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Review Article

Insights into endophytic aquatic hyphomycetes of the Indian subcontinent

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Abstract
Endophytic fungi include a diverse group that differ in plant-associated lifestyles, mutualistic associations and ecological functions in terrestrial, freshwater and marine ecosystems. Freshwater hyphomycetes are a unique group of mitosporic fungi that best thrive in submerged debris (leaf and woody litter) in running freshwater habitats. These are abundant in aquatic and semi-aquatic ecosystems as saprophytes (decomposition and nutrient turnover), epiphytes (plant or tree organ surfaces) and endophytes (internal regions of live plant tissues). Recent research advocates for the occurrence of endophytic aquatic hyphomycetes (EAHs) outside their usual ecosystems (e.g., lentic, terrestrial and tree canopy). The convergence of evolution might be responsible for their adaptation and functions in multiple ecological niches. The root-associated EAHs are diverse, widely distributed and known to produce a wide range of metabolites. Various metabolites of EAHs degrade detritus, help promote plant growth, protect against climate change, evade anthropogenic pressure and show antimicrobial effects. In the Indian subcontinent, the diversity, ecology and bioprospecting of EAHs have been carried out mainly in the Western Himalayas and the Western Ghats. From the ecological and industrial perspective, the present study envisages the diversity, distribution, ecosystem services, and secondary metabolites of EAHs.

Keywords: Bioprospecting, Diversity, Himalayas, Mutualism, Riparian plant roots, Streams, Western Ghats.

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1. Introduction

Recent investigations addressed the diversity, distribution, ecology and bioprospecting of endophytic aquatic hyphomycetes (EAHs) occurring in freshwater habitats (Sandberg et al., 2014; Chauvet et al., 2016; Han et al., 2015; Ghate & Sridhar, 2017; Sridhar, 2019; Altaf & Bisht, 2024; Lazar et al., 2024; Pant et al., 2024). Many hyphomycetes that are present in water have adapted to live in both aquatic and terrestrial ecosystems as saprophytes and endophytes (Seena & Monroy, 2015; Chauvet et al., 2016; Magyar et al., 2021; Lazar et al., 2024; Sridhar, 2024; Strullu-Derrien et al., 2024). They are more poorly studied than marine and terrestrial habitats (Sandberg et al., 2014; Sridhar, 2019; Sridhar, 2024). Quasi-developed roots of riparian plants in the running waters serve as stagnant shelter for aquatic hyphomycetes to colonize and to overcome the elimination from a unidirectional flow of lotic habitats (Sridhar & Bärlocher, 1992a, 1992b). Worldwide, about 60 species of EAHs are known to be associated with the roots of angiosperms, gymnosperms, and pteridophytes submerged in aquatic systems (Chauvet et al., 2016; Pant & Sati, 2018; Sridhar, 2019; Koranga et al., 2021). This accounts for about 17% of known morphospecies of aquatic hyphomycetes (Chauvet et al., 2016; Duarte et al., 2016; Sridhar, 2024). Most of the EAHs were found associated with angiosperms, followed by mosses, pteridophytes and gymnosperms. Due to their adaptability to colonize various substrates across different ecological niches, these fungi can provide ecosystem services beyond their usual lotic environment.

Many aquatic hyphomycetes share common ancestry with terrestrial fungal endophytes (Kong et al., 2000; Liew et al., 2002; Selosse et al., 2008). Waid (1954) demonstrated the activity of aquatic hyphomycetes in soil sites by isolating *Clathrosphaerina zalewskii* and *Varicosporium elodeae* from the surface of roots of beech seedlings in woodland soils. Subsequently, Nemec (1969) established the occurrence of *Tetracladium marchalianum* as an endophyte in the roots of *Fragaria* sp., whereas *Tetracladium setigerum* was found in the roots of *Fragaria* sp. and *Gentiana* sp. by Watanabe (1975). Fisher et al. (1986) observed that the incidence of fungal colonization of endophytes showed a significant tendency with an increase in the age of the host tissue. A report on the occurrence of two EAHs (*Campylospora parvula* and *Tricladium splendens*) in the roots of riparian *Alnus glutinosa* was published by Fisher and Petrini (1989). Further detailed study by Fisher et al. (1991) revealed higher colonization of EAHs in aquatic than in terrestrial roots (30 vs. 12%). Additional studies carried out in western Canada revealed that many aquatic hyphomycetes are endophytic on spruce, maple and birch roots (Sridhar & Bärlocher, 1992a). Generally, colonization was higher in bark than xylem, but xylem segments of spruce roots grown up to 4 to 5 years showed the highest number of species (Sridhar & Bärlocher, 1992b).

Up to 17 EAHs were recorded in riparian tree roots (*Mangifera indica*, *Populus hybrida* and *Salix babylonica*) in Pakistan, with more in bark than in xylem tissues (Iqbal et al., 1995a). The occurrence, ecology and secondary metabolites of endophytic fungi in soil and submerged roots in freshwater and mangrove habitats have been reviewed by Bärlocher (2006). Iqbal et al. (1995b) reported 14 EAHs associated with submerged green leaves in a canal in Pakistan. Woody litter serves as a potential substrate to establish anamorph-teleomorph connections of aquatic hyphomycetes (Webster, 1992; Sivichai & Jones, 2003). Similarly, subcultures of endophytic *Neonectria lugdunensis* isolated from submerged spruce roots exposed to fluorescent light developed its ascomycete teleomorph, *N. lugdunensis*, within six weeks (Sridhar & Bärlocher, 1992a). *Gyoerffyella* spp. were also known to be endophytic in the roots of *Picea abies* (Czacauga & Orlowska, 1997; Selosse et al., 2008). Four new species of EAHs were described in several riparian tree roots extended to aquatic habitats (*Filosporella fistucella, F. versimorpha, Fontanospora fusiramosa* and *Tetracladium nainitalense*) (Marvanová & Fisher, 1991; Marvanová et al., 1992, 1997; Sati et al., 2009).

Many plant species thrive in freshwater habitats such as streams, rivers, lakes, and marshes. In southwest China, certain marsh plants, specifically *Equisetum arvense*, *Myriophyllum verticillatum* and *Ottelia acuminata*, including riparian herbs like *Cardamine multijuga* and *Impatiens chinensis*, are associated with 31 types of endophytic fungi (Li et al., 2010). The medicinal fern *Marsilea minuta*, which grows in aquatic environments, harbors 17 different endophytic fungi (Udayaprakash et al., 2018). Additionally, studies on hydrophytes such as *Nymphaea nouchali* and *Vallisneria spiralis* have identified 18 types of endophytic fungi (Rajagopal et al., 2018). The lower, middle and top regions of another aquatic macrophyte (*Vallisneria spiralis*) yielded two ascomycetes, four coelomycetes and 14 hyphomycetes as endophytes (Govindan & Jalainthararajan, 2020). Submerged macrophytes also serve as potential hosts for EAHs (e.g., *Apium*, *Potamogeton* and *Ranunculus*) (Bärlocher, 1992).

Besides submerged roots and soils, aquatic hyphomycetes have also been reported as endophytes in the aerial plant parts (Widler & Müller, 1984; Bärlocher, 2006; Sokolski et al., 2006; Chauvet et al., 2016; Ghate & Sridhar, 2017; Altaf & Bisht, 2024; Eichfeld et al., 2024; Lazar et al., 2024). Aquatic hyphomycetes have a wider perspective in distribution in different ecological habitats and functions (Chauvet et al., 2016; Sridhar, 2024). In the context of the occupation of different niches by aquatic hyphomycetes, EAHs have special consideration, as they mutualistically occupy root ecosystems of a variety of riparian vegetation. Besides EAHs preferring submerged roots as stagnant refuge, it is likely benefitting the host species by their metabolites, in turn maintaining their inoculum in streams against unidirectional flow. As our knowledge of the mutualism of aquatic fungi is inadequate (Hawksworth, 2021), this review attempts to appraise studies carried out on EAHs in two biodiversity hotspots of the Indian subcontinent (the Western Himalayas and the Western Ghats) in view of their ecological and bioprospecting potential.

2. Taxonomic Diversity

Diversity and distribution of endophytic fungi in aquatic and riparian plants are less studied as compared to terrestrial plants. Several plant species that grow in and around aquatic habitats may serve as possible sites for fungal colonization. A total of 48 aquatic hyphomycetes were recorded as endophytes, with the highest of 41 species in the Western Himalayas and 18 species in the Western Ghats (Table 1). Up to 27 host plant species consist of endophytes in 13 locations. Twenty-nine plant species possess five or more than five endophytes (Fig. 1a). Similarly, 27 EAHs were associated with five or more host plant species (Fig. 1b), while 15 EAHs were found in five or more locations (Fig. 1c).

Table 1. Diversity of root-associated endophytic aquatic hyphomycetes in India.

Endophyte	Host plant (# host)	Region (## location)	Reference
Alatospora acuminata Ingold	*Alnus nepalensis*, *Carpesium cernuum, Equisetum* sp., *Eupatorium adenophorum, Ilex diphyrena, Machilus duthiei, Viburnum mullaha,* unidentified grass and unidentified fern (9)	Uttarakhand (8)	Sati & Belwal, 2005; Sati et al., 2008, 2009a; Sati & Pathak, 2017
Alatospora pulchella Marvanová	Unidentified grass (1)	Uttarakhand (2)	Sati & Belwal, 2005; Sati et al., 2008
Amniculicola longissima (Sacc. & P. Syd.) Nadeeshan & K.D. Hyde	*Mallotus phillipensis* (1)	Uttarakhand (1)	Altaf & Bisht, 2024
Anguillospora crassa Ingold	*Ageratum conyzoides*, *Berberis* sp., *Equisetum* sp. and Unidentified fern (4)	Uttarakhand (3)	Sati et al., 2008, 2009a; Altaf & Bisht, 2024
	Submerged roots (1)	Madhya Pradesh (1)	Chaudhari et al., 2016
	Bambusa sp., *Bischofia javanica,* *Canarium strictum, Ficus arnottiana, Ficus carica, Ficus racemosa, Hydnocarpus pentandra, Madhuca neriifolia, Syzygium cumini* and *Vateria indica* (10)	Karnataka (2)	Ghate & Sridhar, 2017
Anguillospora longissima (Sacc. & Syd.) Ingold	*Alnus nepalensis*, *Berberis* sp., *Botrychium* sp., *Equisetum* sp., *Geranium nepalense*, *Machilus duthiei, Myrica esculenta, Pilea scripta, Rumex hastatulus, Symplocos chinensis,* unidentified grass, unidentified fern and submerged roots (13)	Uttarakhand (6)	Sati & Belwal, 2005; Sati et al., 2008, 2009a; Sati & Singh, 2014; Sati & Pathak, 2017; Singh & Sati, 2017
	Submerged roots (1)	Madhya Pradesh (1)	Chaudhari et al., 2016
	Bambusa sp., *Bischofia javanica, Canarium strictum, Ficus arnottiana, Ficus carica, Ficus racemosa, Hydnocarpus pentandra, Madhuca neriifolia, Syzygium cumini* and *Vateria indica* (10)	Karnataka (2)	Ghate & Sridhar, 2017

Anguillospora mediocris Gönczöl & Marvanová	*Mallotus phillipensis* (1)	Uttarakhand (1)	Altaf & Bisht, 2024
Bacillispora aquatica Sv. Nilsson	*Mimosa pudica* (1)	Uttarakhand (1)	Altaf & Bisht, 2024
Camposporium pellucidum (Grove) S. hughes	*Acer oblongum, Equisetum* sp., *Eupatorium adenophorum, Quercus leucotrichophora, Symplocos chinensis* and unidentified fern (6)	Uttarakhand (5)	Sati et al., 2006, 2008
Campylospora chaetocladia Ranzoni	*Carpesium cernuum, Eupatorium adenophorum, Murraya koenigii, Roscoea alpina, Valeriana wallichii* and unidentified fern (6)	Uttarakhand (4)	Sati & Belwal, 2005; Sati et al., 2008; Sati & Pathak, 2017
	Submerged roots (1)	Madhya Pradesh (1)	Chaudhari et al., 2016
	Canarium strictum, Ficus arnottiana, Ficus carica, Ficus racemosa, Hydnocarpus pentandra, Madhuca neriifolia, Syzygium cumini and *Vateria indica* (8)	Karnataka (2)	Ghate & Sridhar, 2017
Campylospora filicladia Nawawi	*Mallotus phillipensis* (1)	Uttarakhand (1)	Altaf & Bisht, 2024
Campylospora parvula Kuzuha	*Aesculus indica*, *Berberis vulgaris*, *Berberis* sp., *Botrychium* sp., *Lyonia ovalifolia*, *Lyonia ovalifolia, Machilus duthiei, Pilea scripta*, *Quercus floribunda, Rubus ellipticus*, *Symplocos chinensis*, *Viburnum mullaha*, unidentified fern, unidentified grass and submerged roots (15)	Uttarakhand (11)	Sati & Belwal, 2005; Sati et al., 2008, 2009a; Sati & Pant, 2020; Sati et al., 2023; Pant et al., 2024
Clavariana aquatica Nawawi	*Madhuca neriifolia* (1)	Karnataka (2)	Ghate & Sridhar, 2017
Clavariopsis aquatica De Wild.	*Botrychium* sp., *Carpesium cernuum, Elatostema* sp., *Eupatorium adenophorum, Quercus floribunda,* unidentified grass and unidentified fern (7)	Uttarakhand (3)	Sati & Belwal, 2005; Sati et al., 2008; Sati & Pathak, 2017
	Submerged roots (1)	Madhya Pradesh (1)	Chaudhari et al., 2016
	Canarium strictum, Bambusa sp., *Bischofia javanica, Ficus arnottiana, Ficus racemosa, Madhuca neriifolia, Syzygium cumini* and *Vateria indica* (8)	Karnataka (2)	Ghate & Sridhar, 2017

Cylindrocarpon aquaticum (Sv. Nilson) Marvanová & Descals	*Acer oblongum*, *Acer pictum*, *Aesculus indica, Alnus nepalensis, Artemisia vulgaris, Berberis* sp., *Carpesium cernuum, Debregeasia* sp., *Equisetum* sp., *Eupatorium adenophyllum, Geranium nepalense, Machilus duthiei, Myrica esculenta*, *Nepeta leucophylla*, *Pilea scripta, Pyracantha crenulata*, *Quercus floribunda*, *Quercus leucotrichophora*, *Rubus ellipticus*, *Rumex hastatulus, Sarcococca hookeriana*, *Shorea robusta, Symplocos chinensis*, *Valeriana wallichii, Viburnum mullaha,* unidentified grass and unidentified fern (27)	Uttarakhand (9)	Sati & Belwal, 2005; Sati et al., 2008; Singh & Sati, 2014, 2017; Sati & Pathak, 2017
Diplocladiella scalaroides G. Arnaud	*Aesculus indica, Geranium nepalense, Lyonia ovalifolia* and *Shorea robusta* (3)	Uttarakhand (4)	Sati et al., 2006, 2008
Flagellospora curvula Ingold	*Bambusa* sp., *Bischofia javanica*, *Canarium strictum*, *Madhuca neriifolia*, *Ficus arnottiana, Ficus racemosa, Hydnocarpus pentandra, Syzygium cumini* and *Vateria indica* (9)	Karnataka (2)	Ghate & Sridhar, 2017
	Mallotus phillipensis (1)	Uttarakhand (1)	Altaf & Bisht, 2024
Flagellospora penicillioides Ingold	*Acer oblongum*, *Ageratina adenophora*, *Elatostema* sp., *Eupatorium adenophyllum, Eurya acuminata, Quercus leucotrichophora*, *Pilea scripta* and *Valeriana wallichii* (8)	Uttarakhand (3)	Arya & Sati, 2010; Sati & Pathak, 2017; Sati et al., 2025
	Bambusa sp., *Bischofia javanica, Canarium strictum*, *Ficus arnottiana, Ficus racemosa, Madhuca neriifolia, Syzygium cumini* and *Vateria indica* (8)	Karnataka (2)	Ghate & Sridhar, 2017
Helicomyces roseus Link	*Acer pictum, Carpesium cernuum, Eupatorium adenophyllum, Quercus floribunda, Mallotus phillipensis, Roscoea alpina* and	Uttarakhand (3)	Sati & Pathak, 2017; Sati et al., 2008; Altaf & Bisht, 2024

	Valeriana wallichii (7)		
Helicomyces torquatus L.C. Lane & Shearer	*Aesculus indica, Lyonia ovalifolia* and unidentified roots (3)	Uttarakhand (3)	Koranga et al., 2021; Sati et al., 2023
Helicosporium lumbricoides Sacc.	*Carpesium cernuum, Rumex hastatulus, Valeriana wallichii,* unidentified grass and unidentified fern (5)	Uttarakhand (1)	Sati & Pathak, 2017
Isthmotricladia gombakiensis Nawawi	Submerged roots (1)	Uttarakhand (1)	Arya & Sati, 2010
	Bischofia javanica, Canarium strictum, Ficus arnottiana, Ficus racemosa, Madhuca neriifolia, Syzygium cumini and *Vateria indica* (7)	Karnataka (2)	Ghate & Sridhar, 2017
**Kumbhamaya jalapriya* S.K. Nair & Bhat	*Hopea ponga* (1)	Goa (1)	Sreekala & Bhat, 2002
Lemonniera aquatica De Wild.	*Aesculus indica, Acer oblongum*, *Debregeasia* sp. and *Lyonia ovalifolia* (4)	Uttarakhand (3)	Sati & Belwal, 2005; Koranga et al., 2021
	Bischofia javanica, Canarium strictum, Ficus arnottiana, Ficus racemosa and *Madhuca neriifolia* (5)	Karnataka (1)	Ghate & Sridhar, 2017
Lemonniera cornuta Ranzoni	*Lyonia ovalifolia* (1)	Uttarakhand (1)	Sati et al., 2008
Lemonniera pseudofloscula Dyko	*Myrica esculenta*, *Lyonia ovalifolia* and Unidentified roots (3)	Uttarakhand (4)	Sati & Belwal, 2005; Sati et al., 2008, 2023
Lemonniera terrestris Tubaki	*Lyonia ovalifolia* (1)	Uttarakhand (2)	Sati & Belwal, 2005; Sati et al., 2008
Lunulospora curvula Ingold	*Acer oblongum*, *Botrychium* sp., *Eupatorium adenophyllum, Mallotus phillipensis, Quercus floribunda*, *Quercus leucotrichophora* and unidentifired fern (7)	Uttarakhand (6)	Sati & Belwal, 2005; Sati et al., 2008, 2009a; Altaf & Bisht, 2024
	Submerged roots (1)	Madhya Pradesh (1)	Chaudhari et al., 2016

	Coffea arabica, Hevea brasiliensis, Angiopteris evecta, Christela dentata, Madhuca neriifolia, Canarium strictum, Ficus arnottiana, Bischofia javanica Vateria indica, Bambusa sp., *Ficus carica* (11)	Karnataka (3)	Raviraja et al., 1996; Ghate & Sridhar, 2017
Lunulospora cymbiformis K. Miura	*Bambusa* sp., *Bischofia javanica, Canarium strictum, Ficus carica, Ficus racemosa, Hydnocarpus pentandra, Madhuca neriifolia, Syzygium cumini* and *Vateria indica* (9)	Karnataka (2)	Ghate & Sridhar, 2017
Neonectria lugdunensis (Sacc. & Therry) L. Lombard & Crous	*Acer pictum, Berberis* sp., *Botrychium* sp., *Debregeasia* sp., *Geranium nepalense*, *Lyonia ovalifolia, Machilus duthiei, Quercus floribunda, Rosa moschata, Strobilanthes alatus*, *Strobilanthes* sp., *Symplocos chinensis*, submerged roots and unidentified fern (14)	Uttarakhand (7)	Sati et al., 2006, 2008, 2009a; Sati & Belwal, 2005; Sati & Arya, 2010a, 2010b; Arya & Sati, 2011
Pestalotiopsis submersa Sati & N. Tiwari	*Carpesium cernuum, Equisetum* sp., *Eupatorium adenophyllum, Lyonia ovalifolia, Quercus floribunda* and unidentified fern (6)	Uttarakhand (3)	Sati & Belwal, 2005; Sati et al., 2008, 2009a; Sati & Pathak, 2017
Phalangispora constricta Nawawi & J. Webster	*Canarium strictum, Ficus arnottiana, Ficus racemosa* and *Madhuca neriifolia* (4)	Karnataka (1)	Ghate & Sridhar, 2017
Pleuropedium tricladioides Marvanová & S.H. Iqbal	*Hedera nepalensis* and *Wulfenia amherstiana* (2)	Uttarakhand (1)	Koranga & Sati, 2023
Setosynnema isthmosporum D.E. Shaw & B. Sutton	*Carpesium cernuum, Pilea scripta*, *Shorea robusta*, *Mallotus phillipensis, Rumex hastatulus* (5)	Uttarakhand (3)	Sati & Pathak, 2017; Altaf & Bisht, 2024
Speiropsis scopiformis Kuthub. & Nawawi	*Mallotus phillipensis* (1)	Uttarakhand (1)	Altaf & Bisht, 2024
Synnematophora constricta K.R. Sridhar & Kaver.	*Bischofia javanica, Canarium strictum, Ficus arnottiana, Ficus racemosa* and *Madhuca neriifolia* (5)	Karnataka (1)	Ghate & Sridhar, 2017

Tetrachaetum elegans Ingold	*Botrychium* sp., *Lyonia ovalifolia, Pilea scripta, Valeriana wallichii,* unidentified grass, unidentified fern and submerged roots (7)	Uttarakhand (8)	Sati & Belwal, 2005; Sati et al., 2008, 2009a; Sati & Arya, 2010a, 2010b; Arya & Sati, 2011; Pant & Sati, 2018
Tetracladium apiense R.C. Sinclair & Eicker	*Eupatorium adenophorum, Pilea scripta, Valeriana wallichii* and submerged roots (4)	Uttarakhand (2)	Pant & Sati, 2018 Arya & Sati, 2010
Tetracladium breve A. Roldán	*Alnus nepalensis, Eupatorium adenophorum*, *Pyracantha crenulata* and submerged roots (4)	Uttarakhand (5)	Arya & Sati, 2010, 2011; Sati & Arya, 2010b; Pant & Sati, 2018
Tetracladium furcatum Descals	*Angiopteris evecta* and *Christela dentata* (2)	Karnataka (1)	Raviraja et al., 1996
Tetracladium marchalianum De Wild.	*Aesculus indica*, *Berberis vulgaris*, *Botrychium* sp., *Carpesium cernuum, Cedrus deodara*, *Equisetum* sp., *Elatostema* sp.*, Eupatorium adenophorum, Geranium nepalense, Lyonia ovalifolia, Mallotus phillipensis, Machilus duthiei, Parthenium hysterophorus, Querecus floribunda, Salix tetrasperma, Shorea robusta*, *Syzygium cumini*, *Tectona grandis, Viola canescens. u*nidentified grass, *u*nidentified fern and submerged roots (22)	Uttarakhand (9)	Sati & Belwal, 2005; Sati et al., 2008, 2009a, 2023; Sati & Arya, 2010b; Arya & Sati, 2011; Sati & Pathak, 2017; Pant & Sati, 2018; Altaf & Bisht, 2024
	Submerged roots (1)	Madhya Pradesh (1)	Chaudhari et al., 2016
	Canarium strictum and *Ficus arnottiana* (2)	Karnataka (1)	Ghate & Sridhar, 2017
***Tetracladium nainitalense* Sati & P. Arya	*Colocasia* sp., *Eupatorium adenophorum, Lantana camara*, *Rubus ellipticus* and submerged roots (5)	Uttarakhand (4)	Sati et al., 2009b; Sati & Arya, 2010a, 2010b; Arya & Sati, 2011; Pant & Sati, 2018

Tetracladium setigerum (Grove) Ingold	*Acer oblongum*, *Alnus nepalensis, Artemisia vulgaris, Berberis aristata, Berberis vulgaris*, *Botrychium* sp., *Debregessia* sp., *Equisetum* sp., *Eupatorium adenophyllum*, *Geranium nepalensis, Lyonia ovalifolia, Mallotus phillipensis, Machilus duthiei, Murraya koenigii, Oenothera rosea, Oxalis* sp., *Quercus floribunda*, *Rubus ellipticus, Valeriana wallichii*, unidentified grass and unidentified fern (20)	Uttarakhand (13)	Sati & Belwal, 2005, Sati et al., 2008, 2009a; Pant & Sati, 2018; Sati & Pant, 2019, 2020; Pant & Sati, 2023; Altaf & Bisht, 2024
Tricladium indicum Sato & N. Tiwari	*Acer pictum* and *Quercus floribunda* (2)	Uttarakhand (1)	Pant et al., 2019
Tricladium marylandicum J.L. Crane	*Aesculus indica* and *Cedrus deodara* (2)	Uttarakhand (1)	Pant et al., 2019
Triscelophorus acuminatus Nawawi	*Angiopteris evecta, Bambusa* sp., *Bischofia javanica, Canarium strictum, Christela dentata, Coffea arabica, Diplazium esculentum, Ficus arnottiana, Ficus carica, Ficus racemosa, Hevea brasiliensis, Hydnocarpus pentandra, Macrothelypteris torresiana, Madhuca neriifolia, Syzygium cumini* and *Vateria indica* (16)	Karnataka (3)	Raviraja et al., 1996; Ghate & Sridhar, 2017
	Mallotus phillipensis (1)	Uttarakhand (1)	Altaf & Bisht, 2024
Triscelophorus konajensis K.R. Sridhar & Kaver.	*Angiopteris evecta, Canarium strictum, Coffea arabica, Christela dentata, Ficus arnottiana, Macrothelypteris torresiana* and *Madhuca neriifolia* (7)	Karnataka (2)	Raviraja et al., 1996; Ghate & Sridhar, 2017
Triscelophorus monosporus Ingold	*Debregeasia* sp., *Cedrus deodara*, *Equisetum* sp. and *Lantana camara* (4)	Uttarakhand (3)	Sati & Belwal, 2005

	Angiopteris evecta, Bambusa sp., *Bischofia javanica, Canarium strictum, Christela dentata, Coffea arabica, Diplazium esculentum, Ficus arnottiana, Ficus carica, Ficus racemosa, Hydnocarpus pentandra, Macrothelypteris torresiana, Madhuca neriifolia, Syzygium cumini* and *Vateria indica* (15)	Karnataka (3)	Raviraja et al., 1996; Ghate & Sridhar, 2017
Varicosporium elodeae W. Kegel	*Ageratina adenophora* and *Eurya acuminata* (2)	Uttarakhand (1)	Sati et al., 2025

*, new genus and species; **, new species; #, number of host plants; ##, number of locations

Based on EAHs identified up to genus level (6 spp.) (*Campylospora* sp., *Cylindrocrpon* sp., *Lemonnierea* sp., *Mycocentrosopora* sp., *Pleuropedium* sp. and *Tetracladium* sp.), with the addition of three unidentified species, the total EAHs will be 56 species. The top 13 colonized species on the host plant species consist of *Anguillospora crassa, A. longissima, Campylospora chaetocladia, C. parvula, Clavariopsis aquatica, Cylindrocarpon aquaticum*, *Flagellospora penicillioides, Lunulospora curvula, Neonectria lugdunensis, Tetracladium marchalianum, T. setigerum, Triscelophorus acuminatus* and *T. monosporus* (14−27 host species) (Fig. 1b). The top eight most recorded in different locations were *Alatospora acuminata, A. longissima, C. parvula, C. aquaticum*, *L. curvula, Tetrachaetum elegans, T. marchalianum* and *T. setigerum* (8−13 locations) (Fig. 1c).

Sati and Belwal (2005) reported the seasonal occurrence of 17 root endophytes from riparian plants in two high-altitude streams (1150−1775 m above sea level) (m asl) of Nainital and their maximum richness was during winter (November and December). Dominant endophytes include *Anguillospora longissima, Cylindrocarpon aquaticum, Tetracladium marchalianum* and *T. setigerum*. Sati and Pathak (2017) found 12 endophytic hyphomycetes in streams of Nainital (1050−2050 m asl) and their higher occurrence is due to the low temperature range (5−15°C) during the winter season. However, the diversity of EAHs was maximum during autumn and winter in the Nandhaur River of the foothills of the Western Himalayas (221 m asl) at a temperature range of 10−25°C (Altaf & Bisht, 2024).

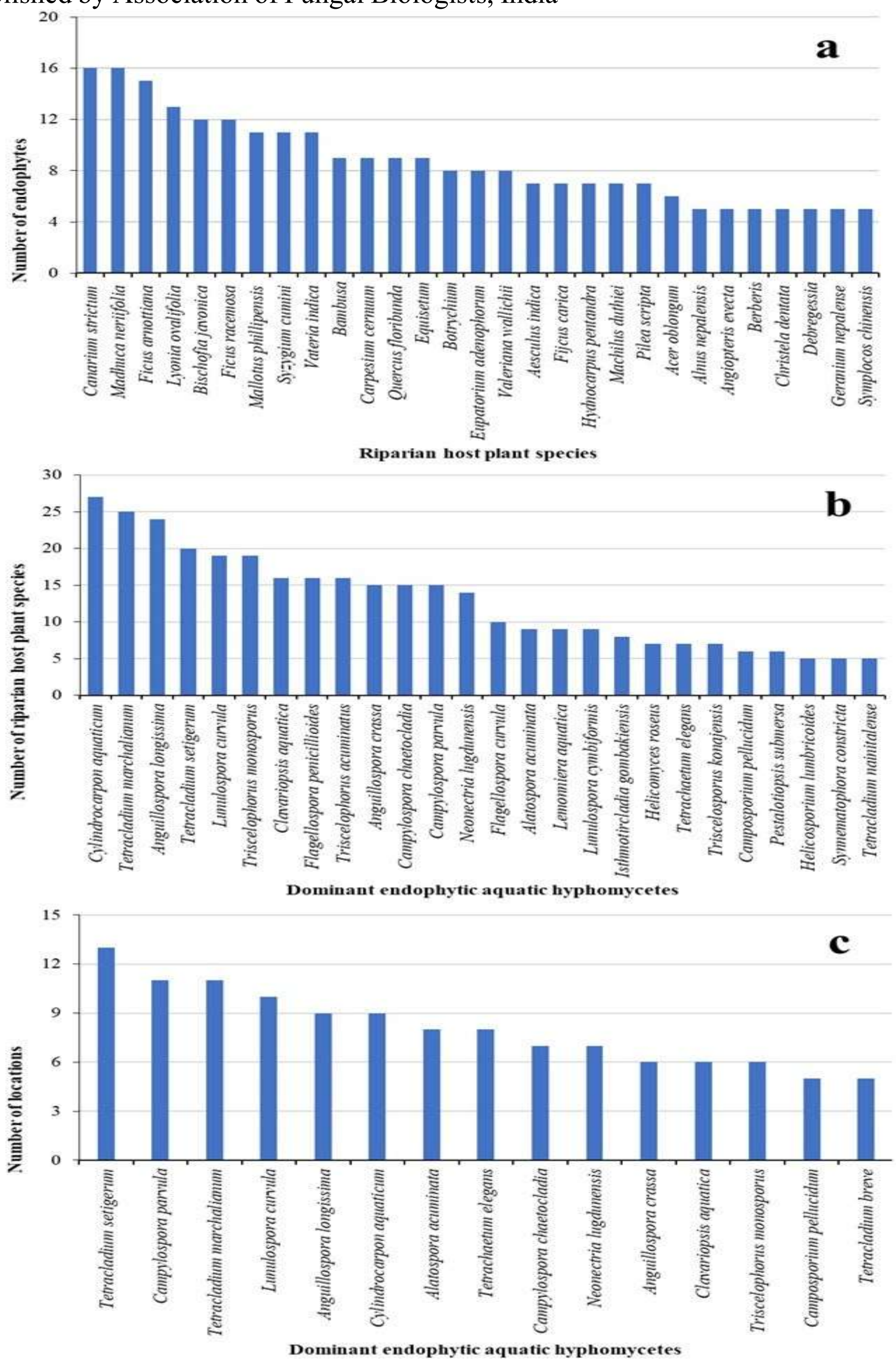

Fig. 1. Roots of 29 host plant species consist of five or more endophytic aquatic hyphomycetes (a); aquatic hyphomycetes are endophytic in roots of five or more host plant species (b); endophytic aquatic hyphomycetes are found in five or more locations (c).

3. Riparian Plant Species

Besides stream debris, submerged roots of riparian plant species are potential niches for colonization by aquatic hyphomycetes. Live roots of riparian angiosperms, gymnosperms, and pteridophytes exposed to water have been colonized by these fungi (Bärlocher, 2006). In the Western Himalayas and the Western Ghats of the Indian subcontinent, aquatic hyphomycetes have mutualistic associations with 67 riparian plant species belonging to climbers (1 sp.), creepers (1 sp.), herbs (20 spp., including 2 ferns), shrubs (18 spp., including 3 ferns) and trees (27 spp., including 1 gymnosperm) (Table 2). Among 61 angiosperms, 60 species were dicots and only one species was a monocot (*Roscoea alpina*). Considering unidentified grasses and unidentified ferns, the total hosts supported by EAHs will be about 70 species. Among 67 host plant species, nine species harbored more than 10 spp. of endophytes: *Canarium strictum* and *Madhuca neriifolia* supported the highest number (16 spp. each), followed by *Ficus arnottiana* (15 spp.), *Lyonia ovalifolia* (13 spp.), *Bischofia javonica, Ficus racemosa* (12 spp. each), *Syzygium cumini, Mallotus phillipensis* and *Vateria indica* (11 spp. each).

Among plant species mutualistic with aquatic hyphomycetes, many possess economic significance (e.g., beverages, charcoal, dyes, edible oils, firewood, fodders, handicrafts, medicinal, nutraceutical, ornamental, rubber and timbers). A maximum of 52 plant species has medicinal value. The IUCN categories of conservation status of EAH-harbored plant species reveal critically endangered (CR, 3 spp.), endangered (EN, 11 spp.), near threatened (NT, 2 spp.) and vulnerable (VU, 8 spp.). The conservation status of threatened endemic flora of the Western Himalayas has been addressed by Slutan-Ud-Din et al. (2016).

Bark as well as xylem of 10 streamside tree species growing in the Western Ghats at two altitudinal ranges (475–500 and 765–800 m asl) consists of 20 species of aquatic hyphomycetes (Ghate & Sridhar, 2017). Three species, *Anguillospora crassa, A. longissima*, and *Cylindrocarpon* sp., were dominant. Xylem possesses higher endophytic hyphomycetes compared to the bark of tree species, which corroborates earlier studies (Sridhar & Bärlocher, 1992a, 1992b; Raviraja et al., 1996). The evidence of higher richness and diversity of saprophytic aquatic hyphomycetes in mid-altitude streams than high-altitude streams is also applicable to root-colonized aquatic hyphomycetes (Raviraja et al., 1998). Among the angiosperms, *Lyonia ovalifolia, Machilus duthiei, Berberis* sp. and *Eupatorium haterophyllum* contributed up to 47.6%, 28.5%, 23.8% and 23.8% diversity, respectively (Sati et al., 2008).

Roots of several ferns provide shelter to endophytic hyphomycetes in the Western Himalayas and the Western Ghats (Raviraja et al., 1996; Sati et al., 2008, 2009a; Altaf & Bisht, 2024). The species richness was highest in *Angiopteris evecta*, while spore output was the highest in *Christella dentata* (Raviraja et al., 1996). In the Western Himalayas (Nainital and Almora), *Mallotus phillipensis* was colonized by the highest number of endophytes (11 spp.), followed by *Botrychium* sp. (8 spp.) and *Equisetum* sp. (5 spp.) (Sati et al., 2008). Similarly, *Botrychium* sp., *Equisetum* sp. and unidentified ferns in high-altitude riparian zones (Jeoli, 1150 m asl; Kilburry, 2160 m asl) harbored seven, four and six species of endophytes, respectively (Sati et al., 2009a).

Botrychium sp. and *Equisetum* sp. contributed up to 38.1% and 23.8% diversity of endophytes, respectively (Sati et al., 2008; 2009a; Zhang et al., 2025).

As root endophytic fungi derive multiple benefits from the hosts, they produce secondary metabolites to survive within the live roots without causing diseases to hosts. Colonization of roots helps fungi to avoid predation from detritus feeders and removal from unidirectional flow. In addition, on senescence of roots, endophytic fungi will profit by degrading and recycling the nutrients through the production of conidia. The released conidia are transporters of nutrients to higher food webs and they have numerous opportunities to colonize new habitats as well as substrates for perpetuation (Seena et al., 2022).

Table 2. Roots of riparian plant species supported endophytic aquatic hyphomycetes.

Plant species	Nature and conservation status*	Number of endophytes colonized	Economic value
Angiosperm - Dicot			
Canarium strictum Roxb.	Tree (CR)	16	Medicinal
Madhuca neriifolia I(Moon) H.J.Lam	Tree (LC)	16	Medicinal and edible oil
Ficus arnottiana (Miq.) Miq.	Tree (NE)	15	Medicinal
Lyonia ovalifolia (Wall.) Drude	Tree (LC)	13	Medicinal
Bischofia javonica Blume	Tree (LC)	12	Timber and medicinal
Ficus racemosa L.	Tree (EN)	12	Medicinal
Mallotus phillipensis (Lam.) Müll.Arg	Tree (LC)	11	Dye-yielding
Syzygium cumini (L.) Skeels	Tree (LC)	11	Medicinal
Vateria indica L.	Tree (VU)	11	Timber and medicinal
Bambusa sp.	Shrub (NC)	9	Medicinal, fodder and handicrafts
Carpesium cernuum L.	Herb (NE)	9	Medicinal
Quercus floribunda Lind. ex A.Camus	Tree (LC)	9	Medicinal, firewood and charcoal
Eupatorium adenophorum (Spreng.) King & H.Rob.	Herb (LC)	8	Medicinal
Valeriana wallichii DC.	Herb (EN)	8	Medicinal
Aesculus indica (Wall. ex Cambess.) Hook.	Tree (VU)	7	Medicinal, fodder and ornamental
Fijcus carica L.	Tree (LC)	7	Medicinal
Hydnocarpus pentandra (Buch.-Ham.) Oken	Tree (VU)	7	Medicinal
Machilus duthiei King	Tree (NT)	7	Medicinal
Pilea scripta (Buch.-Ham. ex D.Don) Wedd.	Herb (EN)	7	Nutraceutical
Acer oblongum Wall. ex DC.	Tree (LC)	6	Timber
Alnus nepalensis D. Don	Tree (LC)	5	Fodder, firewood and charcoal
Berberis sp.	Shrub NC	5	Medicinal
Debregessia sp.	Shrub NC	5	Medicinal

Geranium nepalense Sweet	Herb (NE)	5	Medicinal
Symplocos chinensis (Lour.) Druce	Tree (NE)	5	Timber and medicinal
Coffea arabica L.	Shrub (EN)	4	Beverage
Quercus leucotrichophora A.Camus	Tree (CR)	4	Medicinal and fodder
Rubus ellipticus Sm.	Shrub (VU)	4	Medicinal
Rumex hastatulus Baldw.	Herb (NE)	4	Medicinal
Shorea robusta Roth	Tree (LC)	4	Timber and medicinal
Acer pictum Thunb.	Tree (LC)	3	Timber
Berberis vulgaris L.	Shrub (NT)	3	Medicinal
Elatostema sp.	Herb (NC)	3	Medicinal
Myrica esculenta Buch.-Ham. ex D.Don	Tree (EN)	3	Medicinal
Viburnum mullaha Buch.-Ham. ex D.Don	Shrub (NE)	3	Nutraceutical
Ageratina adenophora (Spreng.) King & H.Rob.	Shrub (VU)	2	Ornamental
Artemisia vulgaris L.	Herb (NE)	2	Medicinal
Eurya acuminata DC.	Shrub (LC)	2	Leaves edible and medicinal
Hevea brasiliensis Müll.Arg.	Tree (LC)	2	Rubber
Lantana camara L.	Shrub (LC)	2	Medicinal and handicrafts
Murraya koenigii L.	Shrub (LC)	2	Medicinal
Pyracantha crenulata (D.Don) M.Roem.	Shrub (LC)	2	Beverage and handicrafts
Tectona grandis Linn. F.	Tree (LC)	2	Timber
Ageratum conyzoides L.	Herb (NC)	1	Medicinal
Berberis aristata DC.	Shrub (CR)	1	Medicinal
Colocasia sp.	Herb (NC)	1	Nutraceutical
Hedera nepalensis K.Koch	Climber (EN)	1	Medicinal
Hopea ponga (Dennst.) Mabberly	Tree (VU)	1	Timber and medicinal
Ilex diphyrena Wall.	Tree (LC)	1	Nutraceutical and ornamental
Mimosa pudica L.	Creeper (LC)	1	Extracts heavy metals
Nepeta leucophylla Benth.	Herb (EN)	1	Medicinal
Oenothera rosea L'Hér. ex Aiton	Herb (NE)	1	Medicinal
Oxalis sp.	Herb (NC)	1	Medicinal
Parthenium hysterophorus L.	Herb (LC)	1	Medicinal
Rosa moschata Herrm	Shrub (LC)	1	Medicinal
Salix tetrasperma Roxb.	Tree (VU)	1	Medicinal
Sarcococca hookeriana Baill.	Shrub (LC)	1	Medicinal
Strobilanthes alatus Nees	Herb (NE)	1	Medicinal
Viola canescens Wall. ex Roxb.	Herb (EN)	1	Medicinal
Wulfenia amherstiana Benth. .Y.Hong	Herb (EN)	1	Medicinal
Angiosperm - Monocot			
Roscoea alpina Royle	Herb (VU)	2	Ornamental
Pteridophyte			
Equisetum sp.	Herb (NC)	9	Medicinal
Botrychium sp.	Herb (NC)	8	Medicinal
Angiopteris evecta (G.Forst.) Hoffm.	Shrub (NE)	5	Medicinal
Christela dentata (Forssk) Brownsey &	Shrub (EN)	5	Medicinal

Jemmy			
Macrothelypteris torresiana (Gaudich.) Ching	Shrub (EN)	3	Medicinal
Gymnosperm			
Cedrus deodara (Roxb.) G.Don	Tree (LC)	3	Medicinal

*IUCN status: CR, critically endangered; EN, endangered; LC, least concerned; NC, not concerned; NE, not evaluated; NT, near threatened; VU, vulnerable.

4. Screening for Secondary Metabolites

Although endophytic fungi other than EAH produce a variety of biologically active unique metabolites, they have not been exploited in view of their contribution towards health, nutrition and environmental conservation (Fig. 2) (Suryanarayanan et al., 2009; Blackwell & Vega, 2018; Barros & Seena, 2022; Eichfeld et al., 2024). The bioprospecting potential of aquatic hyphomycetes is fine-tuned towards the self-cleaning of lotic ecosystems; owing to their versatile adaptations, they become appropriate candidates for aquatic health monitoring (Solé et al., 2008). The outcome of mutualism between host plant species and aquatic hyphomycetes is profound with regard to ecosystem services (Seena et al., 2023). Benefits to the host include defence against pathogenic microbes, prevention from predatory invertebrates, disease abatement and plant growth promotion. Besides, enzymes produced by EAHs facilitate providing mineral nutrition and growth promoters to host plant species. Such benefits will be due to the production of value-added bioactive metabolites by endophytic hyphomycetes. The isolates of EAHs will also offer additional benefits such as enzymes, antimicrobial compounds and antioxidant activities.

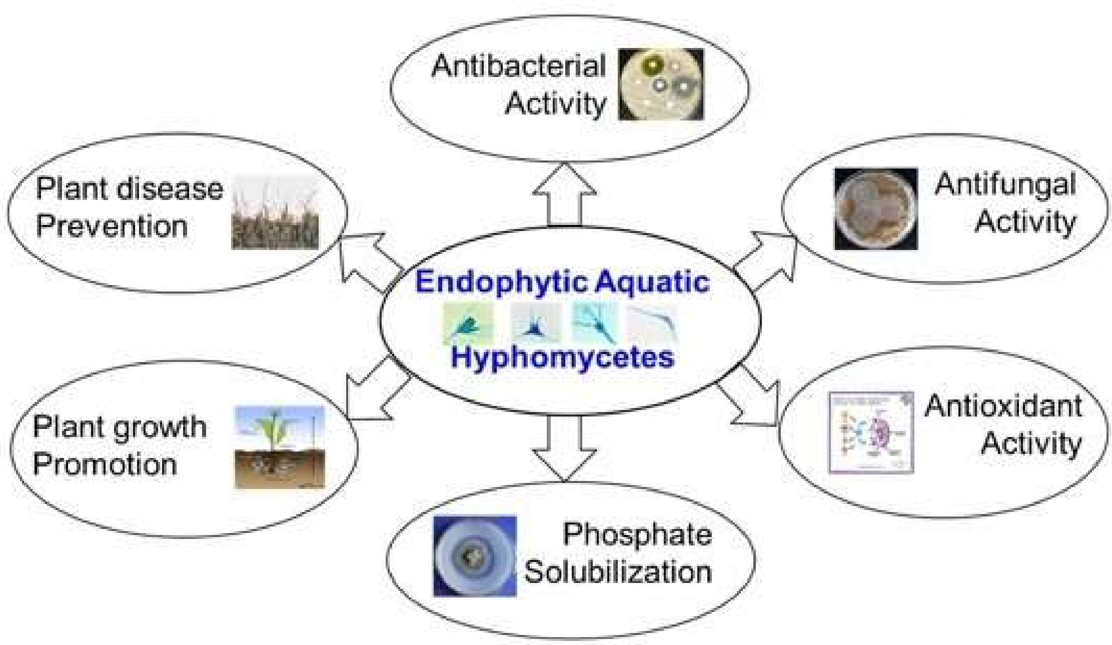

Fig. 2. Bioprospect potential of endophytic aquatic hyphomycetes.

4.1. Plant Growth Promotion

Fungi are known to produce various phytohormones that facilitate plant growth promotion (Gautam & Avasthi, 2019; Fadiji & Babalola, 2020; Kavya et al., 2025). Endophytic *Neonectria lugdunensis* and *Tetrachaetum elegans* (isolated from *Strobilanthus alatus* and *Pilia scripta*, respectively) possess the growth-promotion ability of two angiosperms (*Hibiscus esculentus* and *Solanum melongena*) under greenhouse conditions (Sati & Arya, 2010a). They showed an increase in weight (fresh and dry) and length (shoot and root) without causing disease symptoms. However, a similar test using *Tetracladium nainitalense* did not show any impact on host plants. *Campylospora parvula* and *Tetracladium setigerum* (isolated from *Pilea scripta* and *Berberis vulgaris*, respectively) were assessed for growth promotion of red chili (*Capsicum annum*) in a pot experiment (Sati & Pant, 2020). Both endophytes showed significant increases in total dry biomass, up to 89.9% and 94.2%, respectively. Inoculation of *C. parvula* and *T. setigerum* (isolated from *Pilea scripta* and *Debregessia* sp., respectively) to wheat plants (*Triticum aestivum*) resulted in significant growth promotion (Pant & Sati, 2023).

4.2. Phosphate and Potassium Solubilization

Phosphate-solubilizing microbes are very important in soil and aquatic ecosystems as essential nutrient orthophosphate for plant nourishment (Wang et al., 2009). Many EAHs have agricultural significance, as they are capable of solubilizing phosphate on Pikovskaya agar and broth (Singh & Sati, 2017; Sati & Pant, 2019). So far, seven EAHs have been evaluated for their capability of phosphate solubilization. Root endophytic *Cylindrocarpon aquaticum* and *Anguillospora longissima* showed *in vitro* phosphate solubilization index (PSI) of 1.2 and 1.5, respectively. Similarly, Sati and Pant (2019) demonstrated PSI from 1.3 to 1.5 by an endophytic fungus, *Tetracladium setigerum*, isolated from the live roots of *Berberis vulgaris*. Riparian root endophytic *Campylospora parvula, Helicomyces torquatus, Lemonniera pseudofloscula* and *Tetracladium marchalinum* were tested for phosphate solubilization by Sati et al. (2023). All the isolates showed potency to solubilize phosphate *in vitro* in Pikovskaya's (PVK) agar (https://exodocientifica.com.br/_technical-data/M520.pdf) by showing a hollow zone. In PVK broth, a decrease in pH and increased mycelial weight indicate their capability to grow and solubilize the phosphate. *Helicomyces torquatus* was more potent in phosphate solubilization with high PSI (1.6–3.6), followed by *C. parvula* (1.4–3.4), *T. marchalianum* (1.3–2.9) and *L. pseudofloscula* (1.2–2.3).

Recently, Sati et al. (2025) assessed the release of phosphate and potassium by two EAHs (*Flagellospora penicillioides* and *Varicosporium elodeae*) *in vitro*. The phosphate and potassium solubilization capability of *F. penicillioides* (phosphate, 1.19 mg/l; potassium, 66.48 mg/l) and *V. elodeae* (phosphate, 0.877 mg/l; potassium, 58.31 mg/l) were found to be maximum on 21 days of inoculation into PVK and Aleksandrow's broths. The findings of the above studies collectively highlight the significant potential of EAHs in promoting sustainable agriculture through nutrient solubilization. Further research and field-based evaluations could pave the way for their practical application in enhancing soil fertility and crop productivity, especially in nutrient-deficient or riparian environments.

4.3. Antioxidant Activity

Natural antioxidant compounds obtained from endophytic fungi can be utilized to combat free radicals. Antioxidants are very important, not only for food preservation but also for the defence of living systems against oxidative stress (Masuda et al., 2003). Several studies have shown that endophytic fungi residing inside the medicinal plants can be a potential source of secondary metabolites having antioxidant activity (Gurgul et al., 2020). Ethyl acetate extracts of *Campylospora parvula* and *Tetracladium setigerum* isolated from roots of endangered riparian medicinal shrubs (*Rubus ellipticus* and *Berberis aristata*) from riparian areas (Lamichhane et al., 2023; Goswami et al., 2024) were assessed for DPPH radical-scavenging activity, metal chelation assay (MCA) and ferric reducing antioxidant power (FRAP) (Pant et al., 2024, 2025). The IC50 for the DPPH assay for *C. parvula* and *T. setigerum* was 47.8 and 42.3 µg/ml; for the MCA assay, it was 53.4 and 46.9; and for the FRAP assay, it was 360.5 and 436.7 AAE/g, respectively. These results indicate a positive antioxidant potentiality of root EAHs.

4.4. Antimicrobial Activity

Saprophytic aquatic hyphomycetes are known to produce many antimicrobial metabolites. Field experiments conducted by Chamier et al. (1984) showed inhibitory effects of aquatic hyphomycetes on bacteria. Saprobic *Anguillospora crassa* and *A. longissima* produced a unique antibacterial and antifungal metabolite, anguillosporal (Harrigan et al., 1995). Cyclic depsipeptides produced by another saprobic *Clavariopsis aquatica* inhibited eight plant pathogenic fungi (Soe et al., 2019, Kaida et al., 2001, El-Elimat et al., 2021). Similarly, another antifungal metabolite called quinaphthin has also been obtained from an aero-aquatic fungus, *Helicoon rihonis* (Adriaenssens et al., 1994; Fisher et al., 1988).

Many root-inhabiting EAHs are known to suppress pathogenic bacteria as well as fungi (Table 3). Endophytic *Anguillospora longissima* isolated from riparian roots extending to streams of Nainital possesses antimicrobial potential against pathogenic bacteria such as *Agrobacterium tumefaciens, Bacillus subtilis*, *Erwinia chrysanthemi, Escherichia coli* and *Xanthomonas phaseoli* (Sati & Singh, 2014). Similar results were shown by other EAHs, such as *Campylospora parvula, Cylindrocarpon aquaticum, Tetrachaetum elegans, Tetracladium marchalianum* and *T. setigerum* (Arya & Sati, 2011; Sati & Singh, 2014; Pant & Sati, 2021). However, *Neonectria lugdunensis, Tetracladium breve* and *T. nainitalense* did not show such inhibitory activity (Arya & Sati, 2011). *Neonectria lugdunensis* showed inhibition against plant pathogenic fungi (*Colletotrichum falcatum* and *Rhizoctonia solani*) (Sati & Arya, 2010b), while *T. elegans* showed broad-spectrum inhibition against many phytopathogenic fungi (*C. falcatum, Fusarium oxysporum, Pyricularia oryzae, Sclerotinia sclerotiorum* and *Tilletia indica*) (Sati & Arya, 2010b; Arya & Sati, 2011). Similarly, endophytic *C. parvula* and *T. setigerum* were inhibitory against *Colletotrichum capsici* and *Fusarium oxysporum* (Upadhyay & Sati, 2025). It is interesting to note that *T. elegans* is a versatile endophyte, as it inhibited bacteria (Gram-positive and Gram-negative) as well as plant pathogenic fungi.

Table 3. Antimicrobial activity of root endophytic aquatic hyphomycetes.

Endophyte	Active against		Reference
	Bacteria	Fungi	
Anguillospora longissima	*Agrobacterium tumefaciens, Bacillus subtilis, Erwinia chrysanthemi, Escherichia coli* and *Xanthomonas phaseoli*	ND	Sati & Singh, 2014
Campylospora parvula	*Agrobacterium tumefaciens, Erwinia chrysanthemi, Xanthomonas campestris* and *Xanthomonas phaseoli*	*Colletotrichum capsici* and *Fusarium oxysporum*	Pant & Sati, 2021; Upadhyay & Sati, 2025
Cylindrocarpon aquaticum	*Agrobacterium tumefaciens, Bacillus subtilis, Erwinia chrysanthemi, Escherichia coli* and *Xanthomonas phaseoli*	ND	Singh & Sati, 2014
Neonectria lugdunensis	ND	*Colletotrichum falcatum* and *Rhizoctonia solani*	Sati & Arya, 2010b
Tetrachaetum elegans	*Agrobacterium tumefaciens, Bacillus subtilis, Escherichia coli* and *Xanthomonas phaseoli*	*Colletotrichum falcatum, Fusarium oxysporum, Pyricularia oryzae, Sclerotinia sclerotiorum* and *Tilletia indica*	Sati & Arya, 2010b; Arya & Sati, 2011
Tetracladium marchalianum	*Agrobacterium tumefaciens, Bacillus subtilis, Erwinia chrysanthemi, Escherichia coli* and *Xanthomonas phaseoli*	ND	Arya & Sati, 2011
Tetracladium setigerum	*Agrobacterium tumefaciens, Erwinia chrysanthemi, Xanthomonas campestris* and *Xanthomonas phaseoli*	*Colletotrichum capsici* and *Fusarium oxysporum*	Pant & Sati, 2021; Upadhyay & Sati, 2025

ND = no data available

Similarly, endophytic *C. parvula* and *T. setigerum* were inhibitory against *Colletotrichum capsici* and *Fusarium oxysporum* (Upadhyay & Sati, 2025). It is interesting to note that *T. elegans* is a versatile endophyte, as it inhibited bacteria (Gram-positive and Gram-negative) as well as plant pathogenic fungi.

4.5. Bioactive Compound Assay

Aquatic fungi isolated from different geographic locations are potential sources of bioactive metabolites (El-Elimat et al., 2021; Seena et al., 2023). In many surveys on freshwater hyphomycetes and ascomycetes, nearly half of the species possess antibacterial and antifungal metabolites (Gulis & Stephanovich, 1999; Shearer & Zare-Maivan, 1988). Over the past three decades, 280 compounds with a bioactive potential of 199 compounds have been recorded from freshwater fungi (Gulis & Stephanovich, 1999; El-Elimat et al., 2021). According to Shearer (1992) and Bärlocher (2006), aquatic fungi inhabiting woody litter were more antagonistic than those colonizing leaf litter. It is likely that wood inhabitants acquired the capability to protect themselves from external invaders.

Bioactive compounds like tenellic acids A-D as diphenyl ether derivatives have been obtained from saprobic *Dendrospora tenella* (Oh et al., 1999a). Saprobic *Triclaidum castaneicola* produced seven new bioactive metabolites (tricladolides A-D and tricladic acids A-C) (Han et al., 2015). Saprobic *Massarina aquatica* (the sexual state of *Tumularia aquatica*) grown on oak wood produced bioactive sesquiterpenoids possessing antifungal activities (Fisher & Anson, 1983; Oh et al., 1999b, 2003). It was also similar in other aquatic hyphomycetes (Asthana & Shearer, 1990; Poch et al., 1992). The aero-aquatic fungus *Helicoon rihonis* produced an antifungal metabolite, quinaphthin (Adriaenssens et al., 1994; Fisher et al., 1988).

The GC-MS analysis of an ethyl extract of a root endophyte, *Tetracladium setigerum*, isolated from the endangered medicinal shrub *Berberis vulgaris* in Nainital presents up to 32 compounds (Pant et al., 2025). The major compounds (>10%) include 1,2-benzenedicarboxylic acid, diethyl ester (20.9%); bis(2-ethylhexyl) phthalate (14.8%); and bicyclo[3.2.1]octan-4-on-1-carbonsaeure, 6-, phenol (10.4%). The first two compounds are commonly used as plasticizers to soften the plastics and rubber (Venditti, 2018). Solanesol (4.1%) was another compound prevalent in extracts (also present in Solanaceae members), which has wide application in pharmaceutical industries as an intermediary compound to synthesize coenzyme Q10 and vitamin K2. It has several biological activities, such as antimicrobial, antiviral, anti-inflammatory and anticancer potential; it is not surprising that the ethyl extract of *T. setigerum* has good antioxidant potential. A similar investigation on *Campylospora parvula* isolated from roots of the endangered shrub (*Rubus ellipticus*) also possesses ester (28%), alkene (28%), alcohol (12%), ketone (12%), aldehyde (5%), amine (5%), carboxylic acid (5%) and phenol (5%) (Pant et al., 2024). The major compounds include octanal, 2-(phenylmethylene)- (16.2%) (possesses a jasmine-like odor and is useful in perfumes); 1-(4-Iopropylphenyl)-2-methylpropyl acetate (12.9%) (possesses anti-inflammatory, antihistamine and antitrypanosomal activities); and benzoic acid, 2-hydroxy-, phenylmethyl ester (11.9%) (possesses a balsam-like odor and is useful in skincare products) (Painuli et al., 2015; Pant et al., 2024).

5. Conclusions

Aquatic hyphomycetes and ascomycetes are known to have several terrestrial ancestors. They likely shift their lifestyle from saprophytism to endophytism on colonization of live tissues of plants (mainly roots) in lotic habitats. This hypothesis has been well supported by the occurrence of aquatic hyphomycetes in tree canopies. Some of the EAHs that live within the live tissues of plant species may not normally occur abundantly outside the root tissues. Isolation of aquatic hyphomycetes as an endophyte from roots (submerged as well as terrestrial) and shoot parts of various plants providing direct evidence for the ecological adaptability of these fungi. Being colonizers of the live root tissue, aquatic hyphomycetes have multiple benefits, like seasonal turnover of aquatic roots offering nutritional profits, shelter, protection from predators and preventing their downstream dispersion. Root colonization helps plant species to overcome stress conditions by dealing with pollutants or pollutant degradation (by fungal metabolites), climatic changes and periodic droughts. In addition, EAHs on plant roots offer multiple roles in providing soluble phosphate and potassium, protecting plants against herbivores and evading pathogenic microbes. Besides, bioactive metabolites produced by EAHs due to mutualism will serve as nutrients, bioprotectants and growth promoters of host plant species.

Owing to the adaptation of an endophytic lifestyle, aquatic hyphomycetes are suitable to develop hydroponics of medicinal and other economically valuable plant species. Many medicinal plants occurring in riparian and marshy habitats might have acquired health-promoting potency by colonization of EAHs. For instance, *Campylospora parvula* and *Tetracladium setigerum*, isolated from endangered ethnic medicinal shrubs (*Berberis aristata* and *Rubus ellipticus*), showed considerable antioxidant potential as well as several value-added metabolites of health and industrial concern. As EAHs share a mutualistic association with medicinal plants (52 species), they may be responsible for the value-added metabolites of human health and industrial application.

6. Outlook

Based on various reports on the ecological adaptability of aquatic hyphomycetes in terrestrial environments, it can be inferred that these fungi have strong anamorph and teleomorph connections to survive and disseminate outside their typical aquatic habitats (Sridhar, 2024). The intermingling of endophytic and aquatic hyphomycetous fungi observed on phylogenetic trees in the genus *Tetracladium* by Selosse et al. (2008) provided further support for their dual ecological functions. Anamorph-teleomorph connections (asexual-sexual stages) of aquatic fungi have been established mainly through investigation of woody litter. Asexual and sexual morphs will be induced in endophytic fungi after senescence or death of colonized host tissue. Substrates with minimum moisture or gradual drying might induce teleomorph states. Thus, gradual drying (or other slow-drying techniques) of root segments colonized by EAHs might induce teleomorph states. For example, a subculture of endophytic *Neonectria lugdunensis* isolated from aquatic spruce roots on exposure to fluorescent light (~6 weeks) showed development of ascomycete teleomorph *Nectria lugdunensis* (Sridhar & Bärlocher, 1992a). It is expected that abrupt exposure of substrates colonized by EAHs to *in vitro* conditions may result in induction of the teleomorph state. Most studies on EAHs resulted from surface sterilization and incubation of root segments on antibiotic-amended media. But some studies used the aeration technique of sterile root segments to obtain conidia. In addition to plating, the aeration of sterile segments might be advantageous in a precise assessment of the diversity and richness of EAHs. However, non- sporulating fungi need to be identified by appropriate molecular methods.

This study reveals a huge number of EAHs occupied the submerged roots of a variety of riparian vegetation in the Himalayas and the Western Ghats. It raises many questions: Firstly, what are the benefits to the riparian vegetation by accommodating such diverse EAHs in their roots? Secondly, how the roots of riparian vegetation stimulate the EAHs to produce novel secondary metabolites? Thirdly, what are the roles of secondary metabolites produced by EAHs in their self-defence and defence of host plant species? Given the ecological and agroindustrial significance of EAHs, it is essential to take up more studies on their bioactivity and molecular aspects so as to better understand the basis of their association with live plant tissues.

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Conflict of interest
The authors have no conflict of interest.

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