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Ingoldian fungi in terrestrial damp woody litter of five tree species

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Abstract
Ingoldian fungi are known to occur beyond their preferred lotic habitats. There are many reports on their occurrence in tree canopies (stemflow, through fall and tree holes) and terrestrial leaf litter. This study aimed to assess the assemblage and diversity of Ingoldian fungi in terrestrial damp woody litter of five tree species grown in scrub jungles of the southwest India, following bubble (2 days) and damp chamber (14 days) incubations of segments of bark and cambium samples. Conidia released into water were trapped using Millipore filters, stained and assessed. Total 30 fungal species were recorded, with a higher species richness in bubble chamber as compared to damp chamber incubation method (25 spp. vs. 18 spp.). The bark samples in bubble chamber incubation method yielded more species than cambium samples (19 spp. vs. 16 spp.). The bark samples in bubble chamber incubation also showed the highest number of exclusive species as compared to cambium samples (8 spp. vs. 6 spp.). Simpson and Shannon diversities were higher in bark samples than cambium samples in bubble chamber incubation with low Pielou's equitability. The frequency of occurrence of the top three species (*Anguillospora longissima, Flagellospora curvula* and *Triscelophorus acuminatus*) and top two species (*A. longissima* and *F. curvula*) were same in both samples in bubble and damp chamber incubations, respectively. The bark samples of *Terminalia paniculata* and cambium samples of *Ficus benghalensis* showed the highest number of average species in bubble chamber incubation. The bark samples of *Acacia auriculiformis* as well as *F. benghalensis* possess the highest number of average species in damp chamber incubation, while the cambium samples of *Artocarpus heterophyllus* showed the highest number of average species. All tree species showed the higher number of average conidia in bark samples as compared to cambium samples in bubble chamber incubation, with a highest frequency in *Anacardium occidentale*. The bark of *Acacia auriculiformis* and cambium of *F. benghalensis* showed the highest average conidia in damp chamber incubation. Bubble chamber incubation served as a rapid and efficient method of assessment of Ingoldian fungi in damp woody litter.

Keywords: aquatic hyphomycetes, diversity, incubation techniques, scrub jungles

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Introduction
Ingoldian fungi (also called freshwater or aquatic hyphomycetes) are common in lotic habitats worldwide (Duarte et al. 2016). They serve as an important segment of fungi in aquatic habitats in energy flow from detritus to higher trophic levels (Bärlocher and Sridhar 2014). They produce mainly staurosporus (multiradiate) and scolecosporus (sigmoid) conidia, however

some of them produce spherical or oval and fusiform shaped conidia (Ingold 1975, Marvanová 1997, Gulis et al. 2020). Such complexity of conidial shapes is due to convergent evolution to lead planktonic life in aquatic habitats, dispersal and to adhere to the organic matter for proliferation (Webster and Descals 1981, Webster 1987, Descals 2005, Sridhar 2009). About 335 morphospecies of Ingoldian fungi have been recorded with dominance in freshwater habitats in the mid-latitudinal regions (Wood-Eggenschwiler and Bärlocher 1985, Duarte et al. 2016, Friggens et al. 2017). Being an important fungal community in the lotic ecosystem, it is possible to gain insight on their role in decomposition of organic matter, food web and ecosystem functions (Gulis and Bärlocher 2017). Recently an updated practical guide to study the litter decomposition has been published with several chapters dealing with basic and applied aspects of Ingoldian fungi (Bärlocher et al. 2020).

In spite of the dominance of Ingoldian fungi in the lotic habitats, they also extended their territory beyond their usual aquatic habitats (Sridhar 2009, Chauvet et al. 2016). Their characteristic conidia are common in tree canopies (tree holes, stemflow, throughfall, trapped leaf litter and crown humus) (Sridhar 2009, Ghate and Sridhar 2015, 2016). They are also inhabitants of terrestrial leaf litter of riparian as well as non-riparian tree species (Sridhar and Kaveriappa 1987, Sridhar and Bärlocher 1993, Sridhar et al. 2020). There are two important techniques to study the Ingoldian fungi colonized on plant detritus (damp chamber and bubble chamber incubations) (Bärlocher 2020, Descals 2020, Sridhar et al. 2020). Both methods are efficient in inducing development of conidia by the colonized Ingoldian fungi in leaf litter or agar strips of cultures. Relatively, studies on occurrence of Ingoldian fungi in woody litter submerged in streams in India are limited (e.g., Sridhar et al. 2010, Sridhar and Sudheep 2011). Based on the reports from 11 ecoregions of the Indian Subcontinent (tropical, subtropical and temperate), 200 species of aquatic hyphomycetes (in 70 genera) have been reported (Sridhar et al. 1992, Arya and Sati 2012, Borse et al. 2016, 2017, Sridhar 2021). Duarte et al. (2016) reported global occurrence of 335 morphospecies of aquatic hyphomycetes, hence the Indian subcontinent represents up to 60 % of reported global species.

Figure 1. Tree basins of *Artocarpus heterophyllus* (a) and *Ficus benghalensis* (b) consist of leaf and woody litters.

Although some studies are available on occurrence of these fungi on leaf litter accumulated in terrestrial habitats, assessment of terrestrial woody litter seems to be meagre. Therefore, the

present study aimed to evaluate occurrence of Ingoldian fungi in bark and cambium of damp woody litter accumulated in the basins of five tree species in scrub jungles of southwest India.

Materials and methods

Sampling and processing

Scrub jungles located in the coastal region of Konaje in the Dakshina Kannada district, southwest of Karnataka, India was selected for the study (12°48 'N, 74°55 'E; 104–112 m asl). Damp woody litter accumulated in the basins of three trees each of five common tree species (Figure 1) were sampled during southwest monsoon season (Table 1). Humidity of air (under the canopy) and air temperature (in canopy shade) were measured (Mextech Digital Thermo Hygrometer M288CTHW, Mumbai, India). The soil temperature was measured using mercury thermometer about 8–10 cm depth under the canopy during sampling. Collected damp woody litter was transferred to the laboratory within an hour of sampling. Replicate segments of bark and cambium were separated and dried at 100 °C up to 24 hr to determine the moisture content gravimetrically. Procedure followed to detect the colonized Ingoldian fungi in bark and cambium of woody litter is presented schematically in Figure 2.

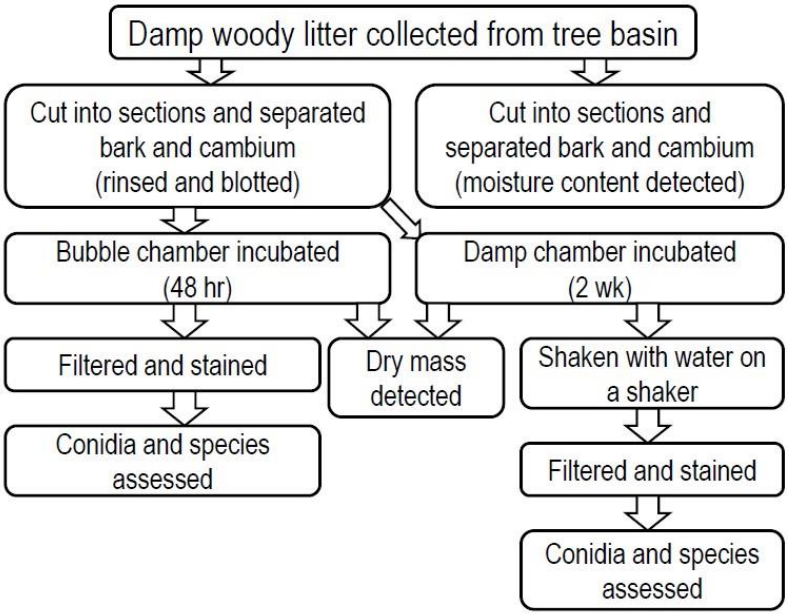

Figure 2. Scheme of assessment of woody litter for Ingoldian fungi.

Woody litter of uniform size with intact bark (~1.5 cm diameter) was selected and excised into 3 cm long segments. From each segment, bark and cambium were separated (~3 × 0.8–1 × 0.2–0.3 cm) for bubble chamber incubation in 150 ml sterile distilled water in 250 ml conical flasks (48 hr) and damp chamber incubation in sterile Petri plates with wet paper towel (2 wk) (Sridhar et al. 2020). Sterile distilled water was added once a while in to the paper towel to avoid desiccation.

Table 1. Temperature and humidity of sampling locations with moisture content of woody litter samples (mean, n=3)

Tree species	Sampling date (2020)	Temperature (°C)		Humidity (%)	Moisture (%)	
		Soil	Air		Bark	Cambium
Acacia auriculiformis A. Cunn. ex Benth.	August 25	24.0	27.0	85.0	40.8	37.8
Anacardium occidentalis L.	August 18	22.1	24.9	92.1	31.4	29.1
Artocarpus heterophyllus Lam.	August 22	25.1	28.0	87.1	64.9	63.2
Ficus benghalensis L.	August 18	22.0	25.0	92.0	54.8	54.1
Terminalia paniculata Roth	August 22	25.0	28.1	87.2	47.7	44.6
Average		23.6	28.1	87.2	47.9	45.8
Range	August 18 to 25	22.0-25.1	24.9-28.1	85.0-92.1	31.4-64.9	29.1-63.2

After 48 hr of bubble chamber incubation, aerated water was filtered through Millipore filters (5 µm), stained with cotton blue in lactophenol and preserved in dark prior to observation. Sections of the filters were mounted on microscope slides followed by addition of a few drops of lactic acid and screened microscopically (Nikon YS100, Nikon Corporation, Tokyo, Japan) to find out the conidia of Ingoldian fungi. Stained conidia on the filters were identified using monographs and individual papers (Nawawi 1985, Marvanová 1997, Gulis et al. 2005, Zhao et al. 2007, Seifert et al. 2011). The dry mass of bark and cambium was assessed gravimetrically by drying at 100 °C for 24 hr in a hot-air oven to present the species and conidial richness per gram dry mass.

After two weeks of damp incubation, bark and cambium segments were transferred to 100 ml conical flasks containing 25 ml sterile distilled water followed by shaking for about 15 min (100 rpm) to release the conidia produced on the wood segments. After shaking, water in the flasks was filtered, processed and observed for the conidia as described in bubble chamber incubation.

Data analysis

The percent frequency of occurrence (FO) of Ingoldian fungi recorded in two methods of incubation (bubble chamber and damp chamber) was calculated based on representation of each species among 15 segments each of bark and cambium pooled from five tree species (Sridhar et al. 2020). Simpson's and Shannon's diversities (Magurran 1988) and Pielou's equitability (Pielou 1975) of the Ingoldian fungi in bark and cambium of woody litter in two methods of incubation were calculated. Significant difference in initial moisture content, average species and conidia (in bark and cambium) of woody litter of five tree species (in two methods of incubation) was assessed by Student's *t*-test.

For comparison of richness of species between the bark and cambium and between the incubation methods, rarefaction indices were followed (Ludwig and Reynolds 1988). The expected number of species [*E(s)*] in a random of *n* samples of bark or cambium taken from a total *N* samples was estimated. Similarly, to compare the richness species between the bark and cambium and between the incubation methods, rarefaction indices were followed. The expected number of species [*E(s)*] in a random sample of *n* conidia from a total of *N* conidia was estimated.

Results

The soil temperature below the canopy of all five tree species was lower than the air temperature (mean, 23.6 vs. 28.1 °C) (Table 1). The humidity was lowest under the canopy of *Acacia auriculiformis* (85 %), while it was the highest in *Anacardium occidentale* (92.1%). The moisture content of bark samples of all tree species was higher than cambium (mean, 47.9 % vs. 45.8 %), however there was no significant difference between bark and cambium of each tree species (*t*-test, p>0.05).

Table 2. Frequency of occurrence (FO %) of Ingoldian fungi in woody litter samples in bubble chamber (BC) and damp chamber (DC) incubations (*, exclusive species in BC incubation; **, exclusive species in DC incubation).

Species	BC		DC	
	Bark	Cambium	Bark	Cambium
Flagellospora curvula Ingold	60	60	40	53
Anguillospora longissima (Sacc. & P. Syd.) Ingold	47	33	47	67
Triscelophorus acuminatus Nawawi	60	33	40	20
Anguillospora crassa Ingold	7	13	47	7
Condylospora spumigena Nawawi (Fig. 3a)	20	-	20	13
Helicosporium griseum Berk. & M.A. Curtis (Fig. 3d)	7	7	-	47
**Ypsilina graminea* (Ingold, P.J. McDougall & Dann) J. Webster & Marvanová	27	20	-	-
Tricladium sp. (Fig. 3i)	33	-	-	7
Trisulcosporium acerinum H.J. Huds. & B. Sutton	-	7	20	7
Phalangispora constricta Nawawi & J. Webster	-	13	7	13
Campylospora parvula Kuzuha	7	7	-	13
Dwayaangam sp. (Fig. 3c)	7	7	7	-
Lemonniera sp. (Fig. 3g)	7	7	-	-
Triscelophorus konajensis K.R. Sridhar & Kaver.	7	7	7	-
Flagellospora penicillioides Ingold	7	-	-	13
***Tumularia aquatica* (Ingold) Descals & Marvanová (Fig. 3j)	-	-	7	13
**Trinacrium subtile* Riess	20	-	-	-
***Speiropsis pedatospora* Tubaki (Fig. 3h)	-	-	7	7
**Actinospora megalospora* Ingold	7	-	-	-
**Diplocladiella scalaroides* G. Arnaud	7	-	-	-
**Dwayaangam dichotoma* Nawawi (Fig. 3b)	7	-	-	-
**Isthmotricladia gombakiensis* Nawawi (Fig. 3f)	7	-	-	-
**Tetracladium marchalianum* De Wild.	7	-	-	-
**Campylospora filicladia* Nawawi	-	7	-	-
**Helicosporium* sp. (Fig. 3e)	-	7	-	-
**Nawawia filiformis* (Nawawi) Marvanová	-	7	-	-
**Triscelophorus monosporus* Ingold	-	7	-	-
***Tetracladium setigerum* (Grove) Ingold	-	-	7	-
***Trisulcosporium* sp.	-	-	7	-
***Campylospora chaetocladia* Ranzoni	-	-	-	7

The bubble chamber incubation yielded 25 species with 19 and 16 species in bark and cambium, respectively (Figure 3, Table 2). Eight species were exclusively found in bark samples, while six species in cambium. The core-group species (frequency of occurrence,

>10%) were also higher in bark than cambium (7 spp. vs. 6 spp.). Except for *Anacardium occidentale*, rest of the tree species consist of higher number of average species in bark than cambium with significant difference in *Artocarpus heterophyllus* and *Terminalia paniculata* (p<0.05) (Figure 4a). However, the conidial output was the highest in bark than cambium in all tree species with significant difference in all tree species (p<0.05) (Figure 4b). The expected number of species against the number of samples in rarefaction curves was higher in bark than cambium (Figure 5a), so also against the number of conidia (Figure 5b). The Simpson's and Shannon's diversities were higher with a lower equitability in bark compared to cambium (Table 3).

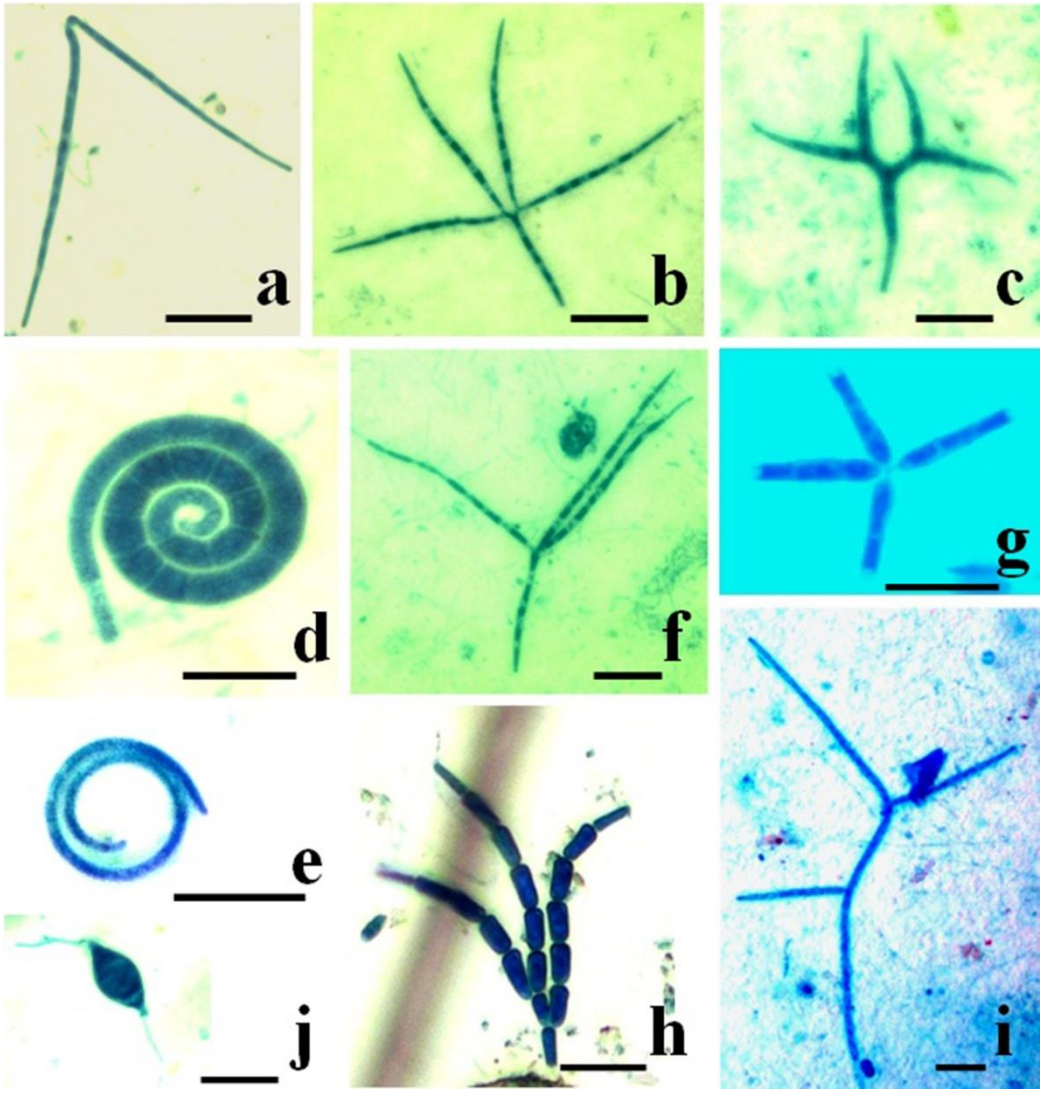

Figure 3. Conidia of *Condylospora spumigena* (a), *Dwayaangam dichotoma* (b), *Dwayaangam* sp. (c), *Helicosporium griseum* (d), *Helicosporium* sp. (e), *Isthmotricladia gombakiensis* (f), *Lemonniera* sp. (g), *Speiropsis pedatospora* (h), *Tricladium* sp. (i) and *Tumularia aquatica* (j) (Scale bar, 20 μm).

The damp chamber incubation consists of total 18 species with higher number of species in cambium than bark (14 spp. vs. 13 spp.) (Figure 3, Table 2). The exclusive species were higher in bark than cambium (4 spp. vs. 3 spp.), while it was opposite for the core-group species (9 spp. vs. 6 spp.). The cambium of *Anacardium occidentale* and *Artocarpus heterophyllus* showed higher number species than bark, while it was reverse in *Acacia auriculiformis*

(p<0.01) and *Ficus benghalensis* and *Terminalia paniculata* showed equal number of species (Figure 4c). *Acacia auriculiformis, A. occidentale* and *T. paniculata* possess higher number of conidia in bark than cambium, while it was opposite in *A. heterophyllus* and *F. benghalensis* with significant difference in all tree species (p<0.05) (Figure 4d). The expected number of species against the number of samples in rarefaction curves was slightly higher in bark than cambium (Figure 5c), while it was opposite for the number of conidia (Figure 5d). The Simpson's diversity was higher in bark than cambium, while it was opposite for Shannon's diversity with a lower equitability (Table 3).

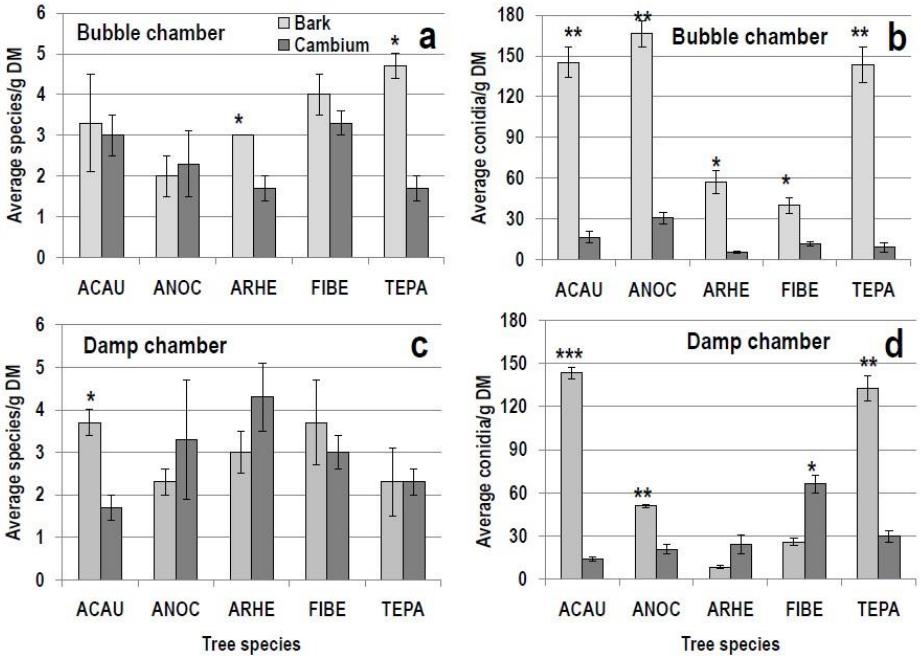

Figure 4. Average species (a) and conidia (b) per gram dry mass in bubble chamber incubation (n=3, mean±SE); average species (c) and conidia (d) per gram dry mass in damp chamber incubation (n=3, mean±SE) (Tree species: ACAU, *Acacia auriculiformis*; ANOC, *Anacardium occidentale*; ARHE, *Artocarpus heterophyllus*; FIBE, *Ficus benghalensis*; TEPA, *Terminalia paniculata*) (*t*-test: *, p<0.05; **, p<0.01; ***, p<0.001).

Table 3 Species richness, diversity and equitability of Ingoldian fungi in bubble chamber (BC) and damp chamber (DC) incubation.

Richness, diversity and equitability	**BC**		**DC**	
	Bark	**Cambium**	**Bark**	**Cambium**
Observed species richness among 15 samples	19	16	13	14
Expected number of species in samples [$Es_{(s35)}$]	14	14	15	14
Expected number of species in conidia [$Es_{(s140)}$]	15	14	14	15
Simpson diversity	0.896	0.878	0.881	0.866
Shannon diversity	3.665	3.489	3.293	3.295
Pielou's equitability	0.863	0.872	0.890	0.866

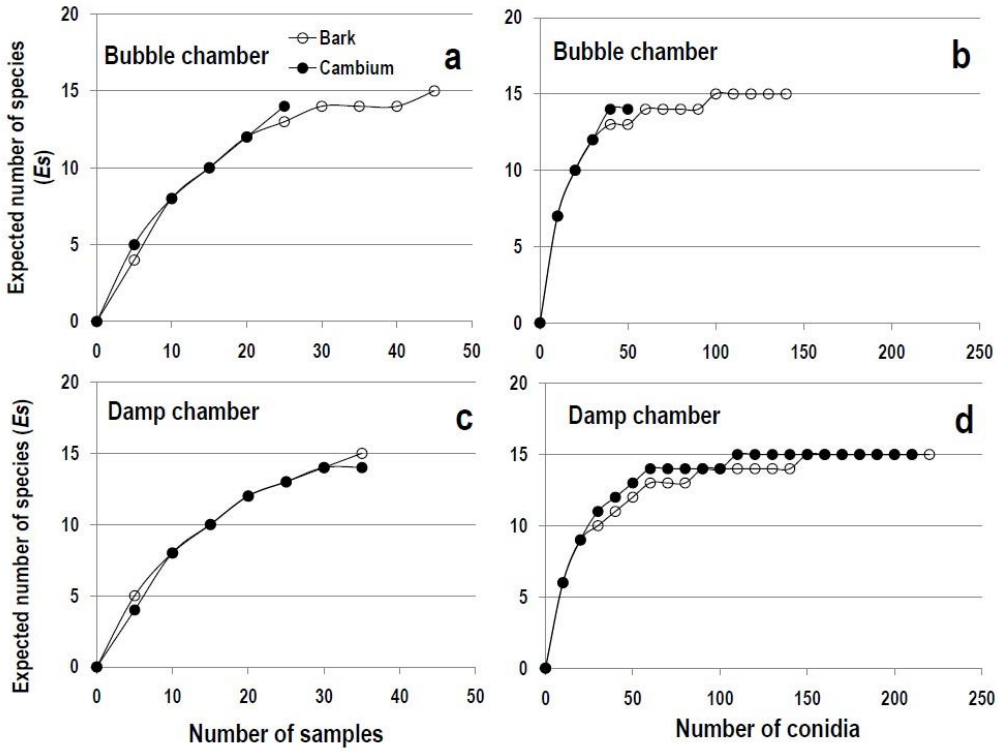

Figure 5. Rarefaction curves of expected number of species [*E(s35)*] of Ingoldian fungi among 35 random bark and cambium samples in bubble chamber (a) and damp chamber (c) incubations; Rarefaction curves of expected number of species [*E(s140)*] of Ingoldian fungi among 140 random conidia in bark and cambium in bubble chamber (b) and damp chamber (d) incubations.

Discussion

The bubble chamber incubation of plant detritus is one of the efficient methods to induce conidial production of colonized Ingoldian fungi (Bärlocher 2020). The jet of air bubbles supplies oxygen for fungal sporulation as well as results in turbulence leading to mechanical stimulation similar to the stream ecosystems. The technique of bubble chamber incubation has also been adapted to study occurrence of Ingoldian fungi in woody litter by Shearer and Webster (1991). Shearer (1992) also found 46 Ingoldian fungi on woody litter in temperate as well as tropical freshwaters based on bubble chamber incubation. Similar study has been carried out by Sridhar et al. (2010) recently to evaluate Ingoldian fungi in submerged woody litter in the Western Ghats and reported 30 species (14 species are common to this study). Sridhar and Sudheep (2011) also adapted the damp and bubble chamber incubation methods to assess the spatial distribution of fungi in decomposing woody litter in the Western Ghat streams and reported 28 species (14 species are common to this study). Thus, nearly 50 % of the Ingoldian fungi are common in stream submerged woody litter as well as damp woody litter in terrestrial conditions.

In the present study, the bubble chamber incubation is a better method than the damp chamber incubation to assess the colonized fungi in damp woody litter in a short duration, which corroborates the observations on terrestrial damp leaf litter (Sridhar et al. 2020). Similarly, the number of conidia released was also higher in bubble chamber than the damp chamber incubation (Figure 4b, d). The bubble chamber incubation also revealed higher exclusive species than the damp chamber incubation (Table 2), while it was almost same in both methods in terrestrial damp leaf litter (Sridhar et al. 2020). In a recent study, assessment of damp leaf litter of 10 tree species in the scrub jungles of southwest India showed the higher species

richness, diversity, core-group fungi, rarefaction curves and conidial output in bubble chamber than the damp chamber incubation (Sridhar et al. 2020). This shows that the damp leaf litter consists of higher species richness as well as diversity of Ingoldian fungi compared to the damp woody litter in scrub jungles possibly due to increased surface area. Similar to the present study, bark of naturally submerged mixed woody litter in 12 high altitude streams of the Western Ghats possesses higher species richness than the cambium (28 vs. 18 spp.) (Sridhar et al. 2010). In addition, although the Ingoldian fungi in bark and cambium of submerged wood showed high similarity (56–77 %), the species richness and conidial output differed significantly (Sridhar et al. 2010) corroborates with the present study. Those woody litter in damp incubation showed lower conidial output in bark than cambium in the present study (e.g., *Artocarpus heterophyllus* and *Ficus benghalensis*) may be due to presence of high quantity of inhibitory substance suberin. The suberin in bark is a lipophilic polyester biopolymer composed of long chain fatty acids (suberin acids and glycerol), those are known to inhibit the fungal colonization (Kolattukudy 2011).

Although the species richness in mixed leaf litter or banyan leaf litter (*Ficus benghalensis*) was lower in a nearby Konaje stream (16–18 spp.) (Sridhar and Kaveriappa 1989, Sridhar et al. 2013) compared to the 10 terrestrial damp leaf litter (31 spp.) (Sridhar et al. 2020) and five terrestrial damp woody litter (30 spp.) (present study), the conidial output was exceptionally higher in submerged leaf litter in the stream (up to 4000 vs. 1000 vs. 170/g dry mass). Increasing order of richness of species and conidia in terrestrial damp litters in scrub jungles is: cambium of woody litter < bark of woody litter < leaf litter.

Conclusions

Occurrence of Ingoldian fungi in terrestrial habitats is well documented in tropical, subtropical and temperate regions. The bubble and damp chamber incubations of damp woody litter accumulated in the basins of five tree species in scrub jungles of southwest India revealed occurrence of 30 species of Ingoldian fungi, which matches with species richness in the streams of the Western Ghats. However, only about 50 % of the species are common to woody litter in streams and damp terrestrial conditions. The bark of damp woody litter possesses more species as well as conidial output based on the bubble chamber incubation. The species richness in terrestrial damp woody litter was lower than the terrestrial damp leaf litter, while higher as compared to the leaf litter in a nearby stream. However, the conidial output was extremely higher in submerged leaf litter in the stream compared to the terrestrial damp leaf as well as woody litters. It is likely the colonization of Ingoldian fungi in terrestrial damp leaf or woody litters is governed by the extent of surface area, moisture content and water activity. The Ingoldian fungi colonized on the damp leaf and woody litters under the canopy may serve as a repository and provide inoculum to the streams during rainy season. Further studies are required to assess the extent of survival of Ingoldian fungi in leaf and woody litters during the dry seasons.

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Conflicts of interest

There are no conflicts of interest by the authors.

Author contribution

Experimental design was performed by the corresponding author. Sample collection, laboratory studies and drafting the manuscript were carried by both the authors.

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