-	-	
	Eurotiomycetes	Eurotiales	9	39.2	5	28	1	11.1	
	Saccharomycetes	Saccharomycetales	-	-	-	-	1	11.1	
	Dothideomycetes	Onygenales	1	4.3	-	-	-	-	
		Plaeosporales	-	-	1	5.5	-	-	
	Orbiliomycetes	Helotiales	-	-	1	5.5	-	-	
Oomycota	Oomycetes	Peronosporales	-	-	1	5.5	-	-	1
Zygomycota	Zygomycetes	Mucorales	-	-	-	-	1	11.1	1
Non identified	-	-	6	26.1	4	22.2	3	33.4	13
		Total	23	100	18	100	9	100	50

Ascomycota, Zygomycota, and Oomycota phylum. Of the total isolated genera, 70% corresponded to the Ascomycota phylum, in which the Sordariomycetes and Eurotiomycetes classes were the predominant fungal strains found. The dominancy of the Ascomycota phylum in mangrove fungal communities has been previously reported. In this sense, species diversity from Eurotiomycetes, Sordariomycetes, Dothideomycetes, and Saccharomycetes in mangrove ecosystems have an important ecological role as saprophyte fungi (Lee et al. 2019, Vanegas et al. 2019, Yang et al. 2021). Likewise, Ascomycota fungi have been found as endophytes in leaves and branches of *Rhizophora mangle*, *Avicennia germinans*, and *Laguncularia racemosa* in mangrove areas affected by oil spills and other anthropogenic activities (De Souza Sebastianes et al. 2013, Simões et al. 2015).

The fungal community decomposes organic matter to make nutrients available for plant growth. The diversity and activity of the fungal community are strongly regulated by biotic and abiotic factors, considered important abiotic factors pH, temperature, and salinity (Frąc et al. 2018). In this sense, in this work, the highest fungi Shannon diversity was found in the preserved area with the lowest level of salinity (35) followed by the semi-preserved (65) and deteriorated (140) areas, with H' = 2.22, 1.73, and 1.60, respectively. These results are similar to those found by Arfi et al. (2012), who found H' values from 0.8 to 2.45 in anoxic-sulphidic mangrove soils. The lower fungal diversity and relative abundance in our study sites were apparent in the semi-preserved and deteriorated areas. The greater fungal diversity in preserved areas supports the importance not only of preserving mangrove conditions,

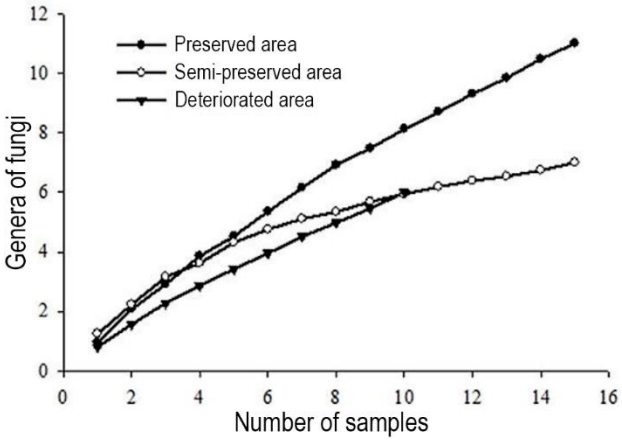

Figure 1. Accumulation curves of fungi genera isolated from rhizosphere sediments as a function of the number of samples in preserved, semi-preserved, and deteriorated mangrove areas.

such as relatively low salinity and oxygen levels no lower than 1 mg L^{-1} (Olguín et al. 2007, Sánchez-Arias et al. 2010), but also of improving mangrove conditions at the semi-preserved and deteriorated areas through restoration initiatives.

The fact that the preserved and semi-preserved areas showed similar fungal diversity indicates that they still share conditions that allow the development of the native mangrove mycota. In contrast, different soil conditions in the deteriorated area harbor a less diverse fungal community. Fungal colonization of deteriorated mangrove areas was reported for other mangroves; for example, various fungi species colonized dead trunks and branches of *R. mangle*, *A. germinans*, *L. racemosa* and *Conocarpus erectus*, which confirms the resilience of mangrove ecosystems and fungi that grows within them (Ananda & Sridhar 2004, Moitinho et al. 2022). Like our results, De Souza-Sebastianes et al. (2013) found no significant changes in fungal diversity among mangrove tree species when comparing preserved and deteriorated areas affected by an oil spill, suggesting that fungi had enough time to adapt.

Regarding the fungal colonization of extreme environments, *Talaromyces* and *Alternaria* have been isolated in sediments from mangroves under similar conditions to those reported in the deteriorated area in our study (Vovides et al. 2011, Arfi et al. 2012), and the ability of *Trichoderma* to grow in marine sediments under anoxic conditions have also been reported (Cathrine & Raghukumar 2009). However, in this study, *Trichoderma*, *Talaromyces*, and *Alternaria* were isolated only in the semi-preserved area, with 65 salinity. Also, *Penicillium*, *Geotrichum*, *Fusarium*, *Aspergillus*,

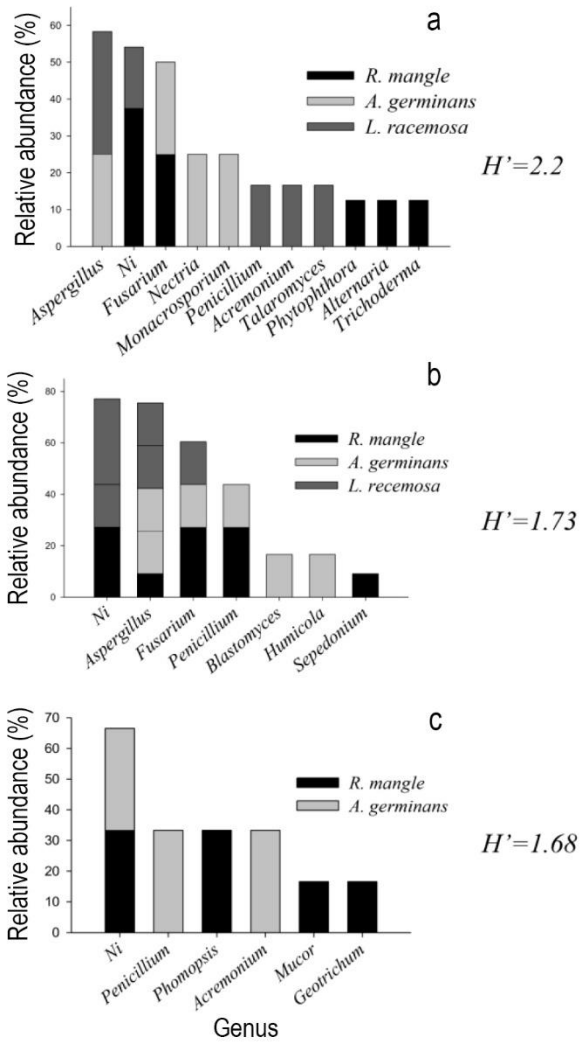

Figure 2. Relative abundance of fungi associated with the rhizosphere of mangrove species at the a) preserved, b) semi-preserved, and c) deteriorated areas.

and *Humicola* have been found in similar conditions to the semi-preserved and deteriorated areas of the Tampamachoco Lagoon (high pH, anoxic sediments, low C content, and low redox potential), with an emphasis on *Fusarium* for its ability to grow under aerobic and anaerobic culture conditions. The isolation of these genera distributed in the two disturbed sites (semi-preserved and deteriorated areas) corroborate their adaptation ability to a wide range of environments. Such is also the case for *Mucor*, found in the deteriorated area. All the above fungi genera mentioned have been reported in studies related to soil fungi, and they are among the most resistant fungi to severe environmental conditions (Samaniego-Gaxiola & Chew-Madinaveitia 2007). Regarding the mangrove species, *R. mangle* showed a higher fungal diversity than *A. germinans* and *L. racemosa*, as reported by

Table 3. Bioactivity level of fungal strains isolated from mangrove species at preserved, semi-preserved, and deteriorated areas. A: GI_{50} = 101-250 µg mL^{-1}, AA: GI_{50} = 0-100 µg mL^{-1}. Rm: *Rhizophora mangle*, Ag: *Avicennia germinans*, Lr: *Laguncularia racemosa*.

Mangrove area	Mangrove species	Strain	Genus	Bioactivity level
Preserved	*R. mangle*	RmS1 A	*Penicillium*	A
		RmS2 A	*Aspergillus*	AA
		RmS2 B	*Penicillium*	AA
		RmS4 B	*Fusarium*	AA
	A. germinans	AgS3 B	*Blastomyces*	A
		AgS4	*Aspergillus*	AA
		AgS5 B	*Fusarium*	A
	L. racemosa	LrS2	*Aspergillus*	AA
Semi-preserved	*R. mangle*	RmC3 A	*Alternaria*	A
		RmC5 A	*Trichoderma*	AA
	A. germinans	AgC1	*Aspergillus*	AA
		AgC3	*Monacrosporium*	A
	L. racemosa	LrC2 B	*Aspergillus*	AA
		LrC5 A	*Talaromyces*	AA
Deteriorated	*R. mangle*	Rm M1 A	*Mucor*	AA
		RmM3 B	*Geotrichum*	A
	A. germinans	AgM1 A	*Penicillium*	A

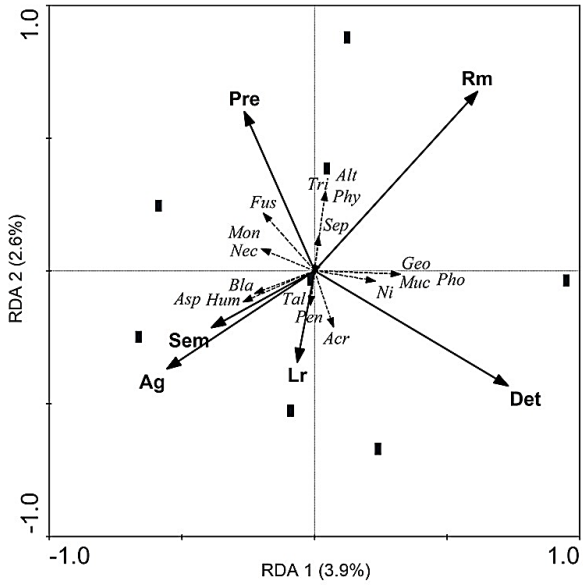

Figure 3. RDA plot showing association among isolated fungi strains to mangrove species and mangrove areas. Pre: preserved, Sem: semi-preserved, Det: deteriorated; Rm: *Rhizophora mangle*; Ag: *Avicennia germinans*; Lr: *Laguncularia racemose*; Fus: *Fusarium*; Mon: *Monacrosporium*; Nec: *Nectria*, Tri: *Trichoderma*; Alt: *Alternaria*; Phy: *Phytophthora*; Sep: *Sepedonium*; Geo: *Geotrichum*; Pho: *Phomopsis*; Muc: *Mucor*; Ni: not identified; Acr: *Acremonium*; Pen: *Penicillium*; Tal: *Talaromyces*; Bla: *Blastomyces*; Asp: *Aspergillus*; Hum: *Humicola*.

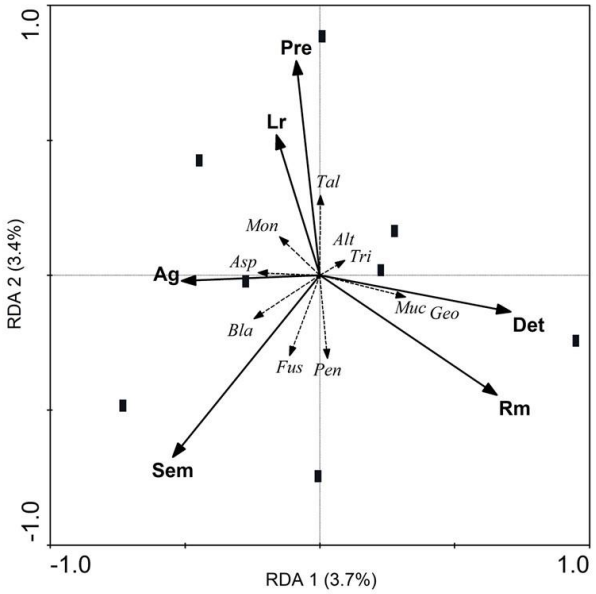

Figure 4. RDA plot showing association among bioactive fungal strains to mangrove species and mangrove areas. Pre: preserved; Sem: semi-preserved; Det: deteriorated; Rm: *Rhizophora mangle*; Ag: *Avicennia germinans*; Lr: *Laguncularia racemosa*; Asp: *Aspergillus*; Mon: *Monacrosporium*; Tal: *Talaromyces*; Alt: *Alternaria*; Tri: *Trichoderma*; Muc: *Mucor*; Geo: *Geotrichum*; Pen: *Penicillium*; Fus: *Fusarium*; Bla: *Blastomyces.*

Sarma & Vittal (2000) and Vittal & Sarma (2006). The fungal diversity found in *R. mangle* could be due to the *R. mangle* rhizosphere, which is more fibrous than *A. germinans* and *L. racemosa* (McKee et al. 1988, Angeles et al. 2002, Menezes 2006).

The fungal community associated with mangroves represents the second group of marine fungi which, in recent years, have gained attention in bioprospecting studies because they represent a valuable source of bioactive compounds that could allow the discovery of diverse and new chemical structures with a potential pharmacological application (Chen et al. 2022). This study identified bioactive fungi strains across the three mangrove areas. Even though there was no significant difference in bioactive fungal strains between mangrove areas, we observed a trend of accumulation of bioactive fungal strains in the preserved area. An analysis of the secondary metabolites isolated from fungi associated with mangroves over the last 30 years has been divulged, highlighting the reports of 1387 new structures (Bibi et al. 2020, Chen et al. 2022). In particular, from fungi associated with mangrove sediments until 2021, 309 bioactive compounds mainly isolated from *Penicillium* sp. and *Aspergillus* sp. (Li et al. 2022) have been reported. Therefore, the fungal community associated with mangrove ecosystems has an ecological role as organic matter decomposers and represents a natural source of secondary metabolites that could have important bioactivities, such as antiproliferative, antiviral, and antibacterial. Finally, this work begins a bioprospecting study in pursuit of new bioactive compounds in which fungal diversity has been explored from mangrove rhizosphere with different disturbing levels and their bioactivity. Hence, bioprospecting studies reinforce the importance of accomplishing preservation programs to recover deteriorated mangroves and maintain preserved mangrove forests.

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