The host range of multi-host endophytic fungi

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Mature leaves of 224 angiosperm plant species belonging to 60 families and growing in Andaman Islands, and the states of Arunachal Pradesh, Kerala and Tamil Nadu were sampled for the presence of endophytic fungi. Fungal genera such as *Alternaria*, *Arthrinium*, *Aureobasidium*, *Chaetomium*, *Cladosporium*, *Glomerella*/*Colletotrichum*, *Drechslera*, *Fusarium*, *Fusicoccum*, *Lasiodiplodia*, *Paecilomyces*, *Pestalotiopsis*, *Phoma*, *Diaporthe/Phomopsis*, *Guignardia*/*Phyllosticta*, *Sporormiella* and *Xylaria* showed an isolation frequency of 5% or more. Species of *Colletotrichum*, *Phyllosticta*, *Phomopsis* and *Xylaria* occurred as endophytes in the leaves of many plant hosts including those that were taxonomically not closely related. The need to address the broad host range of some genera of fungal endophytes is discussed.

Keywords: Diversity, foliar endophytes, fungal endophytes, mutualism.

THE horizontally transmitted endophytic fungi, an integral part of the plant microbiome, infect the above and below ground tissues of all plants without eliciting any disease symptoms. A majority of those endophytes residing in the leaf belong to the subdivision Ascomycotina and are globally distributed in plants growing from the Arctic[1] to the Antarctica[2]. The endophytic lifestyle is exhibited by various ecological groups of fungi including mutualists, latent pathogens and saprotrophs[3–5]. Although universal in occurrence, information regarding endophyte biology such as evolution of endophytism as a lifestyle among fungi, interactions of endophytes with their host plants and other organisms associated with the host plants as well as with the environment is inadequate[6]. For instance, though many independent studies show that certain genera including *Colletotrichum*, *Guignardia* (*Phyllosticta*), *Pestalotiopsis*, *Diaporthe* (*Phomopsis*), and *Xylaria* occur as endophytes in a wide range of plants from different geographical locations, principally, their host range has not been addressed.

Here, using the data gathered in our 20-year long-term study on foliar endophytes of plants from various parts of India, we analyse the distribution of some of the more commonly encountered endophyte genera. The study includes 224 angiosperm plant species belonging to 60 families and were collected from Andaman Islands (Shoal bay – 11°53′52.53″N, 92°46′32.1204″E, Wright myo – 11°47′19.0896″N, 92°43′34.3884″E, Shippighat – 11°39′52.3368″N, 92°44′11.04″E, Corbyn's cove – 11°38′40.7976″N, 92°44′51.3636″E, Manjeri – 11°32′33.36″N, 92°39′8.7588″E, Burmanallah – 11°33′27.3924″N, 92°43′47.3448″E and Chidiyatapu – 11°30′21.9564″N, 92°42′6.0948″E), and the states of Arunachal Pradesh (Ronohills – 27°9′9.702″N, 93°45′56.8116″E), Kerala (Peechi – 10°31′37.3368″N, 76°21′39.0024″E) and Tamil Nadu (Chennai – 13°4′57.648″N, 80°16′14.5848″E, Chengalpattu – 12°41′2.382″N, 79°59′0.0528″E, Pichavaram – 11°25′54.7752″N, 79°46′51.7692″E, Nilgiri Biosphere Reserve – Masinagudi – 11°34′19.8372″N, 76°38′33.774″E, Kargudi and Upper Kargudi – 11°34′30.036″N, 76°33′19.5768″E and Upper Bhavani-11°13′47.1504″N, 76°31′24.7512″E) and included a wide range and variety of hosts including mangroves, hydrophytes and mesophytes.

The methodologies used, such as the criteria for sampling, surface sterilization procedure, size of plant tissue segment screened, growth medium and incubation procedure for isolation of endophytes were the same for all the plants studied[7] so that the data obtained could be compared. To present the results, we consider only those endophyte isolates that appeared in 5% or more of the tissue bits plated for each plant species.

We observed that 17 genera of fungi, viz. *Alternaria*, *Arthrinium*, *Aureobasidium*, *Chaetomium*, *Cladosporium*, *Glomerella*/*Colletotrichum*, *Drechslera*, *Fusarium*, *Fusicoccum*, *Lasiodiplodia*, *Paecilomyces*, *Pestalotiopsis*, *Phoma*, *Diaporthe/Phomopsis*, *Guignardia*/*Phyllosticta*, *Sporormiella* and *Xylaria* exhibited an isolation frequency of 5% or more in many plant hosts (Table 1). A comparison of the data showed that genera such as *Colletotrichum*, *Phyllosticta*, *Phomopsis* and *Xylaria* occur as endophytes in the leaves of plants of disparate families. Of the 224 plant species screened, 167 harboured *Phomopsis* and *Phyllosticta* spp. as endophytes whereas species of *Colletotrichum* and *Xylaria* were present in the leaves of 160 and 124 plant species respectively (Table 1). These four genera were the most common foliar endophytes and could be isolated from 55% to 75% of the plant species screened (Table 1). *Colletotrichum* was endophytic in both members of Lamiaceae and

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Table 1. Endophyte genera (isolation % >5 at least in one of the plant species studied) isolated from leaves of different angiosperm hosts

Family	Host	Location	Dominant endophytes																
			a	b	c	d	e	f	g	h	i	j	k	l	m	n	o	p	q
Acanthaceae (7)	*Acanthus ebracteatus*	Shippighat	●	●	○	●	●	○	○	○	○	○	○	○	○	○	○	○	○
	Acanthus ilicifolius	Wright myo	○	●	○	●	●	○	○	○	○	○	○	○	○	○	○	○	○
	Andrographis echioides	Chengalpattu	○	○	○	●	○	○	○	●	●	○	○	○	○	○	○	○	○
	Avicennia marina	Pichavaram	○	●	○	●	○	●	○	○	○	○	●	○	○	○	○	○	○
	Avicennia officinalis	Pichavaram	○	○	○	○	○	●	○	○	○	●	○	○	○	○	○	○	○
	Justicia adhatoda	Chengalpattu	●	●	○	●	○	○	○	○	○	○	○	○	○	○	○	○	○
	Justicia gendarussa	Chengalpattu	○	○	○	●	○	○	○	○	○	○	○	○	○	○	○	○	○
Altingiaceae (1)	*Altingia excelsa*	Ronohills	●	●	○	●	●	○	○	○	○	○	○	○	○	○	○	○	○
Anacardiaceae (3)	*Anacardium occidentale*	Chennai	●	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
	Mangifera indica	Chennai	●	●	●	●	○	○	○	○	○	○	○	○	●	●	○	○	○
	Semecarpus anacardium	Masinagudi	●	●	●	●	●	●	○	●	●	○	○	○	○	○	○	○	○
Apocynaceae (16)	*Allamanda cathartica*	Chennai	○	○	○	●	○	●	○	○	○	○	●	○	○	○	○	○	○
	Calotropis gigantea	Chennai	●	○	○	●	○	○	●	○	○	○	○	○	○	●	○	○	○
	Cascabela thevetia	Chennai	○	●	○	●	○	●	○	○	○	○	○	○	○	○	○	○	○
	Catharanthus roseus	Chennai	○	●	○	●	○	○	○	○	○	○	○	○	○	●	○	○	○
	Cryptostegia grandiflora	Chennai	○	●	○	●	○	●	○	○	○	○	○	○	○	○	○	○	○
	Gymnema sylvestre	Chennai	○	●	○	●	○	○	○	○	○	○	○	○	○	○	○	○	○
	Hemidesmus indicus	Chennai	○	●	○	●	○	○	○	○	○	○	●	○	○	●	○	○	○
	Nerium oleander	Chennai	●	●	○	○	○	●	○	○	○	○	○	○	○	○	○	○	○
	Oxystelma secamone	Chennai	○	●	○	●	○	●	○	○	○	○	○	○	●	●	○	○	○
	Pentatropis capensis	Chennai	●	●	○	●	○	○	●	○	○	○	○	○	○	●	○	○	○
	Plumeria rubra	Chennai	●	●	○	●	●	●	○	○	○	○	○	○	○	○	○	○	○
	Rauvolfia tetraphylla	Chennai	○	●	○	○	○	○	○	○	○	○	○	○	○	●	○	○	○
	Sarcostemma acidum	Chennai	●	○	○	●	○	○	●	●	○	○	●	○	○	●	○	○	○
	Tabernaemontana divaricata	Chennai	●	●	○	○	●	○	●	○	○	○	○	○	○	○	○	○	○
	Tylophora indica	Chennai	●	●	○	●	○	○	○	○	○	○	○	○	○	●	○	○	○
	Wattakaka volubilis	Chennai	○	●	○	●	○	○	○	○	○	○	○	○	○	○	○	○	○
Aquifoliaceae (2)	*Ilex denticulata*	Upper Bhavani	●	○	○	●	●	○	○	○	○	○	○	○	○	○	○	○	○
	Ilex wightiana	Upper Bhavani	○	○	○	○	●	●	○	○	○	○	○	○	○	○	○	○	○
Araceae (1)	*Pistia stratiotes*	Chennai	○	○	○	○	○	●	○	○	●	○	○	○	○	○	○	●	○
Araliaceae (1)	*Heteropanax fragrans*	Ronohills	○	○	○	●	○	○	○	○	○	○	○	○	○	○	○	○	○
Arecaceae (32)	*Areca catechu*	Peechi	○	○	○	○	●	○	○	○	○	○	○	○	○	○	○	○	○
	Borassus flabellifer	Chennai	○	○	●	○	○	○	●	○	●	○	○	○	○	○	○	○	○
	Calamus andamanicus	Peechi	●	●	○	○	●	○	○	○	○	○	○	○	○	○	○	○	○
	Calamus dransfieldii	Peechi	○	●	○	○	○	○	○	○	○	○	●	○	○	○	○	○	○
	Calamus hookerianus	Peechi	●	●	○	○	●	○	○	○	○	○	○	○	○	○	○	○	○
	Calamus metzianus	Peechi	○	●	○	○	●	○	○	○	○	○	○	○	○	○	○	○	○
	Calamus nagbettai	Peechi	○	●	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
	Calamus pseudotenuis	Peechi	●	●	○	○	●	○	○	○	○	○	○	○	○	○	○	○	○
	Calamus rotang	Peechi	●	●	○	○	●	○	○	○	○	○	○	○	○	○	○	○	○
	Calamus tenuis	Peechi	○	●	○	●	○	○	○	○	○	○	○	○	○	○	○	○	○
	Calamus tetradactylus	Peechi	●	●	○	○	●	○	○	○	○	○	○	○	○	○	○	○	○
	Calamus thwaitesii	Peechi	●	●	○	○	●	○	○	●	○	○	○	○	○	○	○	○	○
	Calamus travancoricus	Peechi	○	●	○	○	●	○	○	○	○	○	○	○	○	○	○	○	○
	Calamus vattayila	Peechi	●	●	○	○	●	○	○	○	○	○	○	○	○	○	○	○	○
	Caryota urens	Chennai	●	●	○	●	●	○	●	○	○	○	○	○	○	○	○	○	○
	Chrysalidocarpus lutescens	Chennai	○	○	○	○	○	●	○	○	○	○	○	○	●	○	○	○	○
	Cocos nucifera	Chennai	●	●	○	○	○	○	●	○	○	○	○	○	●	○	○	○	○
	Corypha macropoda	Chennai	●	○	○	○	●	○	○	○	○	○	○	●	○	○	○	○	○
	Cyrtostachys lakka	Peechi	●	●	○	○	●	○	○	○	○	○	○	○	○	○	○	○	○
	Elaeis guineensis	Chennai	●	●	○	○	○	●	●	○	●	○	○	○	●	○	○	○	○
	Licuala grandis	Peechi	○	●	○	○	○	●	○	○	○	○	○	○	○	○	○	○	○
	Livistona chinensis	Peechi	●	●	○	○	○	●	○	○	○	○	○	○	○	○	○	○	○
	Livistona jenkinsiana	Ronohills	●	○	○	●	●	○	○	○	○	○	○	○	○	○	○	○	○
	Livistona rotundifolia	Peechi	○	●	○	○	●	○	○	○	○	○	○	○	○	○	○	○	○
	Nypa fruticans	Shippighat	●	○	●	●	●	○	○	○	○	○	○	○	○	○	○	○	○
	Phoenix paludosa	Shippighat	●	●	●	○	●	○	○	○	○	○	○	○	○	○	○	○	○
	Phoenix rupicola	Ronohills	○	○	○	●	○	○	○	○	●	○	○	○	○	○	○	○	○
	Phoenix sylvestris	Chennai	○	●	○	●	○	○	●	○	○	○	○	○	○	○	○	○	○
	Pritchardia pacifica	Chennai	○	○	○	○	●	●	●	○	○	○	●	○	○	○	○	○	○

(*Contd*)

Table 1. (*Contd*)

Family	Host	Location	Dominant endophytes																
			a	b	c	d	e	f	g	h	i	j	k	l	m	n	o	p	q
	Ptychosperma macarthurii	Chennai	○	●	○	○	○	○	●	○	○	○	○	○	○	○	○	○	○
	Rhapis excelsa	Chennai	○	○	○	●	●	●	○	○	○	○	○	○	○	○	○	○	○
	Roystonea regia	Chennai	○	○	○	○	○	●	●	○	○	○	○	○	●	○	○	○	○
Asteraceae (1)	*Spilanthes oleracea*	Ronohills	●	●	○	●	●	○	○	○	○	○	○	○	○	○	○	○	○
Bignoniaceae (4)	*Radermachera xylocarpa*	Kargudi	●	●	○	○	●	●	○	○	○	○	○	○	○	○	○	○	○
	Stereospermum angustifolium	Masinagudi	●	●	○	●	●	●	○	○	○	○	○	○	○	○	○	○	○
	Stereospermum personatum	Kargudi	●	●	●	●	●	○	○	○	○	○	○	○	○	○	○	○	○
	Stereospermum tetragonum	Upper Kargudi	●	●	○	●	●	○	○	○	○	○	○	○	○	○	○	○	○
Boraginaceae (4)	*Coldenia procumbens*	Chengalpattu	○	○	○	○	○	○	○	●	○	○	○	○	○	●	○	○	○
	Cordia dichotoma	Kargudi	●	●	○	○	○	●	○	○	○	○	○	○	○	○	○	○	○
	Cordia obliqua	Masinagudi	●	●	○	●	●	○	○	○	●	○	○	○	○	○	○	○	○
	Ehretia canarensis	Masinagudi	●	●	○	●	●	○	○	●	●	○	○	○	○	○	○	○	○
Calophyllaceae (1)	*Mesua assamica*	Ronohills	●	●	○	●	○	○	○	○	○	○	○	○	○	○	○	○	○
Caprifoliaceae (1)	*Viburnum punctatum*	Upper Kargudi	●	●	○	○	●	○	○	○	○	○	○	○	○	○	○	○	○
Celastraceae (3)	*Elaeodendron glaucum*	Masinagudi	●	●	○	●	●	●	○	○	○	○	○	○	○	○	○	○	○
	Euonymus angulatus	Upper Bhavani	●	○	○	●	●	○	○	○	○	○	○	○	○	○	○	○	○
	Maytenus emarginata	Masinagudi	●	●	●	●	●	●	○	○	○	○	○	○	○	○	○	○	○
Colchicaceae (1)	*Gloriosa superba*	Chengalpattu	●	●	●	●	●	○	○	○	○	○	○	○	○	●	○	○	○
Combretaceae (8)	*Anogeissus latifolia*	Masinagudi	●	●	○	●	●	○	○	●	○	○	○	○	○	○	○	○	○
	Lumnitzera littorea	Shoal Bay	●	●	○	○	●	○	○	○	○	○	○	○	○	○	○	○	○
	Lumnitzera racemosa	Manjeri	●	●	○	●	●	○	○	○	○	○	○	○	○	○	○	○	○
	Terminalia alata	Kargudi	●	●	●	●	●	○	○	○	○	○	○	○	○	○	○	○	○
	Terminalia arjuna	Ronohills	●	○	○	●	○	○	○	○	○	○	○	○	○	○	○	○	○
	Terminalia catappa	Ronohills	●	●	○	●	○	○	○	○	○	○	○	○	○	○	○	○	○
	Terminalia chebula	Masinagudi	●	●	●	○	●	●	○	○	●	○	○	○	○	○	○	○	○
	Terminalia crenulata	Kargudi	●	●	●	●	●	○	○	○	○	○	○	○	○	○	○	○	○
Convolvulaceae (1)	*Ipomoea aquatica*	Chennai	●	○	○	●	○	○	○	●	○	○	○	○	○	○	○	○	○
Dioscoreaceae (1)	*Dioscorea* sp.	Ronohills	●	○	○	●	●	○	○	○	○	○	○	○	○	○	○	○	○
Dipterocarpaceae (1)	*Shorea roxburghii*	Kargudi	●	●	●	○	●	○	○	○	○	○	○	○	○	○	○	○	○
Ebenaceae (1)	*Diospyros montana*	Masinagudi	●	●	○	●	●	○	○	○	○	○	○	○	○	○	○	○	○
Elaeocarpaceae (2)	*Elaeocarpus sphaericus*	Ronohills	●	●	○	●	○	○	○	○	○	○	○	○	○	○	○	○	○
	Elaeocarpus serratus	Upper Bhavani	●	○	○	●	●	○	○	○	●	○	○	○	○	○	○	○	○
Elatinaceae (1)	*Bergia aquatica*	Chennai	○	○	○	●	○	○	○	●	○	○	○	○	○	○	○	●	○
Erythroxylaceae (1)	*Erythroxylum monogynum*	Masinagudi	●	●	○	●	●	●	○	○	○	○	○	○	○	○	○	○	○
Euphorbiaceae (10)	*Acalypha indica*	Chennai	●	●	○	●	○	○	○	○	○	○	○	○	○	●	○	○	○
	Bridelia retusa	Masinagudi	●	●	●	●	●	●	●	○	●	○	○	○	○	○	○	○	○
	Daphniphyllum neilgherrense	Upper Bhavani	●	●	○	●	●	○	○	○	○	○	○	○	○	○	○	○	○
	Excoecaria agallocha	Pichavaram	●	●	○	●	○	●	○	○	○	○	○	○	○	○	○	○	○
	Givotia rottleriformis	Masinagudi	●	●	○	●	●	●	○	○	○	○	○	○	○	○	○	○	○
	Glochidion zeylanicum	Upper Bhavani	●	●	○	●	●	○	○	○	○	○	○	○	○	○	○	○	○
	Macaranga peltata	Upper Bhavani	●	○	●	●	○	○	○	○	○	○	○	○	○	○	○	○	○
	Mallotus paniculatus	Ronohills	●	●	○	●	○	○	○	○	○	○	○	○	○	○	○	○	○
	Phyllanthus amarus	Chennai	○	○	○	○	○	○	○	○	○	○	○	○	○	○	●	○	○
	Phyllanthus emblica	Masinagudi	●	●	●	○	●	○	○	○	●	○	○	○	○	○	○	○	○
Fabaceae (18)	*Acacia chundra*	Masinagudi	●	●	○	●	●	○	○	○	○	○	○	○	○	○	○	○	○
	Acacia ferruginea	Masinagudi	●	●	○	○	●	●	○	●	●	○	○	○	○	○	○	○	○
	Acacia leucophloea	Masinagudi	●	●	○	○	●	●	○	○	○	○	○	○	○	○	○	○	○
	Acacia suma	Masinagudi	●	●	○	○	●	○	●	○	○	○	○	○	○	○	○	○	○
	Aeschynomene aspera	Chennai	●	●	○	●	○	○	○	●	○	○	○	○	○	○	○	○	○
	Albizia amara	Masinagudi	●	●	○	●	●	○	●	●	●	○	○	○	○	○	○	○	○
	Albizia saman	Ronohills	○	●	○	●	○	○	○	○	○	○	○	○	○	○	○	○	○
	Bauhinia racemosa	Masinagudi	●	●	○	●	●	●	○	○	○	○	○	○	○	○	○	○	○
	Bauhinia variegata	Chennai	●	●	○	●	●	○	○	○	○	○	○	○	○	○	○	○	○
	Butea monosperma	Masinagudi	●	●	○	●	○	●	○	○	○	○	○	○	○	○	○	○	○
	Caesalpinia pulcherrima	Chennai	○	●	○	○	○	○	○	●	○	○	○	○	○	○	○	○	○
	Cassia fistula	Masinagudi	●	●	○	●	●	●	○	○	○	○	○	○	○	○	○	○	○
	Dalbergia lanceolaria	Masinagudi	●	●	○	●	●	●	○	○	○	○	○	○	○	○	○	○	○
	Dalbergia latifolia	Upper Kargudi	●	●	○	●	●	○	○	○	○	○	○	○	○	○	○	○	○

(*Contd*)

Table 1. (*Contd*)

Family	Host	Location	Dominant endophytes																
			a	b	c	d	e	f	g	h	i	j	k	l	m	n	o	p	q
	Ougeinia oojeinensis	Kargudi	●	●	●	●	○	○	○	○	○	○	○	○	○	○	○	○	○
	Pongamia pinnata	Masinagudi	●	●	●	●	●	○	○	●	○	○	○	○	○	○	○	○	○
	Pterocarpus marsupium	Masinagudi	●	●	○	●	●	●	○	●	●	○	○	○	○	○	○	○	○
	Samanea saman	Masinagudi	●	●	○	○	●	●	○	○	○	○	○	○	○	○	○	○	○
Staphyleaceae (1)	*Turpinia cochinchinensis*	Upper Bhavani	●	●	●	●	●	●	○	○	○	○	○	○	○	○	○	○	○
Lamiaceae (10)	*Callicarpa arborea*	Ronohills	●	○	○	●	○	○	○	●	○	○	○	○	○	○	○	○	○
	Clerodendrum colebrookianum	Ronohills	●	○	○	●	●	○	○	○	○	○	○	○	○	○	○	○	○
	Clerodendrum sp.	Ronohills	●	●	○	●	●	○	○	○	○	○	○	○	○	○	○	○	○
	Gmelina arborea	Kargudi	●	●	○	●	○	○	○	○	○	○	○	○	○	○	○	○	○
	Gmelina asiatica	Masinagudi	●	●	●	●	●	○	●	○	●	○	○	○	○	○	○	○	○
	Leucas aspera	Chengalpattu	○	○	○	○	○	○	○	○	○	●	○	○	○	●	○	○	○
	Premna tomentosa	Masinagudi	●	●	○	●	●	●	○	○	○	○	○	○	○	○	○	○	○
	Tectona grandis	Kargudi	●	●	○	●	○	○	○	○	○	○	○	○	○	○	○	○	○
	Vitex altissima	Kargudi	●	●	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
	Vitex negundo	Chengalpattu	●	●	○	●	○	○	○	●	○	○	○	○	○	●	○	○	○
Lauraceae (10)	*Cinnamomum malabatrum*	Upper Bhavani	●	●	●	●	●	○	○	○	○	○	○	○	○	○	○	○	○
	Cinnamomum wightii	Upper Bhavani	●	○	○	○	●	○	○	○	○	○	○	○	○	○	○	○	○
	Cryptocarya bourdillonii	Upper Bhavani	●	●	○	●	○	○	○	○	○	○	○	○	○	○	○	○	○
	Litsea cubeba	Ronohills	●	●	○	●	●	○	○	○	○	○	○	○	○	○	○	○	○
	Litsea floribunda	Upper Bhavani	●	○	●	●	○	○	○	○	○	○	○	○	○	○	○	○	○
	Litsea oleoides	Upper Bhavani	●	●	○	●	●	○	○	○	○	○	○	○	○	○	○	○	○
	Litsea stocksii	Upper Bhavani	●	○	○	●	●	○	○	○	●	○	○	○	○	○	○	○	○
	Neolitsea zeylanica	Upper Bhavani	●	●	○	●	○	○	○	○	○	○	○	○	○	○	○	○	○
	Persea macrantha	Upper Kargudi	●	●	○	○	○	○	○	○	●	○	○	○	○	○	○	○	○
	Phoebe lanceolata	Upper Bhavani	●	○	○	●	○	○	○	○	○	○	○	○	○	○	○	○	○
Lecythidaceae (1)	*Careya arborea*	Kargudi	●	●	●	○	○	○	○	○	●	○	○	○	○	○	○	○	○
Loganiaceae (1)	*Strychnos potatorum*	Masinagudi	●	●	○	●	●	●	○	●	●	○	○	○	○	○	○	○	○
Lythraceae (4)	*Lagerstroemia microcarpa*	Kargudi	●	●	○	●	●	●	○	○	○	○	○	○	○	○	○	○	○
	Lagerstroemia parviflora	Kargudi	●	●	●	●	●	○	○	○	○	○	○	○	○	○	○	○	○
	Lagerstroemia sp.	Ronohills	○	●	○	●	○	○	○	○	○	○	○	○	○	○	○	○	○
	Sonneratia alba	Wright myo	●	●	○	●	●	○	○	○	○	○	○	○	○	○	○	○	○
Magnoliaceae (1)	*Michelia nilagirica*	Upper Bhavani	●	●	○	●	●	○	○	○	○	○	○	○	○	○	○	○	○
Malvaceae (4)	*Grewia tiliifolia*	Kargudi	●	●	○	●	●	○	○	○	○	○	○	○	○	○	○	○	○
	Helicteres isora	Kargudi	●	●	○	●	○	○	○	○	○	○	○	○	○	○	○	○	○
	Kydia calycina	Kargudi	●	●	○	●	○	○	○	○	●	○	○	○	○	○	○	○	○
	Sida acuta	Ronohills	○	○	○	●	○	○	○	●	●	○	○	○	○	○	○	○	○
Marantaceae (1)	*Phrynium capitatum*	Ronohills	●	●	○	●	●	○	○	○	○	○	○	○	○	○	○	○	○
Melastomataceae (1)	*Memecylon malabaricum*	Upper Bhavani	●	○	○	●	●	○	○	○	○	○	○	○	○	○	○	○	○
Meliaceae (1)	*Xylocarpus granatum*	Burmanallah	●	●	○	●	●	○	○	○	○	○	○	○	○	○	○	○	○
Meliosmaceae (1)	*Meliosma simplicifolia*	Upper Bhavani	●	○	○	●	○	○	○	○	○	○	○	○	○	○	○	○	○
Moraceae (2)	*Ficus benghalensis*	Chennai	●	●	○	○	●	●	○	○	○	○	○	○	○	○	○	○	○
	Ficus religiosa	Ronohills	●	●	○	●	○	○	○	○	○	○	○	○	○	○	○	○	○
Myrsinaceae (1)	*Aegiceras corniculatum*	Corbyn's Cove	●	●	○	●	○	○	○	○	○	○	○	○	○	○	○	○	○
Myrtaceae (4)	*Callistemon viminalis*	Ronohills	●	○	○	●	○	○	○	●	○	○	○	○	○	○	○	○	○
	Rhodomyrtus tomentosa	Upper Bhavani	●	●	○	●	●	○	○	○	●	○	○	○	○	○	○	○	○
	Syzygium cumini	Kargudi	●	●	●	●	●	●	○	○	○	○	○	○	○	○	○	○	○
	Syzygium densiflorum	Upper Bhavani	●	○	○	●	●	○	○	○	●	○	○	○	○	○	○	○	○
Nymphaeaceae (1)	*Nymphaea stellata*	Chennai	○	○	○	●	○	○	○	○	○	○	○	○	○	●	○	○	○
Oleaceae (4)	*Ligustrum roxburghii*	Upper Bhavani	●	●	●	●	●	○	○	○	●	○	○	○	○	○	○	○	○
	Olea glandulifera	Upper Kargudi	●	○	○	●	○	○	○	○	○	○	○	○	○	○	○	○	○
	Olea dioica	Upper Kargudi	○	●	○	●	●	○	○	○	○	○	○	○	○	○	○	○	○
	Schrebera swietenioides	Kargudi	●	●	○	●	○	●	○	○	●	○	○	○	○	○	○	○	○
Orchidaceae (11)	*Aerides odorata*	Ronohills	●	●	○	●	●	○	○	○	○	○	○	○	●	○	○	○	○
	Arundina graminifolia	Ronohills	○	●	○	●	●	○	○	○	○	○	○	○	○	○	○	○	○
	Cymbidium aloifolium	Ronohills	○	●	○	●	●	○	○	○	○	○	○	○	○	○	○	○	○
	Cymbidium ensifolium	Ronohills	●	●	○	●	●	○	○	○	○	○	○	○	○	○	○	○	○

(*Contd*)

Table 1. (*Contd*)

Family	Host	Location	Dominant endophytes																
			a	b	c	d	e	f	g	h	i	j	k	l	m	n	o	p	q
	Dendrobium fimbriatum	Ronohills	○	•	○	•	•	○	○	•	○	○	○	○	○	○	○	○	○
	Dendrobium moschatum	Ronohills	○	•	○	•	•	○	○	○	○	○	○	○	○	○	○	○	○
	Eria flava	Ronohills	•	•	○	○	•	○	○	○	○	○	○	○	○	○	○	○	○
	Paphiopedilum fairrieanum	Ronohills	○	•	○	○	•	○	○	○	○	○	○	○	•	○	○	○	○
	Pholidota imbricata	Ronohills	○	•	○	•	•	○	○	○	○	○	○	○	○	○	○	○	○
	Rhynchostylis retusa	Ronohills	○	○	○	○	•	○	○	○	○	○	○	○	•	○	○	○	○
	Vanilla planifolia	Ronohills	○	•	○	○	•	○	○	○	○	○	○	○	•	○	○	○	○
Pandanaceae (1)	*Pandanus nepalensis*	Ronohills	•	•	•	•	○	○	○	○	•	○	○	○	○	○	○	○	○
Piperaceae (3)	*Piper betle*	Chennai	○	○	○	•	○	○	○	•	•	○	○	○	○	○	○	○	○
	Piper mullesua	Ronohills	•	•	○	•	○	○	○	•	○	○	○	○	○	○	○	○	○
	Piper sp.	Ronohills	•	•	○	•	○	○	○	○	○	○	○	○	○	○	○	○	○
Pontederiaceae (2)	*Eichhornia crassipes*	Chennai	•	•	○	•	○	○	•	○	○	○	○	○	○	○	○	•	○
	Monochoria hastifolia	Chennai	•	○	○	•	○	○	○	○	•	○	○	○	○	•	○	•	○
Rhamnaceae (2)	*Ziziphus jujuba*	Masinagudi	•	•	○	•	•	○	○	○	•	○	○	○	○	○	○	○	○
	Ziziphus xylopyrus	Masinagudi	•	•	○	•	○	•	○	○	○	○	○	○	○	○	○	○	○
Rhizophoraceae (7)	*Bruguiera cylindrica*	Chidiyatapu	•	•	○	•	•	○	○	○	○	○	○	○	○	○	○	○	○
	Bruguiera gymnorhiza	Burmanallah	•	•	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
	Bruguiera parviflora	Shoal Bay	•	•	○	•	•	○	○	○	○	○	○	○	○	○	○	○	○
	Ceriops tagal	Manjeri	•	•	○	○	•	○	○	○	○	○	○	○	○	○	○	○	○
	Rhizophora apiculata	Burmanallah	•	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
	Rhizophora mucronata	Burmanallah	•	○	•	○	•	○	○	○	○	○	○	○	○	○	○	○	○
	Rhizophora stylosa	Chidiyatapu	•	○	○	•	•	○	○	○	○	○	○	○	○	○	○	○	○
Rubiaceae (8)	*Canthium parviflorum*	Masinagudi	•	•	○	•	•	•	○	•	○	○	○	○	○	○	○	○	○
	Catunaregam spinosa	Kargudi	○	○	○	•	○	○	○	•	•	○	○	○	○	○	○	○	○
	Ixora coccinea	Chennai	•	•	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
	Ixora nigricans	Masinagudi	•	•	○	○	•	•	○	○	○	○	○	○	○	○	○	○	○
	Lasianthus venulosus	Upper Bhavani	•	○	•	•	•	○	○	○	○	○	○	○	○	○	○	○	○
	Psychotria bisulcata	Upper Bhavani	•	○	○	•	•	○	○	○	○	○	○	○	○	○	○	○	○
	Randia dumetorum	Masinagudi	•	•	•	•	•	○	○	○	•	○	○	○	○	○	○	○	○
	Scyphiphora hydrophylacea	Shoal Bay	•	•	○	•	○	○	○	○	○	○	○	○	○	○	○	○	○
Rutaceae (3)	*Murraya paniculata*	Upper Kargudi	•	•	○	•	○	○	○	○	○	○	○	○	○	○	○	○	○
	Naringi crenulata	Masinagudi	•	•	○	•	•	•	○	○	○	○	○	○	○	○	○	○	○
	Vepris bilocularis	Upper Bhavani	•	•	○	•	•	○	○	○	○	○	○	○	○	○	○	○	○
Salicaceae (2)	*Casearia esculenta*	Kargudi	•	•	○	•	○	○	○	•	○	○	○	○	○	○	○	○	○
	Salix tetrasperma	Upper Kargudi	•	•	○	•	○	○	○	○	○	○	○	○	○	○	○	○	○
Sapindaceae (1)	*Sapindus emarginatus*	Masinagudi	•	•	•	•	•	•	○	•	•	○	○	○	○	○	○	○	○
Sapotaceae (1)	*Isonandra candolleana*	Upper Bhavani	•	•	○	•	○	•	○	○	○	○	○	○	○	○	○	○	○
Saururaceae (1)	*Houttuynia* sp.	Ronohills	•	•	○	•	○	○	○	○	○	○	○	○	○	○	○	○	○
Scrophulariaceae (1)	*Scoparia dulcis*	Ronohills	•	○	○	•	○	○	○	○	○	○	○	○	○	○	○	○	○
Solanaceae (5)	*Capsicum annuum*	Chennai	•	•	○	•	○	○	•	○	○	○	○	○	○	○	○	○	○
	Datura metel	Chennai	○	•	○	•	○	○	○	•	○	○	○	○	○	•	○	○	○
	Solanum melongena	Chennai	○	•	○	•	○	○	○	○	○	○	○	○	•	•	○	○	○
	Solanum torvum	Ronohills	•	○	○	•	○	○	○	•	○	○	○	○	○	○	○	○	○
	Withania somnifera	Upper Kargudi	•	•	○	•	○	○	○	○	○	○	○	○	○	○	○	○	○
Symplocaceae (2)	*Symplocos cochinchinensis*	Upper Bhavani	•	•	○	•	•	○	○	○	○	○	○	○	○	○	○	○	○
	Symplocos obtusa	Upper Bhavani	•	○	○	○	•	○	○	○	○	○	○	○	○	○	○	○	○
Theaceae (2)	*Eurya nitida*	Upper Bhavani	○	•	○	○	•	○	○	○	○	○	○	○	○	○	○	○	○
	Ternstroemia japonica	Upper Bhavani	•	○	○	•	•	○	○	○	○	○	○	○	○	○	○	○	○
Ulmaceae (1)	*Holoptelea integrifolia*	Masinagudi	•	•	○	•	•	•	•	•	○	○	○	○	○	○	○	○	○
Urticaceae (1)	*Pouzolzia* sp.	Ronohills	○	•	○	•	•	○	○	○	○	○	○	○	○	○	○	○	•
Dominant endophyte genus			a	b	c	d	e	f	g	h	i	j	k	l	m	n	o	p	q
No. of plant hosts harbouring the dominant endophyte genus			167	167	30	160	124	50	19	30	33	2	6	1	11	18	1	4	1
% of plant hosts harbouring the dominant endophyte genus			75	75	13	71	55	22	9	13	15	1	3	0.4	5	8	0.4	2	0.4

Number after family name indicates the number of species screened.

(a) *Phomopsis*; (b) *Phyllosticta*; (c) *Pestalotiopsis*; (d) *Colletotrichum*; (e) *Xylaria*; (f) *Sporormiella*; (g) *Aureobasidium*; (h) *Fusarium*; (i) *Lasiodiplodia*; (j) *Paecilomyces*; (k) *Phoma*; (l) *Fusicoccum*; (m) *Cladosporium*; (n) *Alternaria*; (o) *Chaetomium*; (p) *Dreschlera*; (q) *Arthrinium*. •, Present, ○, Absent or <5% colonization frequency.

Nymphaeaceae, the most distantly related families screened as exemplified by the phylogenetic tree (Figure 1). Similarly, *Phomopsis* could be isolated from disparate families such as Scrophulariaceae and Pandanaeae (Figure 1).

The multi-host nature of some endophyte genera such as *Colletotrichum*, *Pestalotiopsis*, *Phomopsis*, *Phyllosticta* and *Xylaria* is well known[5,8–13]. In the dry tropical forests, these endophytes are not only widespread but also dominate the endophyte assemblage of their plant hosts such that the overall endophyte diversity in these ecosystems is depressed[7]. The present study involving a large sample size attests the wide host range of such endophytes. Although one of the factors critical for a wide host range among pathogens is the high levels of genetic diversity among them[14], with reference to endophytes, it is not known if the same species infecting different plants has evolved traits to overcome the different defence mechanisms of such plant species. One of the *Pestalotiopsis* species recorded in the current study has been shown to escape detection by the plant immune system by modifying its cell wall chitin structure while infecting the plant[15]. In plant–fungus interaction, host sharing among fungi declines as a function of phylogenetic distance between plant hosts[16] and thus closely related plants harbour the same fungal species. This is observed among conifer needle endophytes[17] and tropical leaf pathogens[18] but not for at least some foliar endophytic fungi owing to their multi-host nature. Such a wide host range reflects the high ecological amplitude of these endophytes, since a host plant's defence compounds[19] and nutrient content[20] determines the endophyte community supported by it. Furthermore, their competitive ability should also be high as they are bound to encounter constituents of different microbiomes associated with different plant hosts[21].

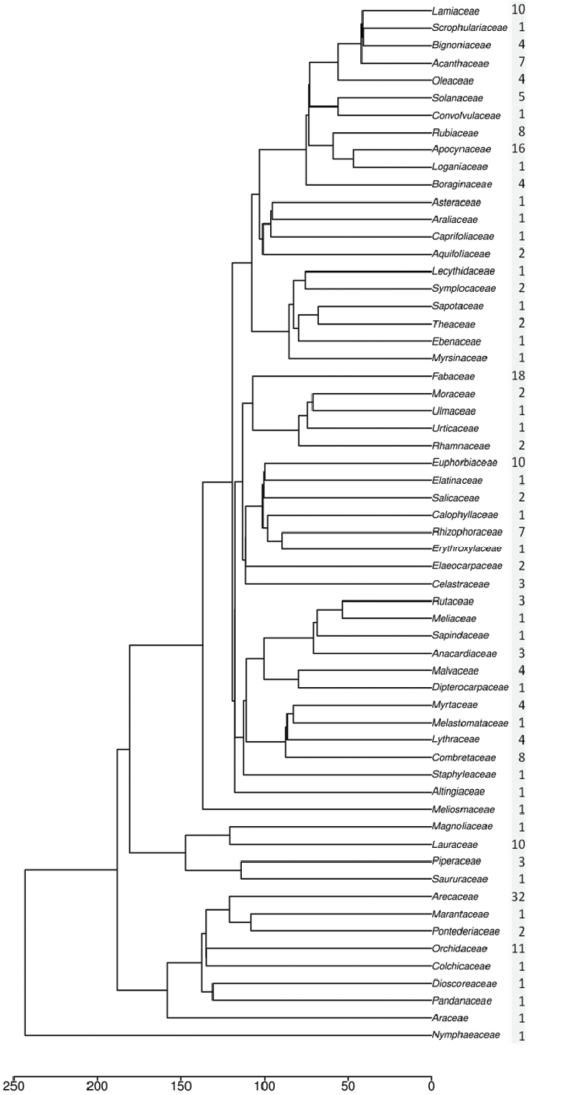

Figure 1. Phylogram of 60 angiosperm families screened for endophytes obtained by using the function S. PhyloMaker. Numbers indicate the number of plant species studied for each family.

It has been argued that generally, evolution should favour host restriction among pathogens. This is because the concomitant functional trade-offs could restrict the fitness of generalists in a given habitat and the possibility of slower evolution in the broad niche occupied by the generalists[14]. However, according to May[22,23], host specificity is low among plant-associated organisms in the tropics due to non-contiguous distribution of a plant host owing to the high plant diversity existing here. This possibly leads to the development of host generalism. Another possibility is the development of common traits by endophytic fungi to survive in unique environments leading to their selection and subsequent survival in different plant hosts. For instance, different endophyte species of dry tropical forests experiencing prolonged dry periods and episodic forest fires have common traits such as thermotolerant spores, tolerance to toxic furaldehydes which are released during biomass burning, and a biphasic life style (endophytic in intact leaves and saprobic in fallen litter)[5,24,25]. Thus, host range expansion in these endophytes could be, apart from co-speciation, due to frequent host jumps as exemplified by some fungal endophytes and pathogens[26,27]. The host could also play a significant role in determining the host range of endophytes. Redman *et al.*[28] showed that for some multi-host endophytes exhibiting both pathogenic and endophytic lifestyles, it is the plant host's metabolism which determines if the invader should survive as a mutualist or a pathogen.

Endophytism is a successful lifestyle among fungi as it evolved about 400 million years ago[29] and is exhibited by several functional groups of fungi. Infection by multi-host and dominant leaf endophyte alters the expression of many defence-linked genes of the plant host[30]. It is not known if prior infection by such an endophyte determines subsequent endophyte colonizers due to its effect on the plant's defence status. Similarly, since there are trade-offs for the host plants even in the beneficial mycorrhizal association[31], it would be worthwhile unravelling the cost

borne by plants for harbouring such multi-host endophytes. Furthermore, since pathogens could survive as endophytes (latent pathogens)[3], and since many species of *Phomopsis*[32] and *Colletotrichum*[33] have a wide host range as symptomless endophytes, it is even more essential to explore the host acquiring ability of such multi-host endophytes. Collectively, to appreciate more completely the evolution of endophytism, it is essential to focus on the question as to how some fungal genera have evolved to become generalist endophytes at a global scale.

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ACKNOWLEDGEMENTS. We thank K. N. Shivaprakash, Ashoka Trust for Research in Ecology and the Environment (ATREE), Bengaluru, for constructing the phylogenetic tree and Dr Uma Shaanker, Department of Crop Physiology, University of Agricultural Sciences, GKVK Campus (Bengaluru) for his valuable comments. T.S.S. thanks DBT, MoEF, DST and ICFRE for funding various research projects to study endophytes and Swami Shukadevananda, Secretary, Ramakrishna Mission Vidyapith (Chennai) for facilities provided.

Received 25 June 2018; accepted 27 July 2018

doi: 10.18520/cs/v115/i10/1963-1969