Phyllosphere Mycobiome: Diversity and Function

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1 Introduction

Fungi are one of most fascinating and enigmatic kingdoms on earth. They occupy enormous habitats in both terrestrial and aquatic environments, driving biogeochemical cycling and influencing the structures of plant and animal communities (Peay et al. 2016; Grossart et al. 2019). Even in extreme ecosystems, such as deep-sea sediments, volcanic vents, and dry valleys of Antarctica, fungi are still the key players of biodiversity and biochemistry (Coleine et al. 2022). Benefiting from the development of high-throughput sequencing and omics technics, we are redrawing the atlas of fungal kingdom on their taxonomic and functional diversity (Nilsson et al. 2019; Fernandes et al. 2021; Tedersoo et al. 2022). For example, current estimates based on high-throughput sequencing suggest that there are at least 6.28 million fungal species on earth (Baldrian et al. 2021), which is larger than the total

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species number previously estimated. In addition, the continuously updated fungal databases of functional traits, such as FUNGuild (Nguyen et al. 2016b), Fun^{Fun} (Zanne et al. 2020), and FungalTraits (Põlme et al. 2021), are designed for rapid functional assignments and predicting how fungal functional diversity varies along certain environmental gradients. Nevertheless, many previous studies focus on the underground fungal diversity and biogeography (Tedersoo et al. 2014, 2021; van der Linde et al. 2018) and mycorrhizal functional ecology (Tedersoo et al. 2020; Tedersoo and Bahram 2019; Genre et al. 2020). The surfaces of phyllosphere fungal diversity and function are barely scratched, despite the highest proportion of unknown fungal species is assumed in plant tissues and lichens (Baldrian et al. 2021).

Phyllosphere is termed as the aerial habitat influenced by plants (Lindow and Leveau 2002), and generally includes the endosphere and episphere (i.e., surface) of plants tissues. In some cases, phyllosphere also includes stems, buds, flowers, and fruits (Whipps et al. 2008); however, most studies on phyllosphere microbiology focus on leaves, the most dominant plant aerial organ. It is estimated that the terrestrial leaf surface area is close to 10^9 km^2 (Lindow and Brandl 2003). Previously, researchers performed lots of work on bacterial diversity and function in phyllosphere (Lindow and Leveau 2002; Lindow and Brandl 2003; Remus-Emsermann and Schlechter 2018). This is because bacterial community is regarded as the most predominant component of phyllosphere microbial community by the traditional view. For example, based on culture method, bacterial cell number was found about 100-fold larger than fungal cell number in the unit weight of the blade (Yang et al. 2013b); however, the difference between phyllosphere bacteria and fungi was not significant at the diversity level (Xiong et al. 2021b; Wei et al. 2022). As far as phyllosphere microbial functions are concerned, both bacteria and fungi play the crucial roles in plant fitness, health, and productivity (Bashir et al. 2022; Xu et al. 2022a, b).

Compared with phyllosphere bacteria, phyllosphere fungi may have the larger differences in morphology, such as filamentous and yeast forms. Moreover, fungi are supposed to more actively enter the internal tissues of plants through leaf stomata or cuticle wounds. Consequently, a large quantity of case studies and reviews on phyllosphere fungi are at the scope of foliar endophytic fungi, including foliar endophytic fungal diversity and their interactions with plant health and fitness (Arnold 2007; Rodriguez et al. 2009; Busby et al. 2016). For example, Busby et al. exemplified foliar endophytic fungi to clarify how the plant microbiomes facilitate reforestation and serve in long-term forest carbon capture and the conservation of biodiversity (Busby et al. 2022). For leaf episphere, Gouka et al. reviewed the updated ecology and functional potential of yeasts; using genomic surveys, they proposed that we only scratched the surface of the largely unexplored functional potential of phyllosphere yeasts (Gouka et al. 2022).

Fungi exhibit a spectrum of life strategies among saprotrophy, mutualism (at most of the time, commensalism), and parasitism in phyllosphere (Schulz and Boyle 2005). At the alive state of leaves, endophytic and epiphytic fungi can mediate host plant growth and health by affecting plant physiology, development, and tolerance to biotic and abiotic stresses (Yang et al. 2013a, 2014; Busby et al. 2016; Costa Pinto et al. 2000; Khan et al. 2015). When leaves fall, some phyllosphere (epiphytic and endophytic) fungi, as the pioneer decomposers of leaf litter, drive the degradation of leaves, and facilitate the nutrient reflux to plants or soil organic matter accumulation (Voriskova and Baldrian 2013; Unterseher et al. 2013; Chen et al. 2022; Osono 2006). Consequently, phyllosphere fungi play a predominant role in global carbon-nitrogen cycle, which has been largely ignored in the past. It is noted that foliar endophytic fungi, epiphytic fungi and both of them can be all termed as phyllosphere fungi. In some studies, epiphytic fungi are also termed as phylloplane fungi (Xiong et al. 2021a, b). The usage of aforementioned terms is determined by the pre-process methods of samples (e.g., leaf surface sterilization or not). Investigations at different compartments (e.g., endosphere vs. episphere) may lead to the distinctive diversity levels, community compositions, and co-occurrence patterns (Yao et al. 2019).

Albert Einstein once said that it is more important to ask a question than to solve it. Around phyllosphere mycobiome, there are many questions that await to be solved. On one hand, high diversity of phyllosphere mycobiome spawns a series of questions about biogeographic patterns, temporal dynamics, and community assembly processes. For example, what are the main environmental factors driving phyllosphere fungal diversity and community composition at different temporal and spatial scales? What are the relative contributions of stochastic and deterministic processes to fungal community assembly in phyllosphere? What are the proportions of phyllosphere fungal community originating from soil, air and water, respectively? On the other hand, the essential functions of phyllosphere mycobiome trigger us to think about the complicated interactions of phyllosphere mycobiome with plant health, changing environments and other biological communities. For example, what are the key functional traits and genes of phyllosphere fungi that can significantly enhance plant fitness and health? Whether do global change factors, such as warming and drought, break the balance of original relationships between phyllosphere fungi and host plants, or impair the beneficial effects of phyllosphere mycobiome? What are the potential roles of phyllosphere mycobiome in future global carbon cycling? By reading the chapter, we are confident that the readers will find most of the answers to the above questions.

2 High Diversity of the Phyllosphere Mycobiome

The phyllosphere supports a massive diversity of yeasts and filamentous fungi. Many of them are epiphytic and then become endophytic by entering the internal tissues. Some phyllosphere fungi could turn to pathogens (Behnke-Borowczyk et al. 2019; Lazarevic and Menkis 2020), while others have antagonistic capacities and influence plant performance (Bashir et al. 2022). Yeasts are the major fungal epiphytes, among which *Cryptococcus*, *Sporobolomyces* and *Rhodotorula* are the commonly occurring genera (Glushakova and Chernov 2004). Yeast-like fungus *Aureobasidium pullulans* is also frequently found in phyllosphere (Inacio et al. 2002). Compared to yeasts, most filamentous fungi tend to be endophytic and commonly belong to *Acremonium*, *Alternaria*, *Aspergillus*, *Cladosporium*, *Mucor* and *Penicillium* (Bashir et al. 2022). Here, we summarize and compare the community composition and diversity of phyllosphere fungi from various plant species in different ecosystems, including natural ecosystems, agroecosystems, and urban ecosystems. We focus on the representative fungal taxa at genus level and summarize the fungal diversities in Table 1.

2.1 Natural Ecosystems

A natural ecosystem is a relatively stable ecosystem maintained by natural regulation within a certain time and space scale. On land, natural ecosystems mainly include forests, grasslands, deserts and wetlands. Among them, forests represent the highly productive ecosystem with hierarchical structure, numerous species and essential ecological functions (Baldrian 2017; Pan et al. 2011). Forests are mainly consisted of and represented by coniferous and broad-leaved trees, and thus the diverse phyllosphere fungi related to these tall trees are summarized at first.

Conifer needles are long lived and thus may harbor diverse fungal taxa (Millberg et al. 2015). *Pinus* is one of the most widely distributed coniferous trees. Previous studies showed that *Alternaria*, *Aspergillus*, *Cladosporium*, *Cryptococcus*, *Lophodermium*, *Penicillium* and *Sydowia* were the most observed fungal genera in *Pinus* (Lazarevic and Menkis 2020; Behnke-Borowczyk et al. 2019; Millberg et al. 2015; Agan et al. 2021; Sun et al. 2021b; Lynikiene et al. 2020; Oono et al. 2015). In these cases, *Cladosporium* and *Lophodermium* were commonly observed in the phyllosphere of *P. sylvestris*, which was one of the most naturally widespread *Pinus* species (Behnke-Borowczyk et al. 2019; Millberg et al. 2015; Agan et al. 2021; Lynikiene et al. 2020). Moreover, higher fungal diversity was observed in needles with disease symptoms compared to healthy ones of *P. sylvestris*, indicating the enrichment of plant pathogens or decomposers (Millberg et al. 2015). In addition, the phyllosphere fungal diversities of *Picea abies* (Nguyen et al. 2016a), *Picea glauca* (Eusemann et al. 2016) and *Sequoia sempervirens* (Harrison et al. 2016) were also investigated. Generally, *Cladosporium* is the most common fungal genus in the phyllosphere of coniferous trees according to our summary. *Alternaria*, *Aspergillus*, *Aureobasidium*, *Cryptococcus*, *Exobasidium*, *Lophodermium*, *Penicillium*, *Phoma*, *Sydowia* and *Taphrina* were frequently observed in phyllosphere as well.

Most of coniferous tree leaves remain alive and green all the year around. Moreover, some broad-leaved tree species are also evergreen or semi-evergreen. It is interesting to explore their phyllosphere fungal composition and to compare the common fungal genera in the phyllosphere of coniferous and these broad-leaved trees. *Euterpe oleracea* is an arborescent multiple stemmed palm with *Xylaria* and *Letendraeopsis* as the most common foliar endophytic fungi (Rodrigues 1994). Another study isolated and identified the phyllosphere fungal communities of five evergreen or semi-evergreen plant species (*Acer monspessulanum*, *Quercus faginea*,

Table 1 Phyllosphere fungal diversity and dominant genera of typical plant species across ecosystems

Ecosystems	Plant Species	Diversity Statistics	Dominant Genera[a]	Detection Methods	Target Regions	References
Natural ecosystems	*Pinus heldreichii*	254 genera (excl. singletons)	*Lophodermium*, *Sydowia*, *Cyclaneusma*, *Phaeosphaeria*	PacBio sequencing	ITS2	Lazarevic and Menkis (2020)
	Pinus massoniana	2127 OTUs (excl. singletons)	*Camptophora*, *Cryptococcus*, *Dictyochaeta*, *Meliniomyces*, *Pestalotiopsis*, *Proliferodiscus*	Illumina HiSeq sequencing	ITS2	Sun et al. (2021b)
	Pinus sylvestris	2429 OTUs (excl. singletons)/602 OTUs (excl. singletons)	*Alternaria*, *Aureobasidium*, *Cladosporium*, *Cryptococcus*, *Coleosporium*, *Curvibasidium*, *Cyclaneusma*, *Phaeococcomyces*, *Lophodermium*, *Sydowia*	PacBio sequencing/454 Pyrosequcing	ITS1/ITS2	Lynikiene et al. (2020) and Millberg et al. (2015)
	Pinus taeda	118 OTUs	*Anthostomella*, *Nemania*, *Nigrospora*, *Podospora*, *Septorioides*	Isolation, cultivation and identification/restriction fragment length polymorphism (RFLP)	ITS–LSU	Oono et al. (2015)
	Picea abies	1737 OTUs (excl. singletons)	*Aureobasidium*, *Celosporium*, *Cladosporium*, *Ceramothyrium*, *Chrysomyxa*, *Epicoccum*, *Phaeocryptopus*, *Sydowia*, *Taphrina*, *Tumularia*	454 pyrosequencing	ITS2	Nguyen et al. (2016a)
	Picea glauca	2009 OTUs	*Articulospora*, *Aureobasidium*, *Catenulostroma*, *Constantinomyces*, *Gyoerffiella*, *Lemonniera*, *Meristemomyces*, *Perusta*, *Pseudocercospora*, *Venturia*, *Xenomycosphaerella*, *Xenophacidiella*, *Zasmidium*	Illumina MiSeq sequencing	ITS1	Eusemann et al. (2016)
	Sequoia sempervirens	1274 OTUs	*Arthroderma*, *Aspergillus*, *Batcheloromyces*, *Caloplaca*, *Catenulostroma*, *Cladophialophora*, *Phaeomoniella*, *Readeriella*, *Taphrina*, *Teratosphaeria*	Illumina MiSeq sequencing	ITS1	Harrison et al. (2016)
	Fagus sylvatica	3713 OTUs/414 OTUs (excl. singletons)	*Aureobasidium*, *Cryptococcus*, *Lalaria*, *Mycosphaerella*, *Penicillium*, *Taphrina*, *Venturia*, *Woollsia*, *Sphaerulina*, *Trametes*	454 pyrosequencing/Illumina MiSeq sequencing	ITS1	Cordier et al. (2012a) and Siddique and Unterseher (2016)

(continued)

Table 1 (continued)

Ecosystems	Plant Species	Diversity Statistics	Dominant Genera[a]	Detection Methods	Target Regions	References
	Betula ermanii	1275 OTUs (excl. singletons)	*Sphaerulina*, *Cylindrium*, *Mrakiella*, *Venturia*, *Allantophomopsis*, *Epicoccum*, *Cladosporium*, *Alternaria*, *Aureobasidium*, *Hymenoscyphus*	454 pyrosequencing	ITS1	Yang et al. (2016b)
	Mussaenda shikokiana	792 OTUs	*Cryptococcus*, *Hannaella*, *Kockovaella*, *Periconia*, *Phomopsis*, *Phoma*, *Rhodotorula*, *Stagonospora*, *Strelitziana*, *Trichomerium*, *Trimmatostroma*	Illumina MiSeq sequencing	ITS2	Qian et al. (2018a)
	Catharanthus roseus	16 species	*Alternaria*, *Chaetomium*, *Colletotrichum*, *Fusarium*, *Lasiodiplodia*, *Phoma*	Isolation, cultivation and identification	ITS full length	Dhayanithy et al. (2019)
Agroecosystems	*Triticum aestivum*	278 OTUs (excl. singletons)/284 OTUs	*Alternaria*, *Arthrinium*, *Ascochyta*, *Bipolaris*, *Blumeria*, *Cladosporium*, *Cryptococcus*, *Dioszegia*, *Epicoccum*, *Fusarium*, *Penicillium*, *Rhodotorula*, *Sporobolomyces*, *Udeniomyces*, *Zymoseptoria*	454 pyrosequencing	ITS1/ITS2	Sapkota et al. (2015) and Karlsson et al. (2017)
	Oryza sativa	45 OTUs	*Aspergillus*, *Bipolaris*, *Bullera*, *Cryptococcus*, *Curvularia*, *Eupenicillium*, *Fusarium*, *Hannaella*, *Hypocrea*, *Isaria*, *Leptosphaerulina*, *Metschnikowia*, *Meyerozyma*, *Penicillium*, *Pseudozyma*, *Sporidiobolus*, *Sporobolomyces*, *Trichoderma*, *Wickerhamomyces*	Restriction fragment length polymorphism (RFLP)	D1-D2 (LSU)	Nasanit et al. (2015)
	Vitis vinifera	897 OTUs for ITS2 and 615 OTUs for D2	*Alternaria*, *Aureobasidium*, *Cladosporium*, *Cryptococcus*, *Davidiella*, *Didymella*, *Endoconidioma*, *Lewia*, *Pleospora*, *Ustilago*	Illumina MiSeq sequencing	ITS2 and D2 (LSU)	Castaneda et al. (2018)
	Brassica oleracea	2038 ASVs	*Alternaria*, *Cystofilobasidium*, *Filobasidium*, *Papiliotrema*, *Purpureocillium*, *Sporobolomyces*	Illumina MiSeq sequencing	ITS2	Kim and Park (2021)
	Lactuca spp.	5 genera	*Cladosporium*, *Cryptococcus*, *Lewia*, *Sporobolomyces*, *Tilletiopsis*	Terminal restriction fragment length polymorphism (TRFLP)	ITS full length	Hunter et al. (2015)
	Cucurbita moschata	399 OTUs	*Alternaria*, *Aureobasidium*, *Davidiella*, *Leptosphaerulina*, *Peniophora*, *Phoma*, *Podosphaera*, *Pseudozyma*, *Rhodotorula*, *Strelitziana*	Illumina MiSeq sequencing	ITS1	Zhang et al. (2018d)

	Solanum lycopersicum	413 OTUs	*Bullera*, *Cladosporium*, *Curvularia*, *Dioszegia*, *Hannaella*, *Moesziomyces*, *Nigrospora*, *Papiliotrema*, *Pseudozyma*, *Saitozyma*,	Illumina MiSeq sequencing	ITS1	Toju et al. (2019)
	Atractylodes lancea	15 genera	*Absidia*, *Acremonium*, *Alternaria*, *Aspergillus*, *botrytis*, *Cephalosporium*, *Curvularia*, *Fusarium*, *Gilmaniella*, *Gliocladium*, *Mucor*, *Penicillium*, *Verticillum*	Isolation, cultivation and identification	SSU	Yang et al. (2013b)
Urban ecosystems	*Quercus macrocarpa*	1232 OTUs	*Alternaria*, *Aureobasidium*, *Cladosporium*, *Davidiella*, *Didymella*, *Epicoccum*, *Erysiphe*, *Mycosphaerella*, *Neofabraea*, *Sporobolomyces*	454 pyrosequencing	ITS1	Jumpponen and Jones (2010)
	Betula pendula	246 OTUs	*Pseudomicrostroma*, *Taphrina*, *Microstroma*, *Aureobasidium*, *Kondoa*, *Ampelomyces*, *Microstromatales*, *Exobasidium*, *Cephalosporium*, *Knufia*	Illumina MiSeq sequencing	ITS full length	Ivashchenko et al. (2022)
	Cinnamomum camphora	5132 OTUs	*Mycosphaerella*, *Zasmidium*, *Trimmatostroma*, *Epicoccum*, *Paraconiothyrium*, *Phoma*, *Cryptococcus*, *Villosiclava*, *Pholiota*, *Preussia*	Illumina MiSeq sequencing	ITS2	Tan et al. (2022)
	Lycoris radiata	27 species	*Colletotrichum*, *Fusarium*, *Gibberella*, *Glomerella*, *Phyllosticta*, *Stagonosporopsis*	Isolation, cultivation and identification	ITS full length	Zhou et al. (2020)

[a] For most studies, approximately ten most abundant fungal genera were listed. For some plant species, several studies were performed, so the most abundant fungal genera overlapped in the studies were listed. *OTUs* operational taxonomic units, *ASVs* amplicon sequence variants

Cistus albidus, *Pistacia lentiscus* and *Osyris quadripartita*) in a mediterranean-type ecosystem; they found that *Alternaria*, *Aureobasidium*, *Cladosporium* and *Penicillium* could be recovered from the leaf samples (Inacio et al. 2002). These four fungal genera were also frequently observed in the phyllosphere of coniferous species, indicating the long-life leaves might harbor the similar fungal taxa.

Although the leaves of some broad-leaved trees are evergreen or semi-evergreen, the leaves of most broad-leaved trees sprout in spring and fall in autumn. Thus, it is interesting to investigate whether these broad-leaved trees harbor different phyllosphere fungal communities compared to evergreen coniferous and broad-leaved trees. Some studies investigated phyllosphere fungal communities of *Fagus sylvatica* and showed that *Mycosphaerella* and *Pseudocercospora* were commonly observed in the phyllosphere (Cordier et al. 2012a, b; Siddique and Unterseher 2016; Unterseher et al. 2016). Other studies surveyed the phyllosphere fungal communities of more deciduous broad-leaved tree species, such as *Betula ermanii* (Yang et al. 2016b), *Mussaenda shikokiana* (Qian et al. 2018a), and *Swida controversa* (Osono and Mori 2005). Summarily, *Cladosporium* and *Phoma* were the most common fungal genera in the phyllosphere of deciduous broad-leaved trees according to our review. Moreover, *Alternaria*, *Aureobasidium*, *Cryptococcus*, *Mycosphaerella*, *Penicillium* and *Pseudocercospora* were frequently observed. Although the life cycles of evergreen and deciduous trees are quite different, they harbor the similar fungal taxa in their phyllosphere.

Besides trees, phyllosphere fungal diversities of shrubs and herbs were explored as well. For *Catharanthus roseus* in the coastal areas, *Alternaria*, *Cophinforma* and *Colletotrichum* were the only three fungal genera isolated from the sterilized leaves (Dhayanithy et al. 2019). The phyllosphere yeast populations of *Oxalis acetosella* were dominated by *Cystofilobasidium*, *Cryptococcus*, *Rhodotorula*, and *Sporobolomyces* (Glushakova and Chernov 2004).

Summarily, *Cladosporium* was the most common fungal genus in the phyllosphere of both coniferous and broad-leaved trees, which was not commonly observed in shrubs and herbs. This difference may be due to different sunshine conditions - the leaves of trees were commonly sampled from the canopy, while the leaves of shrubs and herbs most occupy the shade. In addition, *Alternaria* was frequently observed in the phyllosphere of trees and shrubs, while *Cryptococcus* was frequently observed in the phyllosphere of trees and herbs. It indicates some fungal taxa may horizontally transfer among different plant species. It is worth noting that different plant lineages harbor specific phyllosphere fungal taxa. Various morphological and metabolic characteristics of host plants' leaves may be one of important reasons behind the aforementioned patterns.

2.2 Agroecosystems

Agriculture practices can significantly influence phyllosphere fungal diversity and function. For example, conventional and organic agricultural management differentially affected the fungal community composition on the leaves of grapevines

(Castaneda et al. 2018). Organic farming could increase fungal richness in the phyllosphere of *Triticum aestivum* (Karlsson et al. 2017). Fungicide negatively affected the fungal richness and evenness as well as significantly changed the fungal composition in the phyllosphere of *T. aestivum* (Karlsson et al. 2014). Moreover, agroecosystems are supposed to harbor different fungal taxa compared to natural ecosystems. Recent studies showed that phyllosphere mycobiome is very important to crop health and growth (Sapkota et al. 2015). Thus, understanding the diversity of phyllosphere mycobiome in agroecosystems is crucial to develop new strategies for improving crop growth and adaptation.

In particular, phyllosphere fungal diversity in cereals has been largely explored, considering their importance to global food production. The phyllosphere mycobiome of *Avena sativa*, *Hordeum vulgare*, *Secale cereale*, *T. aestivum* and *Triticum* × *Secale* were explored, and 20 fungal genera were observed in phyllosphere (Sapkota et al. 2015). Each genus was observed at least in two plant species, indicating the possibility of core fungal community in the phyllosphere of diverse cereals. Among them, *Cladosporium* and *Cryptococcus* were the most common genera observed in the phyllosphere of *T. aestivum* (Karlsson et al. 2014, 2017; Larran et al. 2007; Sapkota et al. 2015). Other studies focused on the fungal diversity in the phyllosphere of *Oryza sativa*, the major cereal in Asia. For example, Venkatachalam et al. isolated and identified two morphologically different fungal strains, belonging to *Bipolaris* and *Curvularia* (Venkatachalam et al. 2016). Mwajita et al. showed that *Penicillium*, *Aspergillus* and *Trichoderma* were the common genera in the phyllosphere of *O. sativa* (Mwajita et al. 2013). Nasanit et al. focused on the epiphytic yeast diversity in *O. sativa*; they found that *Bullera*, *Pseudozyma* and *Cryptococcus* were the most common genera (Nasanit et al. 2015). The fungal genera observed in the aforementioned three studies were quite different; the reason may be the significant biogeographic isolation of phyllosphere fungal communities between nations that were revealed by culturable methods.

In addition, some studies explored the phyllosphere fungal communities across different grape species. For example, Singh et al. surveyed the fungal community composition in the phyllosphere of *Vitis pentagona*, *Vitis riparia*, *Vitis vinifera*, *Muscadinia rotundifolia* and *Parthenocissus quinquefolia* by Illumina MiSeq sequencing; they found that *Alternaria*, *Aureobasidium*, *Cladosporium* and *Lachnum* were the most abundant genera observed (Singh et al. 2019). *Alternaria*, *Davidiella* and *Didymella* were most abundant in the phyllosphere of Carménère grapevines (*V. vinifera*) (Castaneda et al. 2018). Moreover, the study showed that the diversity of phyllosphere fungi were highest in the wild, lowest in the conventional, and intermediate in the organic vineyard, respectively (Kernaghan et al. 2017). According to these studies, *Alternaria* was the most common fungal genus in the grape phyllosphere.

Besides cereals and fruits, vegetables are also important crops in agroecosystems. Kim and Park surveyed the fungal diversity in phyllosphere of preharvest and postharvest broccoli (*Brassica oleracea* var. italic); they found that *Cystofilobasidium* and *Purpureocillium* were the representative genera in phyllosphere of preharvest broccoli, while *Filobasidium* and *Sporobolomyces* were the most abundant genera in the phyllosphere of postharvest broccoli (Kim and Park 2021). Another study surveyed 26 lettuce (*Lactuca* spp.) accessions and showed that *Sporobolomyces* and *Cladosporium* were the two dominant genera with significant different abundances among accessions (Hunter et al. 2015). In addition, the researchers analyzed the fungal diversity in the phyllosphere of pumpkin (*Cucurbita moschata*) showing powdery mildew symptoms; they found besides *Podosphaera* (the plant pathogen), *Alternaria*, *Aureobasidium* and *Davidiella* were the most observed genera (Zhang et al. 2018d). Toju et al. surveyed the leaf endophytic fungal community of tomato (*Solanum lycopersicum*) and found that *Cladosporium*, *Dioszegia* and *Moesziomyces* were the most frequently observed genera (Toju et al. 2019).

Moreover, many studies were performed on the phyllosphere mycobiome of medicinal plants, considering their contributions to human health. *Atractylodes lancea* is a traditional Chinese medicinal plant with abundant bioactive terpenoids. *Acremonium*, *Fusarium* and *Penicillium* were the most abundant fungal genera in the phyllosphere of *A. lancea*; besides, some special fungal genera, such as *Absidia*, *Gilmaniella* and *Verticillum*, were also observed in phyllosphere (Yang et al. 2013b). *Ginkgo biloba* is one of the most distinctive trees with an important position in plant evolution, and its dry leaves have multiple medicinal values (Lin et al. 2022). In the leaf interiors of *G. biloba*, *Alternaria*, *Colletotrichum*, *Fusarium* and *Phomopsis* were the most dominant fungal genera (Xiao et al. 2013). For the traditional Brazilian medicinal plant, *Solanum cernuum*, the dominant phyllosphere fungal genera differed between seasons: *Colletotrichum*, *Coprinellus* and *Phoma* were most frequently observed in summer; while *Arthrobotrys*, *Colletotrichum*, *Glomerella*, *Diatrypella*, and *Mucor* were most frequently observed in winter (Vieira et al. 2012). It is noteworthy that medicinal plants tend to harbor special fungal genera in their phyllosphere, which may facilitate the synthesis and accumulation of special bioactive secondary metabolites (Yang and Dai 2013).

Summarily, *Alternaria*, *Cladosporium* and *Cryptococcus* were frequently observed in both natural and agricultural ecosystems. However, *Exobasiduim, Lophodermium* and *Sydowia* were only enriched in natural ecosystems. The phyllosphere of agricultural crops, especially vegetables, harbored some unique fungal taxa, such as *Dioszegia* and *Sporobolomyces*, indicating the interactive effects of agriculture practices and plant species identity. In addition, for most cases, the observed numbers of genera and OTUs in agroecosystems were lower than those in natural ecosystems (Table 1).

2.3 Urban Ecosystems

With an increase in human population, urban area is expanding rapidly. Compared to other ecosystems, urban microbial communities are largely affected by anthropogenic activities, land management, urban heat island effect and air pollution (Perreault and Laforest-Lapointe 2022). For example, *Q. macrocarpa* is a native tree species in Manhattan and often used as an ornamental tree. Fungal richness and other diversity indices in the phyllosphere of *Q. macrocarpa* grown in urban areas were lower than those trees grown in nonurban areas (Jumpponen and Jones 2009), and half of the phyllosphere fungal genera showed distinct and significant seasonal dynamics (Jumpponen and Jones 2010).

Many plant species are cultivated in urban area to purify the air and improve the environment. Some of them could release fragrant and antimicrobial volatiles. *Eucalyptus citriodora* is a widely cultivated tree in Indian cities; *Cladosporium* was dominant in its phylloplane, while *Botrytis* was dominant in its leaf interiors (Kharwar et al. 2010). For *Populus balsamifera* grown in a garden, *Leptosphaerulina* was dominant in the phyllosphere (Balint et al. 2013). Moreover, some flowers were also common ornamental plants cultivated in urban ecosystems, and their phyllosphere mycobiome were explored as well, such as *Camellia japonica* (Osono 2008) and *Lycoris radiata* (Zhou et al. 2020). Among their phyllosphere fungi, *Colletotrichum* was the genus observed in both of the two flowers.

Some studies revealed that the plants grown in polluted areas could harbor more pollutant-degrading microbes. For example, aromatic hydrocarbon (AH) degrading fungi were enriched in the phyllosphere of *Ixora chinensis*, *Ervatamia divaricata*, *Hibiscus rosa-sinensis* and *Amaranthus cruentus*, which were grown on the roadsides of polluted areas (Undugoda et al. 2016). Fungal communities in the phyllosphere of *Cinnamomum camphora* were surveyed in urban, suburban and rural area. The results showed that the fungal diversity was highest in the suburban areas and was strongly affected by the polycyclic aromatic hydrocarbon (PAH) concentrations (Tan et al. 2022); among the ten most abundant fungal genera, *Mycosphaerella*, *Zasmidium*, *Trimmatostoma*, *Epicoccum* and *Paraconiothyrium* were common in rural and suburban area, and *Phoma* was common in urban area.

Generally, all these studies showed that urban ecosystem could harbor special fungal taxa, and their enrichment was related to the environmental pollution induced by urbanization. In summary, common fungal genera could be observed in the phyllosphere of all the three ecosystems, but their abundances varied significantly. Thus, different ecosystems could enrich different fungal genera, indicating that different dominant environmental factors constrain and shape the fungal diversity and community composition accordingly.

3 Fungal Biogeographic Patterns in Phyllosphere

Fungal biogeography is the study of distribution of fungal diversity over space and time; the subject aims to reveal the general patterns and the underlying drivers (Martiny et al. 2006). It is necessary to know which fungi are where, and why they are found there and not somewhere else. These knowledges are the premise and foundation for the protection of fungal diversity and the utilization of fungal resources. The phyllosphere habitat provides an excellent platform to test the biogeographic hypotheses and formulate the associated theories (Andrews and Harris 2000). As early as 1987, researchers had used the theory of island biogeography to explain the fungal distributions on apple leaves (Andrews et al. 1987); they proposed that leaves, like virtual islands, have the natural advantages for biogeographic studies, as they are accessible, replicated and easily manipulated. Other researchers corroborated the geographic isolation and size effect of islands by surveying foliar endophytic fungi of birch trees in the archipelago of Finland (Helander et al. 2007). Based on the framework of current microbial biogeography (Chu et al. 2020), phyllosphere fungal biogeographic distribution is constrained by multiple driving factors, such as plant host identity, leaf functional traits, climatic conditions, geographic distance and other microbial guilds. Of note, microbial biogeographic distribution is spatial scale dependent. At the different spatial scales, the main driving factors may be distinctive (Vaz et al. 2014b). In addition, different detection methods, e.g., culture-based and culture-free methods (e.g., 454 Pyrosequencing, MiSeq Sequencing, and PacBio Sequencing), may lead to the different observed patterns (Bowman and Arnold 2021).

3.1 Fine and Local Scales

At the local-scale tropical forests, there are strong evidence of host tree preference and spatial heterogeneity for phyllosphere fungal communities, regardless of using culture-based or culture-free methods (Arnold et al. 2000; Kembel and Mueller 2014). However, the aforementioned host- and habitat-specificity were not observed for phyllosphere fungal communities of grasses in tropical forests (Higgins et al. 2011, 2014). In other ecosystems, such as mountains, mangroves, and arctic zones, phyllosphere fungi also exhibited host-specificity, namely, different plant species have unique fungal partners (Arfi et al. 2012; Zhang and Yao 2015; Yao et al. 2019; Apigo and Oono 2022). The significant plant identity effect is partly attributed to leaf economic traits (Kembel and Mueller 2014; Tellez et al. 2022), and its extent varies by different plant abundances and lineages (Apigo and Oono 2022).

In order to deeply and extensively explore the other driving factors besides plant species identity, many studies focused on the phyllosphere fungal biogeography of single plant species. Across a Hawaiian landscape, foliar endophytic fungal communities of *Metrosideros polymorpha* were strongly driven by temperature and rainfall (Zimmerman and Vitousek 2012). In a subalpine timberline ecotone on Changbai Mountain, the alpha diversity of foliar endophytic fungi of *B. ermanii* significantly increased with increasing elevation, and fungal community composition differed between different elevation sites; leaf carbon was the main driver of alpha diversity and community composition (Yang et al. 2016b). For *Pinus muricata* and *Vaccinium ovatum* growing across a broad soil nutrient gradient, foliar endophytic fungal richness was constrained by leaf nitrogen-to-phosphorus ratio and sodium content (Oono et al. 2020). The effect of plant within-species variation (i.e., tree genotype) was not observed in the needle mycobiome-*Picea glauca* system at an arctic treeline ecotone (Eusemann et al. 2016). In addition, biotic interactions, such as neighboring plant diversity, fungal-fungal associations, mycorrhizal colonization, and inoculation of endophytes, were found to be significant drivers of phyllosphere fungal communities (Pan and May 2009; Eschen et al. 2010; Nguyen et al. 2017; Yang et al. 2013b). Even at the fine scale, there are still the significant biogeographic patterns; e.g., fungal endophytes *Xylaria* associated with Myrtaceae exhibited leaf fragment preference to petiole and tip (Vaz et al. 2014a).

3.2 Regional Scales

Regional-scale biogeographic studies are commonly carried out over a span of more than 100 km, and thus have the larger geographic distance and broader environmental gradient compared with local-scale studies. Both host species identity and geographic locality were the primary drivers of fungal communities in phyllosphere at the regional scale (Hoffman and Arnold 2008). However, their relative effects were different, and most of the studies showed that host species identity played a more important role than dispersal limitation in shaping phyllosphere fungal biogeographic patterns (Lau et al. 2013; Sapkota et al. 2015; Vincent et al. 2016). Of note, with increasing urbanization, the community dissimilarity of foliar endophytic fungi among different tree species in urban zones significantly decreased compared with that in rural forests (Matsumura and Fukuda 2013). It indicates that human activity exerts a profound effect on fungal biogeographic patterns in phyllosphere, e.g., decrease beta diversity among different tree species (i.e., host specificity).

Strictly, site effect may result from two independent factors – one is geographic distance, and the other is environmental distance (e.g., climatic difference). By focusing on the phyllosphere fungal community of single plant species, researchers found that environmental filtering plays a greater role in structuring foliar fungal communities than dispersal limitation caused by geographic distance (Garcia et al. 2013; Barge et al. 2019; Bowman and Arnold 2021). In addition, fungal community composition in the phyllosphere of *Mussaenda pubescens* was significantly structured by host genotype, and less by geographic distance (Qian et al. 2018b). Manipulative experiments are the important supplement to field surveys in biogeographic studies, as it can uncouple multiple effects directly and test for causality. Commonly, the manipulative experiments are carried out at the local scale. Sometimes, for example, provenance-progeny trails can be carried out at regional scales. Based the provenance-progeny trails of sugar maple as well as switchgrass, researchers found that site effect was the main driver of the variation in phyllosphere fungal communities, whereas seed provenance or host ecotype has no significant effect (Whitaker et al. 2018; De Bellis et al. 2022). Recently, a 7-year old provenance-progeny trail showed that both site and host genetic variation shape the phyllosphere fungal communities of Scots pine (Schonrogge et al. 2022). Therefore, more experiments involving single plant species should be extensively performed to summarize the general pattern of phyllosphere fungal biogeography. In addition, aerial spore communities, rare fungal species and plant genetic distance among different host species were also reported as the drivers for phyllosphere fungal distributions (Oono et al. 2017; Redondo et al. 2022; Sarver et al. 2022; Teng et al. 2022).

3.3 Continental and Global Scales

Phyllosphere fungi cooccur with all major lineages of land plants and are widely distributed across every corner of the earth. However, few studies were really performed to reveal the biogeographic pattern of phyllosphere fungi at the global scale. Previously, Arnold and Lutzoni isolated, cultured and (Sanger) sequenced 1403 endophytic fungal strains involving 28 host plant species from the lowland tropical forest of central Panama to the Canadian arctic; they found the incidence, diversity, and host breadth of foliar endophytic fungi significantly decreased with the increasing latitude (Arnold and Lutzoni 2007). The diversity pattern of foliar endophytic fungi along latitude seems to be similar to the pattern of plants and animals. Later on, the research team examined 4154 endophytic and endolichenic fungal strains involving ca. 20 plant and lichen species across North America; climatic variables, geographic distance, and plant host identity together affected the fungal distributions at the continental scale, among which climatic variables more strongly affected the fungal distributions than geographic distance alone (U'ren et al. 2012). It indicates again that environmental filtering plays a greater role in structuring foliar fungal communities than dispersal limitation at the broad spatial scale. When we study the global-scale phyllophere fungal biogeography, one issue always exists. Considering the turnover of host plants with geography and climate, the relative effects of host species identity, geographic distance, and abiotic environmental variables on foliar fungal biogeography are not clear, especially at the global scale. Also from the progress of Arnold's team, they revealed that host availability, rather than turnover with geographic or environmental distance, drove distributions of foliar endophytic fungi in boreal forest ecosystems at the trans-continent scale (across North America and Eurasia) (U'Ren et al. 2019).

Although there has been a few continental- and trans-continental-scale studies on phyllosphere fungal biogeography, these studies are mainly carried out in the American continent and for foliar endophytic fungi. Therefore, more global-scale integrated studies are needed to form the fundamental knowledge on the biogeography of phyllosphere fungi. Meta-analysis is one of practical approaches to acquire the global-scale understanding. Starting from the raw sequencing data of 10 published studies, researchers corroborated the latitudinal diversity decline and distance-decay relationships, which indicates the similarity in biogeographic patterns between fungi and other organisms (Meiser et al. 2014). Recently, Bladrian et al. complied and analyzed fungal high-throughput sequencing data from 156 publications; they extrapolated fungal diversity to 6.28 million and highlighted the hotspot of unknow diversity in lichen and plant tissues (Baldrian et al. 2021). Of note, phyllophere samples only accounted for one part in the aforementioned meta-analysis studies. Fortunately, some citizen science projects (incl. Dataset construction; Franic et al. 2022) that specify phyllosphere fungi are in progress (https://sisu.ut.ee/funleaf/about). In the near future, it will definitely bring us more insights into the biogeographic patterns of phyllosphere fungi.

4 Fungal Temporal Dynamics in Phyllosphere

4.1 Temporal Factors Shaping Phyllosphere Mycobiome Assembly

A better understanding of fungal temporal dynamics in the phyllosphere is essential for uncovering fundamental ecological processes underpinning the assembly of the plant mycobiome. Changes in phyllosphere mycobiome assembly along plant growth are closely associated with many temporal factors, including plant age, host developmental stage, and seasonal climatic factors (Gao et al. 2020; Xiong et al. 2021b; Vacher et al. 2016; Remus-Emsermann and Schlechter 2018). Growing evidences on maize, sorghum, barley, *Arabidopsis*, and trees have revealed that plant developmental stage and growing season are important factors influencing structure and function of leaf-associated fungal communities and regulating the balance between deterministic and stochastic processes in phyllosphere mycobiome assembly (Table 2). For example, Gao and colleagues showed that leaf-associated fungal communities altered strongly across plant developmental stages (1st to 17th week), and stochastic forces (drift or stochastic dispersal) played a role in shaping leaf fungal community assembly at the early stage of plant development (Gao et al. 2020). Similarly, a recent work on maize grown under different fertilization practices at two contrast sites have suggested that plant developmental stage had the strongest effects on the phylloplane mycobiome, compared with other plant and soil compartments (Xiong et al. 2021b). Null model analysis further showed that the relative importance of deterministic and stochastic processes in the assembly of leaf-associated mycobiome were greatly influenced by plant developmental stage, with a higher relative contribution of stochastic processes mainly belonging to homogenizing dispersal and undominated (e.g., diversification and/or drift) observing for both epiphytic and endophytic phyllosphere fungal communities at the seedling stage (Xiong et al. 2021b). By contrast, deterministic processes dominated the assembly of endophytic phyllosphere fungal community at both tasseling and mature stages (Xiong et al. 2021b). Given that the phyllosphere is an important interface between the plant host and the environment, fungal community assembly in the phyllosphere is not only shaped by temporal factors but also influenced by other biotic and abiotic factors (Vacher et al. 2016; Remus-Emsermann and Schlechter 2018; Vorholt 2012). By using artificial plants made of plastic material as “background controls” in the field during maize developmental stages, Xiong and colleagues found that season-dependent environmental factors like air, dust and rainwater also played a role in phyllosphere fungal community assembly (Xiong et al. 2021b). Source tracking analysis further indicated that atmosphere environment contributed an increasing proportion as the source of the maize phylloplane fungal community across three plant developmental stages (from 86.6% to 92.4%) (Xiong et al. 2021b).

Table 2 Recent studies on fungal temporal dynamics in phyllosphere

Plant species	Leaf Compartment	Research content	Temporal factor	References
Arabidopsis thaliana	Episphere and endosphere	Fungal diversity, composition, and network properties	5 growing seasons	Almario et al. (2022)
45 subtropical tree species	Episphere	Fungal diversity and composition	Dry and wet seasons	Li et al. (2022a)
Hordeum vulgare	Episphere and endosphere	Fungal diversity, composition, and network properties	1st to 18th week	Sapkota et al. (2022)
Schefflera octophylla	Episphere	Fungal composition and network properties	2nd to 6th week	Song et al. (2022b)
Camellia sinensis	Episphere and endosphere	Fungal diversity and composition	4 developmental stages	Xu et al. (2022b)
Gingko biloba, *Pinus bungeana*, and *Sabina chinensis*	Episphere	Fungal diversity, composition, and network properties	2 growing seasons	Bao et al. (2022)
Zea mays	Episphere and endosphere	Fungal diversity, composition, assembly processes, and network properties	3 developmental stages	Xiong et al. (2021b)
Quercus robur	Episphere and endosphere	Fungal diversity and composition	3 growing seasons	Faticov et al. (2021)
Panicum virgatum	Episphere and endosphere	Fungal diversity, composition, and network properties	7 growing seasons	Bowsher et al. (2021)
Sorghum bicolor	Episphere and endosphere	Fungal diversity, composition, and assembly processes	1st to 17th week	Gao et al. (2020)
Olea europaea	Endosphere	Fungal diversity and composition	3 growing seasons	Materatski et al. (2019)
Olea europaea	Episphere and endosphere	Fungal diversity and composition	2 growing seasons	Gomes et al. (2018)
Fraxinus excelsior	Episphere and endosphere	Fungal diversity and composition	9 growing time points	Cross et al. (2017)

In addition, increasing studies indicated that effects of the temporal factors and other drivers on fungal community assembly in the phyllosphere largely depend on changes in plant growth and developmental stages, variation in host identity, and spatial scale (e.g., geographic distance). For example, previous work had showed that plant developmental stage (18–39%) dominated over site (3–26%) in shaping fungal communities in both epiphytic and endophytic phyllosphere of maize (Xiong et al. 2021b). At the plant level, it was reported that plant developmental stage (10.7%) played a more important role than drought treatment (2.6%) and plant cultivar (0.2%) in structuring fungal communities across soil, root, and leaf of sorghum (Gao et al. 2020). Moreover, a recent work on oak had suggested that plant growing season (10%) explained more variation in leaf fungal communities than warming treatment (2%) and host genotype (1%) (Faticov et al. 2021). Study on spring barley reported that plant age (44%) played a more important role than host cultivar (1%) in shaping leaf fungal community (Sapkota et al. 2022). Gomes et al. examined fungal communities in endophytic and epiphytic phyllosphere and demonstrated that season was the major driver of fungal community composition, especially for epiphytic fungal community (Gomes et al. 2018). Wind speed and temperature were important environmental factors influencing epiphytic phyllosphere fungal community, while plant organ, rainfall, and temperature were the major drivers shaping endophytic phyllosphere fungal community (Gomes et al. 2018). All these results suggest that the temporal factors are vital drivers shaping the assembly of leaf-associated fungal communities under different host selection and environmental stresses.

4.2 Temporal Patterns of Fungal Diversity, Composition, and Networks

Increasing works have suggested that the temporal factors also significantly affected diversity, composition, and co-occurrence patterns of the phyllosphere mycobiome (Bowsher et al. 2021; Li et al. 2022a; Faticov et al. 2021; Almario et al. 2022). For instance, the study on the pedunculate oak (*Quercus robur*) across one growing season had showed that phyllosphere fungal species richness increased but evenness decreased during the growing season (Faticov et al. 2021). The relative abundance of Yeasts increased over the time, while putative fungal pathogens decreased (Faticov et al. 2021). A recent work analyzed leaf fungal community of *Arabidopsis thaliana* throughout the plant's natural growing season (extending from November to March) over three consecutive years, and demonstrated that the time of sampling had an important effect on fungal communities (32–40% explained variance) (Almario et al. 2022). The relative abundance of Microbotryales increased throughout the plant's growing season, while that of Sporidiobolales decreased (Almario et al. 2022). Sapkota and colleagues characterized the phyllosphere mycobiome of three spring barley cultivars at weekly intervals during a growth season from seedling emergence to senescence and seed maturity, and showed that the specific members like *Dioszegia* and *Sporobolomyces* of the mycobiome responded differently to plant developmental stage (Sapkota et al. 2022). Moreover, it was found that fungal seasonal dynamics in the phyllosphere differed between phylogenetic groups, with *Aureobasidium* and *Neoascochyta* sp. peaking in early summer and then decreasing across the growing season (Bowsher et al. 2021). By contrast, higher relative abundance of *Epicoccum* sp. were observed at the early stage and then steadily increased throughout much of the growing season (Bowsher et al. 2021). Moreover, previous studies explored fungal diversity and seasonal succession in ash leaves infected by the invasive ascomycete *Hymenoscyphus fraxineus* by high-throughput sequencing and quantitative PCR profiling of *H. fraxineus* DNA, and indicated that plant growing season had a significant impact on fungal composition in the phyllosphere (Cross et al. 2017). Initiation of ascospore production by *H. fraxineus* after overwintering was followed by pathogen accumulation in asymptomatic leaves across plant growing seasons (Cross et al. 2017). Some fungal taxa like genera *Phyllactinia* and *Phoma* were more abundant at the late season and were positively correlated with *Hymenoscyphus*, while some taxa like *Taphrina*, *Tilletiopsis*, *Cladophialophora* were more abundant at the early season and were negatively correlated with *Hymenoscyphus* (Cross et al. 2017). These strong seasonal changes of the phyllosphere fungal community might be explained by the fact that plant metabolisms, leaf physical and chemical traits, and seasonal weather conditions significantly vary across different growing seasons and plant developmental stages (Xu et al. 2022b; Vacher et al. 2016). For example, theophylline was prevalent metabolite at the early shoot development stage and strongly affected fungal communities in the tea plant phyllosphere, in contrast, epigallocatechin gallate was more abundant at the late stage and was identified as the main driver of fungal community assembly (Xu et al. 2022b). Bowsher and colleagues investigated seasonal dynamics of epiphytic phyllosphere fungal communities of switchgrass, and observed a strong impact of plant growing season on fungal community composition, with multiple taxonomic levels exhibiting clear temporal patterns (Bowsher et al. 2021). It was shown that fungal richness index increased after the first time point and remained high until late summer, when it decreased across the final two time points (Bowsher et al. 2021). Further, seasonal patterns in fungal community were significantly correlated to leaf nitrogen concentration, leaf dry matter content, plant height, and minimum daily air temperature(Bowsher et al. 2021), indicating that both host selection and environmental changes contribute to phyllosphere fungal temporal dynamics.

Furthermore, it was reported that fungal network connectivity changed across plant growth stages, with a weak co-occurrence pattern early in the season but increasing dramatically at the late stage (Sapkota et al. 2022). A recent work on maize also revealed that bacterial-fungal interkingdom network patterns in both epiphytic and endophytic phyllosphere changed distinctly across three developmental stages (Xiong et al. 2021b). The fungal network connectivity and the proportion of fungal nodes increased over the time, indicating an increasing role of fungal taxa in the networks (Xiong et al. 2021b). The random forest modeling analysis further indicated that fungal community composition at the mature stage is a strong predictor for crop yield (Sapkota et al. 2022). Additionally, an increasing research effort is to explore core taxa of the phyllosphere mycobiome during plant developmental stages. For instance, six fungal taxa were identified as persistent core taxa (present in at least 95% of samples) for the phyllosphere mycobiome, including two ascomycetes (*Cladosporium* spp.) and four basidiomycete yeast (*Dioszegia* sp., *Itersonilia* sp., *Sporidiobolus* sp., and *Udeniomyces* sp.) (Almario et al. 2022). Taken together, these findings reveal the prominent roles of temporal factors in shaping diversity, composition and co-occurrence networks of the phyllosphere mycobiome under various environmental conditions. These findings can help to form a systematic understanding on the fundamental ecological processes governing plant mycobiome assembly and to develop microbiome-based tools for sustainable plant protection and crop production.

5 Fungal Community Assembly in Phyllosphere

5.1 Community Assembly Processes

Microbial community assembly are driven by four ecological processes: selection, speciation, diversification, and drift based on the theory proposed by Vellend (2010). Selection mirrors deterministic fitness differences between species. Diversification represents evolutionary process of generating new genetic variants. Dispersal relates to the movement of organisms across space, and drift reflects stochastic changes in species abundance (Vellend 2010; Zhou and Ning 2017).

5.1.1 Selection

Leaves present as an extreme environment where phyllosphere fungi withstand low nutrient availability, large moisture fluctuation, intense ultraviolet radiation, and temperature oscillations. These leaf microclimate parameters vary with regional climate and exhibit fine-scale variations due to terrain, vegetation, and canopy structure (Vacher et al. 2016). Thus, environmental factors often exert important selective pressure on phyllosphere fungal communities. For example, climate warming altered the composition of fungal assemblages of *Mycosphaerella punctiformis* along an elevation gradient (Cordier et al. 2012b) or affected phyllophere fungal assemblages of *Quercus robur* in a multifactorial experiment (Faticov et al. 2021). Warming strengthened host plant defenses and filtered out the less adapted fungal taxa in the phyllosphere (Faticov et al. 2021). Precipitation also exerted a significant influence on phyllosphere fungal communities of *Mussaenda kwangtungensis* (Qian et al. 2018a) and *Panicum hallii* (Giauque and Hawkes 2016). Precipitation indirectly influenced fungal community assembly through variation in the local plant community structure (Hawkes et al. 2011). In addition, environmental changes were assumed to decrease the activity of host genes, resulting in the context-dependent expression of genetic variation for plant phenotypic features, which might further alter the community assembly processes of phyllosphere fungi (Wagner et al. 2016).

Since the phyllosphere is an ecological interface between air and host plants. Plant species identity should be an essential driver of community structure of phyllosphere fungi. Previous studies have shown significant different foliar fungal community composition among different plant species (Kembel and Mueller 2014; David et al. 2016) or plant genotypes (Qian et al. 2018b; Balint et al. 2013). Many phenotypic properties including leaf morphology, physiology, and chemistry derived from the host genetic repertoire likely exert selective pressure on the phyllosphere fungal community assembly and the plant-fungal interactions (Friesen et al. 2011). Fungal cells and spores that land on the leaf surface initially contact with the trichomes and cuticles, whose architecture varies greatly depending on environmental conditions and plant identity. Trichomes or hairy extensions can protect the leaf against ultraviolet radiation, ensnare the water, and help spores adhere to the leaf surface (Qian et al. 2020). For instance, some endophytic *Trichoderma* species were found to be intimately associated with *Theobroma cacao* glandular trichomes (Bailey et al. 2009). Cuticle permeability and wettability can influence the diffusion rate of compounds from the apoplast onto the leaf surface and the retention of water droplets on the leaf surface, which will affect the colonization of microbes in the phyllosphere (Schlechter et al. 2019). Additionally, plant traits related to leaf sizes, foliar nutrients (e.g., sulfur, nitrate, and calcium) and leaf secretions (e.g., organic acids, sugars, and secondary metabolites) can also largely influence the phyllosphere fungal diversity and community composition (Larkin et al. 2012; Kivlin et al. 2019; Glushakova et al. 2007; Saunders and Kohn 2009).

5.1.2 Dispersal

Dispersal of foliar microbes is performed primarily by bioaerosols that contain fungal spores, single cells, and fragments of hyphae. Bioaerosols can deposit on nearby plants and travel over a long distance, which relies on the height of release occurs, environmental conditions, local vegetation structures, and the size and density of particles (Vacher et al. 2016). Dispersal limitation theory demonstrates that there will be a decay in the similarity of microbial communities with geographic distance (Hanson et al. 2012). This phenomenon has been found in the fungal communities inhabiting the leaves of *M. pubescens* var. *alba* (Qian et al. 2018b) and *Pinus taeda* (Oono et al. 2017) at regional scales, which highlights the importance of geographic distance as a driver in shaping regional foliar fungal communities.

5.1.3 Diversification and Drift

Given that the current microbial distribution patterns cannot be entirely explained by selection and dispersal, diversification or mutation at the gene level may also act an essential role in determining microbial community assembly (Zhou and Ning 2017). Phyllosphere fungi often cope with intense ultraviolet radiation and reactive oxygen that are considered to accelerate mutation rates (Vorholt 2012). However, we still lack the methods to calculate the relative contribution of diversification in shaping the community structure.

Drift is a purely stochastic process that can function on its own via probabilistic factors, especially in small communities or when the regional pool is enormous in comparison to the size of local communities (Chase 2003). Drift could interact with selection to create multiple stable equilibria and become more important when selection is weak (Chase and Myers 2011). Generally, the majority of phyllosphere fungi are rare taxa, which may be easily influenced by drift, because slight changes in their abundance can lead to extinction on a local scale (Vacher et al. 2016). In addition, the functional redundancy of phyllosphere microbes could increase neutrality and makes functionally redundant members more vulnerable to drift (Zhou and Ning 2017).

5.2 Co-occurrence Networks

In phyllosphere environments, microbial members often interact with each other and live within complicated ecological networks rather than existing in isolation (Faust and Raes 2012). The microbial interactions can be classified as positive (mutualism), neutral (commensalism) or negative (competition, predation, parasitism) and play important roles in determining the fitness of phyllosphere microbes, selecting for specific microbial traits, and shaping the structure of microbial communities (Bashir et al. 2022; Vacher et al. 2016).

Co-occurrence network analysis can reveal how species coexist within a community, disentangle the microbe-microbe and microbe-host interactions, and thus provide comprehensive insights into the assembly process and ecological function of microbial communities (Banerjee et al. 2018). The co-occurrence pattern has been frequently visualized as a network of nodes (microbial taxa) connected by edges (microbial interaction) of varying strength that correspond to the frequency of paired species presence at a site (Kay et al. 2018). Ecological modules are comprised of closely connected microbes, and are usually considered as the result of phylogenetic relatedness, niche differentiation, and/or habitat heterogeneity of the microbial communities (Zhang et al. 2018a; Newman 2006). Network analysis can also help us identify keystone microbes that are highly connected; the keystone species may exert a great influence on the structure and functioning of microbial communities irrespective of their abundance (Banerjee et al. 2018). The removal of these taxa will lead to a dramatic shift in network topology. The network topological properties, such as clustering coefficient, average path length, mean connectivity, and edge density, can be used to speculate microbial assembly and interactions. In particular, co-occurrence network analysis based on amplicon sequencing data has been increasingly used to explore the ecological interactions among multiple-kingdom microbial members as well as microbe-host relationships in various habitats (Teng et al. 2022; Yang et al. 2022).

Recently, several studies have been conducted to explore co-occurrence networks of phyllosphere fungal communities. For instance, Yao et al. found foliar endophytic network had higher levels of specialization and modularity but lower connectance and stronger anti-nestedness than the epiphytic network in a local mangrove forest (Yao et al. 2019). Qian et al. found that the phyllosphere fungal networks of *Mussaenda kwangtungensis* in island regions showed less complex and coherent, but more modular structure than the mainland ones (Qian et al. 2020). At the scale of more than 2000-km span of mountain forests in eastern China, Yang et al. demonstrated that the plant-fungus networks in leaves were significantly higher specialized, modular and stable, but less connected compared to the networks in soils (Teng et al. 2022). Phyllosphere fungal networks of *M. shikokiana* displayed a trend of reduced connectivity and integrity with increasing elevation (Qian et al. 2018a). Nevertheless, we still lack basic knowledge regarding the environmental factors that determine the network structure of phyllosphere fungi. Environmental drivers could influence phylogenetic congruence patterns and the rare taxa involved in coevolved interactions, but exploring the response of networks to environmental change will require linking network architecture with ecosystem functioning, and using multilayer network approaches (Tylianakis and Morris 2017).

5.3 Source Analyses of Phyllosphere Fungi

The phyllosphere recruits microbes via horizontal (from an environmental, free-living symbiont source) or vertical (from the inheritance of the symbiont from the mother or both parents) transmissions (Bright and Bulgheresi 2010; Bashir et al. 2022). Therefore, the sources of phyllosphere fungi are diversified. Epiphytic fungal residents originate from the air, water, or soil and can arrive at the leaf surface through wind, bioaerosols, raindrops or animals (especially insects and herbivores) (Whipps et al. 2008). Once deposited, their establishment and survival will further rely on microbial physiological and genetic features (e.g., acquisition of leaf nutrients, capability to adhere to leaf surface, and adaptation to leaf microclimate) and leaf phenotypic properties in the aspects of morphology, chemistry and physiology (Bashir et al. 2022). Some of them can pass through leaf epidermal openings structure like stomata or hydathodes and become endophytes (Bashir et al. 2022). Yang et al. found more phylogenetically clustered structure for epiphytic and endophytic fungi inhabiting the leaves of *B. ermanii* compared with the corresponding soil fungi, indicating a continuum acted by epiphytes and endophytes in the phyllosphere (Yang et al. 2016a). Some endophytic fungal species (e.g., clavicipitaceous endophytes) can transmit vertically, with maternal plants passing fungi on to offspring through seeds (Rodriguez et al. 2009). Additionally, there is increasing evidence that endophytic microbes in the roots could enter the vascular system and be transferred internally to the leaves where they develop as foliar endophytes (Whipps et al. 2008). For example, many fungal taxa of *Mussaenda kwangtungensis* were shared between the leaf and root endosphere compartments, although the overall community structure can differ significantly (Qian et al. 2019).

The advancement of statistical tools facilitates us to identify the sources of phyllosphere fungi more precisely. For example, SourceTracker is a Bayesian approach to estimate the proportion of contaminants in a given community (Knights et al. 2011); the approach was widely used in high-throughput metagenomic studies (Yang et al. 2021; Zhang et al. 2022). Using SourceTracker, the researchers found that 60% of the foliar endophytic fungal community of healthy Rice was derived from the soil environment. FEAST (i.e., fast expectation-maximization microbial source tracking) is an alternative Bayesian approach to estimate the proportions of microbial sources in a given community based on Gibbs sampling; this method can deal with bigger data information in a timely manner (Shenhav et al. 2019). Using FEAST, the researchers surveyed the sources of the foliar fungal community along the burn severity gradient; they found that the percentages of these sources were strongly affected by the burn severity levels (Dove et al. 2021). In unburned plots, 40% of the foliar fungal taxa were derived from rhizosphere, while bulk soil was the main source of the foliar fungal taxa in burned plots. In addition, airborne fungal community was more derived from leaf surface than soils (Qi et al. 2020). Therefore, soil, air and other plant tissues are potential sources of phyllosphere mycobiome, but their relative contributions vary by plant growth stages and surrounding environments.

6 Fungal Functions in Phyllosphere

Phyllosphere fungi have intimate relationships with plants and exhibit diverse functions, which not only benefit their own survival and growth but also affect plant performance and even the whole ecosystem. They have been reported to increase plant access to nutrients and water, enhance plant resistance to biotic and abiotic stress, degrade organic matters or pollutants, drive plant population and community and so on (Busby et al. 2016; Khan et al. 2015; Rudgers et al. 2010; Russell et al. 2011). However, leaf fungal pathogens induce plant diseases and cause huge losses in agroecosystem (Chen et al. 2021a). Thus, understanding functional diversity of phyllosphere fungi is essential to maintain the sustainability of natural ecosystems, promote the yield in agroecosystems, and benefit to human health in urban ecosystems.

6.1 Functional Traits

Recently, more and more studies focus on fungal functional traits, which are the measurable characteristics that affect organism growth and adaptability in certain environments (Yang 2021). Functional traits can be analyzed based on phenotypic characteristics or inferred from microbial genomes. Microbial functional traits are more sensitive to environmental fluctuations compared to microbial taxonomic composition (Xiang et al. 2020). Currently, several databases of fungal functional traits have been established, including FUNGuild (Nguyen et al. 2016b), Fun^{Fun} (Zanne et al. 2020), and FungalTraits (Põlme et al. 2021), which make the quantification and prediction of diverse fungal traits under different conditions much quicker and easier.

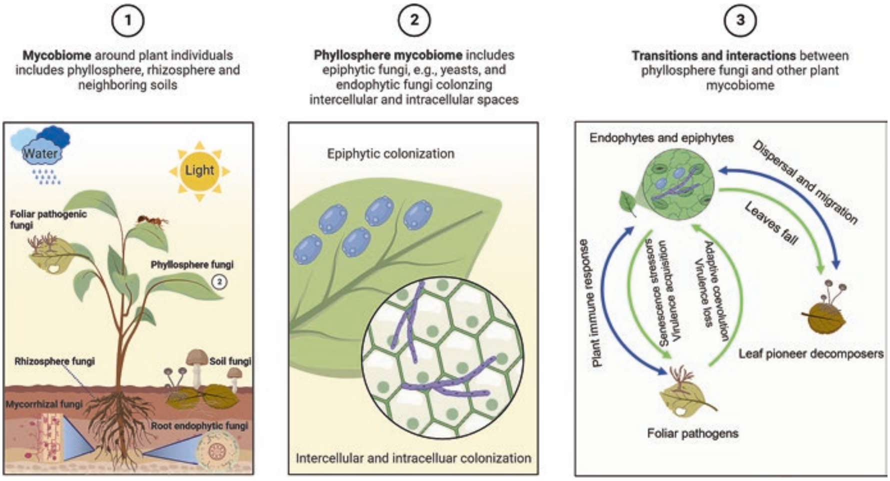

Fig. 1 Dimensions of mycobiome around plant individuals. The transitions in life history and biotic interactions among representative fungal guilds are shown in diagram ③. In the diagram, blue arrows represent biotic interactions between different fungal guilds. For example, endophytes (or epiphytes) and foliar pathogens affect each other by adjusting plant immune responses (Schulz and Boyle 2005). Green arrows represent the transitions in life history between phyllosphere fungi and other plant mycobiomes. For examples, endophytic fungal lineages frequently transit to and from pathogenicity, while endophytic lineages give rise to saprotrophs, but the revisions to endophytism are rare (Arnold et al. 2009). The diagrams are created with the help of BioRender.

Guild, also known as functional group, refers to a group of organisms that utilize the similar environmental resources or have certain niche overlaps, no matter these organisms are phylogenetic related or not (Nguyen et al. 2016b). In FUNGuild, 12 guilds were classified, among which endophytes, pathogens, saprotrophs, and mycorrhizal fungi are plant-associated fungi (Nguyen et al. 2016b). Nevertheless, there are the highly complicated plant mycobiome around plant individuals - different functional guilds (incl. endophytes and epiphytes) transform the life histories and interact with each other closely (Fig. 1). Some fungal endophytes in the phyllosphere could become saprotrophic decomposers after leaf fall (Suryanarayanan 2013). Moreover, *Colletotrichum* (Rojas et al. 2010; Mendgen and Hahn 2002) and Dothideomycetes fungi (Ohm et al. 2012) could transform between non-pathogens and pathogens in response to different environmental conditions or host cues. Dothideomycetes fungi are common in the phyllosphere of many plant species (Qian et al. 2018b; Yao et al. 2019; Teng et al. 2022). The comparison of genome features of 18 Dothideomycetes fungi showed that they could be classified as plant pathogens and saprotrophs, and these pathogens could be further divided into necrotrophs, biotrphs, and hemibiotrophs (Ohm et al. 2012). Further analysis showed that genes involved in carbohydrate degradation and secondary metabolism were expanded in necrotrophs; and necrotrophs also had higher number of genes encoding effectors compared to (hemi)biotrophs, which could lead to the death of leaves and benefit the survival and growth of necrotrophs. Thus, the shift among different life strategies could be predicted by measuring fungal functional traits, such as the production and exudation of lytic enzymes, the suppression of host defenses, and so on (Mendgen and Hahn 2002).

Functional traits that are critical to fungal physiology were also summarized, such as growth rate, respiration rate, spore size and number, stress tolerance (especially through melanin synthesis), demand for nitrogen (N) and phosphorus (P), and extracellular enzyme activity (Zanne et al. 2020). Other functional traits are highly correlated with fungal interactions with plants. For example, some foliar endophytes inhibited *Rhizoctonia solani*, decreasing disease severity and increasing potato yield (Lahlali and Hijri 2010). Among the tested fungal endophytes, *Trichoderma atroviride* acted as a mycoparasite; *Alternaria longipes* and *Epicoccum nigrum* produced antagonistic secondary metabolites; *Phomopsis* sp. competes for nutrients and space with leaf pathogens. Thus, the aforementioned fungal functional traits could be used to predict three-way interactions among plants, pathogens, and mutualists.

As mentioned above, phyllosphere fungi may change their functional guilds in response to changed conditions. Zhang and Elser examined the stoichiometry of different fungal guilds and found that N content was higher while P content was lower in pathogens compared to saprophytes (Zhang and Elser 2017). However, the N/P ratio was much higher in saprophytes than pathogens (Zhang and Elser 2017). Moreover, saprophytes acquire carbon energy by decomposing dead plant matter, so they may harbor more abundant genes encoding carbohydrate-active enzymes (CAZymes) (Zanne et al. 2020). Therefore, for the fungal taxa that can transition from one guild to another, it is essential to understand which fungal traits can specify the guild changes. These functional traits may help to predict fungal functions in phyllosphere more precisely in the future.

6.2 Functional Genes

One microbial strain harbors thousands of functional genes, which are less evolutionarily conserved compared to phylogenetic biomarkers such as 18S rRNA gene or nuclear ribosomal internal transcribed spacer (ITS) gene (Yang 2021). The presence and expression levels of certain functional genes can be used to estimate the fungal functional traits (Zanne et al. 2020). Although the simplest trait is encoded by single genetic locus, most traits are complex (Martiny et al. 2015). Some phyllosphere fungi may obtain certain genes from their host plants and exhibit novel traits through horizontal gene transfer (HGT) (Tiwari and Bae 2020). Thus, it is difficult to summarize all the fungal functional traits by only one or several genes (Escalas et al. 2019). More approaches are needed to ensure the links between functional genes and traits, such as gene knockout and genetic mutant generation.

Fungal community, as a functional library, contains a collection of genes selected by certain environmental conditions (Escalas et al. 2019). A large collection of microbial functional genes have been summarized, which are mainly categorized into nutrient cycling, substance degradation, antibiotic resistance, stress response, and virulence (Escalas et al. 2019). Some functional genes are reported to enrich or delete in phyllosphere mycobiome. For example, phyllosphere fungi harbored specific functional genes related to carbon (C), N, P, sulfur (S) cycles compared to the fungi in other habitats, because carbohydrates, amino acids, and organic acids were released by plants to leaf surface (Xiang et al. 2020). In contrast, powdery mildews lost genes encoding CAZymes, primary and secondary metabolism related enzymes, and transporters, which benefit its biotrophic pathogenicity (Spanu et al. 2010). Thus, the presence and absence of some unique genes in phyllosphere fungal communities can be used to assess their potential phenotypes, functional diversity as well as the healthy state of host plants.

6.3 Omics

Most fungi in the phyllosphere are unculturable in common media and under common culture conditions. Metagenomics is defined as the culture-independent genomic analysis of microbial community (Schloss and Handelsman 2003), which was followed by the emergence of metatranscriptomics, metabolomics, and metaproteomics (Schneider and Riedel 2010). The applications of aforementioned high-throughput techniques will promote the exploration of fungal functions in phyllosphere, providing more comprehensive and accurate information.

6.3.1 Metagenomics

Metagenomics can reveal a much higher fungal diversity in the phyllosphere compared to culture dependent methods (Quince et al. 2017), because the unculturable microbes occupy nearly 99.5% of the entire environmental microbiota (Lloyd et al. 2018). More importantly, metagenomics provides a powerful tool to extend the functional traits from individual to community at the extensive sampling effort (e.g., hundreds or thousands of samples) (Barberan et al. 2012). Individual microbial genomes could be assembled from community metagenomics data, referred to as metagenome-assembled genomes (MAGs), providing an essential basis for genome-centric functional analyses (Luo et al. 2012). Several steps are essential to the accuracy and efficiency of metagenomics. For example, the purity and quality of nucleic acid molecules extracted from environmental samples must be ensured (Hawkes et al. 2021). Then, the improvements in bioinformatic tools and pipelines will further identify and remove contamination sequences. These bioinformatic tools could mimic gene translation progress, converting raw reads generated from metagenomic sequencing into meaningful microbial features. Furthermore, metagenomic sequencing could avoid the biases of PCR amplification that result from the use of target-specific primers (Tedersoo et al. 2015).

Metagenomic analysis showed low functional diversity but highly redundant functions in phyllosphere mycobiome, which may be relevant to fungal adaption to low nutrients, high ultraviolet radiation, and changing temperature and humidity of phyllosphere environment (Stone et al. 2018). Khoiri et al. analyzed the structure and function of microbial community in the sugarcane phyllosphere using the shotgun metagenomics, including archaea, bacteria, fungi, and viruses; they found that different farming practices strongly affected the taxonomic and functional diversity and co-occurrence interactions of phyllosphere microbes (Khoiri et al. 2021). However, several studies used metagenomics to explore fungal taxonomic diversity rather than functions. For example, Ottesen et al. combined amplicon and metagenomic sequencing to reveal the fungal and bacterial diversity in the surface of tomato leaves, stems, roots, flowers, and fruits (Ottesen et al. 2013).

It is noteworthy that metagenomics is the first step to understand microbial community, which could reveal the gene capacity of a community but not the expression of genes and their post-transcriptional modification. Thus, the metatranscriptomics, metabolomics, and metaproteomics should be applied to achieve a more comprehensive picture on the functions of phyllosphere mycobiome.

6.3.2 Metatranscriptomics

Metatranscriptomics could capture gene expression in the plant-associated microbial community, showing the functional profile under certain conditions (Aguiar-Pulido et al. 2016). Since fungal transcripts show different sequence length and GC content from plant transcripts, it is possible to analyze the transcriptome of plants and their phyllosphere fungi together (Delhomme et al. 2015). Delhomme et al. performed *de novo* transcript assembly of more than 1 billion reads from *Picea abies* and obtained a mix of plant and fungal transcripts (Delhomme et al. 2015). They found that fungal transcripts were predominantly from Dothideomycetes and Leotiomycetes, with functional annotation related to glucose intake and processing, indicating active fungal growth and metabolism in the phyllosphere. In other studies, metagenomics and metatranscriptomics were combined to analyze phyllosphere mycobiome. Camargos Fonseca et al. combined amplicon sequencing, shotgun metagenomics, and small RNA transcriptomics to explore the fungal diversity and functions of rubber trees (*Hevea brasiliensis*); they found that most phyllosphere fungi were assigned to saprotrophic ecological mode, with fewer to pathotrophic and symbiotrophic modes, or a combination among them (Camargos Fonseca et al. 2022).

6.3.3 Metabolomics and Metaprotemics

Metabolomics aims to analyze all the metabolites produced by an organism or a community, while metaproteomics aims to identify all the proteins and peptides in a microbial community. Unlike metagenomics and metatranscriptomics that heavily rely on sequencing, both metabolomics and metaproteomics have benefited from the improvement of mass spectroscopy technologies. Moreover, proteins and peptides could also be quantified by analyzing their individual intensity on gels. Generally, metabolomics and metaproteomics provide a more accurate information to the metabolic pathways compared to metagenomics and metatranscriptomics (Levy et al. 2018).

Metabolomics is able to characterize and quantify the chemical outputs of microbial metabolism, which are highly related to the cellular processes under certain conditions (Fiehn 2002). In community, microbes would produce various metabolites, including signaling molecules to communicate with others as well as toxins to kill competitors (Aguiar-Pulido et al. 2016). As such, metabolomics analysis can reveal the role of phyllosphere fungi in the transformation of nutrients and degradation of pollutants. Some fungal endophytes could get host genes through HGT and synthesize plant metabolites (Kusari et al. 2012). Consequently, phyllosphere fungi may be one of most important factors for leaf phytochemical composition (Mogouong et al. 2021). In addition, metabolome is considered as the most direct indicator of the homeostasis of an environment, so certain microbial metabolites could be developed as predictive biomarkers for environmental fluctuations (Lankadurai et al. 2013).

Metaproteomics is defined as a large scale characterization of the entire proteins in microbial communities at a given time point (Wilmes and Bond 2004), which is necessary to reveal the physiology, ecology, and evolution of microbial communities (VerBerkmoes et al. 2009). Currently, metaproteomics has been used to analyze the bacterial functions in the phyllosphere (Lambais et al. 2017; Knief et al. 2012), few studies focused on fungal metaproteomic analysis. In addition, some studies used metaproteomics to reveal fungal functions in soil. For example, Fernandes and colleagues found that the protein functions of soil fungi shifted from metabolism in forests to information processing and storage in shrublands (Fernandes et al. 2021). These existing studies provide some essential technical references to advancing metaproteomics analyses for phyllosphere mycobiome, whose composition and diversity are much simpler than soil mycobiome.

In summary, integrated analysis of metagenomics, metatranscriptomics, metabolomics, and metaproteomics are enabled by the lower cost of sequencing and the advancement of bioinformatic platform. These omics approaches will accelerate our understanding of phyllosphere fungal diversity and functions greatly.

7 Interactions of Phyllosphere Mycobiome with Plants

Phyllosphere mycobiome intimately interacts with host plants and contributes to many processes, from the health of individual plant to the development and function of plant community. Some phyllosphere fungal taxa are reported as latent plant pathogens that may produce negative effects on plant development and growth in some cases. Most of phyllosphere fungi, especially for endophytic fungal group, are able to increase plant fitness by producing phytohormones, increasing plant nutrient uptake, reducing pathogen and herbivore damages, and enhancing plant adaption to stressful environments. Besides influencing the health of individual plant, phyllosphere fungi have a consequence on the plant population and community by

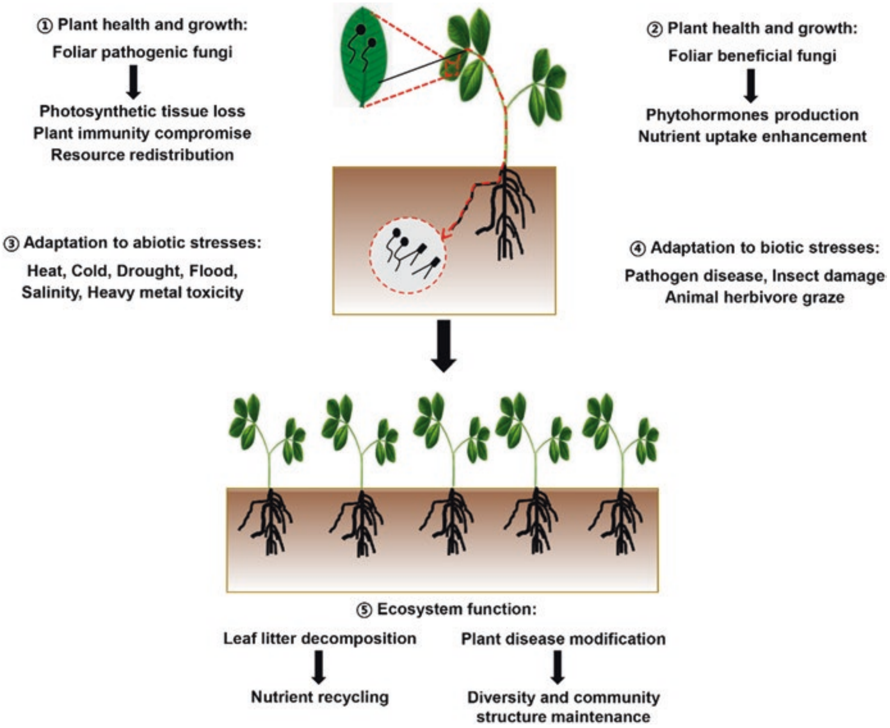

Fig. 2 Roles of phyllosphere mycobiome in plant health and plant community. Phyllosphere fungi can act as latent plant pathogens that produce negative effects on plant development and growth. Some foliar fungi are able to increase plant fitness by producing phytohormones, increasing plant nutrient uptake, reducing pathogen and herbivore damages and enhancing plant adaption to stressful environments. Besides influencing the health of individual plant, foliar fungi have a consequence on the plant population and community by decomposing leaf litter and modifying plant disease. Part ①–④ are at the plant individual level, while part ⑤ occurs at the plant population and community level

decomposing leaf litter (Osono 2006) and modify plant disease (Busby et al. 2016). Here, we focus on the effects of interactions of phyllosphere mycobiome with plants on plant health, growth, biomass, population and community (Fig. 2).

7.1 Roles in Plant Health

7.1.1 Phyllosphere Fungi as Pathogens that Inhibit Plant Health

In the last several decades, the ecology of phyllosphere inhabiting fungi has been studied extensively, but more attentions have been paid on fungal pathogens (Jia et al. 2020). This is not surprising, as 7 in the top 10 most important plant-pathogenic fungi are foliar infection, including *Magnaporthe oryzae, Puccinia* spp., *Fusarium* *graminearum, Blumeria graminis, Mycosphaerella graminicola, Colletotrichum* spp., *Ustilago maydis* and *Melampsora Lini* (Dean et al. 2012). Many previous studies have revealed the molecular mechanisms underlying foliar infection of fungal pathogens, and identified fungal virulence effectors and plant resistance (R) proteins during infection process. For instance, fungal effector AvrPiz-t of *M. oryzae* suppresses rice immunity and promotes virulence by Ca^{2+} sensor-mediated ROS scavenging system (Gao et al. 2021).

Given that leaves are initial infection organ for foliar fungal pathogens, it is reasonable that photosynthesis system would be the prime target by the infection. Foliar fungal infection inevitably deters plant health by directly damaging photosynthetic organelle, chloroplasts, and indirectly interfering plant immunity. Photosynthesis is the fundamental process that fuels plant growth and development (Brestic et al. 2021). Foliar fungal disease causes substantial loss of photosynthetic tissue, reductions in chlorophyll content, net photosynthesis rate (Pn) and other photosynthesis-related parameters, and thus reduces the carbohydrates for plant growth. For instance, maize leaves infection with *Colletotrichum musae* and *Fusarium moniliforme* reduce photosynthetic capacity due to the reduction in chlorophyll content (Pinto et al. 2000). The negative effects on photosynthesis system by foliar fungal and oomycete pathogens are achieved by a cocktail of effectors. During infection, pathogens introduce effectors specifically into chloroplasts, which interact with chloroplast proteins to induce programmed cell death (PCD), interfere chloroplasts function and facilitate pathogen proliferation (Kretschmer et al. 2019). For example, *Pyrenophora tritici-repentis* (Ptr), a necrotrophic fungus, produces host-selective toxins ToxA and ToxB (Ciuffetti et al. 2010), of which ToxA interacts with chloroplast protein ToxA Binding Protein 1 (ToxABP1) in wheat, leading to reductions in levels of PSI and PSII protein (Manning et al. 2010). A haustorium-specific protein (Pst_12806) from wheat stripe rust fungus, *Puccinia striiformis* f. sp. Tritici (Pst) is transported into chloroplasts and interacts with the C-terminal Rieske domain of TaISP protein, which suppresses chloroplast function by reducing electron transport rate, photosynthesis and chloroplast-derived H_2O_2 accumulation (Xu et al. 2019). However, our knowledge of chloroplast-targeted effectors from fungi and oomycete pathogens has lagged behind our knowledge of cytoplasm-targeted effectors, as chloroplast-targeted effectors have not been identified in some of best-characterized fungal pathogens, such as *M. oryzae* and *U. maydis*.

Besides fueling the growth of plants, photosynthesis system also plays central role in early immune responses through the formation of ROS and NO, Ca^{2+} oscillations, and the synthesis of plant defensive phytohormones, including salicylic acid (SA) and jasmonic acid (JA) (Serrano et al. 2016). The biosynthesis of JA and SA is associated with chloroplast. Two different enzymatic pathways are responsible for SA biosynthesis: isochorismate (IC) and phenylalanine ammia-lyase (PAL) pathways, of which IC is operative in chloroplast. IC is catalyzed by the chloroplast-localized IC synthase (ICS), and exported to cytosol by enhanced disease susceptibility 5 (EDS5) (Rekhter et al. 2019). IC is then catalyzed by avrPphB Susceptible 3 (PSB3) to form IC-9-glutamate, which is converted to SA spontaneously or enhanced by pesudomonas susceptibility 1 (EPS1) (Torrens-Spence et al. 2019). Notably, rapid biosynthesis of SA caused by foliar pathogens infection is mainly through ICS pathway. (9S, 13S)-12-oxophytodienoic acid (OPDA), a precursor of JA is synthesized in chloroplast by 13-lipoxygenase (LOX), allene oxide synthase (AOS) and allene oxide cyclase (AOC) (Turner et al. 2002; Zhang et al. 2019). The OPDA is then transported to peroxisome to synthesize JA. It is well known that SA and JA are key components of plant defence against biotrophic and hemibiotrophic (SA-mediated), and necrotrophic (JA-mediated) pathogens, respectively (Bari and Jones 2009). As a consequence, the loss of photosynthetic tissue by the foliar fungal pathogen activity compromises SA- and JA-mediated plant immunity, which further increases plant susceptibility.

To combat foliar fungal infection, the prioritization of carbohydrates synthesized by non-infected of leaves towards production of defense compounds rather than plant growth. As defense compounds biosynthesis imposes a substantial demand for resources, the diversion of plant resources from growth to defense is detrimental to plant growth and reproduction under a fixed total resource budget (Huot et al. 2014; He et al. 2022). This phenomenon is commonly known as "growth-defense tradeoff", which is one of most fundamental principles of "plant economics" (Monson et al. 2022). Consequently, foliar pathogens deter plant health by directly compromising photosynthesis and plant immunity due to the loss of photosynthetic tissue, and indirectly modulating plant resources distribution.

7.1.2 Phyllosphere Fungi as Bio-control Agents that against Pathogens and Herbivores

Besides being pathogens, some fungi inhabiting leaves act as bio-control agents that are beneficial to plant health. Foliar fungi, especially fungal endophytes reduce disease by directly killing pathogenic microbes or insects through the production of toxins, or indirectly activating plant immunity (Jia et al. 2020). The extracts of 5 foliar fungal endophytes (*Diaporthe terebinthifolii* CMRP1430, *D. terebinthifolii* CMRP1436, *D. foliorum* CMRP1321 and *D. malorum* CMRP1438) isolated from *Schinus terebinthifolius* showed the anti-microbial activity in agar diffusion assays, and three key classes of chemical compounds, including ferric chloride, potassium hydroxide, and vanillin-sulfuric acid, were identified (dos Santos et al. 2021). Other studies have shown that the plants infected by endophytic fungi emit volatile organic compounds (VOCs) to inhibit pathogenic fungal growth. For example, the volatile oil extracted from *Epichloë gansuensis*-infected drunken horse grass effectively inhibited the growth of 6 fungal pathogens, including *Alternaria alternata*, *Bipolaris sorokiniana*, *Curvularia lunata*, *F. avenaceum*, *F. solani* and *Trichoderma viride* (Zhang et al. 2015). Moreover, some foliar fungi can produce anti-fungal proteins. For example, *Epichloë* endophytes, can produce an anti-fungal protein, Efe-Afp, which directly impedes the growth of plant pathogen *Sclerotinia homoeocarpa* (Tian et al. 2017).

There is a bit of literature showed that some phyllosphere fungi can function as entomopathogenic fungi that restrict insect activity by producing toxins. Sumarah et al. screened the toxicity of extracts from 150 foliar fungal endophytes from *Picea rubens* (red spruce) needles to the forest pest *Choristoneura fumiferana* (eastern spruce budworm) in dietary bioassays and found that 3 of these strains are toxic to *C. fumiferana* larvae (Sumarah et al. 2010). LC-MS and spectroscopic analyses showed that the extracts of 3 strains contained 9 major metabolites, all of which showed toxicity to *C. fumiferana.* When feeding on *Epichloë*-infected plants, insects begin to metabolize alkaloids into non-toxic compounds. If the energetic cost of such detoxification over other physiological processes, such as growth and reproduction, the fitness of insects can be compromised (Bastias et al. 2017). Moreover, *Epichloë* endophytes-derived alkaloids are harmful to animal herbivores by influencing their gut metabolome and microbiome. Mote et al. investigated the metabolomic features of plasma and urine from steers grazing *Epichloë*-infected tall fescue, and provided evidence that *Epichloë* infection perturbs tryptophan and lipid metabolism (Mote et al. 2017).

Some phyllosphere fungi cannot directly inhibit pathogens and insect growth, but their colonization reduces pathogen and pest disease severity, suggesting that plant immunity is activated by foliar fungi under pathogen and pest challenges. For example, foliar application of leaf-colonizing yeast *Pseudozyma churashimaensis* strain RGJ1 confers pepper's resistance to bacterial and virus pathogens through inducing the expression of resistance marker genes *Capsium annuum Pathogenesis-Related* (*CaPR*)*4* and *CaPR5* (Lee et al. 2017). Although more and more foliar fungi and their metabolites with anti-microbial or anti-insect activities have been isolated and identified, their anti-microbial or anti-insect capacities were determined under controlled conditions, which is far away from the natural situation *in planta*. Future works are required to confirm their pathogens and pest diseases suppression in agricultural and natural ecosystems, which will greatly facilitate their practical use. Moreover, recent studies have reported that dysbiosis in phyllosphere microbiome led to disease symptoms (leaf chlorosis and necrosis) (Chen et al. 2020a), and leaves can recruit beneficial microbes to combat pathogenic diseases (Li et al. 2022b). Although these studies focus on the functions of foliar bacterial community, they promote us to test whether phyllosphere fungi possess the similar functions at community level.

7.2 Effects on Plant Growth and Biomass

7.2.1 Phyllosphere Fungi Promote Plant Growth and Biomass through Producing Phytohormones

Phyllosphere fungi promote plant growth and biomass by producing phytohormones, including indole-3-acetic acid (IAA, a major auxin) and cytokinins (Liu et al. 2020). Auxin is one of the main regulators in plant developmental and physiological processes, including embryogenesis, vascular differentiation, organogenesis, top growth, and root and shoot architecture (Quint and Gray 2006; Zhang et al. 2018c). Khan et al. isolated 17 endophytic fungal strains from leaves and stems of Frankincense tree (*Boswellia sacra*)*;* among them, *Aureobasidium* sp. BSS6 and *Preussia* sp. BSL10 showed high IAA production capacity (Khan et al. 2016). The root inoculation of *Preussia* sp. BSL10 significantly increased plant growth and biomass of *B. sacra* trees. Hoffman et al. reported that the presence of endohyphal bacteria (*Luteibacter* sp., *Xanthomonadales*) enhanced the IAA production of a foliar fungal endophyte (*Pestalotiopsis aff. Neglecta, Xylariales*), suggesting that the production of IAA in foliar fungi can be induced by their interactions with other microorganisms (Hoffman et al. 2013). Recently, several studies have indicated that the microbes-derived auxin plays crucial roles during the infection process by counteracting the plant immunity responses and alleviating ROS toxicity, but the knowledge comes from root-microbe interactions (Tzipilevich et al. 2021). Given that phyllosphere is a nutrient-limited, high ultraviolent radiation and low water availability environment (Vorholt 2012), the auxin production by fungi may contribute to their adaptability in phyllosphere.

7.2.2 Phyllosphere Fungi Promote Plant Growth and Biomass through Increasing Nutrient Uptake

It is well known that root-associated beneficial fungi, such as arbuscular mycorrhizal (AM) fungi, ectomycorrhizal (EcM) fungi, and fungal endophytes promote plant nutrient and water uptake. Emerging evidences show that foliar fungal endophytes can also enhance plant capability to absorb minerals, such as nitrogen (N), phosphorus (P) and potassium (K) (Malinowski et al. 2000). Christian et al. traced the N uptake and distribution of *Theobroma cacao* with or without foliar fungal endophyte (*Colletotrichum tropicale*) inoculation with ^{15}N isotope labeling methods (Christian et al. 2019). The results showed that endophyte-inoculated plants exhibited a greater ^{15}N uptake efficiency than endophyte-free plants. The inoculation of *Epichloë* endophytes improved the survival and biomass of *Lolium perenne* in low fertility soils by increasing N, P and Mn content in leaves, as well as K content in leaves and roots (Chen et al. 2020b). Here, we suggest the two mechanisms that explain the roles of foliar fungal colonization in root nutrients uptake. (1) Foliar fungal colonization upregulates the genes that are associated with plant nutrient uptake (Wang et al. 2018). (2) Foliar fungal colonization alters rhizosphere microbiome by modulating the composition of root exudates (Casas et al. 2011). Previously, Novas et al. reported that the root exudates of *Bromus setifolius* infected by *Neotyphodium* significantly increased AM fungal hyphal branches and length, and thus promote plant nutrient uptake (Novas et al. 2011). However, the internal signals and pathways that mediate the effects of leaf-inhabiting fungi on root exudates or rhizosphere microbiome are largely unknown.

7.2.3 Phyllosphere Fungi Increase Plant Tolerance to Environmental Stresses

The colonization of phyllosphere fungi (in particular endophytes) can confer protection for the host plants against various environmental stressors, such as drought, salinity, heavy metals, cold and flood (Lee et al. 2021). Foliar fungal endophytes increase plant tolerance to drought by increasing root biomass, regulating stomatal closure and accumulating solutes for osmotic stress. For example, Xu et al. investigated the effects of *E. sinensis* endophyte on physiology of *Festuca sinensis* under different soil water conditions, finding that *E. sinensis* infection improved the growth of *F. sinensis* under drought conditions by increasing root and shoot growth, improving photosynthetic rate, accumulating K^+ and Ca^{2+}, and promoting nutrient absorption (Xu et al. 2021). In particular, the inoculation of *E. sinensis* significantly modulated the content of abscisic acid (ABA). Similarly, fungal endophytes *Acremonium strictum* conferred drought tolerance to *Atractylodes lancea* plantlets by increasing the ABA level and root:shoot ratio of host plants (Yang et al. 2014). ABA plays a crucial role in triggering stomatal closure to avoid excessive water loss under drought (Gupta et al. 2020). In addition, foliar fungal infection increased the contents of osmo-protective compounds, such as sugars, proline, glutamic acid and mannitol (Yang et al. 2014). Higher levels of anti-oxidative enzymes, such as superoxide dismutase (SOD), ascorbate peroxidase (APX) and catalase (CAT) are found in foliar fungi-infected plants under drought, which contributes to the migration of damages by scavenging excessive ROS (Zhang and Nan 2007).

Foliar fungal infection also increases plant tolerance to salinity by increasing net photosynthesis, regulating ion transport and improving anti-oxidative system. For example, *Neotyphodium* colonization reduced Na^+ and Cl^- contents in tall and meadow fescues, but increased K^+ contents in the shoots under salinity stress (Sabzalian and Mirlohi 2010). Higher levels of K^+ can balance Na^+, which is crucial for the growth of plants under salinity conditions (Hussain et al. 2021). Pan et al. found that the infection of *E. coenophiala* promoted tall fescue salinity tolerance through lowering Na^{2+} accumulation and decreasing lipid peroxidation, and thus maintained higher plant growth and photochemcial efficiency (Pan et al. 2021). Enzymatic and non-enzymatic anti-oxidants are also induced by foliar fungal infection, which contribute to salinity tolerance of plants by counteracting ROS accumulation. For example, *E. gansuensis* infection increase growth and grass yield of *Achnatherum inebrians* under salinity by enhancing the activity of glucose-6-phosphate dehydrogenase (G6PDH) and plasma membrane (PM) H^+-ATPase activity to reduce ROS content (Wang et al. 2021). Interestingly, foliar fungal infection can regulate plant anatomical structures to acquire salinity tolerance. For example, the presence of *E. bromicola* increased the area of conducting tissues and the thickness of leaf veins, epodermis in stems, cortex and endodermis in roots of wild barley (*Hordeum brevisublatum*) under salinity stress (Chen et al. 2021b). In that way, foliar fungi help wild barley to reduce water loss and inhibit the decrease of transport capacity, and ultimately enhance the salinity tolerance.

Similar to drought and salinity stresses, foliar fungal infection can relieve the symptoms of plants to heavy metal toxicity by promoting plant growth and inducing anti-oxidant systems. For example, the *E. gansuensis*-infected drunken horse grass (*Achnatherum inebrians*) had more biomass and higher values for plant height and tillers compared to non-infected plants under cadmium stress (Zhang et al. 2010). More plant biomass can dilute heavy metal concentrations, and induced anti-oxidant systems can prevent plants from ROS injury under heavy metal stress (Zhang et al. 2010).

7.3 Effects on Plant Population and Community

It has been established that the associations between root and microbial symbionts, such as AM fungi, EcM fungi and rhizobia, largely influence plant population and community (van der Heijden et al. 2016; Keller and Lau 2018; Tedersoo et al. 2020). Mycorrhizal networks connect the conspecific and heterospecific plant individuals belowground, mediating nutrient flow and phytochemcial signals transmission, and ultimately influencing plant population and community (Genre et al. 2020). Given that plant leaves are associated with a large number of fungal species, phyllosphere fungi are also supposed to drive the structure of plant population and community. On one hand, phyllosphere fungi may affect plant population and community by influencing growth and biomass of individual plants. On the other hand, more importantly, phyllosphere fungi drive plant population and community by controlling the degradation rate of leaf litter and the occurrence of plant diseases.

As we described above, foliar fungal infection can influence the health, growth and biomass of individual plant, which depends on the fungal taxa. If the leaves of individual plant infected by pathogens, the health of neighboring plant community will be threatened, as fungal spores can be transported by rainfall, wind and insects (Roper et al. 2010; Kim et al. 2019). In an interesting study, the researchers investigated the dispersal of spores of leaf rust fungus *Puccinia triticina* on the infected wheat plants following a raindrop hits with high-speed photography (Kim et al. 2019). They found the raindrop-induced vortex ring carried the spores beyond the laminar boundary layer of leaves and lead to the long-distance transport of pathogens through the atmosphere. If the phyllosphere fungi are beneficial to health of plants, they will have the positive impacts on plant community establishment and persistence under stressful conditions.

Phyllosphere fungi can indirectly influence plant population and community by acting as pioneer decomposers and regulating the subsequent soil nutrient cycling (Saikkonen et al. 2015; Sun et al. 2020). For example, accumulations of leaf litter create a physical barrier that interferes the arrival of seeds to soil and the emergence of sprouts and seedlings. Vellend et al. reported that the germination of forest sedges (*Carex,* Cyperaceae) is lower for seeds beneath the leaf litter than those on the top of the litter layer (Vellend et al. 2000). In addition, plant litter can intercept light, shading seeds and seedlings, reduce soil water evaporations, and control soil thermal amplitude. As such, the effects of litter on seedling emergency depend to some extent on the litter amount and quality, which can be adjusted by phyllosphere fungi. Additionally, plant litter is the major organic carbon source in ecosystems, especially in forest and grassland ecosystems. During the early stage of leaf litter decay, *Ascomycota* is dominate phylum that involves the decomposition of easily degradable and nutrient-rich compounds, such as oligosaccharides, organic acid, hemicellulose and cellulose (Ma et al. 2013). With the process of degradation, Ascomycota is gradually replaced by the saprotrophs in Basidiomycota, which can degrade highly recalcitrant compounds, such as lignin and suberin (Voriskova and Baldrian 2013). The cooperation of phyllosphere fungi and later decomposer releases nutrients from leaf litter to soil, which increases soil nutrient availability and promotes root nutrient uptake, and ultimately influences plant community.

In addition, based on the Janzen-Connell hypothesis, the researchers reported that pathogenic fungi significantly increased plant diversity, while insect herbivores changed plant community composition in rainforest (Bagchi et al. 2014). Plant diseases caused by fungal pathogens, from some perspectives, are regarded as the modulator of plant diversity and community structure. The occurrence of plant diseases constrains the population density of dominate species and increases the advantage of rare species, maintaining multiple species co-existence. Usually, we name the pattern as conspecific negative density dependence (CNDD). By a long-term monitoring on seedling demographic data in a subtropical forest, Chen et al. found the tree species with higher pathogenic fungal accumulation more suffered from CNDD, whereas the tree species with higher ectomycorrhizal fungal accumulation less suffered from CNDD (Chen et al. 2019). Nevertheless, how diverse phyllosphere fungi regulate plant communities by affecting CNDD is still unknown. In future, the related studies will definitely expand our knowledge on effects of phyllosphere fungi on plant population and community.

8 Interactions of Phyllosphere Mycobiome with Global Change Factors

The Earth and its ecosystems are undergoing radical global changes such as climate change (e.g., global warming, extreme drought and precipitation) and land-use change (e.g., habitat loss, urbanization, and fertilization) (Perreault and Laforest-Lapointe 2022; Zhu et al. 2022). Emerging studies have suggested that these global change factors had an important impact on multiple facets of the phyllosphere mycobiome (Table 3). A better understanding of how the phyllosphere mycobiome and plant-mycobiome interactions response to global change will be a crucial step for harnessing the plant mycobiome to improve plant fitness and productivity.

Table 3 Recent studies showing the impacts of multiple global change factors on the phyllosphere mycobiome

Plant species	Leaf Compartment	Factors	Impacts	References
Quercus robur	Episphere and endosphere	Warming	Decrease fungal species richness and evenness; decrease the relative abundance of putative fungal pathogens	Faticov et al. (2021)
Eucalyptus	Episphere and endosphere	Precipitation	Increase fungal species richness and abundance; increase the relative abundance of putative fungal pathogens	Chen et al. (2021a)
Sorghum bicolor	Episphere and endosphere	Drought	Significantly affect fungal community structure	Gao et al. (2020)
Zea mays, *Triticum aestivum*, and *Hordeum vulgare*	Endosphere	Fertilization	Chemical N fertilizer increased the relative abundance of potential plant pathogen	Xiong et al. (2021a)
Schefflera octophylla	Episphere	Nitrogen deposition	2-week NH3 exposure increased the relative abundance of *Alternaria*, *Cladosporium*, and *Sampaiozyma*.	Song et al. (2022a)
Betula pendula	Episphere	Urbanization	Decrease fungal diversity, DNA amount, and activity; increase microbial respiration	Ivashchenko et al. (2022)
Populus nigra	Episphere and endosphere	Acid rain	Simulated sulfuric and nitric acid rain significantly decreased fungal biomass in the phyllosphere	Du et al. (2020)

8.1 Warming, Precipitation, and Drought

It is unequivocal that human activities result in rapid changes in global climate, and global mean surface temperature is estimated to be increased by 2–3 °C within the next decades (Zhu et al. 2022; Allen et al. 2014). Global warming caused by the "Greenhouse effect" attracts great attention from the general publics and could strongly affect the assembly and function of microbiome (Zhu et al. 2022; Faticov et al. 2021). A lot of efforts have been made to explore impact of warming on diversity, composition, and function of microbial community but mainly focused on bacteria and soil samples (Yuan et al. 2021; Feng et al. 2019; Tao et al. 2020). In addition to affecting bacterial community, growing evidence has suggested that warming significantly influences diversity and structure of the fungal community living in the phyllosphere (Faticov et al. 2021; Zhu et al. 2022; Liu et al. 2019). For example, it was recently showed that warming had a significant effect on fungal community composition of the oak phyllosphere and decreased fungal species richness and evenness (Faticov et al. 2021). Moreover, warming decreased the relative abundance of putative fungal pathogens in the early and late growing seasons (Faticov et al. 2021). Using the common-garden experiment, Balint and colleagues also found that warming significantly decreased fungal diversity in the phyllosphere of *Populus balsamifera*; warming changed the phyllosphere fungal community with the increase of plausible pathogens (Balint et al. 2015).

Liu and colleagues investigated effects of global change on foliar fungal diseases using a 6-year factorial experiment in a natural Tibetan alpine meadow ecosystem, and revealed that warming significantly increased fungal diseases for nine plant species and increased pathogen load of entire host communities (Liu et al. 2019). In contrast, altered precipitation had no significant effect on community pathogen load, indicating that warming has a more important role than precipitation in affecting plant health (Liu et al. 2019). Inconsistent with this finding, it was reported that changes in precipitation can largely influence plant pathogens and plant fitness by altering humidity and water availability (Xin et al. 2016; Romero et al. 2022). For instance, humidity and high temperature are identified as key factors invoking actual fungal plant-disease outbreaks, and *Puccinia* and *Fusarium* are frequently reported as causative agents of plant disease in phyllosphere (Romero et al. 2022). Similarly, a recent study on the phyllosphere of *Eucalyptus* in Australia suggested that precipitation was the most important factor predicting fungal taxonomic diversity and abundance (Chen et al. 2021a). Random forest analysis and structural equation models (SEM) further indicated that precipitation was the best predictor for putative fungal pathogens and can increase its abundance in the phyllosphere (Chen et al. 2021a).

In addition to warming and precipitation, there is a global increase in drought frequency and duration, as well as in extreme weather events including flood and drought (Zhu et al. 2022; Sardans et al. 2008). Increasing researches have showed that drought has important impacts on plant production and health by affecting plant-associated microbiomes and plant-microbiome interactions (Zhu et al. 2022; Santos-Medellin et al. 2021; Gao et al. 2020; Xu et al. 2018; de Vries et al. 2020). Gao and colleagues examined fungal communities associated with soil, root, and leaf compartments of the sorghum under drought stress, and demonstrated that stochastic processes (e.g., drift or stochastic dispersal) dominated mycobiome assembly at the early stage of host development (Gao et al. 2020). Although drought treatment had a significant effect on fungal community structure, there was no signal for stochasticity was observed when drought stress was relieved, indicating that host selection rather than drought plays a more important role in shaping fungal assembly (Gao et al. 2020). All these observations highlighted the importance of improving our understanding of how the phyllosphere mycobiome responses to climate change factors and harnessing the plant mycobiome to improve host fitness under warming, precipitation, and drought stresses.

8.2 Fertilization, Nitrogen Deposition, Acid Rain, and Urbanization

Chemical fertilizers like nitrogen, phosphorus, and potassium are essential for plant growth and health and play a vital role in modern agricultural production. The use of chemical fertilizers, especially for nitrogen fertilizer, is likely to increase significantly in future agricultural production to feed the growing human population (Zhu et al. 2022; Singh et al. 2021). It has been well documented that the overuse of the fertilizers can negatively influence ecosystem function and agricultural production by increasing environmental pollution and soil degradation, such as nitrogen deposition, acid rain, and soil acidification (Carrara et al. 2018; Zhu et al. 2022; Raza et al. 2020). Moreover, increasing evidence showed that excessive chemical fertilization will threaten the diversity, composition, and functioning of soil and plant microbiomes (Fan et al. 2019; Xiong et al. 2021a; Sun et al. 2021a). For example, a recent work on the soil-plant continuum of maize, wheat, and barley has suggested that the excessive application of chemical N fertilizer increased the relative abundance of potential fungal pathogen in the leaf endosphere (Xiong et al. 2021a). Sun and colleagues examined fungal communities associated soil and plant compartments of the sorghum and suggested that the mycobiome in phyllosphere was more resistant than those in soils to fertilization treatments including inorganic, organic, and mixed fertilizations (Sun et al. 2021a). Among the treatments, the NPKM fertilization regime (mineral fertilizers NPK plus organic manure) had a positive effect on fungal alpha diversity in phyllosphere (Sun et al. 2021a). In addition to fertilization regime, agronomic managements (e.g., organic and conventional management) were found to significantly affect microbial diversity and function in soil and plant compartments (Karlsson et al. 2017; Wittwer et al. 2021; Chowdhury et al. 2019). Karlsson and colleagues sampled the wheat leaves from 22 organically and conventionally cultivated fields and found that organic farming increased fungal alpha diversity in the wheat phyllosphere, compared with conventional management (Karlsson et al. 2017).

It has been well documented that nitrogen deposition and acid rain caused by agricultural intensification, industrial pollution, and rapid urbanization are major environmental problems that adversely influence food production, environmental quality, and biogeochemical cycling (Yu et al. 2019; Guo et al. 2010; Zhang et al. 2018b). Previously, numerous studies have explored the impact of nitrogen deposition and acid rain on microbial diversity and composition but still focused on soil and rhizosphere samples (Li et al. 2019; Moore et al. 2021; Zhao et al. 2020). A few recent studies reported that microbial communities living in leaves can take up pollutant nitrogen including wet, dry and gaseous N, and nitrogen deposition and acid rain could drive the assembly changes of the phyllosphere mycobiome (Zhu et al. 2022; Song et al. 2022a, b; Vacher et al. 2016). For example, 2-week NH_3 exposure increased the relative abundance of most fungal genera in phyllosphere, including *Alternaria*, *Cladosporium*, *Sampaiozyma*, *Cystobasidium*, *Gibellulopsis*, and *Cercospora* (Song et al. 2022a). Song and colleagues explored the impact of continuous NO_x exposure on the phyllosphere microbiome and found that NO_x exposure intensify the phyllosphere fungal interactions in co-occurrence networks (Song et al. 2022b). Helander and colleagues tested the influence of simulated acid rain on the occurrence of endophytes and found that the acid rain treatment (pH = 3) decreased approximately 25% of the number of isolated endophytes in the birch phyllosphere (Helander et al. 1993).

In addition, growing evidence has demonstrated a role of rapid urbanization in structuring plant-associated microbial communities (Jumpponen and Jones 2010; Berg and Cernava 2022; Perreault and Laforest-Lapointe 2022). For instance, it was reported that seasonal dynamics of the fungal communities in the *Quercus macrocarpa* phyllosphere differed between urban and nonurban environments, indicating the role of urbanization in the assembly of the phyllosphere mycobiome (Jumpponen and Jones 2010). Imperato and colleagues observed the higher fungal diversity and richness in the phyllosphere of urban environment (Imperato et al. 2019), while Jumpponen et al. found the lower diversity values of that within cities (Jumpponen and Jones 2010). Recently, the researchers investigated the leaves of *Betula pendula* in Moscow at increasing distances from the road; they found that microbial diversity and activity significantly declined with road vicinity, indicating the negative impact of urbanization on phyllosphere fungal diversity and function (Ivashchenko et al. 2022). Taken together, the results demonstrate that multiple global change factors exert the strong effects on many traits of the phyllosphere mycobiome, including fungal diversity, community composition, assembly processes, and biotic interactions. A systematic understanding of ecological and biological mechanisms that govern mycobiome assembly and phyllosphere-mycobiome interactions in the context of global change will provide the pivotal basis for the future plant mycobiome engineering.

9 Future Prospects

Phyllosphere mycobiome owns the extremely high species diversity, and thus should be protected as a hotspot in the global diversity conservation boom. In particular, considering the pressures from deforestation, grassland degradation, irrational use of agricultural fertilizers and pesticides, and urban pollution, it is timely to draw the monitoring of phyllosphere mycobiome into the global biodiversity monitoring network (Guerra et al. 2021). Compared with the phyllosphere fungal studies in natural ecosystems, greater research efforts are needed in agricultural and urban ecosystems. It is because they are more closely correlated with our lives and benefits. Rhizosphere microbiome optimization and synthetic colony techniques has been considered as an important way to solve the future food crisis (Zhang et al. 2017). Obviously, a better understanding of the mechanism of community assembly of phyllosphere fungi will further help us to develop climate-smart agriculture and maintain the crop health (Trivedi et al. 2020). In addition, monitoring the phyllosphere fungal community dynamics in urban greenery will provide new ideas and approaches for monitoring and altering urban environmental pollution.

As phyllosphere fungi are accessible, replicated and easily manipulated, they are well suited for theoretical studies in ecology and biogeography (Andrews and Harris 2000). Several factors that drive the variation in phyllosphere fungal communities have been identified, however, it is more difficult for us to generalize about their distribution patterns and succession dynamics. Currently, we still lack the global-scale and standardized research paradigm for biogeography of phyllosphere fungi. Fungal taxonomic diversity may not be always correlated with their functional diversity. How much is the functional redundancy of phyllosphere mycobiome at the global scale? Trait-based approaches, as an important direction for the phyllosphere mycobiome studies, will hopefully give us some clues (Zanne et al. 2020).

In terms of technology, drone mounted robotic arms will boost the sampling work for phyllosphere fungal researches. Compared with the traditional sampling methods, such as using pruning shears, professional tree climbers and shotgun collection, drone sampling will help us acquire the leaf samples at the high-height canopy more effectively and safely. For example, we may survey the phyllosphere mycobiome of *Sequoia sempervirens* along its whole trunk, which is one of the tallest trees in the world. In addition, the in-depth integration of remote sensing and omics will correlate the fungal taxonomic and functional diversity to the entire ecosystem functioning (e.g., Liu et al. 2022). As Albert Einstein said, the more we see, the less we know. For phyllosphere mycobiome, we only begin to scratch the surface of such important microorganisms. More and more researches and reviews in these areas will be helpful in evaluating and predicting the variation in diversity and function of phyllosphere mycobiome, and providing the new theoretical guide for agricultural application and ecological protection in the context of global change.

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