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ORIGINAL PAPER

Biodiversity of marine fungi in mangroves with reference to Muthupet mangroves, Tamil Nadu, east coast of India

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Abstract

Fungi occur in mangroves as saprobes, pathogens, and endophytes of a wide range of timber host substrates and may also be isolated from the water column and bottom sediments. In this study, we explore their biodiversity within a single mangrove forest at Muthupet, Tamil Nadu, India. The study showed a rich diversity of fungi on five decaying host substrates (out of seven host substrates) collected in the intertidal zone, resulting in 78 marine fungal taxa in 67 genera from 11 field collections and 6215 samples. Of the 78 taxa, 56 species (in 47 genera) belong to the *Ascomycota* and two species (2 genera) to *Basidiomycota* with the remaining 20 species representing asexual fungi (18 genera). Some fungal species were repeatedly reported: *Verruculina enalia* (21.65%) was the most frequently collected fungus; *Marinosphaera mangrovei* (9.2%), *Rimora mangrovei* (9.15%), *Okeanomyces cucullatus* (8.7%), *Halocryptosphaeria bathurstensis* (6%) in the frequent category, *Paraconiothyrium cyclothyroides* (4.5%), *Hysterium rhizophorae* (3.5%), *Sclerococcum haliotrephum* (3.6%), *Lulworthia* sp. (3.6%), and *Farasanispora avicenniae* (3%) were infrequently collected. Of the host substrates, *Avicennia marina* wood pieces harbored 49 fungal species of which 19 were unique. Two-way ANOVA revealed that fungal species richness was not affected irrespective of the collection season ($P = 0.239$) but was significantly dependent on the wood species ($P < 0.001$).

Keywords Fungal diversity · Indian mangroves · Mangrove fungi · *Suaeda monoica*

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Introduction

Mangroves are tropical and subtropical swampy plants that grow in estuaries, bogs, deltas, and lagoons, and harbor marine fungi in trunks and roots that are permanently or intermittently submerged in water (Kohlmeyer and Kohlmeyer 1979; Hyde and Jones 1988; Hyde and Lee 1995). Mangrove forests are of immense ecological, economic, and of traditional importance (Kathiresan and Bingham 2001). They are considered as the second largest habitat of the Earth's marine fungal diversity (Jones 2011). Mangroves are the biodiversity hotspots for marine fungi (Shearer et al. 2007). Marine fungi in mangrove environment play a vital role in nutrient recycling by secreting extracellular degradative enzymes (Pointing 1999). The global distribution of marine fungi is understudied in contrast to other microbes, plants, and animals. Schmit and Shearer (2003) reported 625 mangrove fungi of terrestrial, fresh water, and marine origin from 72 mangrove plants distributed across different parts of the world. Marine fungal diversity from east coast of India has been documented by Ravikumar and Vittal (1996), Sarma and Vittal (2000, 2001a), (Sarma et al.

(2001), Vittal and Sarma (2006), (Sarma 2016), and (Sridhar 2009), to mention but a few. The species diversity in the west coast of India has been documented by Patil and Borse (1983, 1985), Borse and Hyde (1989), Chinnaraj and Untawale (1992), Chinnaraj (1993), Maria and Sridhar (2003, 2004), Raveendran and Manimohan (2007), Hyde and Sarma (2000), and Sarma and Raghukumar (2013). A comprehensive list of marine fungi from India was provided by Borse et al. (2013, 2018). A total of 17 new higher marine fungi were discovered and documented from India until 2014. The number of new marine fungi has increased significantly as different habitats and substrates are examined for marine fungi (Hyde et al. 2017, 2018). Indian mangroves are vast and support various mangrove trees and salt marsh plants. The Indian mangroves have a total area of around 6749 km^2, the fourth largest mangrove area in the world that includes about 59 plant species in 41 genera and 29 families (Naskar and Mandal 1999; Kathiresan and Rajendran 2005; Singh et al. 2012). The east coast of India has the largest mangrove area (80%) in contrast to west coast of India (20%) due to major river deltas of Brahmaputra, Cauvery, Ganges, Godavari, Krishna, and Mahanadi flowing east ward into the Bay of Bengal (Kathiresan and Rajendran 2005). The marine fungi of the Godavari and Krishna deltas have been documented by Sarma and Vittal (2000, 2001a), while the Pichavaram mangroves have been documented by Ravikumar and Vittal (1996) and Sridhar (2009). These studies have shown that in spite of their proximity, 50% of the fungal species found were different at each location with few overlapping species. Mangrove fungal diversity has been studied intensively from a wide range of tropical and subtropical mangrove ecosystems of the Atlantic (Bahamas, Bermuda, Brazil, Cuba, East Mexico, Florida in the USA, Sierra Leone in West Africa and South Africa), Indian (East South Africa, Egypt, India, Java, Kenya, Mauritius, Pakistan, South Australia, Seychelles, Sri Lanka, Sumatra), and the Pacific oceans (Australia, Brunei, China, Hawaii, Japan, Malaysia, New Zealand, Philippines, Singapore, Taiwan, Thailand) (Kohlmeyer and Kohlmeyer 1979; Schmit and Shearer 2003). For example, a total of 99 marine fungi were recorded on decaying woody substrata from mangroves of Thailand (Suetrong et al. 2017), and 37 reported on decaying wood of *Avicennia marina* from the Red Sea coast of Saudi Arabia (Abdel-wahab et al. 2014). Ninety-two marine fungi were reported from seven different mangrove sites of the Bahamas Islands (Jones and Abdel-Wahab 2005). A total of 64 marine fungi were recorded on woody litter of *Rhizophora apiculata* and 55 on *Avicennia officinalis* from mangroves of the Godavari and Krishna deltas of the east coast of India (Sarma and Vittal 2001a). Fifty-eight marine fungi were recorded on *Avicennia officinalis* and *Rhizophora mucronata* from Udayavara mangroves of the west coast of India (Maria and Sridhar 2003).

Salt marshes are a vital borderline coastal ecosystem determined by tidal movement and are formed by the interface of the halophytic vegetation and sediment from inundating water. Studies on marine fungi associated with diverse salt marsh plants shows no overlap between the fungal decay communities, which highlights the specificity of the chemical and structural characteristics of each plant (Newell and Porter 2002; Blum et al. 2004; Torzilli et al. 2006). Studies on salt marsh plants such as *Spartina alterniflora*, *Juncus roemerianus*, and *Phragmites australis* have indicated a rich diversity of marine fungi similar to many woody mangrove plants (Fell and Hunter 1979; Cuomo et al. 1982, 1985; Poon and Hyde 1998; Barata 2002; Kohlmeyer and Volkmann-Kohlmeyer 2002; Wong and Hyde 2002; Van Ryckegem and Verbeken 2005). The salt marsh plant *Suaeda maritima* is commonly distributed in India and across several countries, and *Suaeda monoica* is less commonly found. To our knowledge, the latter salt marsh plant has not been surveyed for marine fungi, while few marine fungi have been documented for the former. Muthupet mangroves include a vast area of salt marsh plants with species such as *Suaeda monoica* and *Suaeda maritima* distributed in the intertidal zone.

The objectives of the study were to document fungal diversity of a mangrove habitat previously not surveyed; to determine if host substrates support different fungal communities; and to survey fungi occurring on the salt marsh plant *Suaeda monoica* at Muthupet mangrove, Tamil Nadu, India.

Materials and methods

Study site and sample collection

Studies on mangrove fungi were carried out from 2015 to 2018. Intertidal and attached dead and decomposing mangrove wood and stem pieces of *Aegiceras corniculatum*, *Avicennia marina*, *Excoecaria agallocha*, *Rhizophora mucronata*, and *Suaeda monoica* were collected from Muthupet mangroves (10.4°N, 79.5°E), Kaveri River Delta, Tamil Nadu, southeast coast of India (Fig. 1) Natural earth (2012), QGIS Development team (2016). Samples were placed in sterile plastic bags and transported to the laboratory. The mangrove plants *Acanthus ilicifolius* and *Suaeda maritima* were collected from the same geographic area but only during the first 2 years of the survey (2015 and 2016). If needed, mud and debris were washed from samples under running tap water. Samples were incubated in a plastic box lined with a layer of sterile tissue paper and kept moist by spraying with sterile seawater and stored at room temperature until examined (Kohlmeyer and Kohlmeyer 1979). There are mainly two seasons in India: summer (January to June) and rainy

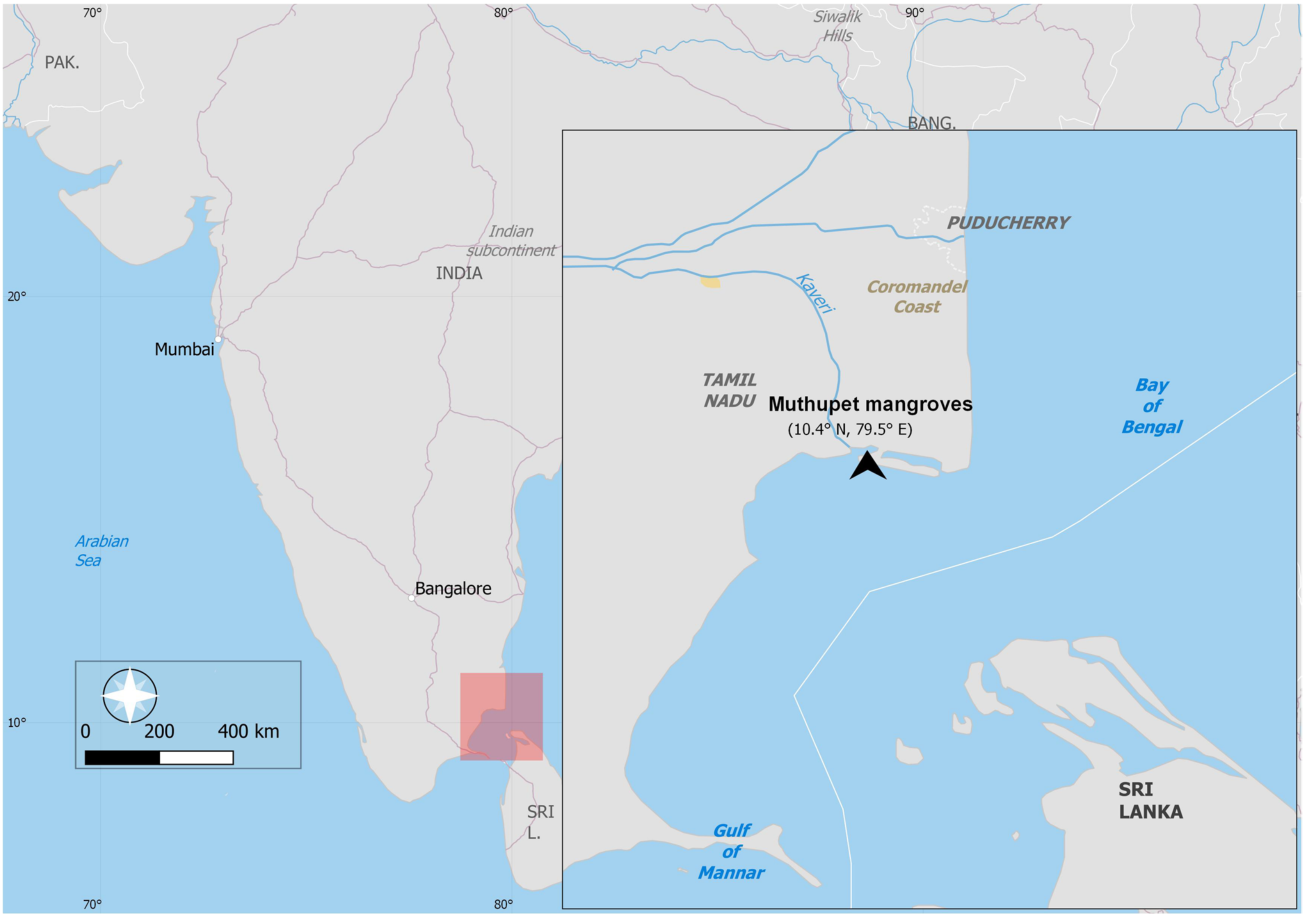

Fig. 1 Map of the study site Muthupet mangroves, Tamil Nadu, East coast of India

(July to December). The fungal colonization and percentage of occurrence of marine fungi on mangrove samples were determined during these seasons.

Morphological studies, isolation, and characterization

The direct examination method was carried out, with magnifications between 7 and 45× using an Optika stereo zoom SZM-LED1 microscope allowing the images of the ascomata, pycnidia, synnemata, and basidiomata located on the twigs to be captured. The fruiting bodies were cut with a sterile razor blade, and the contents of the ascomata were scooped out for microscopic examination under a compound microscope. Microslides were prepared by mounting the fungal material in sterile seawater or lactophenol, and photomicrographs were taken using a Nikon ECLIPSE TiU upright microscope with DIC objectives fitted with Nikon DS-Fi2 digital camera. Measurements were made with Nikon NIS-Elements-Imaging Software version 4.4 program, and images were processed with Adobe Photoshop CS6 updated version 13.0.1 software (Adobe Systems Inc., USA). The fungi observed were then identified based on the latest keys (Kohlmeyer and Volkmann-Kohlmeyer 1991; Hyde and Sarma 2000; Jones et al. 2009). However, for the identification of few asexual species, we referred to earlier and recent literature (Ellis 1971, 1976; Sutton 1980; Seifert et al. 2011).

All the marine fungal cultures were initiated using the single-spore isolation method as outlined in Devadatha et al. (2017). Colony morphology and their growth rate were observed and measured after 3 weeks to ensure that single-spore isolates obtained were of the same species. Pure cultures were deposited at the National Fungal Culture Collection of India (NFCCI), Pune, India. The herbarium materials were deposited at Ajrekar Mycological Herbarium (AMH), Agharkar Research Institute (ARI), Pune, India. The molecular characterization of novel marine fungi was performed as described in Devadatha et al. (2017). Facesoffungi, Index Fungorum, and MycoBank numbers are provided for the new species discovered from this study (Jayasiri et al. 2015).

Statistical analyses

Percentage colonization and frequency of occurrence of each fungus were calculated as follows:

$$\text{Percentage colonization} = \frac{\text{Number of samples supporting fungi}}{\text{Number of samples examined}} \times 100$$

$$\text{Frequency of occurrence of each fungus} = \frac{\text{Number of collections of a particular fungus}}{\text{Total number of sporulating fungal records}} \times 100$$

The univariate community statistics used in this study are: (1) number of species in a sample (richness); (2) number of individuals in a sample (abundance); (3) Simpson diversity index (1-D) (Simpson 1949), where $D = sum((n_i/n)^2)$ where n_i is number of individuals of taxon i; (4) Shannon diversity index: $H = sum((n_i/n)ln(n_i/n))$, where n is the total number of individuals; (5) evenness, calculated as the logarithm of Shannon diversity (Shannon 1948), divided by the number of taxa as: eH/S, where H is a measure of Shannon diversity and S is the number of taxa; and (6) Margalef's richness index: (S-1)/ln(n), where S is the number of taxa, and n is the number of individuals. Jaccard's similarity coefficient (%) M/(M + N) (where *M* is the number of matches and *N* stands for total number of taxa) was determined pair-wise for plant type based on the presence or absence of each species. They were calculated using PAST software version 1.89 (Hammer et al. 2001). Two-way ANOVA (followed by Holm-Sidak's post-hoc method) was applied to evaluate the influence of season (wet and dry) and plant species on species richness of marine fungi (SigmaPlot, version 11, Systat Inc., San Jose, USA). A 1:74 m and a 1:10 m vector polyline shapefile from the natural Earth (NE) river and lakes' centerlines base data layers were used to derive the final India and Muthupet mangrove location map using QGIS. Upset plot generated by UpSetR (version 1.3.3) was used for the quantitative analysis of overlapping species between the five mangrove plant wood (Lex et al. 2014), instead of Venn diagram. The bar chart was generated using GraphPad Prism 5.03 software for Windows (www.graphpad.com).

Results

Diversity, occurrence, and distribution of marine fungi in Muthupet

The examined *Acanthus ilicifolius* and *Suaeda maritima* samples yielded few marine fungi records (< 5) and were excluded from further analysis.

In total, 6215 samples were collected from the intertidal zone of Muthupet mangroves and examined for the presence of marine fungi, with 2198 samples (36.10%) supporting sporulating fungi. Seventy-eight fungal species in 67 genera were recorded, including 56 *Ascomycota* (72%), two *Basidiomycota* (2%), and 20 asexual morphs (26%) (Table 1).

Percentage of occurrence was calculated as mentioned in the Materials and Methods section, and frequency groups were defined as follows: very frequent (> 10%), frequent (> 5–10%), infrequent (> 1–5%), and rare (less than 1%) (Table 2). The only fungus occurring very frequently was *Verruculina enalia* (21.65%); frequent fungi included *Rimora mangrovei* (9.15%), *Marinosphaera mangrovei* (9.2%), *Okeanomyces cucullatus* (8.7%), and *Halocryptosphaeria bathurstensis* (6%), while infrequent fungi were *Paraconiothyrium cyclothyrioides* (4.50%), *Hysterium rhizophorae* (3.5%), *Sclerococcum haliotrephum* (3.60%), *Lulworthia* sp. (4.00%), and *Farasanispora avicenniae* (3.00%) (Table 2).

Percentage fungal diversity among different hosts of Muthupet

Among the different hosts examined, *Avicennia marina* was found to support the highest number of marine fungi (49), followed by the salt marsh plant *Suaeda monoica* (34) (Fig. 2).

Twelve marine fungal species were recorded from *Aegiceras corniculatum* which included nine *Ascomycota* (75.5%) and three asexual morphs (25%), (Figs. 2, 3), with *Hysterium rhizophorae* (44.85%), *Rimora mangrovei* (21.80%), and *Verruculina enalia* (17.95%) as the most frequently recorded species. Colonization of *A. corniculatum* substrates by marine fungi was 38.7% (Table 3). Two new country records (*Falciformispora lignalitis*, *Hysterium rhizophorae*) were recorded for *A. corniculatum*. Photomicrographs of the propagules of the marine fungi recorded in the present study are included in figure plates (Fig. 4a–dd; Fig. 5a–bb; and Fig. 6a–t).

Forty-nine marine fungal species belonging to 44 genera were recorded from *Avicennia marina*, which included 37 *Ascomycota* (75.5%), two *Basidiomycota* (4.0%), and 10 asexual morphs (20.4%) (Figs. 2, 3). *Verruculina enalia* (27.40%) was found to be the most frequently recorded fungus on this host followed by *Marinosphaera mangrovei* (12.00%), *Halocryptosphaeria bathurstensis* (9.25%), *Okeanomyces cucullatus* (8.70%), *Rimora mangrovei* (6.15%), *Sclerococcum haliotrephum* (6.00%), and *Paraconithyrium cyclothyroides* (4.00%). Colonization of *A. marina* by marine fungi was 35.4% (Table 3).

Seventeen marine fungal species belonging to 17 genera were recorded from *Excoecaria agallocha* which included 11 *Ascomycota* (64.7%) and six asexual fungi (35.2%) (Figs. 2, 3). *Verruculina enalia* (41.11%) was

Table 1 Percentage occurrence of higher marine fungi recorded from Muthupet mangroves, Tamil Nadu, East Coast of India

Fungal species	Sample collection												
	28-04-2015	15-08-2015	28-11-2015	30-03-2016	29-06-2016	29-09-2016	24-12-2016	29-03-2017	23-06-2017	25-10-2017	25-02-2018	Total collections fungus	Percentage occurrence
Ascomycota (Sexual morphs)													
Aigialus parvus	_	1	2	3	_	3	_	_	_	_	_	9	0.40
Amphisphaeria mangrovei	_	1	_	_	_	1	_	1	_	_	1	4	0.18
Aniptodera chesapeakensis	3	2	5	8	3	2	1	_	_	_	_	24	1.09
Aniptodera haispora	3	2	_	1	_	_	_	_	_	_	_	6	0.27
Antennospora quadricornuta	2	_	_	_	_	_	5	_	_	_	_	7	0.31
Anthostomella sp.	11	1	2	_	1	1	_	_	_	_	1	17	0.77
Arenariomyces trifurcatus	_	_	1	_	_	_	5	_	_	_	_	6	0.27
Calonectria sp.	_	_	1	_	_	_	_	_	_	_	_	1	0.04
Deniquelata vittalii	_	1	_		_	_	_	1	_	_	_	2	0.09
Dyfrolomyces rhizophorae	_	_	_	_	_	7	_	_	_	_	_	7	0.31
Falciformispora lignalitis	_	_	1	_	_	_	_	_	_	_	_	1	0.04
Farasanispora avicenniae	1	11	15	5	8	4	3	5	_	10	5	67	3.00
Fusicolla bharatavarshae	_	_	1	_	_	_	_	_	_	_	_	1	0.04
Halocryptosphaeria avicenniae	_	_	_	_	_	_	_	_	_	3	_	3	0.13
Halocryptosphaeria bathurstensis	24	20	15	10	14	9	12	17	_	7	3	131	6.00
Halomassarina thalassiae		_	1	_	_	1	_	_	_	5	_	7	0.31
Halosarpheia marina	_	1	_	14	8	1	2	_	3	5	2	36	1.63
Hayinga salina		_	1	1	_	_	_	_	_	1	_	3	0.13
Hypoxylon teeravasti	_	_	2	_	_	_	_	_	1	1	1	5	0.22
Hysterium rhizophorae		1	11	6	4	5	9	20	15	3	6_	80	3.63
Lanspora cylindrospora	_	_	_	__	_	_	1	_	_	_	1	2	0.09
Leptosphaeria australiensis	2	2	1	11	12	_	_	1	_	_	3	32	1.45
Lignincola laevis	1	_	_	2	_	1	1	_				5	0.22
Lulworthia sp.	2	3	6	11	11	26	5	6	_	5	4	79	3.60
Marinosphaera mangrovei	10	20	16	33	30	37	20	6	10	7	13	202	9.20
Medicopsis romeroi	_	_	_	_	_	_		1	_	_	_	1	0.04
Melaspilea mangrovei	_	_	_	1	_	_	2	_	_	_	_	3	0.13
Morosphaeria muthupetensis	_	_	_	_	_	1	_	_	_	_	_	1	0.04
Morosphaeria ramunculicola	_	_	_	_	_	1	_	_	_	_	_	1	0.04
Morosphaeria velatispora	1	_	1	_	_	_	_	_	_	_	_	2	0.09
Neptunella longirostris	_	_	_	_	_	1	_	_	_	_	_	1	0.04
Paraconiothyrium cyclothyroides	19	1	19	9	3	3_	3	6	7	7	21	98	4.45
Patellaria atrata	_	1	_	2	_	_	3	10	4	5	3	28	1.27
Pedumispora rhizophorae	_	_	_	_	2	1	_	1	_	_	4	8	0.36
Peroneutypa indica	_	2	5	_	_	_	_	7	10	15	14	53	2.41
Peroneutypa polysporae	_	1	_	_	_	2	1	2	3	_	_	9	0.40

Table 1 (continued)

Fungal species	Sample collection											Total collec-tions fungus	Percentage occurrence
	28-04-2015	15-08-2015	28-11-2015	30-03-2016	29-06-2016	29-09-2016	24-12-2016	29-03-2017	23-06-2017	25-10-2017	25-02-2018		
Phaeoseptum carolshearerianum	–	–	1	–	–	–	1	–	–	–	–	2	0.09
Phaeoseptum manglicola	1	–	1	–	–	1	–	2	–	–	–	5	0.22
Pontoporeia mangrovei	–	–	–	–	–	–	1	1	–	–		2	0.09
Pseudoastrosphaeriellopsis kaveriana	–	6	16	4	2	1	–	3	–	–	–	32	1.45
Raghukumaria keshaphalae	–	–	–	—	–	–	1	–	–	–	–	1	0.04
Rimora mangrovei	–	13	44	27	13	19	34	24	9	12	6	201	9.15
Saagaromyces glitra	–	1	1	–	1	1	–	2	1	2	1	10	0.45
Sammeyersia grandispora	–	–	–	5	4	17	–	–	–	–	–	26	1.18
Savoryella lignicola	2	–	–	1	–	–	–	1	–	–	–	4	0.18
Savoryella longispora	–	–	1	–	–	1	2	–	–	–	1	5	0.22
Sclerococcum haliotrephum	–	1	10	21	12	6	3	5	7	10	5	80	3.60
Sedecmiella taiwanensis	1	–	–	–	–	–	–	–	–	–	–	1	0.04
Spororimiella sp.	–	–	–	–	–	–	–	–	–	–	1	1	0.04
Thyridariella mahakoshae	–	–	–	–	–	–	–	1	–	–	–	1	0.04
Thyridariella mangrovei	–	–	–	–	–	–	–	1	–	–	2	3	0.13
Verruconis mangrovei		2	6	3	3	1	–	1	1	–	1	18	0.81
Verruculina enalia	10	16	46	79	76	58	38	37	19	60	45	476	21.6
Vaginatispora microarmatispora	–	–	2	–	–	–	–	–	–	–	–	2	0.09
Zopfiella indica	–	–	1	–	–	–	–	–	–	–	–	1	0.04
Zopfiella sp.	–	–	–	–	–	–	–	–	–	–	1	1	0.04
Ascomycota (Asexual morphs)													
Arthrobotrys sp.	–		1	–	–	–	–	–	–	–	–	1	0.04
Biatrispora borsei	–	1	–	–	–	–	1	–	–	–	–	2	0.09
Camarosporium roumeguerei	–	–	–	–	–	–	–	1	–	–	–	1	0.04
Cytospora rhizophorae	–	5	–	–	–	13	–	–	–	–	–	18	0.81
Fusarium solani	–	–	1	–	–	–	–	–	–	–	–	1	0.04
Halenospora varia	1	1	–	2	10	–	–	–	–	–	–	14	0.63
Hydea pygmea	–	–	1	–	3	–	–	–	–	–	–	4	0.18
Lasiodiplodia theobromae	1	–	–	–	–	–	–	1	1	–	–	3	0.13
Moleospora maritima	2	–	–	4	9	3	8	–	–	–	–	26	1.18
Moromyces varius	7	–	4	5	3	–	–	–	–	–	–	19	0.86
Okeanomyces cucullatus	40	11	40	66	6	12	16	–	–	–	–	191	8.68
Paradictyoarthrinium diffractum	–	–	1	–	–	–	–	–	–	–	–	1	0.04
Phaeosaria clematidis	–	–	1	–	–	–	–	–	–	–	–	1	0.04
Phoma sp.	–	17	6	12	–	14	–	–	–	–	–	49	2.22
Phomopsis mangrovei	–	1	2	–	–	7	2	4	–	–	–	16	0.72
Scedosporium aurantiacum	–	–	1	–	–	–	–	–	–	–	–	1	0.04

Table 1 (continued)

Fungal species	Sample collection											Total collections fungus	Percentage occurrence
	28-04-2015	15-08-2015	28-11-2015	30-03-2016	29-06-2016	29-09-2016	24-12-2016	29-03-2017	23-06-2017	25-10-2017	25-02-2018		
Scedosporium dehoogii	–	–	1	–	–	–	–	–	–	–	–	1	0.04
Sporidesmium sp.	–	1	–	–	–	–	–	13	–	–	–	14	0.63
Sporidesmium tropicale	–	–	1	–	–	–	–	–	–	–	–	1	0.04
Zygosporium gibbum	–	–	–	1	–	–	–	–	–	–	–	1	0.04
Basidiomycota													
Halocyphnia villosa	–	–	4	–	–	9	–	–	–	–	–	13	0.59
Marasmiellus sp.	–	–	3	–	–	–	3	–	–	–	–	6	0.27
No. of twigs supporting sporulating fungi	**144**	**147**	**302**	**347**	**230**	**270**	**183**	**181**	**91**	**158**	**145**	**2198**	
No. of twigs examined	**420**	**540**	**650**	**635**	**612**	**627**	**580**	**596**	**460**	**535**	**560**	**6215**	

found to be the most frequent fungus followed by *Rimora mangrovei* (13.33%), *Antennospora quadricornuta* (7.77%), *Arenariomyces trifurcatus* (6.66%), and *Halenospora varia* (4.44%), with 17.7% of substrates colonized by fungi (Table 3).

Twenty marine fungal species belonging to 19 genera were recorded from *Rhizophora mucronata* which included 12 *Ascomycota* (60%), one *Basidiomycota* (5%), and seven asexual morphs (35%) (Figs. 2, 3). *Lulworthia* sp. (14.55%) was found to be the most frequent fungus followed by *Sammeyersia grandispora* (12.2%), *Phoma* sp. (10.8%), *Rimora mangrovei* (7.98%), *Okeanomyces cucullatus* (7.98%), *Verruculina enalia* (6.57%), *Cytospora rhizophorae* (6.14%), and *Halocyphnia villosa* (4.2%). Colonization of *R. mucronata* by marine fungi was 42.2% (Table 3). *Morosphaeria muthupetensis* is recorded as specific to this host.

Thirty-four marine fungal species belonging to 32 genera were recorded on *Suaeda monoica* including 23 *Ascomycota* (67.5%), two *Basidiomycota* (5.8%), and nine asexual morphs (26.4%) (Figs. 2, 3). *Rimora mangrovei* (14.05%) was found to be the most frequent fungus followed by *Farasanispora avicenniae* and *Peroneutypa indica* (13.10%), *Paraconithyrium cyclothyrioides* (11.10%), *Okeanomyces cucullatus* (8.65%), *Verruculina enalia* (8.65%), and *Marinosphaera mangrovei* (7.15%). Colonization of *S. monoica* by marine fungi was 44.4% (Table 3).

Statistical analyses

Species richness was greatest for *Avicennia marina* followed by *Suaeda monoica* and *Rhizophora mucronata*. Shannon-Weiner index accounting for entropy in an ecosystem was greatest for *A. marina*, *S. monoica*, and *R. mucronata* but lower in *Aegiceras corniculatum*. A similar profile was observed by the Simpson index indicating that *Aegiceras corniculatum* has lower diversity in comparison with other plants. Evenness was highest in *R. mucronata* and lowest in *A. marina*, hinting that it may have a single species dominance (Table 4 and Table 5).

A two-way ANOVA showed that fungal species richness was significantly affected by plant species ($P < 0.001$) but not by season ($P = 0.239$) (Table 6). There was no significant effect of season on fungal richness (season × plant, $P = 0.369$). Based on multiple comparisons with the Holm-Sidak method, a significant difference was observed in the overall species richness between *Avicennia marina* and *Aegiceras corniculatum*, *Avicennia marina* and *Excoecaria agallocha*, *Avicennia marina* and *Rhizophora mucronata*, *Avicennia marina* and *Suaeda monoica* ($P < 0.001$), and *Suaeda monoica* and *Aegiceras corniculatum* ($P = 0.003$) (Table 6).

Table 2 Summary of very frequent, frequent and infrequent fungi recorded from Muthupet mangroves

Very frequent (> 10%)	Frequent (> 5–10%)	infrequent (> 1′5%)
Verruculina enalia	*Okeanomyces cucullatus*	*Sclerococcum haliotrephum*
	Rimora mangrovei	*Lulworthia sp*
	Marinosphaera mangrovei	*Paraconiothyrium cyclothyroides*
	Halocryptosphaeria bathurstensis	*Hysterium rhizophorae*
		Farasanispora avicenniae

Discussion

The current number of accepted marine fungi in the world is 1692 species in 685 genera, 222 families, and 88 orders as listed in the website: marinefungi.org (28 Sep 2020). A significant proportion of that is accounted for by the number documented for mangrove habitats especially over the past 10 years (Suetrong et al. 2017; Sarma 2016).

Current status of marine fungal diversity in Indian mangroves

A total of 850 mangrove fungi have been reported from different mangroves distributed across the world (Devadatha et al. 2021). The number of marine fungi recorded for India is (339) greater than other countries surveyed, e.g., Thailand (303) and Malaysia (171) (Devadatha et al. 2021). Sarma and Devadatha (2020) listed 414 mangrove fungi, including the lower marine fungi, from Indian mangroves. A comparison of fungal diversity between east (225 marine fungi) and west coast (306) of India showed that 117 species were common to both coasts (Sarma and Devadatha 2020). The current study demonstrated that Muthupet mangroves have a rich marine fungal diversity with 20% of total recorded for India. These studies highlight the rich fungal diversity of India reflecting the widespread and extensive areas of mangroves on the east and west coasts.

Marine fungi initially described elsewhere from Muthupet mangroves

Fungal species diversity at Muthupet mangrove was higher (78 taxa) when compared to other tropical locations: Mauritius (67 species, (Poonyth et al. 1999)); Seychelles (63 species, (Hyde and Jones 1989)), Andaman and Nicobar Islands, India (63 species, Chinnaraj (1993)); and Belize (46 species, (Kohlmeyer and Volkmann-Kohlmeyer 1987)), with lower numbers reported for Mandai mangrove, Singapore (41 species, (Tan et al. 1989)).

The survey of Muthupet mangroves resulted in the discovery of many new taxa and have been described elsewhere. These include three novel genera: *Thyridariella* (*T. mangrovei*, *T. mahakoshae*) (Devadatha et al. 2018a), *Pseudoastrosphaeriellopsis* (*P. kaveriana*) (Phookamsak et al. 2019), and *Raghukumaria* (*R. keshaphalae*) (Jones et al. 2020). The new species described from Muthupet mangroves include: *Vaginatispora microarmatispora* (Devadatha et al. 2017), *Pontoporeia mangrovei* (Devadatha and Sarma 2018), *Deniquelata vittalii* (Devadatha et al. 2018c), *Morosphaeria muthupetensis* (Devadatha et al. 2018b), *Amphisphaeria mangrovei*, *Hypoxylon teeravasati*, *Zopfiella indica*

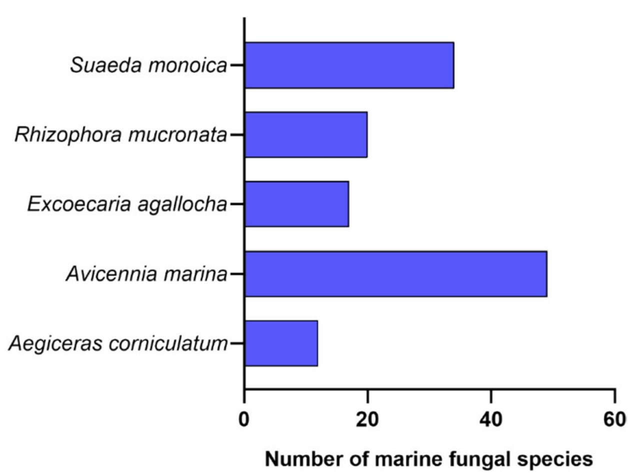

Fig. 2 Bar diagram showing number of marine fungal species retrieved from different mangrove plants of Muthupet

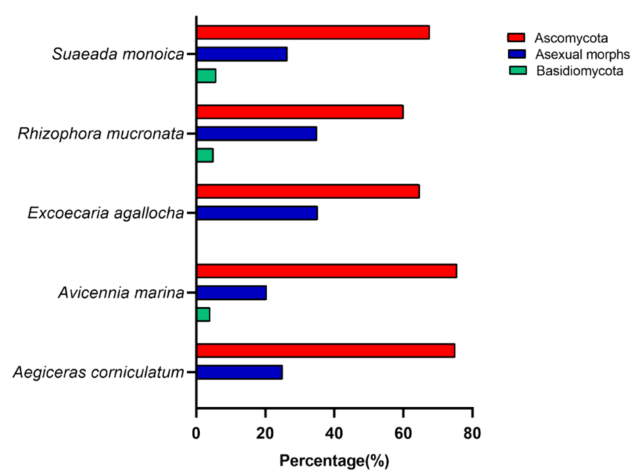

Fig. 3 Bar diagram showing percentage occurrence of marine fungal groups on different mangrove plants of Muthupet

Table 3 Percentage occurrence of higher marine fungi recorded from different hosts of Muthupet mangroves, Tamil Nadu, East Coast of India

Fungal species	*Avicennia marina*		*Aegiceras corniculatum*		*Excoecaria agallocha*		*Rhizophora mucronata*		*Suaeda monoica*		Total number of collections of each fungus	Percentage of occurrence
	No. occurrences	% occurences	No. occurrences	% occurrences	No. occurences	% occurences	No. occurences	% occurences	No. occurences	% occurences		
Ascomycota (Sexual morphs)												
Aigialus parvus	6	0.45	_	_	_	_	_	_	3	0.74	9	0.41
Amphisphaeria mangrovei	_	_	_	_	_	_	_	_	**3**	0.74	3	0.13
Aniptodera chesapeakensis	18	1.36	_	_	2	2.22	3	1.4	1	0.24	24	1.09
Aniptodera haispora	5	0.37	_	_	_	_	1	0.46	_	_	6	0.27
Antennospora quadricornuta	_	_	_	_	7	7.77	_	_	_	_	7	0.32
Anthostomella sp.	17	1.28	_	_	_	_	_	_	_	_	17	0.77
Arenariomyces trifurcatus	_	_	_	_	6	6.66	_	_	_	_	6	0.27
Calonectria sp.	1	0.07	_	_	_	_	_	_	_	_	1	0.04
Halocryptosphaeria avicenniae	3	0.22	_	_	_	_	_	_	_	_	3	0.13
Halocryptosphaeria bathurstensis	122	9.25	_	_	_	_	_	_	9	2.22	131	6.00
Deniquelata vittalii	_	_	_	_	_	_	_	_	2	0.49	2	0.09
Dyfrolomyces rhizophorae	_	_	_	_	_	_	7	3.28	_	_	7	0.32
Falciformispora lignalitis	_	_	1	0.6	_	_	_	_	_	_	1	0.04
Farasanispora avicenniae	14	1.06	_	_	_	_	_	_	53	13.08	67	3.07
Fusicolla bharatavarshae	1	0.07	_	_	_	_	_	_	_	_	1	0.04
Halomassarina thalassiae	6	0.45	_	_	_	_	1	0.46	_	_	7	0.32
Halosarpheia marina	36	2.73	_	_	_	_	_	_	_	_	36	1.64
Hayinga salina	3	0.22	_	_	_	_	_	_	_	_	3	0.13
Hypoxylon teeravasti	4	0.3	_	_	_	_	_	_	1	0.24	5	0.22
Hysterium rhizophorae	2	0.15	70	44.9	_	_	8	3.75			80	3.66
Lanspora cylindrospora	_	_	_	_	_	_	_	_	2	0.49	2	0.09
Leptosphaeria australiensis	29	2.2	_	_	3	3.33	_	_	_	_	32	1.46
Lignincola laevis	5	0.37	_	_	_	_	_	_	_	_	5	0.22
Lulworthia sp.	37	2.8	1	0.64	3	3.33	31	14.55	7	1.72	79	3.62
Marinosphaera mangrovei	158	11.98	_		2	2.22	_	_	29	7.16	189	8.66
Medicopsis romeroi	_	_	_	_	_	_	_	_	1	0.24	1	0.04
Melaspilea mangrovei	_	_	_	_	_	_	3	1.4	_	_	3	0.13
Morosphaeria muthupetensis	_	_	_	_	_	_	1	0.46	_	_	1	0.04
Morosphaeria ramunculicola	_	_	1	.64	_	_	_	_	_	_	1	0.04
Morosphaeria velatispora	1	0.07	_	_	1	1.11	_	_	_	_	2	0.09
Neptunella longirostris	1	0.07		_	_	_	_	_	_	_	1	0.04
Paraconiothyrium cyclothyroides	53	4.02	_	_	_	_	_	_	45	11.11	98	4.49
Patellaria atrata	18	1.36	_	_	_	_	_	_	10	2.46	28	1.28
Pedumispora rhizophorae	_	_	_	_	_	_	8	3.75			8	0.36
Peroneutypa indica	_	_	_	_	_	_	_	_	53	13.08	53	2.42

Table 3 (continued)

Fungal species	*Avicennia marina*		*Aegiceras corniculatum*		*Excoecaria agallocha*		*Rhizophora mucronata*		*Suaeda monoica*		Total number of collections of each fungus	Percentage of occurrence
	No. occurrences	% occurences	No. occurrences	% occurrences	No. occurences	% occurences	No. occurences	% occurences	No. occurences	% occurences		
Peroneutypa polysporae	_	_	_	_	_	_	_	_	9	2.22	9	0.41
Phaeoseptum carolshearerianum	1	0.07	_	_	_	_	_	_	1	0.24	2	0.09
Phaeoseptum manglicola	4	0.3	_	_	_	_	_	_	1	0.24	5	0.22
Pontoporeia mangrovei	1	0.07	_	_	_	_	_	_	1	0.24	2	0.09
Pseudoastrosphaeriellopsis kaveriana	20	1.51	_	_	2	2.22			10	2.46	32	1.46
Raghukumaria keshaphalae	_	_	1	0.64	_	_	_	_	_	_	1	0.04
Rimora mangrovei	81	6.15	34	21.79	12	13.33	17	7.98	57	14.07	201	9.21
Saagaromyces glitra	10	0.75	_	_	_	_	_	_	_	_	10	0.45
Sammeyersia grandispora	_	_	_	_	_	_	26	12.2	_	_	26	1.19
Savoryella longispora	3	0.22	_	_	_	_	_	_	2	0.49	5	0.22
Savoryella lignicola	4	0.3	_	_	_	_	_	_	_	_	4	0.18
Sclerococcum haliotrephum	80	6.00	_	_	_	_	_	_	_	_	80	3.66
Sedecmiella taiwanensis	1	0.07	_	_	_	_	_	_	_	_	1	0.04
Spororimiella sp.	1	0.07	_	_	_	_	_	_	_	_	1	0.04
Thyridariella mahakoshae	1	0.07	_	_	_	_	_	_	_	_	1	0.04
Thyridariella mangrovei	3	0.22	_	_	_	_	_	_	_	_	3	0.13
Verruconis mangrovei	8	0.6	8	5.12	2	2.22	_	_	_	_	18	0.82
Verruculina enalia	361	27.3	28	17.94	37	41.11	14	6.57	35	8.64	475	21.76
Vaginatispora microarmatispora	_	_	2	1.28	_	_	_	_	_	_	2	0.09
*Zopfiella indica**	_	_	_	_	_	_	_	_	_	_	_	_
Zopfiella sp.	_	_	_	_	_	_	_	_	1	0.24	1	0.04
Ascomycota (Asexual morphs)												
Arthrobotrys sp.	_	_	_	_	_	_	_	_	1	0.24	1	0.04
Biatrispora borsei	2	0.15	_	_	_	_	_	_	_	_	2	0.09
Camarosporium roumeguerei	1	0.07	_	_	_	_	_	_	_	_	1	0.04
Cytospora rhizophorae	_	_	_	_	_	_	18	8.45	_	_	18	0.82
Fusarium solani	_	_	_	_	1	1.11	_	_	_	_	1	0.04
Hydea pygmea	_	_	_	_	_	_	4	1.877			4	0.18
Halenospora varia	_	_	_	_	4	4.44	10	4.69	_	_	14	0.64
Lasiodiplodia theobromae	_	_	_	_	3	3.33	_	_	_	_	3	0.13
Moleospora maritima	20	1.51	_	_	_	_	5	2.34	1	0.24	26	1.19
Moromyces varius	12	0.91	6	3.84	1	1.11	_	_	6	1.48	25	1.14
Paradictyoarthrinium diffractum	1	0.07	_	_	_	_	_	_	_	_	1	0.04
Okeanomyces cucullatus	130	9.86	3	1.92	1	1.11	17	7.98	35	8.64	186	8.52
Phaeosaria clematidis	_	_	_	_	_	_	_	_	1	0.24	1	0.04
Phoma sp.	19	1.44	_	_	3	3.33	23	10.79	4	0.98	49	2.24

Table 3 (continued)

Fungal species	*Avicennia marina*		*Aegiceras corniculatum*		*Excoecaria agallocha*		*Rhizophora mucronata*		*Suaeda monoica*		Total number of collections of each fungus	Percentage of occurrence
	No. occurrences	% occurences	No. occurrences	% occurrences	No. occurences	% occurences	No. occurences	% occurences	No. occurences	% occurences		
Phomopsis mangrovei	4	0.3	1	0.64	–	–	–	–	11	2.71	16	0.73
Scedosporium aurantiacum	1	0.07	–	–	–	–	–	–	–	–	1	0.04
Scedosporium dehoogii	–	–	–	–	–	–	–	–	1	0.24	1	0.04
Sporidesmium sp.	7	0.53	–	–	–	–	7	3.28			14	0.64
Sporidesmium tropicale	–	–	–	–	–	–	–	–	1	0.24	1	0.04
*Zygosporium gibbum**	–	–	–	–	–	–	–	–	–	–	–	–
Basidiomycota												
Halocyphnia villosa	1	0.07	–	–	–	–	9	4.22	3	0.74	13	0.59
Marasmelius sp.	1	0.07	–	–	–	–	–	–	5	1.23	6	0.27
Total number of samples supporting sporulating fungi	**1318**	–	**156**	–	**90**	–	**213**	–	**405**	–	**2182**	
Samples without sporulating fungi	**2398**	–	**247**	–	**418**	–	**291**	–	**507**	–	**3861**	
Number of samples examined	**3716**	–	**403**	–	**508**	–	**504**	–	**912**	–	**6043**	
% colonization	**35.4**		**38.7**		**17.7**		**42.2**		**44.4**			

*Collected on unkown drift mangrove wood

(Phookamsak et al. 2019), *Halocryptosphaeria avicenniae* (Dayarathne et al. 2020b), *Lanspora cylindrospora*, *Verruconis mangrovei* (Hyde et al. 2020b), *Biatriospora borsei* (Hongsanan et al. 2020), *Fusicolla bharathavarshae* (Jones et al. 2020), *Peroneutypa polysporae*, *P. indica, Phaeoseptum carolshearerianum*, and *Ph. manglicola* (Dayarathne et al. 2020a). The fact that of the 78 species recorded 3 are new genera and 20 are new species indicates a rich marine fungal diversity in this mangrove formation. The main reason could be the new host plant *Suaeda monoica* examined. Our study demonstrates the value of exploring new mangrove locations and host substrates. Hence, further fungal diversity can be expected when mangrove forests hitherto not surveyed, such as mangroves in Africa, Bangladesh, China, Indonesia, Myanmar, Pakistan, South America, and Sri Lanka, are investigated (Hyde and Jones 1989; Jones et al. 2019).

First report of pathogenic marine fungi in Muthupet mangroves

From this study, it is evident that pathogenic fungi, often reported from humans and other sources, may also occur in the marine environment. For example, the sexual and asexual morphs of the human pathogen *Medicopsis romeroi* were recovered from woody stems of *Suaeda monoica*. *Medicopsis romeroi* is commonly reported from mycetoma in humans and immunocompromised hosts and also occasionally on plant materials. *Paraconithyrium cyclothyrioides* (asexual morph) is a coelomycetous fungal species recognized as an opportunistic pathogen in immunocompromised patients and causes cutaneous phaeohyphomycosis (Gordon et al. 2012). The sexual morph of *P. cyclothyrioides* was also frequently recorded on *S. monoica* (Hyde et al. 2020a). Similarly, we have found *Scedosporium aurantiacum* as a saprobe on decaying woody stems of the halophyte *S. monoica* from marine habitats. *Scedosporium aurantiacum* is an opportunistic human pathogen known to cause various infections in lungs, ears, respiratory sinuses, and subcutaneous abscess in patients of diabetes and malignant lymphoma (Kondo et al. 2018).

Core mangrove fungi

Various researchers have attempted to characterize core mangrove fungi, but this is difficult as the study methods and documentation differ (Hyde et al. 1998; Sarma and Hyde 2001; Alias et al. 2010; Sridhar et al. 2012). The most frequent fungi from Muthupet mangroves were *Verruculina enalia*, *Rimora mangrovei*, *Marinosphaera mangrovei*, *Okeanomyces cucullatus*, and *Halocryptosphaeria bathurstensis*. According to earlier reports, the most frequent marine fungi from east coast of India were *V. enalia*, *Rimora*

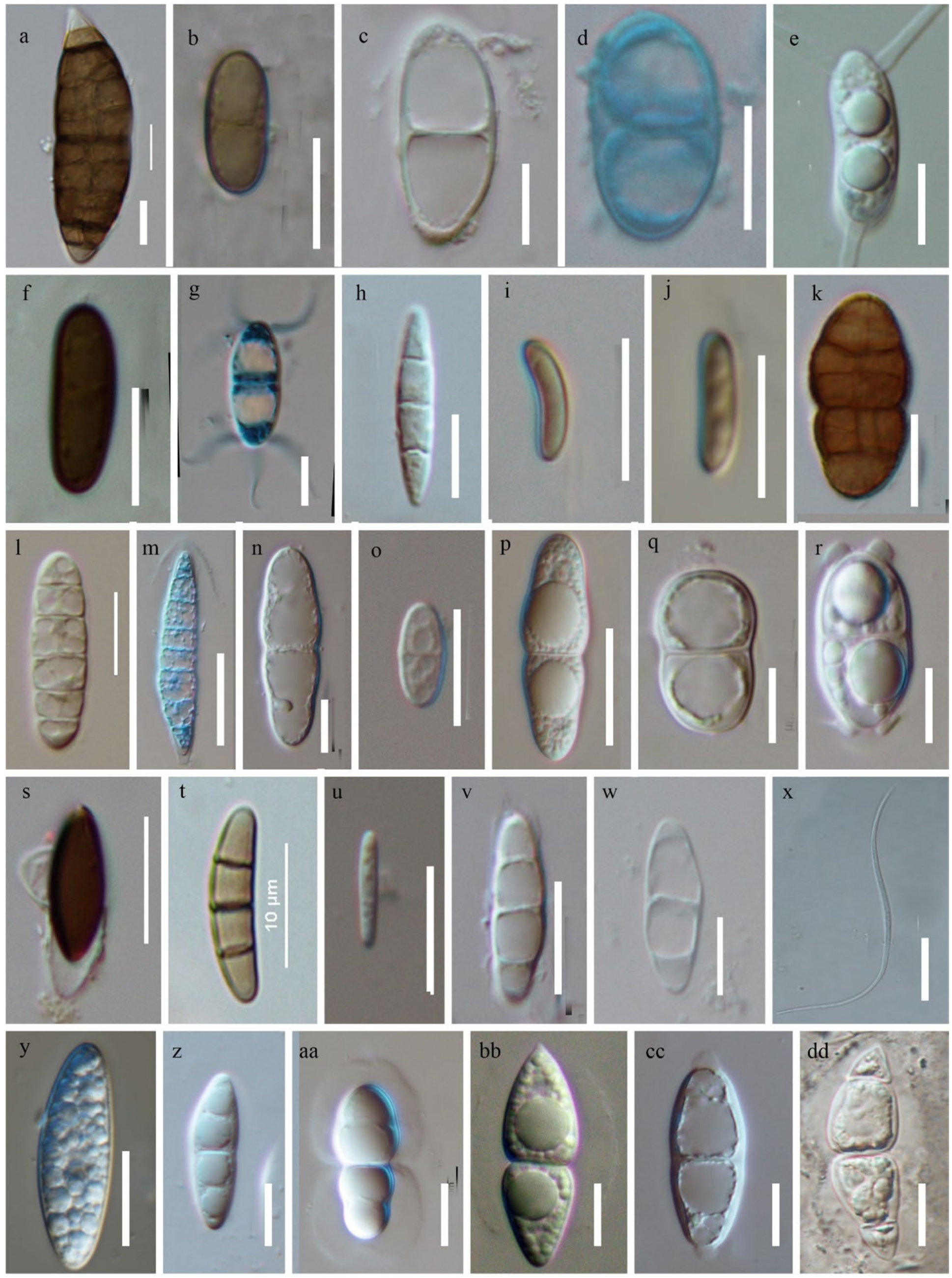

Fig. 4 Ascomycetes found from Muthupet mangroves. **a** *Aigialus parvus*; **b** *Amphisphaeria mangrovei*; **c** *Aniptodera chesapeakensis*; **d** *Aniptodera haispora*; **e** *Antennospora quadricornuta*; **f** *Anthostomella* sp.; **g** *Arenariomyces trifurcatus*; **h** *Calonectria* sp.; **i** *Deniquelata vittalii*; **j** *Dyfrolomyces rhizophorae*; **k** *Falciformispora lignalitis*; **l** *Farasanispora avicenniae*; **m** *Fusicolla bharatavarshae*; **n** *Halocryptosphaeria avicenniae*; **o** *Halocryptosphaeria bathurstensis*; **p** *Halomassarina thalassiae*; **q** *Halosarpheia marina*; **r** *Hayinga salina*; **s** *Hypoxylon teeravasti*; **t** *Hysterium rhizophorae*; **u** *Lanspora cylindrospora*; **v** *Leptosphaeria australiensis*; **w** *Lignincola laevis*; **x** *Lulworthia* sp.; **y** *Marinosphaera mangrovei*; **z** *Medicopsis romeroi*; **aa** *Melaspilea mangrovei*; **bb** *Morosphaeria muthupetensis*; **cc** *Morosphaeria ramunculicola*; **dd** *Morosphaeria velatispora*. Scale bars: a–dd = 10 µm

mangrovei, *Halocryptosphaeria bathurstensis*, *Rhizophila marina*, *Sclerococcum haliotrephum*, *Halorosellinia oceanica*, and *Halocyphnia villosa* (Sarma and Vittal 2000; Sarma and Hyde 2001; Sarma et al. 2001). *Aniptodera mangrovei*, *Hydea pygmea*, *Lignincola laevis*, and *Savoryella lignicola* are the core marine fungi documented for the Indian west coast (Maria and Sridhar 2002, 2003, 2004; Sridhar and Maria 2006). The frequency of occurrence of mangrove fungi differs significantly among different studies; normally, few fungi will dominate a given area, whereas others will be infrequently encountered (Cooke and Rayner 1984, Sarma and Hyde 2001, Sarma et al. 2001).

Prevalence of *Ascomycota* in mangroves

The *Ascomycota* is the predominant group of fungi in the marine environment, as in our study, while *Basidiomycota* is poorly represented (Alias et al. 1995; Sarma and Vittal 2001a; Binder et al. 2006; Vittal and Sarma 2006; Jones et al. 2019). Worldwide a total of 21 filamentous marine basidiomycetes in 17 genera and 75 marine basidiomycete yeasts in 26 genera were recorded in marine environments (marinefungi.org). Of these, 19 filamentous basidiomycetes in 14 genera and 39 basidiomycete yeasts in 20 genera were recorded from mangrove habitats (Devadatha et al. 2021).

Fig. 5 Ascomycetes and Basidiomycetes found from Muthupet mangroves. **a** *Neptunella longirostris*; **b** *Paraconiothyrium cyclothyroides*; **c** *Patellaria atrata;* **d** *Pedumispora rhizophorae*; **e** *Peroneutypa indica*; **f** *Peroneutypa polysporae*; **g** *Phaeoseptum carolshearerianum*; **h** *Phaeoseptum manglicola*; **i** *Pontoporeia mangrovei*; **j** *Pseudoastrosphaeriellopsis kaveriana*; **k** *Raghukumaria keshaphalae*; **l** *Rimora mangrovei*; **m** *Saagaromyces glitra*; **n** *Sammeyersia grandispora*; **o** *Savoryella lignicola*; **p** *Savoryella longispora*; **q** *Sclerococcum haliotrephum*; **r** *Sedecmiella taiwanensis*; **s** *Spororimiella* sp.; **t** *Thyridariella mahakoshae*; **u** *Thyridariella mangrovei*; **v** *Verruconis mangrovei*; **w** *Verruculina enalia*; **x** *Vaginatispora microarmatispora*; **y** *Zopfiella indica*; **z** *Zopfiella* sp.; **aa** *Halocyphnia villosa*; **bb** *Marasmiellus* sp. Scale bars: a–z = 10 µm; aa–bb = 200 µm

Only two basidiomycetes were reported in comparison to 56 *Ascomycetes* in the present study. However, basidiomycetes, like *Ganoderma* sp., *Hexogonia* sp., and *Schizophyllum commune*, were noted on the aerial parts of mangrove trees of Muthupet. In general, the basidiomes of marine *Basidiomycota* are small and rarely greater than 5 mm. Several reasons have been advanced to explain why so few basidiomata-forming basidiomycetes are reported from the marine environment, and these include wave action which may hamper formation of larger fruiting structures and need to tolerate tidal fluctuations and immersion in seawater and formation and dispersal of basidiospores in an aquatic environment (Jones 1982; Binder et al. 2001; Jones et al. 2019). *Ascomycetes* are better adapted to an aquatic habitat with minute or microscopic ascomata, often immersed in the host substrate, passive release of ascospores, and or active discharge in the intertidal region.

Host specificity and common mangrove fungi among different hosts were collected during 2015 to 2018

Studies of mangrove fungi suggest they are not host specific, with the exception of those growing on the brackish

Fig. 6 Asexual fungi found from Muthupet mangroves. **a** *Arthrobotrys* sp.; **b** *Biatrispora borsei*; **c** *Camarosporium roumeguerei*; **d** *Cytospora rhizophorae*; **e** *Fusarium solani*; **f** *Halenospora varia*; **g** *Hydea pygmea*; **h** *Lasiodiplodia theobromae*; **i** *Moleospora maritima*; **j** *Moromyces varius*; **k** *Okeanomyces cucullatus*; **l** *Paradictyoarthrinium diffractum*; **m** *Phaeosaria clematidis*; **n** *Phoma* sp.; **o** *Phomopsis mangrovei*; **p** *Scedosporium aurantiacum*; **q** *Scedosporium dehoogii*; **r** *Sporidesmium* sp.; **s** *Sporidesmium tropicale*; **t** *Zygosporium gibbum*. Scale bars: a–t = 10 µm

water palm *Nypa fruticans* with Loilong et al. (2012) listing 31 that are unique to this host, e.g., *Anthostomella nypae*, *Bacusphaeria nypae*, *Fasciatispora nypae*, *Helicascus nypae*, *Manglicola guatemaelensis*, *Pleurophomopsis nypae* and *Tirisporella baccariana* (Jones et al. 1996; Hyde and Alias 1999; Suetrong et al. 2009; Loilong et al. 2012; Abdel-Wahab et al. 2017). To date, most mangrove fungi have been found growing on woody substrates, while plants in the salt marsh zones of mangroves have been little studied in the tropics, e.g., *Suaeda monoica*. In the current study, we examined the colonization of five timber host plants, and the results are presented in UpSet plot (Fig. 7). Fewer fungi were recorded on two mangrove associates: *Acanthus ilicifolius* and *Suaeda maritima* as collections were made only in 2015–2016 with fewer samples, and hence, they were not accounted in ecological observations. The herbaceous nature of these substrata seems to be not favorable for fungal colonization, in contrast to other mangrove plants. UpSet plot indicates that *A. marina* supported 19 unique fungal species, while *S. monoica* and *R. mucronata* have 11 each, while *E. agallocha* and *R. mucronata* have four unique fungal taxa (Fig. 7). Only four fungal taxa (*Lulworthia* sp., *Okeanomyces cucullatus*, *Rimora mangrovei*, *Verruculina enalia*) were found to be common to all host substrates, indicating that certain fungal species have very particular niche colonization. Few host-specific marine fungi have been found in this study. However, six species are specific to *Avicennia marina* (*Biatrispora borsei*, *Halocryptosphaeria avicenniae Fusicolla bharatavarshae*, *Hypoxylon teeravasti*, *Thyridariella mangrovei*, and *T. mahakoshae*), five to *Suaeda monoica* (*Amphisphaeria mangrovei*, *Deniquelata vittalii*, *Lanspora cylindrospora*, *Peroneutypa indica*, and *P. polysporae*), two to *A. corniculatum* (*Raghukumaria keshaphale* and *Vaginatispora microarmatispora*), and one to *Rhizophora mucronata* (*Morosphaeria muthupetensis*). These taxa are recently introduced, and further studies are required to determine if they are host specific. It is interesting to note that *Suaeda maritima*, which is more common in mangroves throughout the world, did not support a rich fungal diversity. This may be attributed to the herbaceous nature of *S. maritima*,

Table 4 Alpha diversity measures

Alpha diversity indices	*Avicennia marina*	*Aegiceras corniculatum*	*Excoecaria agallocha*	*Rhizophora mucronata*	*Suaeda monoica*
Species richness	49	12	17	20	34
Individuals	1318	156	90	213	405
Simpson 1-D	0.8795	0.7141	0.7938	0.9177	0.9095
Shannon_H	2.673	1.571	2.143	2.675	2.712
Evenness_e^H/S	0.2955	0.4011	0.5017	0.726	0.443
Margalef	6.682	2.178	3.556	3.544	5.496

Jaccard's similarity ranged from 15 to 38.9%, with a higher species similarity between *A. marina* and *S. monoica*, while lowest was seen between *Ae. corniculatum* and *S. monoica* (Table 5)

Table 5 Jaccard's similarity (%) of mangrove fungi in five plant species

Plant species	*Avicennia marina*	*Aegiceras corniculatum*	*Excoecaria agallocha*	*Rhizophora mucronata*
Aegiceras corniculatum	15.38			
Excoecaria agallocha	22.3	26		
Rhizophora mucronata	21.42	18.51	24.13	
Suaeda monoica	38.98	15	21.42	18.6

while *S. monoica* is woody. This study is the first to document the colonization of woody tissues of *S. monoica* and again demonstrates the need to sample a wider range of host mangrove plants. Many low- and high-salt marsh plants also form part of the mangrove ecosystem such as *Juncus kraussii* in Australia and remain to be surveyed for fungi (Sainty et al. 2012).

Species richness, diversity, and evenness of marine fungi recovered from Muthupet mangroves

A higher species richness and fungal incidence was observed in *Aviccenia marina* followed by *S. monoica* compared to other plant species (Fig. 2). The higher occurrence of marine fungi on *A. marina* and *S. monoica* may be due to larger number of available substrata and greater susceptibility to colonization. Another reason is dominance of *A. marina* and *S. monoica* plants when compared to other mangrove plants in Muthupet. However, two exceptions are *E. agallocha* and *S. maritima*. Even though these plants are dominant in Muthupet, they did not support a rich fungal diversity. The evenness was lower in *A. marina*, while it was highest in *R. mucronata* possibly due to dominant fungal species in *A. marina* (*H. bathurstensis, V. enalia* and *M. mangrovei*) indicating that *R. mucronata* harbors an even fungal community on it. Simpson's diversity index (1-D) was highest for *R. mucronata* followed by *S. monoica* and *A. marina* indicating that *R. mucronata* harbored a highly diverse fungal species compared to the other tree species. Margalef's index and Shannon index are dependent on the total number of species and were hence higher in *A. marina* and *S. monoica* (Table 4).

Conclusions

Despite several studies on mangrove fungi, many mangrove sites in India remain unexplored. This also applies to many other countries with extensive mangroves: Africa, Australia, and South America. Previous studies of Indian mangroves yielded circa 17 new marine fungi. In the current study, 78

Table 6 Two-way ANOVA of the impact of plant species and season (wet and dry) on richness of species of mangrove fungi in five mangrove plants followed by multiple comparison with Holm-Sidak method

Treatment	df	F	P
Season	1	1.476	0.239
Plant	4	23.495	< 0.001
Season × plant	4	1.133	0.369
Multiple comparison for plant (Holm-Sidak method)			
Comparison	Diff of means	P value	Significance
AM vs. AC	16.167	< 0.001	Yes
AM vs. EA	15.000	< 0.001	Yes
AM vs. RM	13.500	< 0.001	Yes
AM vs. SM	9.833	< 0.001	Yes
SM vs. AC	6.333	0.003	Yes

df degrees of freedom; *F* ratio of two mean square values; *P* level of significance. Plant species: *AM Avicennia marina*, *AC Aegiceras corniculatum*, *RM Rhizophora mucronata*, *SM Suaeda monoica*, *EA Excoecaria agallocha*

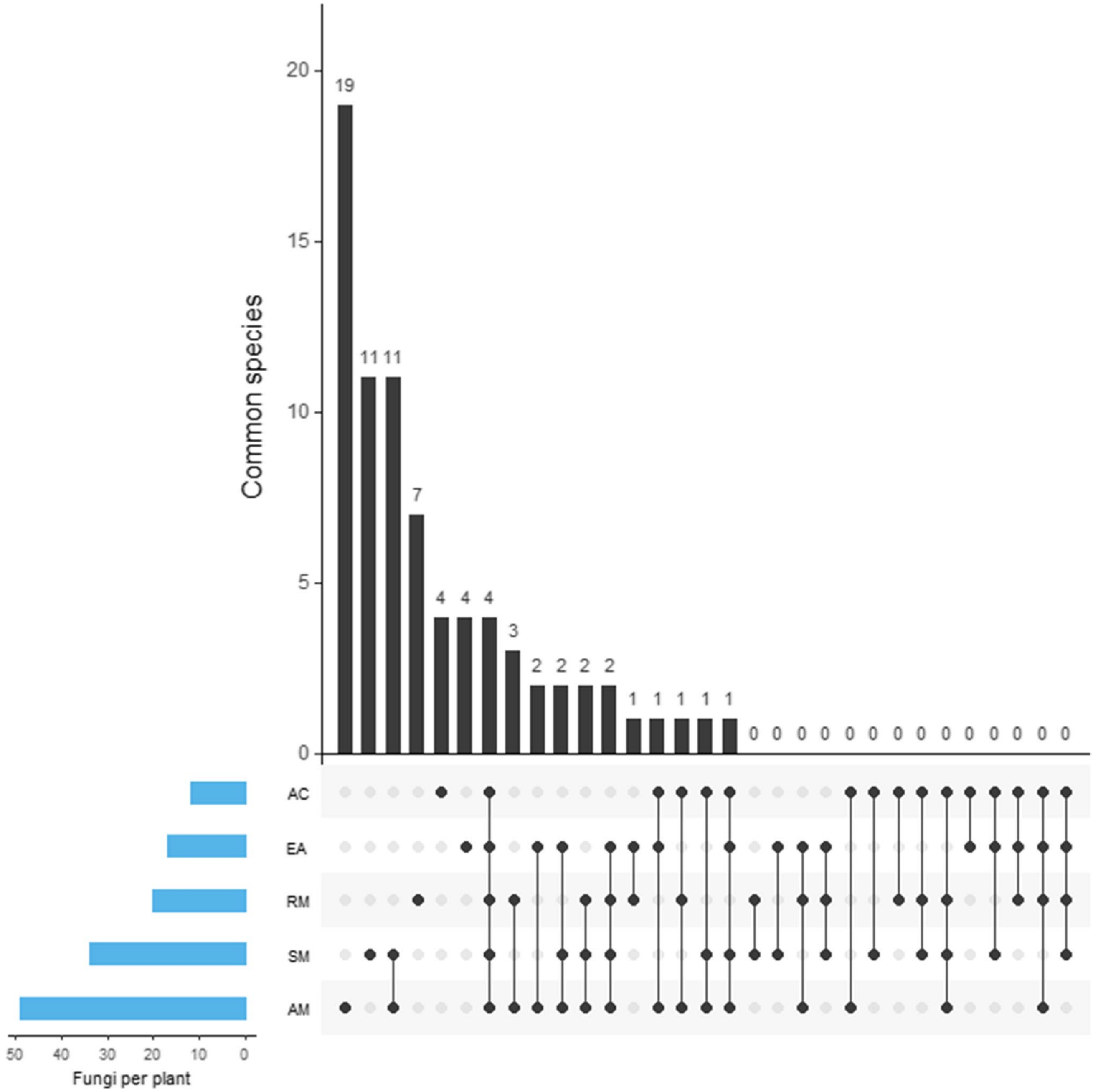

Fig. 7 UpSet plot showing common mangrove fungal species among different mangrove plants (AC = *Aegiceras corniculatum*; EA = *Excoecaria agallocha*; RM = *Rhizophora mucronata*; SM = *Suaeda monoica*; AM = *Avicennia marina*)

marine fungal taxa were reported, of which three were new genera and 19 new species, which were reported elsewhere (Devadatha et al. 2017, 2018a, b, c, 2019, Devadatha and Sarma 2018, Dayarathne et al. 2020a, b, Hongsanan et al. 2020, Hyde et al. 2020b, Jones et al. 2020, Phookamsak et al. 2019). This highlights the need for intensive sampling supported by sequencing data. Reports of marine fungi from mangrove soil and leaf litter are few in number; hence, further studies are required to explore their diversity in mangroves. Additional studies are required to reveal the fungal community structure associated with decomposition of mangrove plants, including metagenomic/transcriptomic-based analyses on marine fungi from mangrove litter, soil, water, and wood in order for a better understanding of the nature of fungal interactions in mangroves. While these surveys enhance our knowledge of the diversity of marine fungi in mangrove ecosystems, studies involving high-throughput sequencing techniques are urgently required to form a more robust statistical evaluation of fungal activity and occurrence of non-sporulating taxa.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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Author contribution BD contributed in the investigation of the research work, methodology, formal analysis, software, data curation, writing the original draft of the manuscript, review, editing, and visualization. SG contributed in the statistical analyses, software, formal analysis, writing-review, editing type face, and data curation. EBG has contributed in review and editing of the manuscript, visualization and validation. VVS contributed in conceptualization, methodology, resources, supervision, project administration, funding acquisition, and review and editing of the manuscript. All authors reviewed and approved the manuscript.

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