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Distribution and diversity of foliar endophytic fungi in the mangroves of Andaman Islands, India

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ABSTRACT

Fungal endophytes represent a major component of plant microbiomes. Various aspects of these fungi such as their diversity and technological potential have been studied in detail. However, their distribution and diversity in a mangrove community has not been addressed. In this study, we report the presence of culturable fungal endophytes from 20 obligate mangrove hosts from south Andaman Islands. *Phomopsis/Diaporthe* was isolated from all the mangrove species studied while *Xylaria*, *Colletotrichum* and *Phyllosticta* were recorded from the majority of the mangroves studied. A phylogenetic analysis of representative *Phomopsis/Diaporthe* isolates clearly indicated the broad host range of this genus. Our study also highlighted the fact that leaf endophytes of mangroves are not unique with reference to their species diversity and frequency of occurrence when compared to those of terrestrial plants. These observations suggest that the extraordinary success of some fungal endophytes in colonizing taxonomically disparate hosts could be due to development of traits specific to their ecosystem.

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1. Introduction

Endophytic fungi infect and live within plant tissues without inducing any disease. They are ubiquitous and constitute an integral component of the plant microbiome. Endophyte association increases plant host fitness by enhancing its tolerance to abiotic (Yamaji et al., 2016; Lata et al., 2018) and biotic (Estrada et al., 2015; Suryanarayanan et al., 2018) stressors; these filamentous fungi are thus being investigated for their potential to improve crop fitness (Vega et al., 2008; Raghavendra and Newcombe, 2013). Furthermore, endophytic fungi represent a source of novel bioactive molecules (Suryanarayanan et al., 2009; Kharwar et al., 2011; Kusari et al., 2012) and industrially important enzymes (Thirunavukkarasu et al., 2011, 2015; Suryanarayanan et al., 2012; Sengupta et al., 2017). There are many studies on endophytes residing in the leaves of individual angiosperm plants and a few of them address the status of the foliar endophyte of plant communities (Suryanarayanan et al., 2003, 2011; Arnold and Lutzoni, 2007; Sudhakara Reddy et al., 2016). Here, we report on the distribution and diversity of culturable foliar endophytes of mangroves of Andaman Islands, India.

Mangroves are plants of the tidal habitats and survive in the ecotone between the terrestrial and marine ecosystems. Mangroves constitute an unique ecosystem which provides crucial ecosystem services including fisheries, shoreline shield, carbon sequestration and bioremediation of wastes (Lee et al., 2014). Furthermore, mangrove forests support a wide biodiversity and constitute the most carbon rich forests of the tropics (Donato et al., 2011). Current satellite data confirm that anthropogenic activity is leading to the loss of mangrove forests globally (Thomas et al., 2017).

While macroscopic basidiomycetes (Gilbert and Sousa, 2002; Maekawa et al., 2003; Sakayaroj et al., 2012; Nogueira-Melo et al., 2014) and marine fungi (Sarma and Hyde, 2001) of mangroves have been studied for their diversity and distribution at the community level, investigations on endophytes of mangroves pertain only to a few mangrove species (Suryanarayanan et al., 1998; Kumaresan and Suryanarayanan, 2001; Costa et al., 2012; de Souza Sebastianes et al., 2013; Li et al., 2016) or to their ability to produce novel bioactive metabolites and extracellular enzymes (Maria et al., 2005; Aly et al., 2010; Debbab et al., 2013). To our knowledge, there are no studies involving simultaneous sampling of many mangrove species to address the diversity and distribution of foliar

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endophytes in them. Furthermore, according to Niranjan and Sarma (2018) there are no studies on the endophytes of Andaman and Nicobar Islands. We chose to investigate this facet of endophytes of Andaman Islands (in the Bay of Bengal, east of India, 11.7401° N, 92.6586° E) since 13% of the total mangrove cover of India is present here (Forest Survey of India, 2013), and the mangroves of this region exhibit the highest density and growth among the mangroves of the country (Dagar et al., 1991).

2. Materials and methods

2.1. Sample collection

We chose South Andaman for our study as it supports 23 of the 25 mangrove species and all the 10 mangrove families distributed in the Andaman and Nicobar Islands (Goutham-Bharathi et al., 2014). Mature and healthy leaves of 20 obligate mangrove species (Goutham-Bharathi et al., 2014) belonging to 10 families were collected from the following seven different locations in South Andaman Island (Fig. 1, Table 1) and sampled for their endophyte presence - Burmanallah, Chidiyatapu, Corbyn's Cove, Manjeri, Shippighat, Shoal Bay and Wright Myo. The leaves were transported to the laboratory in sterile bags and screened for endophyte presence within 48 h of collection, by surface sterilizing and plating them on nutrient agar medium. The study involved a one time sampling between May 2016 and February 2017.

2.2. Surface sterilization

For each mangrove species, a total of 40 leaves were collected from 4 individual plants (10 leaves/individual). From these, 120 tissue segments (0.5 cm^2 each) were cut from the midrib region (including the lamina portion) -one each from the apical, middle and the basal region of the leaf. Of these, 100 leaf segments were surface sterilized and screened. These leaf segments were surface sterilized by immersing them in 70% ethanol for 5 s, followed by treatment with sodium hypochlorite (4% available chlorine) for 90 s and rinsing in sterile distilled water for 10 s (Suryanarayanan et al., 1998). The tissue segments were then plated in Petri dishes (9 cm dia.) containing antibiotic-amended (Chloramphenicol, 150 mg/l) Potato Dextrose Agar (PDA) medium (20 ml). We had previously used this sampling design for studying leaf endophytes of trees of different forest types occurring in the Western Ghats (Suryanarayanan et al., 2002, 2011; Govinda rajulu et al., 2013; Sudhakara Reddy et al., 2016).

2.3. Incubation procedure and isolation of endophytes

The efficacy of the sterilization protocol in removing the surface microbes was confirmed (Schulz et al., 1998) and each Petri dish with ten leaf segments was incubated in a light chamber (12 h light: 12 h dark cycle, 2200 lux of light) at 26 °C for 4 weeks (Suryanarayanan, 1992). The endophytes which grew out of the tissue segments were isolated, cultured on PDA slants and identified using standard manuals (Barnett and Hunter, 1998; Ellis, 1971, 1976; Ellis and Ellis, 1988; Sutton, 1980; Onions et al., 1981). Isolates which failed to sporulate were given codes based on culture characteristics such as growth rate, colony surface texture and hyphal pigmentation (Suryanarayanan et al., 1998) and were assumed to be different taxonomic species (Bills and Polishook, 1994). Since the identification was done primarily based on spore morphology, the anamorph (asexual state) and teleomorph (sexual state) were enumerated separately.

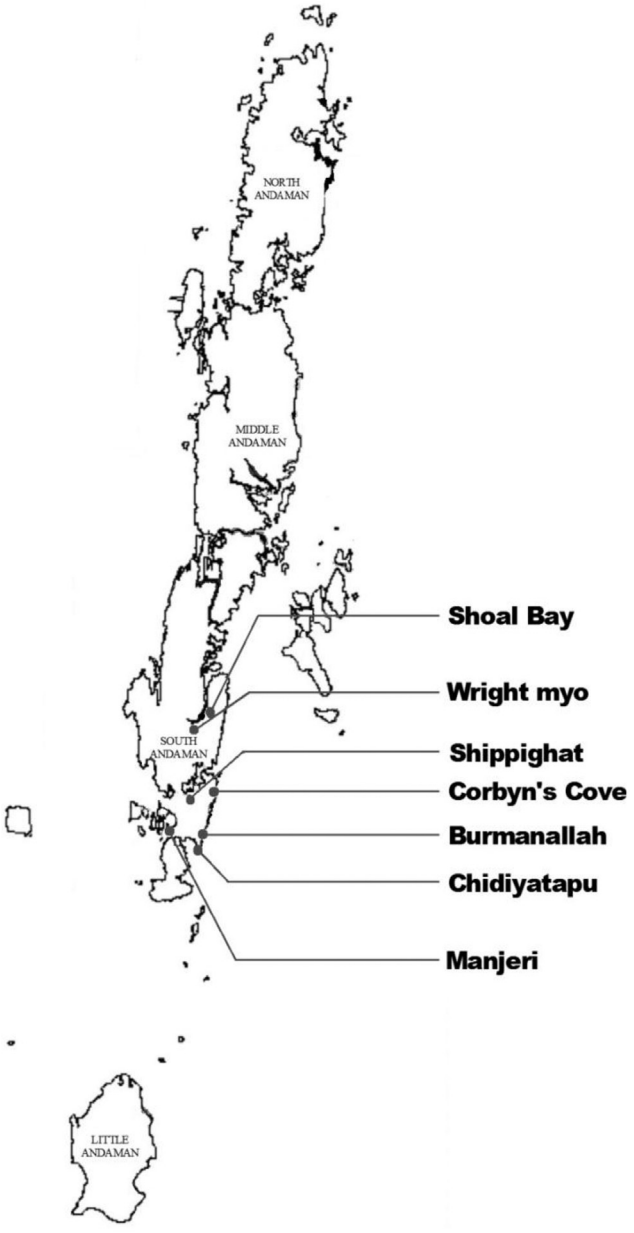

Fig. 1. Map of Andaman Islands showing the places of sample collection.

2.4. Genomic DNA extraction

The genomic DNA was extracted from fresh mycelia collected from 7 d old cultures growing in PDA medium. For this, the phenol-chloroform method was used (Sudhakara Reddy et al., 2016). The extracted DNA was resuspended in 50 μl of sterile distilled water and stored at −80 °C for further studies. For PCR amplification, the samples were thawed, concentration of the genomic DNA was checked in a 1% agarose gel and then used.

2.5. PCR amplification and sequencing of ITS region

A polymerase chain reaction was performed to amplify the ITS region and its flanking sequences. Fungal specific primers ITS4 and ITS5 were used for the reaction (White et al., 1990). The PCR reaction mix consisted of PCR buffer, forward and reverse primers, dNTPs, Taq Polymerase, DMSO, $MgCl_2$ and fungal DNA and was

Table 1
Mangrove species of Andaman Islands, India studied for foliar fungal endophytes.

Code	Mangrove Plant	Family	Collection Site	Co-ordinates
AE	*Acanthus ebracteatus* Vahl	Acanthaceae	Shippighat	11° 39′ 52.3368″ N92° 44′ 11.04″ E
AI	*Acanthus ilicifolius* L.	Acanthaceae	Wright myo	11° 47′ 19.0896″ N92° 43′ 34.3884″ E
AC	*Aegiceras corniculatum* (L.) Blanco	Myrsinaceae	Corbyn's Cove	11° 38′ 40.7976″ N92° 44′ 51.3636″ E
AM	*Avicennia marina* (Forssk.) Vierh.	Avicenniaceae	Burmanallah	11° 33′ 27.3924″ N92° 43′ 47.3448″ E
AO	*Avicennia officinalis* L.	Avicenniaceae	Corbyn's Cove	
BC	*Bruguiera cylindrica* (L.) Blume	Rhizophoraceae	Chidiyatapu	11° 30′ 21.9564″ N92° 42′ 6.0948″ E
BG	*Bruguiera gymnorhiza* (L.) Lam.	Rhizophoraceae	Burmanallah	
BP	*Bruguiera parviflora* (Roxb.) Wight &Arn. exGriff.	Rhizophoraceae	Shoal Bay	11° 53′ 52.53″ N92° 46′ 32.1204″ E
CT	*Ceriops tagal* (Perr.) C.B. Rob.	Rhizophoraceae	Manjeri	11° 32′ 33.36″ N92° 39′ 8.7588″ E
EA	*Excoecaria agallocha* L.	Euphorbiaceae	Burmanallah	
LL	*Lumnitzera littorea* (Jack) Voigt	Combretaceae	Shoal Bay	
LR	*Lumnitzera racemosa* Willd.	Combretaceae	Manjeri	
NF	*Nypa fruticans* Wurmb	Arecaceae	Shippighat	
PP	*Phoenix paludosa* Roxb.	Arecaceae	Shippighat	
RA	*Rhizophora apiculata* Blume	Rhizophoraceae	Burmanallah	
RM	*Rhizophora mucronata* Lam.	Rhizophoraceae	Burmanallah	
RS	*Rhizophora stylosa* Griff.	Rhizophoraceae	Chidiyatapu	
SH	*Scyphiphora hydrophyllacea* C.F. Gaertn.	Rubiaceae	Shoal Bay	
SA	*Sonneratia alba* Sm.	Lythraceae	Wright myo	
XG	*Xylocarpus granatum* J. Koenig	Meliaceae	Burmanallah	

carried out in a 25 μl reaction volume. The reaction conditions were: 94 °C for 3 min; 34 cycles consisting of 94 °C for 30 s, 54 °C for 30 s and 72 °C for 60 s; followed by 72 °C for 10 min. The PCR amplicons were run in agarose gel and gel eluted for purification. The sequencing reaction was carried out using one of the primers and sequenced in ABI 3130 Genetic Analyzer. After manual editing, an initial search was carried out using BLAST to identify the closest matches. The sequences obtained in the current study were then aligned with sequences of type materials and sequences showing higher similarity in Blast search using ClustalW. The aligned sequences were then manually realigned again and the phylogenetic tree was constructed using MEGA6 (Tamura et al., 2013). A maximum likelihood analysis was performed to understand the phylogenetic relationship between the isolates. A bootstrap analysis with 1000 replicates was performed and the consensus tree was constructed using MEGA6. The sequences were submitted to GenBank and accession numbers were obtained (MH371241-MH371256).

2.6. Statistical analysis

The colonization frequency (CF%) of each endophyte was calculated by the method of Hata and Futai (1995).

$$CF\% = \frac{\text{Number of segments colonized by each endophyte}}{\text{Total number of segments observed}} \times 100$$

Fisher's α was used to estimate the species diversity of endophytes. The formula for estimating this value is $S = a^{*}\ln(1 + n/a)$, where S is the number of taxa, n is the number of individuals, ln is the natural logarithm and a is the Fisher's alpha. This index was preferred as it has been shown to be less affected by the abundance of common species (Magurran, 2004). Statistical programmes Pro version 2 (The National History Museum and The Scottish Association for Marine Science) and EstimateS software version 9.1.0 (Robert K. Colwell, University of Connecticut) [http://viceroy.eeb.uconn.edu/estimates] were used for calculating the ecological parameters. To avoid the influence of sample sequence on the progress of species accumulation, unique species and singleton curves, the data were randomized 100 times before analysing and plotting the curves (Suryanarayanan et al., 2011).

3. Results

The number of endophyte isolates that were recovered varied from 39 in *Avicennia marina* to 236 in *Excoecaria agallocha*; the number of endophyte species isolated ranged from 8 in *Bruguiera parviflora* to 23 in *Rhizophora apiculata* (Supplementary Table 1). The species diversity of the endophytes was lowest for *B. parviflora* (2.1) and highest for *R. apiculata* (11.4) (Supplementary Table 1). *Phomopsis* was the most common endophyte genus recorded and was isolated from all the 20 mangrove species screened; it accounted for 377 isolates of the total 2180 isolates obtained from all the mangroves and hence isolates belonging to this genus were selected for further molecular characterisation (Fig. 2, Table 2). Species of *Xylaria* and *Colletotrichum* were present in the leaves of 19 mangroves. *Phyllosticta capitalensis* was the densest endophyte as 545 isolates of it were isolated from 18 mangrove species. *Colletotrichum gloeosporioides, Phyllosticta capitalensis, Phomopsis* spp. (along with the teleomorph *Diaporthe* spp.), or *Xylaria* spp. (along with the anamorph *Nodulisporium* spp.) dominated or occurred as co-dominant species in the endophyte assemblage of different mangrove species studied (Table 3). *C. gloeosporioides* dominated the endophyte assemblages of AE and XG (abbreviations are expanded in Table 1), *P. capitalensis* was dominant in AI, BG, EA, LL, LR and SH and co-dominat in AE and SA, *Phomopsis* spp. was dominant in AC, AM, AO and RM and co-dominant in AI, BG, LR, PP, RA and RS, *Xylaria* spp. was dominant in BC, BP, CT, NF, PP and RS and co-dominant in AM, AO, BC, BP, CT, LL, RM, SH and XG (Table 3). An ITS sequence analysis of the 16 *Phomopsis/Diaporthe* isolates showed that these belonged to 10 different species (Table 2). *Diaporthe pseudomangiferae* was endophytic in the leaves of AC, AM, AO and CT. *D. discoidispora* was present in BP, LL, and RM while *D. hongkongensis* was isolated from NF and PP. *D. longicolla, D. kyushuensis, Phomopsis heveicola, D. eucalyptorum, D. liquidambaris, D. perseae* and *D. tectonae* were isolated from the leaves of AI, BC, BG, LR, SH, SA, and XG respectively. A bootstrap consensus tree constructed based on maximum likelihood approach showed that the *Phomopsis/Diaporthe* isolates could be grouped into several distinct clades (Fig. 2). Many species of *Phomopsis/Diaporthe* were isolated from different mangroves indicating very little host specificity among the endophytic isolates. We also could not discern any clusters based on the location from which these isolates were obtained. Statistical analyses revealed that while the number of endophyte isolates increased with increasing sample size, the

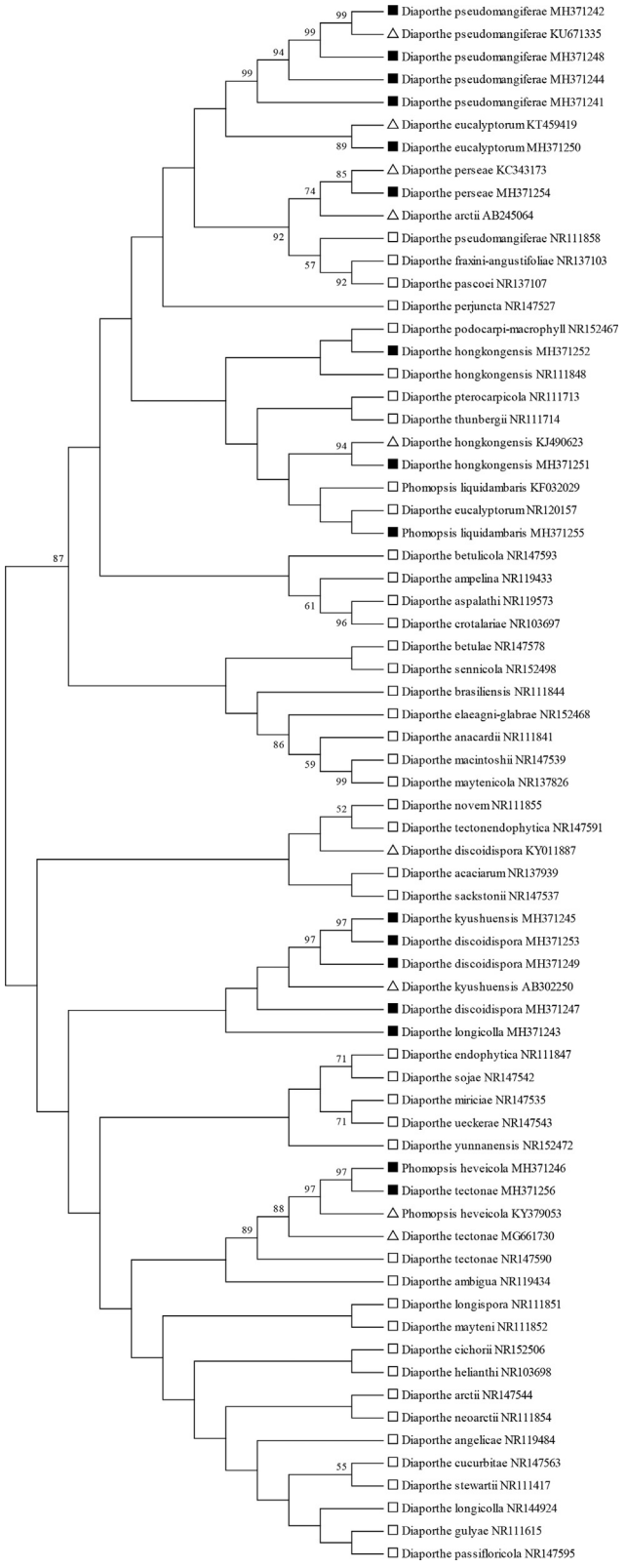

Fig. 2. Bootstrap consensus tree based on Maximum Likelihood method for *Phomopsis/Diaporthe* isolates obtained in the study. Black squares indicate sequences obtained in the present study, open squares represent type sequences while open triangles represent other sequences.

Table 2
Phomopsis/Diaporthe species identified based on ITS-sequences and their GenBank accession number (Refer Table 1 for host code).

Host Code	Isolate	GenBank Accession No.
AI	*Diaporthe longicolla*	MH371243
AC	*Diaporthe pseudomangiferae*	MH371242
AM	*Diaporthe pseudomangiferae*	MH371241
AO	*Diaporthe pseudomangiferae*	MH371244
BC	*Diaporthe kyushuensis*	MH371245
BG	*Phomopsis heveicola*	MH371246
BP	*Diaporthe discoidispora*	MH371247
CT	*Diaporthe pseudomangiferae*	MH371248
LL	*Diaporthe discoidispora*	MH371249
LR	*Diaporthe eucalyptorum*	MH371250
NF	*Diaporthe hongkongensis*	MH371251
PP	*Diaporthe hongkongensis*	MH371252
RM	*Diaporthe discoidispora*	MH371253
SH	*Diaporthe liquidambaris*	MH371255
SA	*Diaporthe perseae*	MH371254
XG	*Diaporthe tectonae*	MH371256

numbers of endophyte species (Fig. 3), unique species and singletons (Fig. 4) decreased with increasing sample size.

4. Discussion

The leaves of all the mangrove species studied harboured culturable fungal endophytes. In community level investigations, the sample size should be large enough to inform the diversity of the organisms studied. The sample size in the present study was rigorous enough to represent the diversity of foliar endophytes of the mangrove community existing at the time of sampling. This is borne out by the observation that the accumulation of endophyte species, as well as the unique and singleton species among them, although increasing initially, started to decrease with increasing sample size (Longino, 2000; Henderson, 2003; Suryanarayanan et al., 2011). The total CF% of the endophytes (which is also equal to the total number of isolates since 100 tissue segments were screened for each mangrove species) was higher than 100% in nine mangrove species due to the growth of more than one endophyte species from a tissue segment. This indicated that the density of colonization of the leaves by endophytes is high.

Leaf endophytes enhance the tolerance of terrestrial host plant to pathogen (Arnold et al., 2003) and herbivores (Estrada et al., 2015). Mangrove endophytes have not been investigated for such a role in biotic stress tolerance of mangroves. Furthermore, as speculated by Suryanarayanan (2013), dense colonization of leaves by endophytes could affect photosynthesis negatively by draining photosynthates or positively by creating localized zones of low photorespiration in the leaf due to their respiration. This aspect gains importance as the air in mangrove canopy is low in CO_2 and its microclimate is different from that of the terrestrial plants due to tidal inundation (Al-Saidi et al., 2009).

In the present study, species of *Colletotrichum, Phomopsis, Phyllosticta* and *Xylaria* were more commonly isolated as endophytes and were present in different mangrove species. These fungi have a wide host range as foliar endophytes and have been reported from mangroves of Hong Kong (Pang et al., 2008), Thailand (Chaeprasert et al., 2010), Brazil (Wanderley et al., 2012; de Souza Sebastianes et al., 2013) and China (Li et al., 2016). These fungi as endophytes are known to have loose plant host affiliation and occur even in taxonomically unrelated terrestrial plants distributed throughout the world (Pandey et al., 2003; Murali et al., 2006; Govinda rajulu et al., 2013; Unterseher et al., 2016). Although, low host specificity is a rule among several guilds of tropical fungi including the endophytes (Suryanarayanan, 2011), of particular

Table 3
Dominant and Co-dominant endophyte species present in the leaves of mangrove plants of Andaman Islands, India (Refer Table 1 for host code).

Host Code	Dominant endophyte		Co-dominant endophyte	
	Name	Order	Name	Order
AE	*Colletotrichum gloeosporioides*	Glomerellales	*Phyllosticta capitalensis*	Botryosphaeriales
AI	*Phyllosticta capitalensis*	Botryosphaeriales	*Diaporthe longicolla*	Diaporthales
AC	*Diaporthe pseudomangiferae*	Diaporthales	Sterile form 4	–
AM	*Diaporthe pseudomangiferae*	Diaporthales	*Nodulisporium* sp. 1	Xylariales
AO	*Diaporthe pseudomangiferae*	Diaporthales	*Xylaria* sp. 2	Xylariales
BC	*Xylaria* sp. 1	Xylariales	*Nodulisporium* sp. 1	Xylariales
BG	*Phyllosticta capitalensis*	Botryosphaeriales	*Phomopsis heveicola*	Diaporthales
BP	*Xylaria* sp. 1	Xylariales	*Nodulisporium* sp. 2	Xylariales
CT	*Xylaria* sp. 1	Xylariales	*Nodulisporium* sp. 1	Xylariales
EA	*Phyllosticta capitalensis*	Botryosphaeriales	*Graphium* sp.	Microascales
LL	*Phyllosticta capitalensis*	Botryosphaeriales	*Xylaria* sp. 1	Xylariales
LR	*Phyllosticta capitalensis*	Botryosphaeriales	*Diaporthe eucalyptorum*	Diaporthales
NF	*Xylaria* sp. 1	Xylariales	*Penicillium* sp. 1	Eurotiales
PP	*Nodulisporium* sp. 1	Xylariales	*Diaporthe hongkongensis*	Diaporthales
RA	*Aspergillus fumigatus*	Eurotiales	*Phomposis* sp. 2	Diaporthales
RM	*Diaporthe discoidispora*	Diaporthales	*Xylaria* sp. 1	Xylariales
RS	*Xylaria* sp. 1	Xylariales	*Phomposis* sp. 1	Diaporthales
SH	*Phyllosticta capitalensis*	Botryosphaeriales	*Xylaria* sp. 1	Xylariales
SA	*Pestalotiopsis* sp.	Amphisphaeriales	*Phyllosticta capitalensis*	Botryosphaeriales
XG	*Colletotrichum gloeosporioides*	Glomerellales	*Xylaria* sp. 1	Xylariales

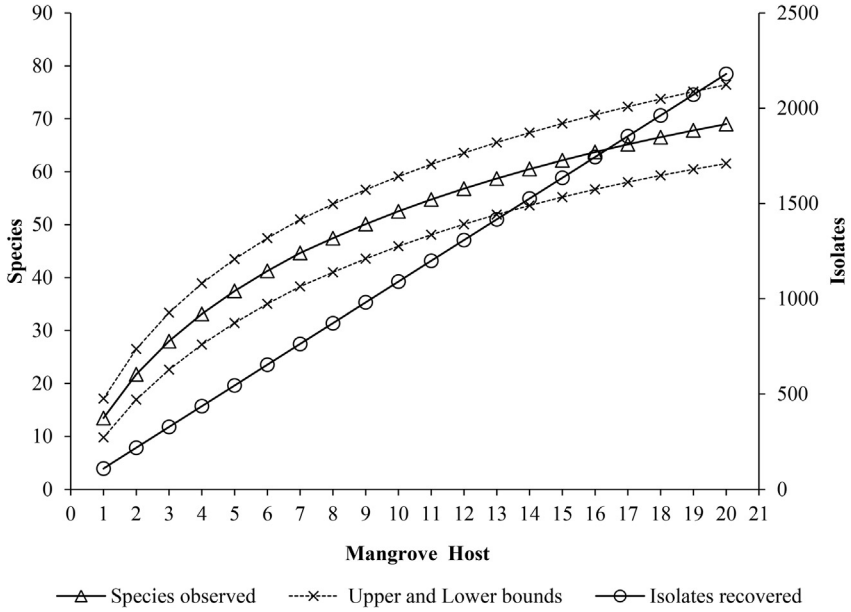

Fig. 3. Species accumulation curve for foliar endophytes isolated from twenty mangrove species. Dotted lines represent 95% confidence interval limits (upper and lower bounds) for species observed. Data were randomized 100 times for plotting the graph.

interest is the wide host range of *Diaporthe* (*Phomopsis*) spp. observed in the present study which is indicative of their ecological success. For instance, in our study, *Phomopsis* (*Diaporthe*) species were isolated from all the mangrove species. Of the 20 isolates from the 20 mangrove species, 4 (from AE, EA, RA and RS) failed to grow upon further sub-culturing and the other 16 were taken up for identification at the species level using ITS sequencing since morphological characters of this genus are unreliable (Gomes et al., 2013; Dissanayake et al., 2017). Interestingly we did not observe any host specificity among the *Phomopsis* isolates since the same species were isolated from different mangroves. This further attests to the loose host affiliation seen among major fungal endophytes, especially in tropical climates, and might be a major contributing factor in their extraordinary success as an endophyte in wide and disparate hosts.

The present survey involving more mangrove species than earlier studies confirms that leaf endophytes of mangroves are not unique with reference to their species diversity and frequency of occurrence when compared to those of terrestrial plants. Mangrove leaves accumulate salt as they mature (Cram et al., 2002) to levels which are 3–12 times higher when compared to terrestrial plants (Dissanayake and Amarasena, 2009). They are also rich in tannins (Maie et al., 2008) which are inhibitory to fungal growth (Harrison, 1971; Dix, 1979). The common foliar endophytes of mangroves are tolerant of high concentrations of both salt and tannins (Kumaresan et al., 2002). Selection of fungi with traits to survive in the salt and tannin-rich leaves of mangroves could be the reason for the wider ecological amplitude of certain endophyte genera in the mangrove forest.

Fungi in general, along with bacteria and oomycetes, are known

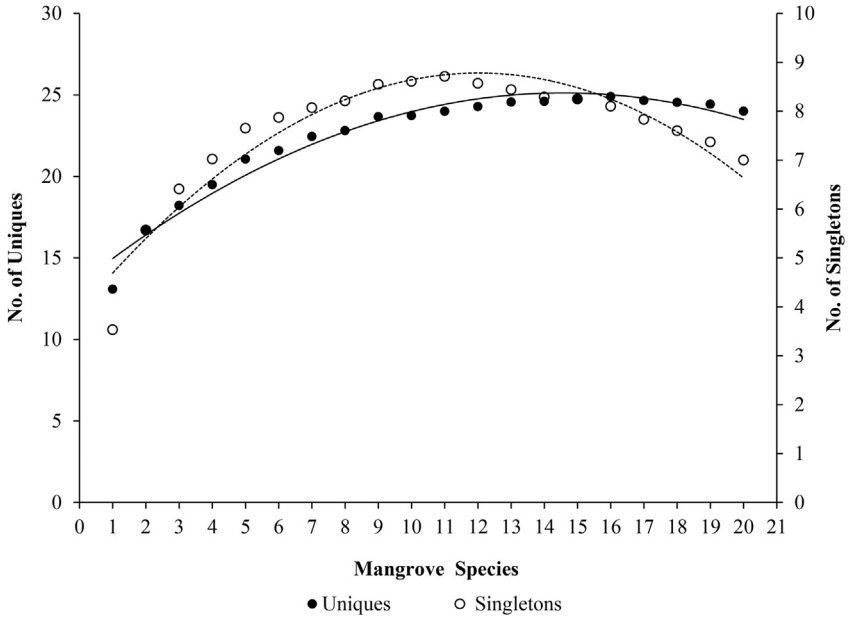

Fig. 4. Number of singleton and unique endophyte species isolated from twenty mangrove species. Data were randomized 100 times for plotting the graph. The curve represents a polynomial trendline.

to decompose mangrove litter (Kristensen et al., 2008). It is now established that foliar endophytic fungi remain in fallen leaves, switch to a saprotrophic mode (Unterseher et al., 2013; Guerreiro et al., 2017) and, owing to their ability to produce different extracellular enzymes, aid in litter decomposition (Suryanarayanan et al., 2012). Kumaresan and Suryanarayanan (2002) reported that the density of colonization of endophytic *Glomerella* sp. and *Pestalotiopsis* sp. in the leaves of the mangrove *R. apiculata* increases in fallen leaves with time and that these fungi produce biomass destructuring enzymes indicating their role in mangrove litter decomposition. *Talaromyces stipitatus*, a root endophyte in the mangrove *Avicennia marina*, elaborates salt-tolerant chitin modifying enzymes (Paranetharan et al., 2018). The specific role of mangrove endophytes in litter decomposition has to be addressed to understand their contribution to carbon dynamics in mangrove ecosystem. Since endophyte association confers salt tolerance in some plants, (Rodriguez et al., 2008; Khan et al., 2015), it could be worthwhile to investigate the contribution of endophytes to the fitness of mangroves.

To conclude, the mangrove ecosystem supports diverse microorganisms which perform various functions. The diversity and roles of archaea (Bhattacharyya et al., 2015) and bacteria (Basak et al., 2016; Chen et al., 2016) in this ecosystem are well established. With reference to fungi, only the manglicolous (Sahoo and Dhal, 2009) and mycorrhizal fungi (D'Souza, 2016) have been studied in detail. Considering the importance of endophytes in enhancing host plant's fitness and recycling nutrients, this cryptic ecological group of fungi of the mangroves deserves more attention to get a holistic view of the mangrove ecosystem.

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Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.funeco.2018.09.007.

References

D'Souza, J., 2016. Arbuscular mycorrhizal diversity from mangroves: a Review. In: Pagano, M.C. (Ed.), Recent Advances on Mycorrhizal Fungi. Fungal Biol. Springer, Cham, pp. 109–116.
Al-Saidi, A., Fukuzawa, Y., Ueno, M., Baba, S., Kawamitsu, Y., 2009. Temporal and vertical variations in photosynthetic drivers in mangrove canopies, Okinawa, Japan. Plant Prod. Sci. 12, 336–340.
Aly, A.H., Debbab, A., Kjer, J., Proksch, P., 2010. Fungal endophytes from higher plants: a prolific source of phytochemicals and other bioactive natural products. Fungal Divers. 41, 1–16.
Arnold, A.E., Lutzoni, F., 2007. Diversity and host range of foliar fungal endophytes: are tropical leaves biodiversity hotspots? Ecology 88, 541–549.
Arnold, A.E., Mejia, L.C., Kyllo, D., Rojas, E.I., Maynard, Z., Robbins, N., Herre, E.A., 2003. Fungal endophytes limit pathogen damage in a tropical tree. Proc. Natl. Acad. Sci. Unit. States Am. 100, 15649–15654.
Barnett, H.L., Hunter, B.B., 1998. In: Illustrated Genera of Imperfect Fungi, fourth ed. APS press, St. Paul.
Basak, P., Pramanik, A., Sengupta, S., Nag, S., Bhattacharyya, A., Roy, D., Pattanayak, R., Gosh, A., Chattopadhyay, D., Bhattacharyya, M., 2016. Bacterial diversity assessment of pristine mangrove microbial community from Dhulibhashani, Sundarbans using 16S rRNA gene tag sequencing. Genomics Data 7, 76–78.
Bhattacharyya, A., Majumder, N.S., Basak, P., Mukherji, S., Roy, D., Nag, S., Haldar, A., Chattopadhyay, D., Mitra, S., Bhattacharyya, M., Ghosh, A., 2015. Diversity and Distribution of Archaea in the Mangrove Sediment of Sundarbans. Archaea 2015, ID 968582.
Bills, G.F., Polishook, J.D., 1994. Abundance and diversity of microfungi in leaf litter of a lowland rain forest in Costa Rica. Mycologia 86, 187–198.
Chaeprasert, S., Piapukiew, J., Whalley, A.J.S., Sihanonth, P., 2010. Endophytic fungi from mangrove plant species of Thailand: their antimicrobial and anticancer potentials. Bot. Mar. 53, 555–564.
Chen, Q., Zhao, Q., Li, Z., Jian, S., Ren, H., 2016. Mangrove succession enriches the sediment microbial community in South China. Sci. Rep. 6, 27468.
Costa, I., Maia, L.C., Cavalcanti, M.A., 2012. Diversity of leaf endophytic fungi in mangrove plants of northeast Brazil. Braz. J. Microbiol. 43, 1165–1173.
Cram, J.W., Peter, G.T., Rose, D.A., 2002. Salt allocation during leaf development and leaf fall in mangroves. Trees (Berl.) 16, 112–119.
Dagar, J.C., Mongia, A.D., Bandyopadhyay, A.K., 1991. Mangroves of Andaman and Nicobar Islands. Oxford & IBH Pub. Co.
de Souza Sebastianes, F.L., Romao-Dumaresq, A.S., Lacava, P.T., Harakava, R., Azevedo, J.L., de Melo, I.S., Pizzirani-Kleiner, A.A., 2013. Species diversity of

culturable endophytic fungi from Brazilian mangrove forests. Curr. Genet. 59, 153–166.
Debbab, A., Aly, A.H., Proksch, P., 2013. Mangrove derived fungal endophytes-a chemical and biological perception. Fungal Divers. 61, 1–27.
Dissanayake, N.P., Amarasena, K.M.C., 2009. Assessment and comparison of salt content in mangrove plants in Sri Lanka. Ruhuna J. Sci. 4, 21–27.
Dissanayake, A.J., Phillips, A.J.L., Hyde, K.D., Yan, J.Y., Li, X.H., 2017. The current status of species in *Diaporthe*. Mycosphere 8, 1106–1156.
Dix, N.J., 1979. Inhibition of fungi by gallic acid in relation to growth on leaves and litter. Trans. Br. Mycol. Soc. 73, 329–336.
Donato, D.C., Kauffman, J.B., Murdiyarso, D., Kurnianto, S., Stidham, M., Kanninen, M., 2011. Mangroves among the most carbon-rich forests in the tropics. Nat. Geosci. 4, 293–297.
Ellis, M.B., 1971. Dematiaceous Hyphomycetes. CMI, Kew, Surrey, UK.
Ellis, M.B., 1976. More Dematiaceous Hyphomycetes. CMI, Kew, Surrey, UK.
Ellis, M.B., Ellis, J.P., 1988. Microfungi on Miscellaneous Substrates: an Identification Handbook. Croom Helm Ltd, London, UK.
Estrada, C., Degner, E.C., Rojas, E.I., Wcislo, W.T., Van Bael, S.A., 2015. The role of endophyte diversity in protecting plants from defoliation by leaf-cutting ants. Curr. Sci. 109, 55–61.
Forest Survey of India, 2013. India State of Forest Report. Forest Survey of India, Ministry of Environment and Forests, Dehradun, India.
Gilbert, G.S., Sousa, W.P., 2002. Host specialization among wood-decay polypore fungi in a Caribbean mangrove forest. Biotropica 34, 396–404.
Gomes, R.R., Glienke, C., Videira, S.I., Lombard, L., Groenewald, J.Z., Crous, P.W., 2013. *Diaporthe*: a genus of endophytic, saprobic and plant pathogenic fungi. Persoonia: Molecular Phylogeny and Evolution of Fungi 31, 1–41.
Goutham-Bharathi, M.P., Dam Roy, S., Krishnan, P., Kaliyamoorthy, M., Immanuel, T., 2014. Species diversity and distribution of mangroves in andaman and nicobar islands, India. Bot. Mar. 57, 421–432.
Govinda rajulu, M.B., Thirunavukkarasu, N., Babu, A.G., Aggarwal, A., Suryanarayanan, T.S., Sudhakara Reddy, M., 2013. Endophytic Xylariaceae from the forests of Western Ghats, southern India: distribution and biological activities. Mycology 4, 29–37.
Guerreiro, M.A., Brachmann, A., Begerow, D., Persoh, D., 2017. Transient leaf endophytes are the most active fungi in 1-year-old beech leaf litter. Fungal Divers. 89, 237–251.
Harrison, A.F., 1971. The inhibitory effect of oak leaf litter tannins on the growth of fungi, in relation to litter decomposition. Soil Biol. Biochem. 3, 167–172.
Hata, K., Futai, K., 1995. Endophytic fungi associated with healthy pine needles and needles infested by the pine needle gall midge *Thecodiplosis japonensis*. Can. J. Bot. 73, 384–390.
Henderson, P.A., 2003. In: Practical Methods in Ecology, third ed. Blackwell Science Ltd, Oxford.
Khan, M.I., Fatma, M., Per, T.S., Anjum, N.A., Khan, N.A., 2015. Salicylic acid-induced abiotic stress tolerance and underlying mechanisms in plants. Front. Plant Sci. 6, 462.
Kharwar, R.N., Mishra, A., Gond, S.K., Stierle, A., Stierle, D., 2011. Anticancer compounds derived from fungal endophytes: their importance and future challenges. Nat. Prod. Rep. 28, 1208–1228.
Kristensen, E., Bouillon, S., Dittmar, T., Marchand, C., 2008. Organic carbon dynamics in mangrove ecosystems: a review. Aquat. Bot. 89, 201–219.
Kumaresan, V., Suryanarayanan, T.S., 2001. Occurrence and distribution of endophytic fungi in a mangrove community. Mycol. Res. 105, 1388–1391.
Kumaresan, V., Suryanarayanan, T.S., 2002. Endophyte assemblages in young, mature and senescent leaves of *Rhizophora apiculata*: evidence for the role of endophytes in mangrove litter degradation. Fungal Divers. 9, 81–91.
Kumaresan, V., Suryanarayanan, T.S., Johnson, J.A., 2002. Ecology of mangrove endophytes. In: Hyde, K.D. (Ed.), Fungi of Marine Environments. Fungal Diversity Research Series 9. Fungal Diversity Press, Hong Kong, pp. 145–166.
Kusari, S., Hertweck, C., Spiteller, M., 2012. Chemical ecology of endophytic fungi: origins of secondary metabolites. Chem. Biol. 19, 792–798.
Lata, R., Chowdhury, S., Gond, S.K., White Jr., J.F., 2018. Induction of abiotic stress tolerance in plants by endophytic microbes. Lett. Appl. Microbiol. 66, 268–276.
Lee, S.Y., Primavera, J.H., Dahdouh-Guebas, F., McKee, K., Bosire, J.O., Cannicci, S., Diele, K., Fromard, F., Koedam, N., Marchand, C., Mendelssohn, I., Mukherjee, N., Record, S., 2014. Ecological role and services of tropical mangrove ecosystems: a reassessment. Global Ecol. Biogeogr. 23, 726–743.
Li, J.L., Sun, X., Chen, L., Guo, L.D., 2016. Community structure of endophytic fungi of four mangrove species in Southern China. Mycology 7, 180–190.
Longino, J.T., 2000. What to do with the data. In: Agosti, D., Majer, J.D., Alonso, L.E., Schultz, T.R. (Eds.), Ants Standard Methods for Measuring and Monitoring Biodiversity. Smithsonian Institution Press, Washington, pp. 186–203.
Maekawa, N., Suhara, H., Kondo, R., Kinjo, K., 2003. Corticioid fungi (Basidiomycota) in mangrove forests of the islands of Iriomote and Okinawa, Japan. Mycoscience 44, 403–409.
Magurran, A.E., 2004. Measuring Biological Diversity. Blackwell science limited, UK.
Maie, N., Pisani, O., Jaffé, R., 2008. Mangrove tannins in aquatic ecosystems: their fate and possible influence on dissolved organic carbon and nitrogen cycling. Limnol. Oceanogr. 53, 160–171.
Maria, G.L., Sridhar, K.R., Raviraja, N.S., 2005. Antimicrobial and enzyme activity of mangrove endophytic fungi of southwest coast of India. J. Agri. Technol. 1, 67–80.
Murali, T.S., Suryanarayanan, T.S., Geeta, R., 2006. Endophytic *Phomopsis* species: host range and implications for diversity estimates. Can. J. Microbiol. 52, 673–680.
Niranjan, M., Sarma, V.V., 2018. A check-list of fungi from andaman and nicobar islands, India. Phytotaxa 347, 101–126.
Nogueira-Melo, G.S., Santos, P.J., Gibertoni, T.B., 2014. The community structure of macroscopic basidiomycetes (fungi) in Brazilian mangroves influenced by temporal and spatial variations. Rev. Biol. Trop. 62, 1587–1595.
Onions, A.H.S., Allsopp, D., Eggins, H.O.W., 1981. In: Smith's Introduction to Industrial Mycology, seventh ed. London, UK.
Pandey, A.K., Sudhakara Reddy, M., Suryanarayanan, T.S., 2003. ITS-RFLP and ITS sequence analysis of a foliar endophytic *Phyllosticta* from different tropical trees. Mycol. Res. 107, 439–444.
Pang, K.L., Vrijmoed, L.L.P., Goh, T.K., Plaingam, N., Jones, E.B.G., 2008. Fungal endophytes associated with *Kandelia candel* (rhizophoraceae) in mai Po nature reserve, Hong Kong. Bot. Mar. 51, 171–178.
Paranetharan, M.S., Thirunavukkarasu, N., Rajamani, T., Murali, T.S., Suryanarayanan, T.S., 2018. Salt-tolerant chitin and chitosan modifying enzymes from *Talaromyces stipitatus*, a mangrove endophyte. Mycosphere 9, 215–226.
Raghavendra, A.K.H., Newcombe, G., 2013. The contribution of foliar endophytes to quantitative resistance to *Melampsora* rust. New Phytol. 197, 909–918.
Rodriguez, R.J., Henson, J., Van Volkenburgh, E., Hoy, M., Wright, L., Beckwith, F., Kim, Y.O., Redman, R.S., 2008. Stress tolerance in plants via habitat-adapted symbiosis. ISME J. 2, 404–416.
Sahoo, K., Dhal, N.K., 2009. Potential microbial diversity in mangrove ecosystems: a review. Indian J. Mar. Sci. 38, 249–256.
Sakayaroj, J., Preedanon, S., Suetrong, S., Klaysuban, A., Jones, E.G., Hattori, T., 2012. Molecular characterization of basidiomycetes associated with the decayed mangrove tree *Xylocarpus granatum* in Thailand. Fungal Divers. 56, 145–156.
Sarma, V.V., Hyde, K.D., 2001. A review on frequently occurring fungi in mangroves. Fungal Divers. 8, 1–34.
Schulz, B., Guske, S., Dammann, U., Boyle, C., 1998. Endophyte-host interactions. II. Defining symbiosis of the endophyte-host interaction. Symbiosis 25, 213–227.
Sengupta, A., Zabala, A., Tan, S.Y., Broadstock, A., Suryanarayanan, T.S., Gopalan, V., 2017. Characterization of an ionic liquid-tolerant β-xylosidase from a marine-derived fungal endophyte. Biochem. Cell Biol. 95, 585–591.
Sudhakara Reddy, M., Murali, T.S., Suryanarayanan, T.S., Govinda rajulu, M.B., Thirunavukkarasu, N., 2016. *Pestalotiopsis* species occur as generalist endophytes in trees of Western Ghats forests of southern India. Fungal Ecol 24, 70–75.
Suryanarayanan, T.S., 1992. Light-incubation: a neglected procedure in mycology. Mycologist 6, 144.
Suryanarayanan, T.S., 2011. Diversity of fungal endophytes in tropical trees. In: Prittila, A.M., Carolin, F.A. (Eds.), Endophytes of Tropical Trees. Forestry Sciences Series 80. Springer, pp. 67–80.
Suryanarayanan, T.S., 2013. Endophyte research: going beyond isolation and metabolite documentation. Fungal Ecol 6, 561–568.
Suryanarayanan, T.S., Kumaresan, V., Johnson, J.A., 1998. Foliar fungal endophytes from two species of the mangrove *Rhizophora*. Can. J. Microbiol. 44, 1003–1006.
Suryanarayanan, T.S., Murali, T.S., Venkatesan, G., 2002. Occurrence and distribution of fungal endophytes in tropical forests across a rainfall gradient. Can. J. Bot. 80, 818–826.
Suryanarayanan, T.S., Venkatesan, G., Murali, T.S., 2003. Endophytic fungal communities in leaves of tropical forest trees: diversity and distribution patterns. Curr. Sci. 85, 489–493.
Suryanarayanan, T.S., Thirunavukkarasu, N., Govinda rajulu, M.B., Sasse, F., Jansen, R., Murali, T.S., 2009. Fungal endophytes and bioprospecting. Fungal Biol. Rev. 23, 9–19.
Suryanarayanan, T.S., Murali, T.S., Thirunavukkarasu, N., Govinda rajulu, M.B., Venkatesan, G., Sukumar, R., 2011. Endophytic fungal communities in woody perennials of three tropical forest types of the Western Ghats, southern India. Biodivers. Conserv. 20, 913–928.
Suryanarayanan, T.S., Thirunavukkarasu, N., Govinda rajulu, M.B., Gopalan, V., 2012. Fungal endophytes: an untapped source of biocatalysts. Fungal Divers. 54, 19–30.
Suryanarayanan, T.S., Govinda rajulu, M.B., Vidal, S., 2018. Biological control through fungal endophytes: gaps in knowledge hindering success. Curr. Biotechnol. 7, 185–198.
Sutton, B.C., 1980. The Coelomycetes. Fungi Imperfecti with Pycnidia, Acervuli and Stromata. CMI, Kew, Surrey, UK.
Tamura, K., Stecher, G., Peterson, D., Filipski, A., Kumar, S., 2013. MEGA6: molecular evolutionary genetics analysis, version 6.0. Mol. Biol. Evol. 30, 2725–2729.
Thirunavukkarasu, N., Suryanarayanan, T.S., Murali, T.S., Ravishankar, J.P., Gummadi, S.N., 2011. L-asparaginase from marine derived fungal endophytes of seaweeds. Mycosphere 2, 147–155.
Thirunavukkarasu, N., Jahnes, B., Broadstock, A., Govinda rajulu, M.B., Murali, T.S., Gopalan, V., Suryanarayanan, T.S., 2015. Screening marine-derived endophytic fungi for xylan-degrading enzymes. Curr. Sci. 109, 112–120.
Thomas, N., Lucas, R., Bunting, P., Hardy, A., Rosenqvist, A., Simard, M., 2017. Distribution and drivers of global mangrove forest change, 1996-2010. PloS One 12 e0179302.
Unterseher, M., Peršoh, D., Schnittler, M., 2013. Leaf-inhabiting endophytic fungi of European Beech (*Fagus sylvatica* L.) co-occur in leaf litter but are rare on decaying wood of the same host. Fungal Divers. 60, 43–54.
Unterseher, M., Siddique, A.B., Brachmann, A., Peršoh, D., 2016. Diversity and composition of the leaf mycobiome of beech (*Fagus sylvatica*) are affected by

local habitat conditions and leaf biochemistry. PloS One 11 e0152878.
Vega, F.E., Posada, F., Aime, M.C., Pava-Ripoll, M., Infante, F., Rehner, S.A., 2008. Entomopathogenic fungal endophytes. Biol. Con. 46, 72–82.
Wanderley, I.P.M., Maia, C.L.C., Cavalcanti, M.A., 2012. Diversity of leaf endophytic fungi in mangrove plants of northeast Brazil. Braz. J. Microbiol. 43, 1165–1173.
White, T.J., Bruns, T.D., Lee, S.B., Taylor, J.W., 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics (1990. In: Innis, M.A., Gelfand, D.H., Shinsky, J.J., White, T.J. (Eds.), PCR Protocols: a Guide to Methods and Applications. Wiley, New York, pp. 315–322.
Yamaji, K., Watanabe, Y., Masuya, H., Shigeto, A., Yui, H., Haruma, T., 2016. Root fungal endophytes enhance heavy-metal stress tolerance of *Clethra barbinervis* growing naturally at mining sites via growth enhancement, promotion of nutrient uptake and decrease of heavy-metal concentration. PloS One 11 e0169089.