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ORIGINAL ARTICLE

Minor species of foliar fungal endophyte communities: do they matter?

M. B. Govinda Rajulu[1] · T. S. Suryanarayanan[1] · T. S. Murali[2] · N. Thirunavukkarasu[3] · G. Venkatesan[4]

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Abstract

Studies on the diversity and technological potential of leaf fungal endophytes invariably focus on the dominant fungal species among them. There is hardly any information on the diversity and role of endophytic fungi present in low frequencies (minor species) inside leaves. Hence, we studied the diversity of the minor species of leaf endophytes and speculate on the possible roles such fungi could play in the ecosystem. Mature leaves of twenty-five woody tree species from tropical dry thorn (DT), dry deciduous (DD), and montane evergreen (ME) forests of the Nilgiri Biosphere Reserve, southern India, were screened for the presence of minor species of fungal endophytes (colonization frequency of < 5%). We recorded 47, 35, and 51 minor species in DT, DD, and ME forests, respectively. Species of *Aspergillus*, *Cladosporium*, *Corynespora*, *Drechslera*, *Eurotium*, *Gliocladium*, *Lasiodiplodia*, *Nigrospora*, *Nodulisporium*, *Paecilomyces*, *Penicillium*, and *Phoma* were present in the leaves of trees growing in all the forests studied. *Lasiodiplodia* spp. were most common among the minor endophytes and could be isolated from 32 tree species from the 3 different forest types. Isolates of *Lasiodiplodia* spp. produced enzymes including β-glucosidase, cellulase, laccase, pectinase, pectate transeliminase, and protease as well as antifungal metabolites. This study highlights the need to study leaf endophytes exhibiting low frequency of occurrence to know their influence in selecting, constituting, and functioning of the plant microbiome.

Keywords Plant microbiome · Core species · Endophyte community · Plant endobiome

Introduction

Fungal endophytes, which are a universal and indispensable constituent of a plant microbiome, have a long evolutionary history as plant symbionts (Krings et al. 2007). Foliar fungal endophytes (FFE) which reside inside leaf tissues are ubiquitous and have been isolated from leaves of plants of the Arctic (Zhang and Yao 2015), Antarctic (Rosa et al. 2009), deserts (Suryanarayanan et al. 2005; Massimo et al. 2015), tropical (Arnold et al. 2000; Suryanarayanan et al. 2011), temperate (Matsumura and Fukuda 2013), and mangrove forests (Suryanarayanan et al. 1998; Rajamani et al. 2018). Such a long-time symbiosis which is unrestricted by the geography and taxonomy of the host plants goes to show that endophytism is a successful life strategy among fungi. Recent investigations have revealed many functional roles of FFE in the establishment and performance of plants. They enhance their host plant's ability to tolerate abiotic (Chitnis et al. 2020) and biotic (Estrada et al. 2013) stressors. Furthermore, it is envisaged that a plant's response to climate change could be modulated by the endophytes it harbours (Suryanarayanan and Uma Shaanker 2021). Such features of FFE which modify their plant host's traits have encouraged viewing them as alternatives to genetic modifications and dependence on chemicals to improve crop production (Vega 2018; Chitnis et al. 2020). A few FFE persist in fallen leaves to initiate litter degradation and thus help in nutrient recycling (Prakash et al. 2015; Guerreiro

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✉ T. S. Suryanarayanan
t_sury2002@yahoo.com

[1] Vivekananda Institute of Tropical Mycology, Ramakrishna Mission Vidyapith, Chennai 600004, India

[2] Department of Biotechnology, Manipal School of Life Sciences, Manipal Academy of Higher Education, Karnataka, Manipal 576104, India

[3] PG & Research Department of Botany, Ramakrishna Mission Vivekananda College, Chennai 600004, India

[4] Department of Botany, Mannai Rajagopalaswamy Government Arts College, Mannargudi, Thiruvarur, India

et al. 2017). Furthermore, fungal endophytes are known to produce many industrially important bioactive metabolites (Pimentel et al. 2011). Despite such appealing characteristics of fungal endophytes, few studies address their interactions with plants and co-occurring microbes and within tissue distribution (Suryanarayanan 2013). For instance, although it is well established that certain genera such as *Colletotrichum*, *Guignardia* (*Phyllosticta*), *Pestalotiopsis*, *Diaporthe* (*Phomopsis*), and *Xylaria* exist as dominant FFE irrespective of their plant hosts' taxonomic or geographic connectivity (Suryanarayanan et al. 2018), there is no information on fungi present in low frequencies (minor species) inside leaves. The roles of minor species in a community could be disproportionate to their numbers. It is known that minor species of soil bacteria reduce invasion by alien species, protect plants from pathogen invasion, and determine plant's responses during rhizosphere colonization (Dawson et al. 2017). Among plant communities, minor species influence the abundance of the dominant species (Boeken and Shachak 2006) and functional similarities between dominant and minor species aid in the resilience of ecosystem function under changing environmental conditions (Walker et al. 1999). Hence, we analysed the results obtained from our study on 75 tree species of 32 families growing in three different types of tropical forests to understand the pattern of distribution of minor FFE exhibiting very low frequency of occurrence — a colonization frequency of less than 5% in any tree leaf.

Materials and methods

Collection sites

Twenty-five woody tree species, each group from tropical dry thorn (DT), dry deciduous (DD), and montane evergreen (ME) forests situated in the Nilgiri Biosphere Reserve (Latitude 11°33′0″N, Longitude 76°37′30″E), were sampled for their FFE. These are not primary forests; they receive a mean annual rainfall of 700–1000 mm, 1000–1400 mm, and 1300–3000 mm, respectively (Kodandapani et al. 2009; Suryanarayanan et al. 2011). All collections were made from private lands or unprotected regions and the data accumulated in a 10-year study (from 2000 to 2009) are analysed here.

Sample collection

The most common tree species recorded in each forest type were screened (Table 1). Trees with more than 10-cm diameter at breast height (DBH) were chosen since trees of these forests do not have discernable annual rings for age determination. Three individual trees for each host species

Table 1 Tree species and the forest type studied for minor FFE

Family	Tree species	Forest
Aquifoliaceae (2)	*Ilex wightiana*	ME
	Ilex denticulata	ME
Barringtoniaceae (1)	*Careya arborea*	DD
Bignoniaceae (2)	*Stereospermum angustifolium*	DT
	Stereospermum personatum	DD
Boraginaceae (4)	*Cordia dichotoma*	DT
	Ehretia canarensis	DT
	Cordia dichotoma	DD
	Cordia obliqua	DD
Celastraceae (3)	*Elaeodendron glaucum*	DT
	Euonymus angulatus	ME
	Maytenus emarginata	DT
Combretaceae (5)	*Anogeissus latifolia*	DD
	Terminalia chebula	DT
	Anogeissus latifolia	DT
	Terminalia alata	DD
	Terminalia crenulata	DD
Dipterocarpaceae (1)	*Shorea roxburghii*	DD
Ebenaceae (1)	*Diospyros montana*	DT
Erythroxylaceae (1)	*Erythroxylum monogynum*	DT
Euphorbiaceae (5)	*Daphniphyllum neilgherrense*	ME
	Glochidion zeylanicum	ME
	Bridelia retusa	DT
	Givotia rottleriformis	DT
	Phyllanthus emblica	DD
Fabaceae (9)	*Acacia ferruginea*	DT
	Cassia fistula	DT
	Bauhinia racemosa	DT
	Butea monosperma	DT
	Dalbergia lanceolaria	DT
	Pterocarpus marsupium	DT
	Cassia fistula	DD
	Ougeinia oojeinensis	DD
	Pongamia pinnata	DT
Lauraceae (6)	*Litsea floribunda*	ME
	Cinnamomum malabatrum	ME
	Cryptocarya bourdillonii	ME
	Litsea stocksii	ME
	Neolitsea zeylanica	ME
	Phoebe lanceolata	ME
Loganiaceae (1)	*Strychnos potatorum*	DT
Lythraceae (2)	*Lagerstroemia parviflora*	DD
	Lagerstroemia microcarpa	DD
Magnoliaceae (1)	*Michelia nilagirica*	ME
Malvaceae (1)	*Kydia calycina*	DD
Melastomataceae (1)	*Memecylon malabaricum*	ME
Myrtaceae (3)	*Syzygium densiflorum*	ME
	Rhodomyrtus tomentosa	ME
	Syzygium cumini	DD

Table 1 (continued)

Family	Tree species	Forest
Oleaceae (2)	*Ligustrum roxburghii*	ME
	Schrebera swietenioides	DD
Pedaliaceae (1)	*Radermachera xylocarpa*	DD
Rhamnaceae (2)	*Ziziphus jujuba*	DT
	Ziziphus xylopyrus	DT
Rubiaceae (5)	*Lasianthus venulosus*	ME
	Catunaregam spinosa	DD
	Randia dumetorum	DT
	Psychotria bisulcata	ME
	Ixora nigricans	DT
Rutaceae (1)	*Vepris bilocularis*	ME
Sabiaceae (1)	*Meliosma simplicifolia*	ME
Samydaceae (1)	*Casearia esculenta*	DD
Sapotaceae (1)	*Isonandra candolleana*	ME
Staphyleaceae (1)	*Turpinia nepalensis*	ME
Sterculiaceae (1)	*Helicteres isora*	DD
Symplocaceae (2)	*Symplocos cochinchinensis*	ME
	Symplocos obtusa	ME
Ternstromiaceae (1)	*Eurya nitida*	ME
Tiliaceae (1)	*Grewia tiliifolia*	DD
Verbenaceae (6)	*Gmelina asiatica*	DT
	Premna tomentosa	DT
	Gmelina arborea	DD
	Premna tomentosa	DD
	Tectona grandis	DD
	Vitex altissima	DD

DT, dry thorn; *DD*, dry deciduous; *ME*, montane evergreen

were chosen and 20 mature, healthy, symptomless leaves were collected (total 60 leaves/tree species) and screened for endophytes. Leaf sampling was done only during the months of November, December, and January, thus avoiding the dry and monsoon seasons.

Endophyte isolation

From each leaf, three segments (0.5 cm^2) were cut from its apical, middle, and basal regions of the lamina and the 180 segments thus obtained from 60 leaves for each host species were surface disinfected by the method of Suryanarayanan et al. (1998). From these, 150 segments were randomly selected and plated on chloramphenicol-amended Potato Dextrose Agar (PDA) medium contained in 9-cm diam. petri dishes. Such petri dishes (10 segments/dish) were incubated in a light chamber (12-h light:12-h dark cycle) for 28 days at 26 ± 1 °C to induce sporulation in the growing endophytes (Suryanarayanan 1992). The surface imprinting method of Schulz et al. (1998) was followed to ensure the effectiveness of the surface disinfection in killing the epiphyllous microbes. The tissue segments were observed periodically and the fungi growing out of them were isolated and identified based on their spore morphology and spore development (Ellis 1976; Subramanian 1971; Sutton 1980; Onions et al. 1981; Ellis and Ellis 1988; Nag Raj 1993; Hyde et al. 2000). Sterile mycelia which differed in their colony structure (colour and growth characteristics in culture) were treated as morphospecies. Foliar fungal endophytes which had a colonization frequency (CF%) of less than 5% were considered minor species for the analysis. In very few cases, genera such as *Alternaria*, *Colletotrichum*, *Fusarium*, *Pestalotiopsis*, *Phomopsis*, *Phyllosticta*, *Sporormiella*, and *Xylaria* exhibited < 5 CF%; these were not considered for the analysis since they are universally dominant FFE (Suryanarayanan et al. 2011). Representative endophyte fungal cultures were deposited in the culture collection centres of India (The Microbial Type Culture Collection (MTCC) and National Fungal Culture Collection of India (NFCCI)); these include dry thorn forest, *Corynespora* sp. (MTCC 8466), *Drechslera rostrata* (NFCCI 2312, GB), and *Lasiodiplodia theobromae* (MTCC 10,347); dry deciduous forest, *Corynespora* sp. (MTCC 8467) and *Nigrospora oryzae* (MTCC 8465); and montane evergreen forest, *Chaetomium* sp. (MTCC 8385) and *Sordaria fimicola* (MTCC 10,342). In a parallel work addressing the technological potential of endophytes, *Curvularia* sp. and *Drechslera rostrata* isolated as minor endophytes were identified using their ITS sequences and their GenBank accession numbers are KF135619 and HQ909080, respectively.

Statistical analyses

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

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

Margalef's richness index (R1) was used to measure the species richness and Fisher's α, which is less affected by the abundance of common species (Magurran 2004), was used to estimate the species; $R1 = S - 1/ln\ (n)$, where S is the total number of species in the community and "n" is the total number of individuals observed. Fisher's α was calculated by $S = a*ln\ (1 + n/a)$, 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. Using the software BiodiversityPro, a principal component analysis (PCA) was done to detect any difference in the minor endophyte assemblage of trees from different forests.

Qualitative test for antifungal metabolites

Since *Lasiodiplodia* was the most common among the minor endophytes obtained in the present study, isolates of this fungus were screened for the production of antifungal metabolites by the autobiogram method (Schulz et al. 1995). Each isolate was grown in 200 mL Potato Dextrose broth at 26 °C for 3 weeks. The mycelium was filtered, and the culture filtrate was extracted with methanol and concentrated to 1.5 mL under vacuum. The methanol extract (50 µL) was spotted on a TLC (20 × 20 cm silica gel 60 F254-coated aluminium sheet, Merck, Germany) sheet and was developed in a dichloromethane:methanol (9.6:0.4) solvent system. After drying, the chromatogram was sprayed with a suspension of *Cladosporium cucumerinum* spores in 2% glucose solution and incubated for 5 days at 26 °C. The appearance of inhibition zone in the growth of the *C. cucumerinum* on the TLC plates confirmed the production of antifungal secondary metabolite(s). As a control, methanol (50 µL) was run and tested.

Qualitative test for production of biomass degrading enzymes

The production of biomass degrading enzymes such as cellulase, β-glucosidase, laccase, lipase, pectinase, pectate transeliminase, and protease was detected by agar plate assay after growing the fungus on a suitable medium for 5 days (Rohrmann and Molitoris 1992; Thirunavukkarasu et al. 2017). For detecting cellulase activity, the fungus was grown on yeast extract and peptone agar medium containing Na-carboxymethylcellulose (0.5%). Then, the colony was flooded with 0.2% Congo red and destained with 1 M NaCl. Yellow areas around the fungal colony indicated cellulase activity. Laccase activity was visualized by growing the fungus in glucose, yeast extract, and peptone agar medium with 0.05 g α-napthol/L. Appearance of blue colour in the growth medium due to the oxidation of α-naphtol indicated the presence of laccase. For detecting lipase activity, the fungus was grown in peptone agar medium with 1% Tween 20. Clearing or precipitation around the fungal colony indicated lipase activity. For detecting pectinase, the fungus was grown in pectin agar medium (5.0 g pectin, 1.0 g yeast extract) and then the colony was flooded with 1% aqueous solution of hexadecyl trimethyl ammonium bromide. A clear zone that formed around the fungal colony indicated pectinolytic activity. Pectate transeliminase production was seen at pH 7.0 and pectinase activity at pH 5.0 of the medium. For detecting protease activity, the fungus was cultured in glucose yeast peptone agar medium amended with 0.4% gelatin. The growth was then flooded with an aqueous saturated solution of ammonium sulphate and the presence of a clear zone around the fungal colony confirmed the production of the enzyme. β-Glucosidase activity was detected by growing the fungus on yeast extract peptone liquid medium with 0.5% of Na-carboxymethyl cellulose and the culture filtrate was centrifuged and the supernatant was used for assay. One hundred millilitres of 4% agar in 0.2 M sodium acetate buffer (pH 5.0) was autoclaved and maintained at 50 °C. One hundred millilitres of 0.2% esculin (Sigma) was mixed with 6 mL of 1% $FeCl_3$ solution and heated up to 50 °C in a water bath; this was mixed with the agar solution and poured in petri dishes (20 mL per plate). After solidification, four wells of 0.5-cm dia. were cut and 75 µL of a supernatant was poured into each well and incubated at 37 °C for 5 h. The appearance of brown colour around the well indicated enzyme activity (Saqib and Whitney 2006).

Results

We screened 11,250 leaf tissue segments (3750 for each forest type) of the 75 tree species for the presence of endophytes. We recorded 86 species belonging to 51 fungal genera (including sterile morphospecies) as minor endophytes (CF% < 5) from the 3 forests (Fig. 1, Table 2). From the 25 tree species screened from each forest type, we obtained 47, 35, and 51 minor species in DT, DD, and ME forests respectively (Table 2). Twelve fungi including *Aspergillus*, *Cladosporium*, *Corynespora*, *Drechslera*, *Eurotium*, *Gliocladium*, *Lasiodiplodia*, *Nigrospora*, *Nodulisporium*, *Paecilomyces*, *Penicillium*, and *Phoma* were present in the leaves of trees growing in all the forests studied.

Lasiodiplodia spp. were not host restricted and could be isolated from 32 of the 75 tree species from the 3 different forests; the total CF% of this genus were 22, 22, and 10 in DT, DD, and ME forests, respectively. *Aspergillus niger*, *Cladosporium cladosporioides*, *Corynespora cassiicola*, *Drechslera halodes*, *Eurotium* sp., *Gliocladium roseum*, *Lasiodiplodia theobromae*, *Nigrospora oryzae*, *Nodulisporium gregarium*, *Paecilomyces* sp. 1, *Penicillium* sp. 1, and *Phoma* sp. 1 were present as minor species in all the forests (Table 2). Of these, *C. cladosporioides*, *Lasiodiplodia theobromae*, *N. oryzae*, *Paecilomyces* sp. 1, and *Phoma* sp. 1 showed a wider host range and were present in more than 10 different tree species. Some endophytes including *Aspergillus* sp. 3, sp. 4, and sp. 5, *Beltrania rhombica*, *Chaetomium globosum*, *C. verrucichaeta*, *Curvularia eragrostidis*, *C. pallescens*, *Diplococcium* sp. 1, *Ellisiopsis* sp. 1, *Fusicoccum* sp. 1, *Gliocladium* sp. 1, *Graphium penicillioides*, *Humicola* sp. 2, *H. grisea*, *Monodictys levis*, *Paecilomyces* sp. 2, *Penicillium* sp. 8, *Phaeotrichoconis* sp. 1, *Phoma* sp. 2, *Pithomyces graminicola*, *Polynema* sp. 1, *Rhizopus* sp. 1, *Sordaria* sp. 1, and sp. 2, and *Ulocladium botrytis* could be isolated from only one of the 75 trees sampled (Table 2).

Margalef's richness R1 of FFE reduced from 8.7 to 3.6, 7.9 to 3.9, and 9.4 to 3.3 and Fisher's α reduced from 12.6 to 4.5,

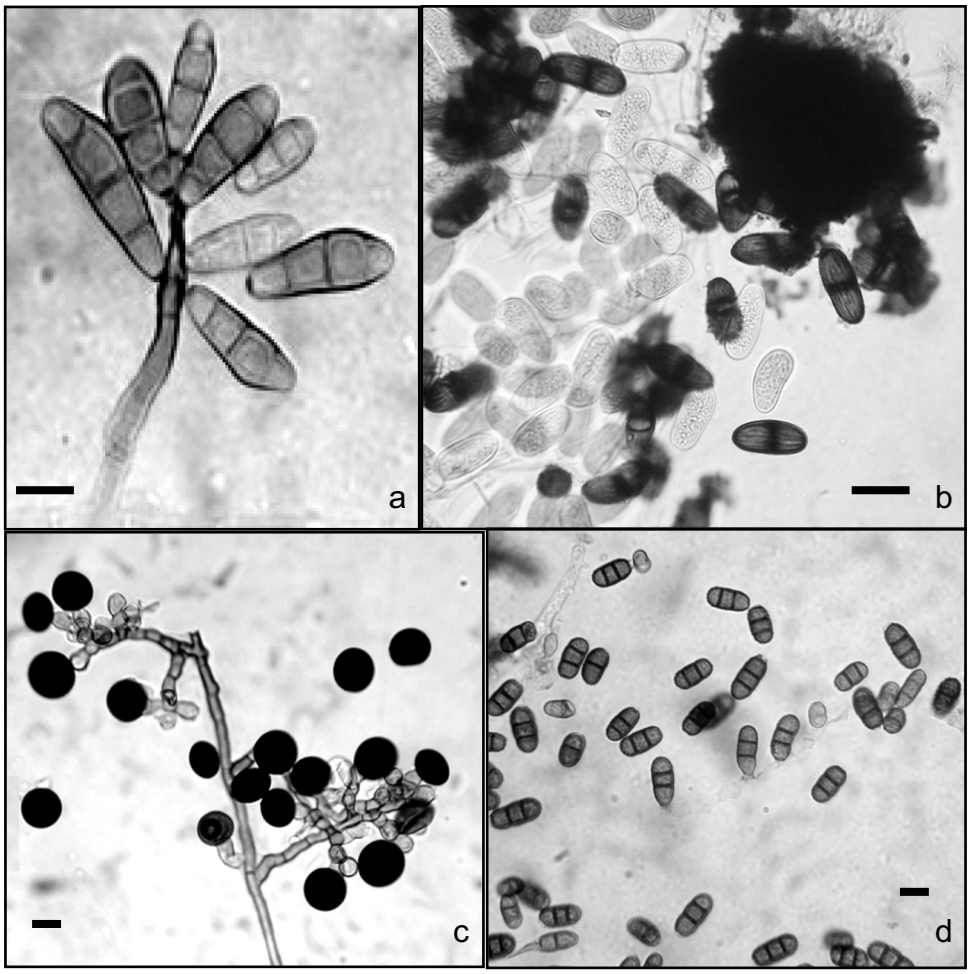

Fig. 1 Conidia of some of the minor species of endophytes. **a** *Curvularia* sp. **b** *Lasiodiplodia theobromae* **c** *Nigrospora* sp. **d** *Pithomyces* sp. Scale bars: a, b = 30 µm, c, d = 15 µm

11.2 to 4.9, and 14.5 to 7.2 in DT, DD, and ME, respectively, when the minor FFE were not considered (Table 3).

Since *Lasiodiplodia* exhibited a wider host range infecting 32 tree species and also occurred in all three forests, it was taken up for further study. Three isolates (VIG 454, 671, and 113) from three different tree hosts of DT and one isolate (VIG 307) from a tree host of DD forest were screened for enzyme production and antifungal activity (Table 4). Qualitative agar plate assay showed that out of the 4 isolates of this minor endophyte screened, 3 produced cellulase and β-glucosidase enzyme (Table 4); 2 were positive for protease; and 1 produced pectinase, pectate transeliminase, and elaborated laccase. An autobiogram test showed that 2 isolates produce antifungal metabolites (Table 4).

Discussion

Unlike the mycorrhizae, endophytes have not been studied in detail for their roles in the ecosystem (Naranjo-Ortiz and Gabaldón 2019). There are limited studies on the diversity and ecological significance of FFE at the plant community level (Arnold and Lutzoni 2007; Sanchez-Azofeifa et al. 2012). Again, such studies focus on the dominant FFE species (Suryanarayanan et al. 2002, 2011, 2018; Rajamani et al. 2018), and thus information on the diversity and ecological importance of the minor FFE is lacking. Our current preliminary study underscores this gap in knowledge by looking at the diversity of minor FFE of three different types of tropical forests.

It is important for studies quantifying diversity to ensure that the sample size used effectively reflects the diversity. Using species accumulation and unique species curves (Longino 2000; Henderson 2003), we had determined earlier that a sample size of 25 tree species/forest type is sufficient to report the overall species diversity of FFE of these three forests (Suryanarayanan et al. 2011).

Generally, most communities are represented by a few dominant species and many species with low abundance (Walker et al. 1999) — a situation which is also exhibited by the FFE community. A leaf is densely colonized by 15–20 species of FFE such that their infection frequency is high; however, their CF% is skewed due to the dominance of one or two core species (which shows high CF%) (Fig. 2) (Vaz

Table 2 Minor FFE (< 5% CF) from trees of DT, DD, and ME forests. No. of tree species harbouring an endophyte and its total CF%

Fungus	DT (No. tree/ total CF%)	DD (No. tree/ total CF%)	ME (No. tree/ total CF%)
Arthrinium phaeospermum	2/2	0/0	0/0
Arthrinium sp. 1	0/0	2/2	2/2
Aspergillus flavus	1/1	1/1	0/0
Aspergillus niger	1/1	4/5	2/5
Aspergillus sp. 1	2/3	8/11	0/0
Aspergillus sp. 2	1/1	0/0	1/1
Aspergillus sp. 3	0/0	1/1	0/0
Aspergillus sp. 4	1/2	0/0	0/0
Aspergillus sp. 5	0/0	1/1	0/0
Aspergillus sp. 6	0/0	3/5	0/0
Aureobasidium pullulans	0/0	1/1	1/1
Beltrania rhombica	0/0	0/0	1/1
Botrytis cinerea	4/6	0/0	0/0
Botrytis sp. 1	1/1	0/0	5/7
Chaetomium globosum	0/0	1/1	0/0
Chaetomium sp. 1	3/5	0/0	2/2
Chaetomium verrucichaeta	0/0	0/0	1/1
Cladosporium cladosporioides	5/8	2/4	9/17
Cladosporium sp. 1	1/2	3/5	0/0
Corynespora cassiicola	3/4	4/7	1/2
Corynespora sp. 1	5/8	7/15	0/0
Curvularia eragrostidis	0/0	0/0	1/1
Curvularia lunata	3/7	2/7	0/0
Curvularia pallescens	1/2	0/0	0/0
Curvularia robusta	2/3	0/0	0/0
Curvularia sp. 1	0/0	0/0	6/8
Diplococcium sp. 1	0/0	0/0	1/1
Drechslera halodes	6/10	3/6	2/4
Drechslera hawaiiensis	1/2	0/0	8/15
Drechslera rostrata	1/1	2/2	0/0
Drechslera sp. 1	3/5	0/0	1/1
Ellisiopsis sp. 1	0/0	0/0	1/1
Emericella sp. 1	2/2	0/0	0/0
Eurotium sp. 1	7/18	2/5	2/2
Fusicoccum sp. 1	0/0	0/0	1/1
Geotrichum sp. 1	0/0	1/1	1/1
Gliocladium roseum	2/5	1/2	2/5
Gliocladium sp. 1	1/1	0/0	0/0
Glomerella cingulata	0/0	5/9	0/0
Glomerella sp. 1	5/8	0/0	0/0
Graphium penicillioides	0/0	1/2	0/0
Graphium sp. 1	1/2	0/0	2/3
Humicola grisea	0/0	0/0	1/1
Humicola sp. 2	0/0	0/0	1/1
Lasiodiplodia theobromae	12/22	13/22	7/10
Monodictys levis	0/0	1/1	0/0
Nigrospora oryzae	10/20	1/1	9/18
Nigrospora sphaerica	0/0	2/4	0/0
Nodulisporium gregarium	2/4	2/3	1/1
Nodulisporium sp. 1	3/7	0/0	6/11
Paecilomyces sp. 1	1/3	2/2	13/24
Paecilomyces sp. 2	1/1	0/0	0/0
Paecilomyces sp. 3	1/1	0/0	1/1
Penicillium sp. 1	2/3	2/3	4/5
Penicillium sp. 2	0/0	3/5	0/0
Penicillium sp. 8	0/0	0/0	1/1
Periconia byssoides	3/6	0/0	5/10
Periconia sp. 1	1/2	0/0	1/1
Phaeotrichoconis sp. 1	0/0	0/0	1/1
Phialophora sp. 1	0/0	2/3	1/1
Phoma sp. 1	4/8	6/17	5/5
Phoma sp. 2	0/0	0/0	1/1
Pithomyces graminicola	0/0	0/0	1/2
Polynema sp. 1	0/0	0/0	1/1
Rhizopus sp. 1	1/1	0/0	0/0
Sordaria sp. 1	0/0	0/0	1/1
Sordaria sp. 2	0/0	0/0	1/1
Stachylidium bicolor	2/4	0/0	0/0
Sterile form 1	0/0	1/1	0/0
Sterile form 2	0/0	4/5	0/0
Sterile form 3	0/0	0/0	1/4
Sterile form 4	0/0	0/0	1/1
Sterile form 5	0/0	0/0	1/1
Sterile form 6	0/0	0/0	1/1
Sterile form 7	0/0	0/0	1/1
Sterile form 8	0/0	0/0	2/2
Sterile form 9	2/2	0/0	0/0
Sterile form 10	1/1	0/0	0/0
Sterile form 11	1/1	0/0	2/2
Sterile form 12	1/3	0/0	0/0
Sterile form 13	1/2	0/0	0/0
Torulomyces lagena	3/4	0/0	0/0
Torulomyces sp. 1	5/9	0/0	7/11
Trichoderma sp. 1	0/0	1/1	5/8
Trichurus spiralis	0/0	2/2	0/0
Ulocladium botrytis	1/2	0/0	0/0

et al. 2018). Our earlier screening of single leaves of eight tree species of DD and 12 of ME confirmed that a similar trend exists in these forests (Suryanarayanan et al. 2011). Invariably, these core species are those of *Colletotrichum*, *Pestalotiopsis*, *Phomopsis*, *Phyllosticta*, and *Xylaria*; they also exhibit a wide host range and infect plants irrespective

of the geographic and taxonomic distance of the host plants (Suryanarayanan et al. 2018). Probably owing to their dominance, these core endophytic fungi have been the subject of intense screening for their technological potential (Lu et al. 2000; Zou et al. 2000; Okane et al. 2003; Liu et al. 2010; Chapla et al. 2014; Ratnaweera et al. 2014; Yang et al. 2015) and interaction with their plant hosts (Chen et al. 2013; Mejía et al. 2014). In general, such core fungal species directly report any ecological shifts and their increased occurrence reflects increased stability of the system (Unterseher et al. 2011). Foliar fungal endophytes showing very low frequency of colonization are merely recorded in studies and no information is available regarding their host preference and distribution in the leaf tissue, and role

Table 3 Minor FFE status of dry thorn, dry deciduous, and montane evergreen forests

	Dry thorn forest (DT)	Dry deciduous forest (DD)	Montane evergreen forest (ME)
No. of tree species screened	25	25	25
No. of tissue segments screened	3750	3750	3750
No. of endophyte isolates	4833	4360	2364
No. of endophyte species	75	68	75
No. of minor FFE species	47	35	52
Margalef's index (R1) — with and without the minor species	8.7/3.6	7.9/3.9	9.4/3.3
Fisher's α — with and without the minor species	12.6/4.5	11.4/4.9	14.7/7.2

Table 4 Production of biomass degrading enzymes and antifungal compounds by isolates of foliar endophytic *Lasiodiplodia* spp

Isolate	Host	Cellulase	β-Glucosidase	Laccase	Pectinase	Pectate transelimi-nase	Protease	*Anti-fungal activity*
VIG 454	*Bridelia retusa* (DT)	+	+	−	−	−	+	+
VIG 671	*Randia dumetorum* (DT)	+	+	−	−	−	−	+
VIG 307	*Tectona grandis* (DD)	−	−	−	−	−	−	−
VIG 113	*Ziziphus jujuba* (DT)	+	+	+	+	+	+	−
	No. of strains tested positive	3	3	1	1	1	2	2

−, tested negative; +, tested positive; *DD*, dry deciduous forest; *DT*, dry thorn forest

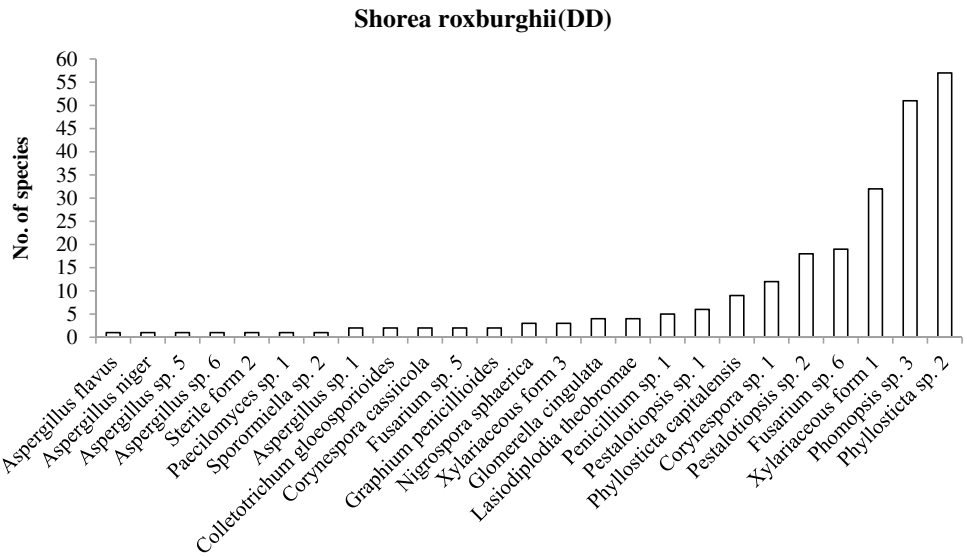

Fig. 2 Representative diagram showing the pattern of occurrence of FFE in a tree species

in their plant host microbiome or the ecosystem. The present study showed that although their colonization frequency is very low, the occurrence of many different fungi as minor species influenced the FFE diversity. Both species richness and species diversity indices were lower for the endophyte community of the forests when the minor endophyte species were not considered (Table 3).

We also show that some minor endophytes including *Lasiodiplodia* have a wide host range, though there are some fungi such as *Diplococcium* with restricted host range (Slippers and Wingfield 2007). A PCA showed a clustering pattern of the 86 species of 51 genera of minor fungi despite the variations in the elevation, rainfall, and tree host taxonomy among the three forests (Fig. 3). This was suggestive of a broad ecological amplitude of the minor endophytes of these forests.

The present study reveals for the first time that a broad host range may be characteristic of some minor FFE species such as *Lasiodiplodia*. Currently, twenty-six species of *Lasiodiplodia* are recognized (Coutinho et al. 2017); many of these cause different diseases including dieback, gummosis, leaf spot, and fruit rot. In the present study, this endophyte was isolated from 19 of the 32 families (32 of the 75 trees) as a minor fungus. It is intriguing that this fungus is not a core species in any plant species studied despite its ability to infect a broad range of plant hosts including trees of the Eastern Amazon (Vaz et al. 2018), *Magnolia* forests of China (de Silva et al. 2019), mangrove plants of Andaman Islands (Rajamani et al. 2018), and orchids of Northeastern India (Govinda Rajulu et al. 2016). The colonization frequency of *L. theobromae* as a minor endophyte is not static but increases in *Piper betle* as the leaf ages (Thirumalai et al. 2021). Thus, it needs to be determined if its limited colonization is due to its low competitive ability or dispersal limitation. The age of the leaf could also affect the CF% of this minor endophyte.

Several bacterial and fungal endophytes including species of *Lasiodiplodia* (Sakai et al. 2021) produce different types of antibiotics, siderophores, and volatile compounds which could determine the plant's stable endobiome composition (Schulz et al. 2015; Hassani et al. 2018; González-Teuber et al. 2020; Christian et al. 2020). We observed that endophytic *Lasiodiplodia* spp. produce antifungal compounds and plant biomass degrading enzymes (Table 4). This fungus is known to occur as a litter degrading saprotroph in shed leaves in the DD forest (Prakash et al. 2015). These characteristics are exemplified by many core endophyte species of these forests (Govinda Rajulu et al. 2013; Prakash et al. 2015). Such functional redundancies with the dominant species of FFE along with their low infection density could render minor FFE unimportant. However, considering the importance of minor species in other communities such as plants, their diversity and influence on host performance need to be studied to appreciate their contribution to functional diversity. Although Unterseher et al. (2011) opine that minor species of ecological groups of fungi including phyllosphere, ectomycorrhiza, and arbuscular mycorrhiza are transient inhabitants and contribute negligibly to ecosystem functions, the situation could be different with FFE as they are known to influence several host traits (Harrison et al. 2021). *Lasiodiplodia* spp. are known to metabolize plant host defense compounds (Paolinelli-Alfonso et al. 2016) and produce phytohormones suggesting that they could affect their plant host's physiology (Eng et al. 2016). Furthermore, latent pathogenic forms of this genus surviving as endophytes in plants are triggered to become pathogenic under environmental stress conditions (Paolinelli-Alfonso et al. 2016). Considering such traits, it is likely that in some plants or under certain ecological conditions, a minor

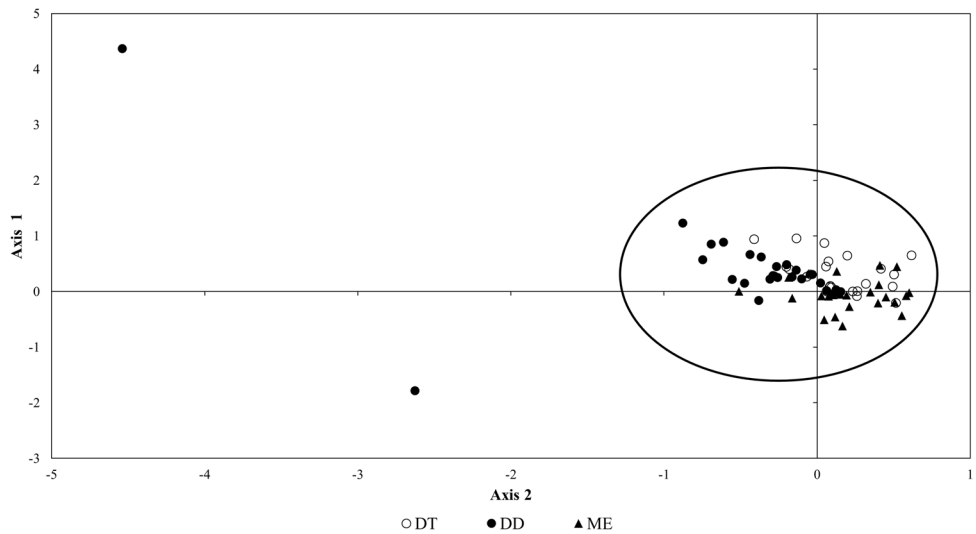

Fig. 3 Principal component analysis for minor FFE

FFE could function as a keystone species leading to a cascade of interactions which may ultimately determine the homeostasis of the plant endobiome (Vandenkoornhuyse et al. 2015; Banerjee et al. 2018). Furthermore, the endophyte community status in a leaf is not static but changes with the age of the leaf (Suryanarayanan and Thennarasan 2004) and factors such as dispersal limitation and local extinctions determine the microbial assembly (Peay et al. 2010). Hence, periodic sampling of leaves is essential to fully understand the status of minor FFE.

To sum up, our study using a large sample size suggests indirectly that minor FFE could have a disproportionate influence in selecting, constituting, and functioning of the plant endomicrobiome (Jones et al. 2019). We used the conventional methods for identifying the fungi because of the huge number of isolates obtained. With molecular methods, the actual number of minor foliar endophyte species in these forests could be less or more than that reported here. However, considering the projected roles of fungal endophytes in enhancing their host plants' tolerance to abiotic and biotic stress (Chitnis et al. 2020) and resilience of plants to climate change (Suryanarayanan and Uma Shaanker 2021), it is essential to know the role played by minor endophyte species in individual plant microbiome and in the ecosystem.

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Author contribution TSS conceived the work, obtained funding, and contributed to the experimental design. MBG and GV collected samples, and isolated endophytic fungi from the trees of the dry thorn forest. TSM collected samples, and isolated endophytic fungi from the trees of the dry deciduous forest. NT collected samples, and isolated endophytic fungi from the trees of the montane evergreen forest. MBG, TSM, NT, and GV collected and analysed the data. All the authors contributed equally to writing the manuscript.

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Declarations

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