

MINIREVIEW

Viruses of fungi and oomycetes in the soil environment

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ABSTRACT

Soils support a myriad of organisms hosting highly diverse viromes. In this minireview, we focus on viruses hosted by true fungi and oomycetes (members of Stamenopila, Chromalveolata) inhabiting bulk soil, rhizosphere and litter layer, and representing different ecological guilds, including fungal saprotrophs, mycorrhizal fungi, mutualistic endophytes and pathogens. Viruses infecting fungi and oomycetes are characterized by persistent intracellular nonlytic lifestyles and transmission via spores and/or hyphal contacts. Almost all fungal and oomycete viruses have genomes composed of single-stranded or double-stranded RNA, and recent studies have revealed numerous novel viruses representing yet unclassified family-level groups. Depending on the virus–host combination, infections can be asymptomatic, beneficial or detrimental to the host. Thus, mycovirus infections may contribute to the multiplex interactions of hosts, therefore likely affecting the dynamics of fungal communities required for the functioning of soil ecosystems. However, the effects of fungal and oomycete viruses on soil ecological processes are still mostly unknown. Interestingly, new metagenomics data suggest an extensive level of horizontal virus transfer between plants, fungi and insects.

Keywords: mycovirus; RNA virus; soil ecosystem; soil microorganisms; virome; virus effects

INTRODUCTION

Soils are inhabited by a variety of microorganisms required for the functioning of soil ecosystem services. These microbial groups, including bacteria, archaea, protozoa, algae, fungi and oomycetes, all harbor viruses, intracellular infectious agents depending on a living host cell for replication. Of their viruses, bacteriophages hosted by bacteria are by far the most common and diverse virus group (Pratama and van Elsas 2018; Williamson, Fuhrmann and Wommack 2017). The soil bacterial virome shows habitat-type specificity and greater diversity than in any other ecosystem, including the extensively studied marine ecosystem (Paez-Espino et al. 2016; Williamson,

Fuhrmann and Wommack 2017; Graham et al. 2019, unpublished). This possibly reflects the spatial soil structure that supports separate microhabitats having the potential for accelerating parallel evolution (Pratama and van Elsas 2018). In contrast to marine ecosystems, where the contribution of bacterial viruses to carbon and nutrient cycling is well recognized (Breitbart 2012), the putative role of soil viruses to ecological processes is only beginning to unravel. Recently, auxiliary metabolic genes associated with the decomposition of soil organic matter have been discovered from soil viromes, implicating that bacteriophages could potentially transfer these genes among hosts and, thus, contribute to soil carbon cycling (Emerson et al. 2018; Trubl et al. 2018; Graham et al. 2019, unpublished). Furthermore,

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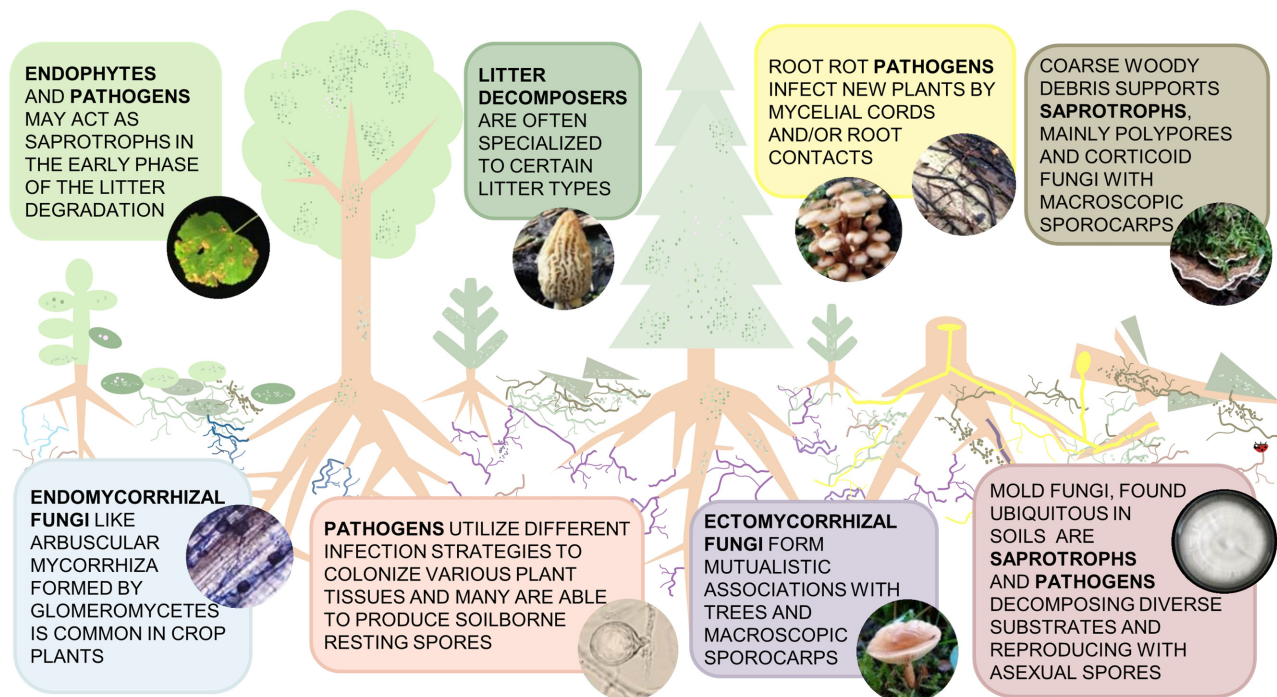


Figure 1. Illustration presenting main ecological guilds of fungi and oomycetes inhabiting soil, rhizosphere and plant debris (litter layer). Here, the hosts are categorized as saprotrophs, mycorrhizal fungi, mutualistic endophytes and pathogens based on their utilization of environmental resources. However, it is common that the same species may utilize more than one ecological niche depending on the environment, and possible plant host, which aids them to thrive in diverse conditions. In particular, the life strategy of endophytes seems to be plant-specific, and, thus, an endophyte can function as a commensalist with one plant species and as a pathogen with another. Even though many endophyte species complete their life cycle above the ground, many are also found present in soil after litterfall or as spores. Arbuscular mycorrhizal picture courtesy of Sannakajsa Velmala.

Graham et al. (2019, unpublished) showed that viruses could aid the transfer of metabolic functions as fungal chitinase was detected in soil bacteriophage sequences. Still, the viruses of archaea, protozoa and microalgae (e.g. Pagnier et al. 2013; Aherfi et al. 2016; Büdel et al. 2016; Nagasaki 2008; Krupovic et al. 2018; Lefkowitz et al. 2018; Schulz et al. 2018) as well as fungi and oomycetes have remained less well known, and very little is known about their ecological effects in soil habitats.

In this minireview, we will focus on viruses infecting two important microbial groups sharing similar life strategies and partly related virus communities: true fungi and oomycetes (members of Stramenopila, Chromalveolata). These organisms exhibit filamentous mycelial growth, reproduction by spores, and similar nutrition acquisition strategies by secreting extracellular enzymes to break down complex nutrients and recovering simple sugars by osmotrophy (Richards et al. 2006). Moreover, they inhabit comparable ecological niches and host persistent virus infections. Soils harbor highly diverse fungal communities shaping the structure of microbial and plant communities and playing key roles in the decomposition of organic matter and nutrient cycling (Tedersoo et al. 2014; Treseder and Lennon 2015; Peay, Kennedy and Talbot 2016; Fraç et al. 2018). The high phenotypic plasticity of fungi and oomycetes enables them to colonize dissimilar microhabitats and sustain variable environmental conditions, which is advantageous in spatially and temporally heterogeneous habitats like soil. For instance, they are able to resist unfavorable conditions by producing survival structures such as resting spores, and, furthermore, some fungi may form resistant mycelial chords facilitating an effective spread from one resource to another. Besides being able to adopt different forms in response to environmental conditions, their capability

to degrade complex polymers enables them to utilize diverse life strategies and contribute to most ecological processes occurring in soils (Peay, Kennedy and Talbot 2016; Fraç et al. 2018).

In a study addressing the global diversity of soil fungi, Tedersoo et al. (2014) detected more than 80 000 fungal species-level operational taxonomic units (OTUs) from 365 separate locations representing divergent soil ecosystems such as arctic tundra, boreal, tropical and temperate forests, grassland or shrubland, and savanna and Mediterranean vegetation. Overall, the most abundant fungal ecological guilds present in soils were saprotrophs, ectomycorrhizal mutualists and plant pathogens. These fungal groups have very different life strategies, and the two latter groups are closely associated with living plants. For this reason, the present minireview will cover soil-dwelling fungi in a broad sense, i.e. including fungal species capable of growing and reproducing in bulk soil, but also species present in the rhizosphere, plant roots and litter layer, as outlined in Fig. 1.

Taxonomically, the largest proportion of fungal species-level OTUs detected by Tedersoo et al. (2014) consisted of members of Basidiomycota, Ascomycota, Mortierellomycotina and Mucoromycotina, all of which are known to host viruses. Besides these dominant soil-associated fungi, viruses also occur in Glomeromycotina as well as in many basal clades of kingdom Fungi. For example, viruses with RNA genomes are harbored by *Allomyces arbuscula* (Khandjian et al. 1977), a member of Blastocladiomycota, including many saprobic or parasitic species dwelling in tropical soils and fresh water bodies. RNA viruses are also present in an animal parasitic microsporidium of phylum Cryptomycota (Pyle, Keening and Nibert 2017), and *Entomophthora muscae*, a member of Zoopagomycota (Nibert et al. 2019). Moreover, fungi of genus *Olpidium* (phylum

Olpidiomycota) act as vectors for many plant viruses [see the chapters on virus families *Virgaviridae*, *Ophioviridae* (currently *Aspiviridae*) and *Tombusviridae* in the ninth report of the International Committee on Taxonomy of Viruses (ICTV) by King et al. 2011]. Regardless of these intriguing findings, fungal and oomycete virology has so far concentrated on viruses infecting important plant pathogens. Therefore, most fungi known to host viruses originate from agricultural or forest habitats, and much less is known about the viromes of fungi inhabiting natural habitats like wetlands, grasslands, deserts and tundra. Moreover, the virus communities of saprotrophic or mutualistic fungi are still poorly known, despite their central role in the maintenance of soil ecosystem services.

Virus diversity and classification among fungi and oomycetes

Most fungal viruses (mycoviruses) have small genomes encoding only a few proteins (Ghabrial et al. 2015; Lefkowitz et al. 2018). The simplest of all known viruses are mitoviruses in the family *Narnaviridae* (Table 1; Fig. 2), which encode only a single protein, the RNA-dependent RNA polymerase (RdRp) required for virus replication. Moreover, members of the virus families *Partitiviridae* and *Totiviridae* typically encode only a polymerase and a capsid protein providing a protective coat for the virus genome. The mature virion may include one or several genome segments (Table 1; Fig. 2), and the polymerase may be associated with the genomic nucleic acid within the virus particle. The vast majority of fungal and oomycete viruses found so far have single-stranded RNA (ssRNA) or double-stranded RNA (dsRNA) genomes, corresponding to the so-called Baltimore classes III, IV and V (Baltimore 1971). Viruses in genus *Mitovirus* of family *Narnaviridae* (and possibly members of family *Botourmiaviridae*) replicate inside host mitochondria, whereas other known fungal viruses are cytosolic. The cellular location of the viruses may have an effect on their mode of replication and transmission, as well as the resistance towards host RNA silencing (Shahi et al. 2019).

Fungal and oomycete viruses with RNA genomes represent viral realm *Riboviria*, which was recently proposed to include six phyla (Koonin et al. 2019; the ICTV taxonomic proposal 2019.006G.N.v1.Riboviria). Fungal viruses with positive-sense ssRNA (+RNA) genomes are currently included in eight families (Table 1), whereas only one family (*Mymonaviridae*) encompasses viruses with negative-sense ssRNA genomes (Lefkowitz et al. 2018). Moreover, numerous mycoviruses representing at least seven different families have dsRNA genomes (Table 1). Most fungal viruses have unenveloped protein capsids, but many are also capsidless. These virus groups, such as members of families *Hypoviridae*, *Narnaviridae* and *Endornaviridae*, have been found to be associated with lipid vesicles derived from the host and show phylogenetic affinities to +RNA viruses with dsRNA replicative intermediates (Koonin and Dolja 2014). The lack of capsid proteins among many mycoviruses is considered to result from their intracellular mode of transmission (see below).

The only mycoviruses with single-stranded DNA (ssDNA) genomes found so far are included in family *Genomoviridae*. Moreover, a unique double-stranded DNA virus (*Rhizidiomyces* virus) has been found in the aquatic stramenopile *Rhizidiomyces* (Dawe and Kuhn 1983). Virus families *Metaviridae* and *Pseudoviridae* produce virus-like capsids, but represent noninfectious retrotransposable elements found in ascomycetous yeast fungi, plants, insects and nematodes (Lefkowitz et al. 2018).

In addition to these approved families and genera, several newly discovered virus groups await classification. Many of them are dsRNA viruses that can be affiliated with the proposed phylum 'Pisugruviricota' (Koonin et al. 2019), formerly referred to as the 'Picornavirus supergroup' (Koonin and Dolja 2014; Wolf et al. 2018). These include viruses with bisegmented genomes related to the mutualistic *Curvularia* Thermal Tolerance virus, nonsegmented viruses tentatively named 'unimaviruses' (Kotta-Loizou, Sipkova and Coutts 2015) and 'ustiviruses' (Herrero 2016), and viruses with segmented genomes named 'polymycoviruses' (Kotta-Loizou and Coutts 2017; see Table 2). There are also at least three novel groups affiliated with phylum 'Pisugruviricota' that have nonsegmented +RNA genomes. These include 'fusariviruses' (Zhang et al. 2014) and 'yadokariviruses' (Hisano et al. 2018), and the unclassified *Sclerophthora* macrospora virus B resembling plant sobemoviruses (Yokoi et al. 1999). Two unique astro-like +RNA viruses also infect the oomycete *Phytophthora infestans*. Another proposed phylum named 'Duplornaviricota' encompasses dsRNA viruses (Wolf et al. 2018; Koonin et al. 2019), and three unclassified mycovirus groups, tentatively named 'fusagraviruses' (Wang et al. 2016a), 'phlegviruses' (Petrzik et al. 2016) and 'alternaviruses' (Kozlakidis et al. 2013), can be affiliated with this phylum.

In turn, several new mycovirus groups with +RNA genomes can be affiliated with the proposed phylum 'Kitrinoviricota' (Koonin et al. 2019), which includes the so-called 'Alphavirus supergroup' (Wolf et al. 2018). The unclassified *Sclerotinia* sclerotiorum RNA virus L resembles members of family *Hepeviridae* and tobamoviruses (Liu et al. 2009), and tobamo-like viruses (family *Virgaviridae*) also occur in the powdery mildew fungus *Podosphaera prunicola* (Pandey, Naidu and Grove 2018a). The oyster mushroom spherical virus resembles tymoviruses (Yu, Lim and Lee 2003). Noda-Tombus-like +RNA viruses occur in the oomycetes *Sclerophthora macrospora* and *Plasmopara halstedii* (Yokoi, Yamashita and Hibi 2003; see Table 2), and members of the proposed family 'Ambiguiviridae' (Gilbert et al. 2019, unpublished) also show resemblance to family *Tombusviridae*. Also bunya-type negative-sense ssRNA viruses (putative members of phylum *Negarnaviricota*) have been recently found in fungi, including *Fusarium poae* (Osaki et al. 2016) and *Botrytis cinerea* (Donaire, Pagán and Ayllón 2016). Furthermore, virus sequences related to plant negative-sense ophioviruses (*Aspiviridae*) have been found in *Rhizoctonia solani* (Marzano et al. 2016).

The constant discovery of novel virus species and family-level groups suggests that a large part of viral diversity among fungi and oomycetes still remains unknown. Transcriptomic (RNA-Seq) data collected from fungi have been exploited to determine numerous novel mycoviral sequences in various fungal hosts (Gilbert et al. 2019, unpublished). Moreover, the accumulating availability of high-throughput sequencing datasets has recently allowed identification of a plethora of new viruses with mycovirus affinities in insect-derived sequences. This has revealed several new representatives of yet unclassified virus groups and therefore changed our view of their occurrence in various hosts (Shi et al. 2016).

Mycovirus transmission within and between host species

In contrast to bacteriophages, fungal and oomycete viruses are not known to cause lysis of host cells. Instead, they cause persistent infections and are transmitted intracellularly during cell division, hyphal anastomosis and the formation of

Table 1. List of currently recognized virus families with fungal and oomycete members. The data are based on Howitt et al. (2001; 2006), Suzuki et al. (2004), King et al. (2011), Tidona and Darai (2011), Lin et al. (2012) and Lefkowitz et al. (2018).

Virus family or realm	Genera infecting fungi/oomycetes	Type species or representative mycovirus. Exemplar fungal or oomycete genera hosting similar viruses	Nucleic acid	Number and size of genome segments	Morphology
Genomoviridae	Gemycircularvirus	<i>Sclerotinia gemycircularvirus</i> 1	ssDNA	1 (2.2 kb, circular)	20–22 nm virion, isometric protein capsid
Not determined	Rhizidiavirus	<i>Rhizidiomyces virus</i>	dsDNA	1 (Mr = 16.8 × 10 ⁶)	60-nm virion, isometric protein capsid
Chrysoviridae ^a	Alphachrysovirus	<i>Penicillium chrysogenum virus</i> . Also found in <i>Aspergillus</i> , <i>Cryphonectria</i> , <i>Fusarium</i> , <i>Helminthosporium</i> , <i>Isaria</i> , <i>Macrophomina</i> , <i>Verticillium</i>	dsRNA	4 (2.4–3.6 kb)	35–40 nm virion, isometric protein capsid
	Betachrysovirus	<i>Botryosphaeria dothidea chrysovirus</i> . Also found in <i>Alternaria</i> , <i>Colletotrichum</i> , <i>Fusarium</i> , <i>Magnaporthe</i> , <i>Penicillium</i>			
Megabirnaviridae ^b	Megabirnavirus	<i>Rosellinia necatrix megabirnavirus</i> 1	dsRNA	2 (7.2–8.9 kb)	50-nm virion, isometric protein capsid
Riboviria	Botybirnavirus ^c	<i>Botrytis porri botybirnavirus</i> 1	dsRNA	2 (5.9–6.2 kb)	Virions ca. ~35 nm in diameter
Partitiviridae ^d	Alphapartitivirus	<i>Helicobasidium mompa partitivirus</i> V70. Also found in <i>Chondrostereum</i> , <i>Flammulina</i> , <i>Heterobasidium</i> , <i>Rosellinia</i>	dsRNA	2 (1.4–2.4 kb)	30–40 nm virion, isometric protein capsid
	Betapartitivirus	<i>Atkinsonella hypoxylon virus</i> . Also found in <i>Fusarium</i> , <i>Heterobasidium</i> , <i>Pleurotus</i> , <i>Rhizoctonia</i> , <i>Rosellinia</i>			
	Gammapartitivirus	<i>Penicillium stoloniferum virus</i> S. Also found in <i>Aspergillus</i> , <i>Fusarium</i> , <i>Gremmeniella</i> , <i>Ophiostoma</i>			
Reoviridae	Mycoreovirus ^e	<i>Mycoreovirus</i> 1	dsRNA	11–12 (0.7–4.1 kb)	80-nm double-shelled virion, icosahedral protein capsid
Totiviridae	Totivirus ^f	<i>Saccharomyces cerevisiae virus</i> L-A. Also found in <i>Scheffersomyces</i> , <i>Tuber</i> , <i>Ustilago</i> , <i>Xanthophyllomyces</i>	dsRNA	1 (4.6–6.3 kb)	30–40 nm virion, isometric protein capsid
	Victorivirus ^g	<i>Helminthosporium victoriae virus</i> 190S. Also found in <i>Aspergillus</i> , <i>Beauveria</i> , <i>Coniothyrium</i> , <i>Epichloë</i> , <i>Gremmeniella</i> , <i>Helicobasidium</i> , <i>Helminthosporium</i> , <i>Magnaporthe</i> , <i>Rosellinia</i> , <i>Sphaeropsis</i> , <i>Tolyocladium</i> , <i>Thielaviopsis</i>			
Quadriviridae	Quadrivirus	<i>Rosellinia necatrix quadrivirus</i> 1	dsRNA	4 (3.7–4.9 kb)	45-nm virion, isometric protein capsid
Alphaflexiviridae	Botrexvirus	<i>Botrytis virus</i> X	ssRNA (+)	1 (7.0 kb)	720-nm flexuous rod-shaped particle
	Sclerodarnavirus	<i>Sclerotinia sclerotiorum</i> debilitation-associated RNA virus			
Barnaviridae	Barnavirus ^h	<i>Mushroom bacilliform virus</i>	ssRNA (+)	1 (4.0 kb)	18–20 × 48–53 nm bacilliform virions
	Mycoflexivirus	<i>Botrytis virus</i> F	ssRNA (+)	1 (6.8 kb)	720-nm flexuous rod-shaped particle
Gammaflexiviridae ⁱ	Deltaflexivirus	<i>Sclerotinia deltaflexivirus</i> 1. Also found in <i>Fusarium</i>	ssRNA (+)	1 (6.7 kb)	Probably not encapsidated
Endornaviridae ^j	Alphaendornavirus	<i>Helicobasidium mompa alphaendornavirus</i> 1. Also found in <i>Erysiphe</i> , <i>Phytophthora</i> , <i>Rhizoctonia</i>	ssRNA (+)	1 (9.7–17.6 kb)	Vesicle-like structures, no capsid
	Betaendornavirus	<i>Sclerotinia sclerotiorum betaendornavirus</i> 1. Also found in <i>Alternaria</i> , <i>Botrytis</i> , <i>Gremmeniella</i> , <i>Tuber</i>			
Hypoviridae	Hypovirus ^k	<i>Cryphonectria hypovirus</i> 1	ssRNA (+)	1 (9.1–12.7 kb)	50–80 nm pleomorphic vesicles, no true virion
Narnaviridae	Narnavirus ^l	<i>Saccharomyces</i> 20S RNA narnavirus	ssRNA (+)	1 (2.3–3.6 kb)	Ribonucleoprotein complex, no true virion

Table 1. Continued

Virus family or realm	Genera infecting fungi/oomycetes	Type species or representative mycovirus. Exemplar fungal or oomycete genera hosting similar viruses	Nucleic acid	Number and size of genome segments	Morphology
	Mitovirus ^m	<i>Cryphonectria mitovirus</i> 1. Also found in <i>Ophiostoma</i>			
Botourmiaviridae	Botoulivirus	<i>Botrytis botoulivirus</i> . Also found in <i>Sclerotinia</i>	ssRNA (+)	1 (2.4–3.2 kb)	Unencapsidated
	Magoulivirus	<i>Magnaporthe magoulivirus</i> 1. Also found in <i>Rhizoctonia</i>			
Mymonaviridae ⁿ	Scleroulivirus	<i>Sclerotinia scleroulivirus</i> 1			
	Sclerotimonavirus	<i>Sclerotinia sclerotimonavirus</i>	ssRNA (–)	1 (10 kb)	Filamentous helical nucleocapsid of 22 × 200–2000 nm
Pseudoviridae	Pseudovirus	<i>Saccharomyces cerevisiae</i> Ty1 virus	ssRNA	1 (5–9 kb)	60–80 nm virus-like particles
	Hemivirus	<i>Saccharomyces cerevisiae</i> Ty5 virus. Also found in <i>Candida</i>			
Metaviridae ^o	Metavirus	<i>Saccharomyces cerevisiae</i> Ty3 virus. Also found in <i>Cladosporium</i> , <i>Fusarium</i> , <i>Schizosaccharomyces</i>	ssRNA	1 (4–10 kb)	Virus-like particles, undetermined size

Unclassified fungal and oomycete viruses in the NCBI Taxonomy Browser (13 May 2019):

^aUnclassified Chrysoviridae: *Agaricus* (bisporus virus 1, La France disease), *Beauveria*.

^bUnclassified Megabirnaviridae: *Ceratobasidium*, *Entoleuca*, *Fusarium*, *Pleosporales*, *Rhizoctonia*, *Sclerotinia*.

^cUnclassified Botybirnavirus: *Alternaria*, *Sclerotinia*.

^dUnclassified Alphapartitivirus: *Rhizoctonia*; Betapartitivirus: *Rosellinia*; Betapartitivirus: *Lentinula*, *Rosellinia*; Gammapartitivirus: *Pythium*.

^eUnclassified Mycoreovirus: *Sclerotinia*.

^fUnclassified Totivirus: *Aspergillus*, *Botryotinia*, *Gremmeniella*, *Helicobasidium*, *Ophiostoma*, *Phomopsis*.

^gUnclassified Victorivirus: *Alternaria*, *Botryosphaeria*, *Botrytis*, *Fusarium*, *Nigrospora*, *Sclerotinia*, *Ustilaginoidea*.

^hUnclassified Barnavirus: *Rhizoctonia*.

ⁱUnclassified Gammaflexiviridae: *Entoleuca*.

^jUnclassified Endornaviridae: *Agaricus*, *Arthrocladiella*, *Botrytis*, *Ceratobasidium*, *Gyromitra*, *Leucostoma*, *Morchella*, *Rosellinia*, *Thielaviopsis*.

^kUnclassified Hypovirus: *Ceratobasidium*, *Entoleuca*, *Fusarium*, *Macrophomina*, *Phomopsis*, *Rosellinia*, *Sclerotinia*, *Sclerotium*, *Setosphaeria*, *Trichoderma*, *Valsa*.

^lUnclassified Narnavirus: *Aspergillus*, *Beauveria*, *Fusarium*.

^mUnclassified Mitovirus: *Agaricus*, *Alternaria*, *Aspergillus*, *Botrytis*, *Buergenerula*, *Ceratobasidium*, *Clitocybe*, *Colletotrichum*, *Cronartium*, *Cytospora*, *Entomophthora*, *Erysiphe*, *Fusarium*, *Gigaspora*, *Gremmeniella*, *Helicobasidium*, *Heterobasidium*, *Hymenoscyphus*, *Leptosphaeria*, *Leucostoma*, *Loramycetes*, *Macrophomina*, *Nigrospora*, *Ophiocordyceps*, *Puccinia*, *Rhizoctonia*, *Rhizophagus*, *Sclerotinia*, *Setosphaeria*, *Thielaviopsis*, *Tuber*, *Valsa*.

ⁿUnclassified Mymonaviridae: *Botrytis*.

^oUnclassified Metaviridae: *Penicillium*.

sexual and asexual spores. Therefore, the horizontal transmission of fungal viruses is regulated by host systems controlling hyphal fusion, including somatic (vegetative) incompatibility, mating type incompatibility and intersterility (Cortesi et al. 2001; Ihrmark, Stenström and Stenlid 2004; Wu et al. 2017). Consequently, virus transmission usually occurs only between strains of the same fungal species.

The establishment of mycelial contacts largely depends on the continuous availability of suitable growth substrates for the interacting fungi. In addition, cellular contacts may form between established mycelia and spores landing on the same substrate. Vegetative (conidial) and sexual spores provide means for both long- and short-range dispersal for the fungus via insect vectors, watersplashes or wind, and a concomitant spread of mycoviruses. In many ascomycetous microfungi, such as *Aspergillus nidulans*, *Penicillium stoloniferum*, *Ustilaginoidea virens* and *Ophiostoma ulmi*, viruses are efficiently transferred to asexual conidial spores, and up to 90–100% of single conidia harbor viruses (Demarini et al. 1977; Rogers, Buck and Brasier 1986; Coenen et al. 1997; Jiang et al. 2015). Virus transmission by anastomosis and virus presence in 100% of asexual zoospores have also been observed in the oomycete *Phytophthora infestans* (Cai et al. 2018).

However, virus transmission into sexual spores is usually very limited in ascomycetes. For example, in the plant

pathogens *Gremmeniella abietina* and *Rosellinia necatrix*, viruses are usually eliminated during ascospore formation, while ascospores of the rice blast fungus (*Magnaporthe grisea*) harbor viral dsRNA elements (Chun and Lee 1997; Ikeda et al. 2004). Transmission of dsRNA elements through conidia as well as ascospores with an incidence of 30–100% was also reported in the wheat pathogen *Fusarium graminearum* (Chu et al. 2004). Among basidiomycetous root rot fungi, dsRNA viruses have been detected both in conidial spores (Ihrmark et al. 2002) and basidiospores of *Heterobasidium* species (Vainio et al. 2015), whereas in *Helicobasidium mompa*, basidiospores seem to be devoid of viruses (Ikeda et al. 2004).

After successful virus transmission from one host to another, mycovirus propagation can be regulated by host RNA silencing, which serves as an antiviral defense system targeting various fungal viruses (Segers et al. 2007; Hammond et al. 2008; Chiba et al. 2013a; Yaegashi et al. 2013a; 2016; Mochama et al. 2018). Preexisting viral infections in a mycelium may also affect the transmissibility of other viruses. For example, the transmission of *Rosellinia necatrix* partitivirus 1 is hindered by the presence of a mycoreovirus in the recipient fungal mycelium (Yaegashi et al. 2011). On the other hand, the presence of a debilitation-associated mycovirus may turn down host incompatibility, enhancing the establishment of subsequent virus infections as seen in the white mold fungus *Sclerotinia sclerotiorum* (Wu

Table 2. List of unclassified fungal and oomycete virus groups (see the text for references). The higher level affiliations (proposed virus phyla) are based on the phylogenetic analysis of RdRp sequences by Wolf *et al.* (2018) and a recent ICTV taxonomic proposal (IC2019.006G.N.v1.Riboviria) by Koonin *et al.* (2019).

Proposed virus phylum	Proposed name or affiliation with known families	Representative mycovirus (GenBank accession in parentheses). Exemplar fungal or oomycete genera hosting similar viruses	Nucleic acid	Number and size of genome segments	Morphology
'Duplornaviricota'	'Fusagravirus'	<i>Fusarium graminearum</i> virus 3 (GQ140626). Also found in <i>Rosellinia</i> , <i>Sclerotinia</i> , <i>Botrytis</i> , <i>Macrophomina</i> , <i>Phlebiopsis</i> , <i>Diplodia</i>	dsRNA	1 (9 kb)	Probably not encapsidated
'Duplornaviricota'	'Alternaviridae'	<i>Alternaria alternata</i> virus 1 (AB438027–9; AB368492). Also found in <i>Aspergillus</i> , <i>Fusarium</i>	dsRNA	3–4 (1.4–3.6 kb)	Isometric 33-nm virions
'Duplornaviricota'	'Phlegivirus'	<i>Phlebiopsis gigantea</i> mycovirus dsRNA 1 (AM111096). Also found in <i>Thelephora</i> , <i>Lentinula</i> , <i>Rhizoctonia</i>	dsRNA	1 (10–11.6 kb)	Probably not encapsidated
'Pisugruviricota'	Partiti-like	<i>Curvularia Thermal Tolerance</i> virus (EF120984–5). Also found in <i>Penicillium</i> , <i>Cryphonectria</i> , <i>Heterobasidion</i> , <i>Gremmeniella</i> , <i>Fusarium</i> , <i>Lactarius</i> , <i>Rhizoctonia</i>	dsRNA	2 (1.8–2.2 kb)	Isometric 27-nm virions found in <i>Curvularia</i> sp.
'Pisugruviricota'	'Unirnavirus'	<i>Alternaria longipes</i> dsRNA virus 1 (KJ817371). Also found in <i>Beauveria</i> , <i>Penicillium</i> , <i>Ustilaginoidea</i>	dsRNA	1 (2.7–3.4 kb)	Unknown
'Pisugruviricota'	'Ustivirus'	<i>Ustilaginoidea vires</i> nonsegmented virus 1 (KJ605397). Also found in <i>Nigospora</i> , <i>Purpureocillium</i>	dsRNA	1 (2.9–3.8 kb)	Unknown
'Pisugruviricota'	'Polymycoviridae'	<i>Aspergillus fumigatus</i> polymycovirus-1 (HG975302–5). Also found in <i>Beauveria</i> , <i>Botryosphaeria</i> , <i>Cladosporium</i> , <i>Sclerotinia</i> , <i>Penicillium</i>	dsRNA	4–7 (0.9–2.4 kb)	No virions found
'Pisugruviricota'	'Fusariviridae'	<i>Fusarium graminearum</i> virus DK21 (AY533037). Also found in <i>Rosellinia</i> , <i>Sclerotinia</i> , <i>Pleospora</i> , <i>Penicillium</i> , <i>Macrophomina</i> , <i>Neofusicoccum</i> , <i>Agaricus</i> , <i>Nigospora</i> , <i>Sclerotinia</i> , <i>Alternaria</i>	ssRNA (+)	1 (6–7.8 kb)	Probably not encapsidated
'Pisugruviricota'	'Yadokariviridae'	Yado-kari virus 1 (LC006253) of <i>Rosellinia necatrix</i> . Also found in <i>Fusarium</i> , <i>Aspergillus</i> , <i>Penicillium</i>	ssRNA (+)	1 (6.3 kb)	Trans-encapsidated with the totivirus Yado-nushi virus
'Pisugruviricota'	Sobemo-like	<i>Sclerophthora macrospora</i> virus B (AB012756) (unique among fungi)	ssRNA (+)	1 (5.5 kb)	32-nm isometric particles
'Pisugruviricota'	Astro-like	<i>Phytophthora infestans</i> RNA virus 1 (FJ373316–18; unique)	ssRNA (+)	2 (2.7–3.1 kb)	No virions found
Undetermined	Astro-like?	<i>Phytophthora infestans</i> RNA virus 2 (MH013270; unique)	ssRNA (+)	1 (11.2 kb)	No virions found
'Kitrinoviricota'	Tymo-like	Oyster mushroom spherical virus (AY182001). Also found in <i>Agaricus</i> , <i>Rhizoctonia</i>	ssRNA (+)	1 (5.8 kb)	Isometric 27-nm virions
'Kitrinoviricota'	'Hepelivirus'	<i>Sclerotinia sclerotiorum</i> RNA virus L (EU779934). Also found in <i>Rhizoctonia</i>	ssRNA (+)	1 (6 kb)	No virions found
'Kitrinoviricota'	Tobamo-like	<i>Podospaera prunicola</i> tobamo-like virus (KY420046). Also found in <i>Macrophomina</i> , <i>Acidomyces</i>	ssRNA (+)	1 (9.7–11 kb)	Unknown (discovered by high-throughput sequencing)
'Kitrinoviricota'	Noda/Tombus-like	<i>Sclerophthora macrospora</i> virus A (AB083060–62). Also found in <i>Plasmopara</i>	ssRNA (+)	2–3 (1–3 kb)	Isometric 30-nm particles
'Kitrinoviricota'	'Ambiguiviridae'	<i>Diaporthe</i> RNA virus (AF142094). Also found in <i>Magnaporthe</i> , <i>Verticillium</i> , <i>Sclerotinia</i>	ssRNA (+)	1 (2.6–4.5 kb)	Probably not encapsidated
'Negarnaviricota'	Phlebovirus-like	<i>Fusarium poae</i> negative-stranded RNA virus 2 (LC150619)	ssRNA (–)	1 segment found (ca. 6.6–8.5 kb)	Unknown
	Tospovirus-like	<i>Botrytis cinerea</i> negative-stranded RNA virus 1 (LN827956); <i>Pythium polare</i> bunya-like RNA virus 1			
'Negarnaviricota'	Aspiviridae-like	<i>Rhizoctonia solani</i> negative-stranded virus 2 (KP900920); <i>Fusarium poae</i> negative-stranded RNA virus 1 (LC150618)	ssRNA (–)	1 segment found (7.7–8.2 kb, partials)	Unknown

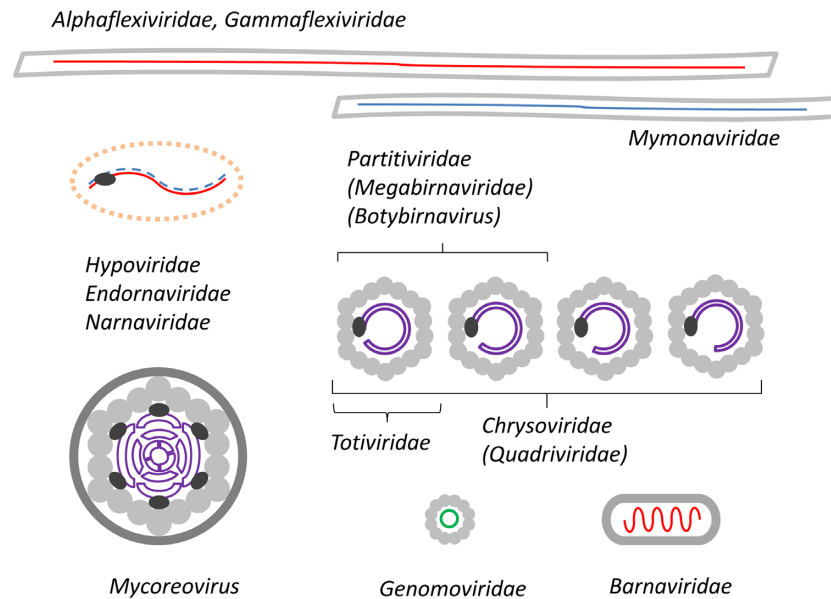


Figure 2. Schematic presentation of virus morphologies in classified mycovirus taxa (see Table 1). Colours indicate the genome type as follows: red, ssRNA (+); blue, ssRNA (-); violet, dsRNA; green, ssDNA. Protein capsids are shown in gray, mycoreoviruses being double-shelled. The dotted oval line demarcates host-derived lipid structures in members of three capsidless +RNA virus families. The polymerase is shown in black if associated with the genome. Different genome segments of single viruses may be encapsidated in one to four separate particles. Virus taxa shown in parentheses are presumed to have indicated morphologies. The readers are referred to the latest ICTV report available online (Lefkowitz et al. 2018) for electromicrographs and 3D models.

et al. 2017). In *Heterobasidion* root rot fungi, moderately related partitiviruses may enhance each other's transmission, whereas highly similar viruses tend to exclude each other, thereby preventing mixed virus infections (Kashif et al. 2019). Antagonistic and mutualistic interactions between mycoviruses have been recently reviewed by Hillman, Annisa and Suzuki (2018).

Despite the limitations posed by cellular incompatibility, mycoviruses are occasionally transmitted across species borders. Viruses have been shown to transmit between different species of genera *Aspergillus* (Coenen et al. 1997; van Diepeningen, Debets and Hoekstra 1998) and *Sclerotinia* (Melzer, Ikeda and Boland 2002). Moreover, a cellular contact between two intersterile *Heterobasidion* species, *H. ecrustosum* and *H. abietinum*, resulted in the subsequent death of the cells involved, but allowed for between-species transmission of the alphapartitivirus *Heterobasidion partitivirus 3* (Vainio et al. 2010). Viruses can also be artificially introduced to more distantly related host species by transfecting fungal protoplasts with purified virions. This has been accomplished, for example, for viruses of the apple root rot pathogen *Rosellinia necatrix* (Kanematsu et al. 2010; Chiba et al. 2013b).

There are no known natural vectors for most mycoviruses. However, the ssDNA virus *Sclerotinia gemycircularvirus 1* of family *Genomoviridae* is infectious as a free particle (Yu et al. 2013), and transmittable by an insect vector (Liu et al. 2016a). Similar genomoviruses are very common in environmental samples (Kraberger et al. 2013; Sikorski et al. 2013). The appearance of novel mycoviruses in *R. necatrix* mycelia during soil incubation has led to the hypothesis that feeding by microarthropods or nematodes may facilitate interspecies transmission of RNA viruses (Yaegashi and Kanematsu 2016). This view is supported by the observation that a 'phlegivirus' of the ectomycorrhizal fungus *Telephora terrestris* occurs in oribatid mites (Petrzik et al. 2016). Further indications of mycovirus transmission between distantly related fungi have been obtained by analyzing

mycoviral sequences in different host species at single habitats (Feldman, Morsy and Roossinck 2012; Vainio et al. 2017).

Based on phylogenetic analysis, it is also probable that virus transmission occasionally occurs between fungi and plants. For example, both plant and fungal viruses are included in the genera *Alphapartitivirus* and *Betapartitivirus*. It has also been demonstrated by *in vitro* transfection that *Penicillium aurantiogriseum partitivirus 1* is capable of replicating in the *Nicotiana tabacum* BY2 cell line (Nerva et al. 2017). On the other hand, tobacco mosaic virus is able to replicate and trigger RNA silencing in the oomycete *Phytophthora infestans* (Mascia et al. 2019). Moreover, the cucumber mosaic virus was recently found to naturally infect the basidiomycetous plant pathogen *Rhizoctonia solani* (Andika et al. 2017). Also mitoviruses, previously shown to infect only fungi, have been recently found in various plant species (Nibert et al. 2018). As mentioned above, *Olpidium* fungi may also serve as vectors for plant viruses, providing a possible route for horizontal virus transmission between plants and fungi. The extensive level of horizontal virus transfer between plants, fungi and insects suggested by recent metagenomics data is discussed by Dolja and Koonin (2018) and Roossinck (2018). Thus far, this view is supported mainly by phylogenetic evidence, and the cellular mechanisms of cross-kingdom virus transmission remain to be elucidated. However, the intimate association between plants and fungal endophytes or pathogens infecting them may provide opportunities for horizontal virus transmission, which may be facilitated by feeding by microarthropods, as mentioned above.

Occurrence of viruses among ecological guilds of soil-dwelling fungi and oomycetes

In this section, we will describe case examples of fungal viruses in the context of their host classified to ecological guilds (Nguyen et al. 2016) as follows: fungal saprotrophs, mycorrhizal fungi,

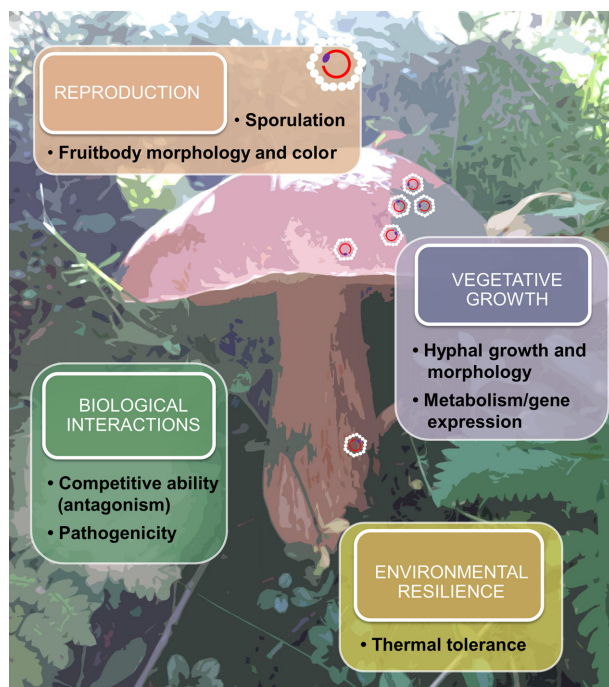


Figure 3. Diverse effects of mycovirus infections on their fungal hosts. Mycovirus infection may decrease host growth, sporulation, virulence and mycotoxin production and cause fruitbody deformation, as described in the text. In turn, infection by certain mycoviruses improves the abiotic stress tolerance, pathogenicity or competitive ability of their host fungi.

mutualistic endophytes and pathogens (Fig. 1). In addition, we cover viruses of oomycetes that share similar ecological roles with fungi (Richards et al. 2006). It should be noted that many fungi can be categorized in more than one ecological guild (Kariman et al. 2018; Selosse, Schneider-Maunoury and Martos 2018); for instance, species of *Heterobasidion* are capable of acting as both necrotrophic pathogens and saprotrophs, while species of *Paxillus* act as both mycorrhizal symbionts and litter decomposers.

Most mycoviruses seem to be associated with asymptomatic persistent infections of their hosts. However, there are several important exceptions (Fig. 3). Because some mycoviruses mediate phenotypic debilitation in their host, they have been investigated for the use as biocontrol agents against plant pathogenic fungi (Xie and Jiang 2014; see below). The model organism for studying mycovirus–host interactions is the Chestnut blight pathogen *Cryphonectria parasitica*, which harbors hypoviruses causing attenuation of host virulence. Hypovirus infections have been shown to alter *C. parasitica* gene expression (Chen et al. 1996; Allen, Dawe and Nuss 2003; Dawe et al. 2003), affect several signaling pathways (Larson, Choi and Nuss 1992; Chen et al. 1996; Turina, Zhang and Van Alfen 2006; Li et al. 2018), perturb host secretion pathways (Kazmierczak et al. 2012; Wang et al. 2016b) and alter DNA methylation of promoter regions (Li et al. 2018). Similarly, mycovirus infections have been shown to affect the transcription levels of genes associated with basic cellular functions in different fungal hosts (e.g. Li et al. 2008; Lee et al. 2014; Ejmal et al. 2018; Vainio et al. 2018). Some mycoviruses are also able to suppress host RNA silencing (Segers et al. 2007; Yaegashi et al. 2013a; Chiba et al. 2016). The reduced host virulence induced by mitoviruses has been connected to mitochondrial malformation and subsequent attenuation of mitochondrial function, and interference of the shikimate pathway

(Rogers, Buck and Brasier 1987; Lakshman, Jian and Tavantzis 1998; Wu et al. 2010).

In contrast, some mycoviruses can provide a selective or competitive advantage to their host fungi. The most striking example is the tripartite symbiotic relationship between the *Curvularia thermal tolerance virus* (CThTV) and its endosymbiotic fungal host infecting the roots of a panic grass, resulting in thermal tolerance at high soil temperatures (Márquez et al. 2007). Based on transcriptome data, the possible mechanisms of heat tolerance may be connected to osmoprotectants, melanin and heat shock proteins (Morsy et al. 2010). Some viruses also benefit plant or animal pathogenic fungi and oomycetes by enhancing their virulence (Ahn and Lee 2001; Lau et al. 2018; Cai et al. 2018). Moreover, the toxin/antitoxin system encoded by satellite elements of certain totiviruses provides a competitive advantage to yeast hosts (see below).

Viruses in saprotrophic fungi of ecological and industrial importance

Saprotrophic fungi are by far the most diverse and dominant ecological fungal guild inhabiting soils (Tedersoo et al. 2014). By degrading organic matter saprotrophs, including litter decomposers, wood decay fungi as well as molds and yeasts release considerable amounts of nutrients and carbon dioxide.

A wide range of microfungi that do not produce large fruiting bodies but spread by abundant asexual spores with characteristic morphological features are commonly referred to as ‘mold fungi’. Soil and plant roots are inhabited by numerous mold fungi of ascomycetous genera *Acremonium*, *Alternaria*, *Aspergillus*, *Fusarium*, *Penicillium*, *Botrytis*, *Sclerotinia* and *Trichoderma*, and also members of genera *Mucor*, *Mortierella* (*Umbelopsis*) and *Rhizopus*, formerly classified as zygomycetes. Viruses have been detected in members of all these genera (see Tables 1 and 2). Many of these fungi have been extensively studied in the laboratory for their industrial uses for the production of antibiotics, enzymes and lipids, but many also cause severe plant diseases, storage rot and toxin production. Some of the first fungal viruses found were strains of partitiviruses and chrysovirus described in *Penicillium stoloniferum* and *P. chrysogenum*, the latter of which is used for the production of penicillin (Banks et al. 1969; Bozarth et al. 1971). More recently, viruses of putative family ‘Fusagraviridae’ have been found in species of *Trichoderma* (Lee et al. 2017), which are ubiquitous in agricultural and forestry soils, and may be used as biocontrol organisms and biostimulants in agricultural crop production. Viruses of pathogenic mold fungi are described in more detail in the following section considering viruses of fungal pathogens.

Litter decomposer fungi are mainly basidiomycetes and ascomycetes capable of degrading plant-derived polymers such as cellulose and hemicellulose in forest and grassland biotopes. In contrast to the richness and ecological importance of litter decomposers, their viruses are poorly known even though the first-known mycovirus was discovered in the commercially cultivated litter decomposer fungus *Agaricus bisporus* (Hollings 1962). This unique barnavirus (Table 1), called Mushroom bacilliform virus, causes a severe die-back disease. It has later been found that the virome of cultivated *A. bisporus* strains is highly diverse and dynamic, and probably supplemented with novel virus infections from wild *Agaricus* populations (Deakin et al. 2017). Among litter decomposers, viruses have also been found in *Clitocybe odora* (Heinze 2012), *Coprinopsis lagopus* (Shahriari, Kirkham and Casselton 1973), *Gymnopus peronatus* (Mori et al.

1978), *Megacollybia platyphylla* (Vainio et al. 2017), *Neolentinus lepideus* (Mori et al. 1978), *Phaeolepiota aurea* (Mori et al. 1978) and putative *Preussia* sp. (Feldman, Morsy and Roossinck 2012). A recent unpublished study by Gilbert et al. (2019) reports finding viral sequences also in many more litter decomposers, including *Gyromitra esculenta*, *Loramyces juncicola*, *Morchella importuna* and *Rutstroemia firma*, in addition to the dung decomposers *Delitschia confertaspera* and *Thelebolus microsporus*.

The species mainly responsible for the decomposition of coarse woody debris are basidiomycetous macrofungi, such as polypores and corticiaceous fungi capable of degrading complex organic polymers, including lignin, cellulose and hemicellulose (white rot fungi) or only the latter two compounds (brown rot fungi). Recently, Mäkipää et al. (2017) showed that 31% of fungal OTUs detected in forest soil and dead wood were shared by both substrates. The pioneer wood decay species include, for example, *Phlebiopsis gigantea*, which is also used as a biocontrol agent against the *Heterobasidion* root rot of conifer trees. This aphylloroid fungus hosts a 'phlegivirus' (named after the host), which has been associated with alterations in the host phenotype (Lim et al. 2011). On the other hand, several edible wood decay fungi have been shown to harbor mycoviruses, as recently reviewed by Sahin and Akata (2018). These wood decomposers include many cultivated species such as the Oyster mushroom (*Pleurotus ostreatus*), shiitake mushroom (*Lentinula edodes*), enokitake mushroom (*Flammulina velutipes*) and maitake mushroom (*Grifola frondosa*) (Yu, Lim and Lee 2003; Magae and Sunagawa 2010; Magae 2012; Komatsu et al. 2019). In these cases, viruses may cause diseases that affect crop production or alter the morphology of the fruiting bodies.

Another important research line in mycovirology has concentrated on viruses of commercially utilized yeasts. Both ascomycetous and basidiomycetous yeasts, characterized by their single-celled form of growth, are common in soil, rhizosphere, plant detritus and phyllosphere, and mostly use simple sugars as a nutritional source. In Baker's yeast, the satellite elements of certain totiviruses, such as *Saccharomyces cerevisiae* virus L-A, provide the host fungus a competitive advantage by encoding a toxin against other yeast strains and an antidote to protect the host (Wickner, Fujimura and Esteban 2013). Yeast strains with such a capacity are described as 'killer yeasts'. Similar toxin systems are found in several other fungi of the *Saccharomycetaceae* family, but also in the corn smut pathogen hosting the unclassified totivirus *Ustilago maydis* virus P4, which produces a toxin benefiting its basidiomycetous host (Allen et al. 2013).

Viruses in mycorrhizal fungi

More than 90% of vascular plants are forming mycorrhizal symbiosis with fungal partners of Ascomycota, Basidiomycota, Glomeromycotina and Mucoromycotina (Brundrett and Tedersoo 2018; Hoystedt et al. 2018). In addition to directly enhancing plant fitness, mycorrhizal fungi play a role in several vital ecosystem processes, including weathering of soil minerals, controlling the decomposition of organic matter, solubilization of mineral nutrients, soil acidification and carbon cycling (Kariman et al. 2018). Mycorrhizas connect root systems of different plant individuals as well as species via mycelial networks, enabling the movement of nutrients, water and carbon products among plant individuals and fungi. Of the principal mycorrhizal types arbuscular, ectomycorrhizal, ericoid and orchid (Brundrett and Tedersoo 2018), all but ericoid mycorrhizae forming fungal species have been shown to harbor mycoviruses; yet, the effects

of viruses on the phenotype or symbiotic ability of mycorrhizal fungi remain mostly unknown.

Most land plants are able to form arbuscular mycorrhizal symbiosis with members of Glomeromycotina (Vigneron, Radhakrishnan and Delaux 2018). So far, mycoviruses have been reported only in few arbuscular mycorrhizal genera, including *Gigaspora* and *Rhizophagus*. *Rhizophagus clarus* strain RF1 (previously known as *Glomus* sp. strain RF1) was found to harbor a 4.6-kb dsRNA element named *Glomus* sp. strain RF1 virus-like medium dsRNA (GRF1V-M), which was related to but distinct from members of family Totiviridae (Ikeda et al. 2012). Moreover, GRF1V-M was found to be more closely related to a protozoan *Giardia* virus and animal viruses than known mycoviruses. The GRF1V-M-free fungal strain RF produced a 2-fold greater number of spores in addition to promoting the growth of perennial grass *Miscanthus sinensis* more efficiently than the GRF1V-M containing lines. Recently, *Gigaspora margarita* was found to harbor a virus similar to GRF1V-M and hence named *G. margarita* *Giardia*-like virus 1 (GmGLV1, Turina et al. 2018). Both GRF1V-M and GmGLV1 resemble members of a newly proposed family 'Megatotiviridae' found in *Rosellinia necatrix* (Arjona-Lopez et al. 2018). Mitoviruses have been reported in both *Rhizophagus* sp. (Ikeda et al. 2012; Kitahara et al. 2014; Neupane et al. 2018) and *G. margarita* (Turina et al. 2018). In addition, *G. margarita* was shown to harbor a putative ourmia-like virus clustering outside the newly classified family *Botourmiaviridae* (Turina et al. 2018). Interestingly, the occurrence of this ourmia-like virus was regulated by the presence or absence of endobacterium *Candidatus Glomeribacter gigasporarum* in the fungal host.

Members of Endogonomycetes, Pezizomycetes and Agaricomycetes form ectomycorrhizal symbiosis with members of 2 Gymnospermae and 28 Angiospermae lineages (Brundrett and Tedersoo 2018). Mycoviral particles have been detected in the macromycete species *Boletus edulis* (Huttinga, Wichers and Dieleman-van-Zaayen 1975), *Craterellus tubaeformis* (Blattný and Králík 1968), *Hebeloma circinans* (Bai et al. 1997), *Laccaria* sp. (Blattný and Králík 1968), *Peziza ostracoderma* (Dieleman-van Zaayen, Igesz and Funch 1970) and *Phaeolepiota aurea* (Mori et al. 1978). More recently, mycoviruses have been found in the macromycete fungal genera *Lactarius*, *Telephora* and *Tuber*. Thus, bisegmented viruses related to the mutualistic CThTV were discovered in *Lactarius rufus* and *L. tabidus* (Vainio et al. 2017), whereas *Telephora terrestris* was found to harbor a 'phlegivirus' (Petřzik et al. 2016). *Tuber* species have been shown to harbor mitoviruses (Stielow et al. 2011a; 2012) in addition to endorna- (Stielow et al. 2011b) and totiviruses (Stielow and Menzel 2010). The putative effects of these viruses on their hosts are still unknown, and thus far, only the occurrence of an uncharacterized globular virus with 28-nm virions has been connected to the fruitbody deformation in *Laccaria laccata* (Blattný and Králík 1968).

Orchid species are highly dependent on orchid mycorrhizal fungi, which include members of Ceratobasidiaceae, Pezizales, Serendipitaceae and Tulasnellaceae, in addition to some fungi typically categorized as ectomycorrhizal symbionts (Brundrett and Tedersoo 2018). Of orchid mycorrhizal fungal isolates, mycoviruses have been detected in the *Ceratobasidium* and orchid-associated multiniche fungi *Aspergillus*, *Penicillium* and *Rhizoctonia*. Australian *Ceratobasidium* isolates have been shown to host several endornaviruses and partitiviruses (Ong et al. 2016, 2017), and, remarkably, single *Ceratobasidium* isolates have been shown to host at least 5 and up to 10 different alpha- and beta-partitiviruses (Ong et al. 2017). Furthermore, based on the *de novo* assembly of RNA-Seq reads, the *Ceratobasidium* isolate F-2012

harbored viral strains similar to toti-, hypo-, megabirna- and mitoviruses, in addition to viruses resembling but distinct from toti- and mitoviruses (Ong et al. 2018).

Mycoviruses in mutualistic endophytes

A variety of fungal species originating from diverse fungal clades can inhabit plants without causing negative effects (Kariman et al. 2018). Mutualistic fungal endophytes have the ability to promote the fitness of plants by several different means, including enhanced mineral uptake and stress resistance (Kariman et al. 2018). Endophytes can be grouped into four classes (Rodríguez et al. 2009), which all have been shown to harbor mycoviruses (Bao and Roossinck 2013). In the current minireview, we cover only fungal hosts belonging to families that have been detected in soil samples (Tedersoo et al. 2014), so clavicipitaceous class 1 endophytes inhabiting the shoots of grasses, such as *Epichloë* (Romo et al. 2007), are not included. Moreover, it should be noted that the trophic strategy of fungal isolates harboring mycoviruses has not been confirmed in every case.

Class 2 endophytes, with members of Pezizomycotina, Agaricomycotina and Pucciniomycotina, inhabit plant roots, stems and leaves, and have a limited diversity in individual hosts but can have high infection frequencies, especially when hosts grow in high-stress habitats (Rodríguez et al. 2009). Mutualistic class 2 endophytes hosting mycoviruses include *Colletotrichum* (Rosseto et al. 2016), *Curvularia protuberata* (Márquez et al. 2007), *Fusarium culmorum* (Herrero, Sánchez Márquez and Zabalgoeazcoa 2009) and *Phoma* sp. (Feldman, Morsy and Roossinck 2012). As mentioned above, the three-way symbiosis of panic grass (*Dichantheium lanuginosum*), mycobiont *C. protuberata* and CThTV enables the plant and the fungus to survive at temperatures neither can tolerate in insolation (Redman et al. 2002; Márquez et al. 2007). CThTV is a vertically transmitted isometric partiti-like mycovirus with a bisegmented genome (Table 2) harbored by *C. protuberata*, which is capable of inhabiting several plants and conferring heat tolerance also to tomatoes (Rodríguez et al. 2008). Related viruses occur in several other fungal species (see Table 2), but none of them have been connected to thermal tolerance.

Thus far, there are only few reports on the mycoviruses of class 3 and 4 endophytes. The third functional endophyte class comprises horizontally transmitted fungi inhabiting above-ground tissues of plants (Rodríguez et al. 2009). The diversity of these endophytes can be extremely high, and, thus, the ecological roles of different species have not been evaluated. Feldman, Morsy and Roossinck (2012) detected several different mycoviral sequences in *Alternaria alternata* hosted by prairie plants. Class 4 endophytes comprise primarily ascomycetous dark septate endophytes colonizing roots of almost 600 different angiosperm and gymnosperm species (Rodríguez et al. 2009; Kariman et al. 2018). The plant–endophyte combination as well as environmental conditions determine whether the interaction is beneficial for the plant partner. Class 4 dark septate endophyte *Phialophora graminicola* acts as a mutualistic endophyte of annual grass *Vulpia ciliata* ssp. *ambigua* (Newsham 1999). Virus-like particles of size 30 nm have been found in one *P. graminicola* isolate (Rawlinson and Muthyalu 1974).

In addition, several entomopathogenic fungi, also found present in soils, have been reported to inhabit plants similarly as endophytes (Vega 2008; Jaber and Ownley 2018). Entomopathogenic fungal endophytes harboring mycoviruses include *Beauveria bassiana* (e.g. Herrero, Sánchez Márquez and Zabalgoeazcoa 2009; Koloniuk, Hrabáková and Petrzik 2015;

Kotta-Loizou and Coutts 2017) and *Cladosporium* sp. (Feldman, Morsy and Roossinck 2012).

Viruses of soil-borne fungal pathogens and their potential use as biocontrol agents

Research efforts on mycoviruses have largely focused on viruses capable of inducing hypovirulence (reduced virulence) in plant pathogenic fungi. These studies have identified a diverse group of mycoviruses that cause phenotypic debilitation in their host fungi and, thus, show the potential to be biocontrol agents. Implementation of these results has been successful in the case of the Chestnut blight fungus, *Cryphonectria parasitica*, in which hypoviruses significantly reduce the pathogenicity of the host. The fungus causes cankers and the mortality of Chestnut trees, and has practically destroyed the natural Chestnut forests in North America. In Europe, the disease is controlled by hypoviruses, which are now spreading naturally among closely related European *C. parasitica* strains (Milgroom and Cortesi 2004; Rigling and Prospero 2018). However, the use of mycoviruses as biocontrol agents may be challenging due to their intracellular nature, limited spread between hosts and variable host tolerance (e.g. Cortesi et al. 2001; Vainio et al. 2018). While numerous mycoviruses have been described from plant pathogenic fungi, this section will focus on those that have been associated with host effects.

Some plant pathogenic fungi have a worldwide distribution, wide ranges of host plants as well as tissue types and a ubiquitous presence in various kinds of soils. These ‘cosmopolitans’ usually either produce very durable survival structures (such as sclerotia, microsclerotia or chlamydospores) and/or have an abundant spore production (as e.g. molds), contributing to their success. They can be opportunistic pathogens that cause severe plant diseases in agricultural, horticultural or silvicultural systems, crop losses in postharvest storage, as well as infections in animals. The viromes of these species have been extensively studied, and many of them are associated with a debilitated host phenotype. Among species of *Botrytis* (gray molds), *B. porri* is infected by the hypovirulence-causing botybirnavirus (Wu et al. 2012), and *Botrytis cinerea* RNA virus 1 representing the tentative virus family ‘Fusagraviridae’ is also associated with host hypovirulence (Yu et al. 2015). *Botrytis cinerea* also hosts a debilitation-associated mitovirus (Wu et al. 2010). The multihost white mold fungus *S. sclerotiorum* uses soil litter as a reservoir for sclerotia, which produce sporulating fruiting bodies, and hosts several hypovirulence-causing viruses, such as the alphaflexivirus *Sclerotinia sclerotiorum* debilitation-associated RNA virus (Xie et al. 2006), the unclassified betapartitivirus *Sclerotinia sclerotiorum* partitivirus 1 and the previously mentioned gemy-circularvirus (Yu et al. 2010). Moreover, the related dollar spot fungus *S. homeocarpa* hosts a hypovirulence-causing mitovirus (Deng, Xu and Boland 2003).

The viromes of many species of *Fusarium* have also been investigated. *Fusarium graminearum* virus 1, an unclassified ‘fusarivirus’, perturbs host developmental processes and causes hypovirulence in the wheat pathogen *Fusarium graminearum* (Chu et al. 2002; Cho et al. 2012). The hypovirulence effect has also been reported with *Fusarium graminearum* mycovirus-China 9 and *Fusarium oxysporum* f. sp. *dianthi* mycovirus 1, both of which are chrysovirus (Darissa et al. 2011, 2012; Lemus-Minor et al. 2018; Torres-Trenas et al. 2019). Among 44 isolates of *F. virguliforme*, isolates containing large dsRNAs (later described as members of the proposed genus ‘Fusagraviridae’)

were also significantly less virulent than isolates without dsRNAs (Marvelli et al. 2014). However, two strains of mitoviruses seemed to increase the pathogenicity of the host *F. circinatum*, the causal agent of pine pitch canker disease (Muñoz-Adalia et al. 2016). Other widespread soil-borne plant pathogens include, for example, *Macrophomina phaseolina* and *Alternaria* spp. hosting mitoviruses, and *Ustilagoideae virens* hosting totiviruses, 'ustiviruses' and putative partitiviruses (Jiang et al. 2015). In addition to the above-mentioned ascomycetous plant pathogens, some species of the basidiomycetous genus *Rhizoctonia* spp. are opportunistic plant pathogens of agricultural plants or tree seedlings. An unclassified alphapartitivirus found in *Rhizoctonia solani* confers hypovirulence in its host on rice plants (Zheng et al. 2014).

Regarding animal pathogenic molds, *Aspergillus fumigatus* partitivirus 1 and *Aspergillus fumigatus* chrysovirus have been found to mediate a reduced growth rate, conidiation and pigmentation in *A. fumigatus* (Bhatti et al. 2011), a common toxin-producing mold species that may infect immunosuppressed humans. On the other hand, the gammapartitivirus *Talaromyces marneffei* partitivirus 1 enhances the virulence of its native host, causing opportunistic infections in mammals (Lau et al. 2018).

Necrotrophic tree root pathogens causing root-system decay are generally able to colonize the otherwise healthy host root tissue through wounds or natural openings. Many of them also spread vegetatively via root contacts and form large clonal individuals. The viromes of the fruit tree root pathogens *Helicobasidium mompa* and *Rosellinia necatrix* reviewed by Kondo, Kanematsu and Suzuki (2013) and conifer pathogens of genus *Heterobasidium* (Vainio and Hantula 2016) have been extensively studied. In nature, clonally spreading mycelia of these long-living root rot pathogens typically consist of virus-infected and virus-free hyphal sections (Ikeda et al. 2005; Yaegashi et al. 2013b; Vainio et al. 2015). This may be due to mycelial fragmentation (losing the connectivity between different parts of the mycelium), and the loss of viruses during mycelial growth, as mycoviruses may be unevenly distributed within an advancing mycelium (Yaegashi et al. 2011), and hyphal tips may be free of viruses. On the other hand, isolates of these long-living pathogens are often co-infected with multiple closely or distantly related viruses (Ikeda et al. 2005; Vainio et al. 2015). Root rot pathogens have also been shown to harbor viruses with host effects. For example, *Heterobasidium partitivirus* 13 causes growth reduction and alters the gene expression of its host (Vainio et al. 2018), and the presence of dsRNA viruses in the fruitbody of *Heterobasidium anno-sum* was found to reduce the germination frequency of basidiospores (Ihrmark, Stenström and Stenlid 2004). In *H. mompa*, the causal agent of the so-called violet root rot in apple and other woody horticultural plants, host virulence is attenuated by the presence of an endornavirus or a totivirus (Ikeda, Nakamura and Matsumoto 2003; Suzaki et al. 2005). In *R. necatrix*, host hypovirulence is mediated by a reovirus (Kanematsu et al. 2004). In some cases, host symptoms develop only during viral co-infection: a mixed infection by *Rosellinia necatrix* partitivirus 1 and megabirnavirus 2 leads to host hypovirulence, while the individual viruses seem to be cryptic (Sasaki, Nakamura and Suzuki 2016).

Ophiostomoid fungi causing vascular wilts as well as wood discoloration in forest and ornamental trees are disseminated by bark beetles, but they can also spread through root contacts. These blue-stain fungi are Ascomycetes of polyphyletic origins, including species from Ophiostomatales and Microascales (De Beer, Seifert and Wingfield 2013). The most famous example of

vascular wilts is the devastating Dutch Elm disease caused by *Ophiostoma ulmi* and *O. novo-ulmi*. These fungi are infected by numerous species of mitoviruses, some of which are associated with deleterious effects on the growth and sporulation of the host fungus (Cole et al. 1998). Remarkably, a single diseased isolate of *O. novo-ulmi* was found to harbor 12 dsRNAs, including at least seven independently replicating mitoviruses (Doherty et al. 2006). Other blue-stain fungi include, e.g. *Endoconidiophora resinifera* and *E. polonica* (formerly *Ceratocystis resinifera* and *C. polonica*, respectively), between which a natural horizontal virus transfer has likely occurred (Deng and Boland 2007).

Finally, many pathogenic (or endophytic) fungi complete their life cycle above the ground, but reach the soil as spores or in fallen shoots or leaves. Some also overwinter and sporulate in decomposing leaves or needles. These shoot pathogens (which include, e.g. rusts, powdery mildews, leaf spots, needle casts and blights, as well as some so-called anthracnose, dieback and canker causing fungi) are not covered in detail in this minireview. However, mycoviruses have been found in several such pathogens, for example, *Hymenoscyphus fraxineus* (Schöbel, Zoller and Rigling 2014), *Fusarium circinatum* (Martínez-Álvarez et al. 2014), *Erysiphe necator* (Pandey, Naidu and Grove 2018b), *Discula destructiva* (Rong et al. 2002), *Puccinia striiformis* f.sp. tritici (Zheng et al. 2017), *Sphaeropsis sapinea* (Ghabrial and Nibert 2009), *Gremmeniella abietina* (Botella and Hantula 2018) and *Cronartium ribicola* (Liu et al. 2016b).

Viruses of soil-borne oomycetes

Oomycetes are heterotrophic saprophytes or parasites of diverse plant and animal hosts. Many oomycetes and fungi share similar lifestyles, but oomycetes are more closely related to brown algae and belong to the Kingdom Stramenopila (Heterokonta). The class Oomycota includes up to 12 orders (Beakes, Glockling and Sekimoto 2012), where the basal ones mainly include marine holocarpic pathogens of nematodes, algae, crustaceans and mollusks (Thines and Choi 2016). The majority and the most well-known oomycetes belong to the lineages Peronosporomycetidae and Saprolegniomycetidae (Beakes, Glockling and Sekimoto 2012; Ascunze et al. 2017), which primarily include mycelia forming microbes with sexual oospores accounting for genetic variability and survival, and asexual self-motile zoospores that are responsible for dispersal and infection (Latijnhouwers, de Wit and Govers 2003; Thines and Choi 2016). Where the majority of species of the Saprolegniomycetidae lineage are saprotrophs, they also include important animal pathogens (Phillips et al. 2007). The species in the peronosporalean groups mainly include plant pathogens with varying infectious lifestyles (Jiang and Tyler 2012). In general, relatively little is known about virus communities inhabiting oomycetes.

The genus *Phytophthora* of Peronosporales mainly consists of plant pathogens generally with broad host ranges. They are notorious for causing enormous losses as introduced pathogens in agriculture, silviculture and natural ecosystems all over the world (e.g. Jung et al. 2018). An alphaendornavirus was described by Hacker, Brasier and Buck (2005) in the *Phytophthora* taxon 'douglasfir' in the USA, and similar virus strains were also later found in *P. ramorum* isolates from several hosts in Europe (Kozlakidis et al. 2010). The causal agent of potato late blight, *P. infestans*, has been shown to host four dsRNA viruses named PiRV1–4 (Cai et al. 2009; 2012; 2013; 2019). PiRV1 and PiRV2 seem to represent novel virus families, whereas PiRV3 is affiliated with the newly proposed family 'Fusagraviridae' and PiRV4 is likely

an unclassified member of *Narnaviridae*. Recently, the unique virus PiRV2 was shown to stimulate the sporangia production of *P. infestans*, thereby enhancing its virulence (Cai *et al.* 2018). The virus was also 100% transmittable through asexual reproduction.

Downy mildews are obligate biotrophic plant parasites, which overwinter in the soil in fallen leaf tissues, germinate in wet conditions and infect the above-ground plant parts by zoospores in water splashes. The few viruses described in downy mildews include the three above-mentioned unclassified ssRNA viruses of *Sclerophthora macrospora* or *Plasmopara parasitica* (Yokoi *et al.* 1999; Yokoi, Yamashita and Hibi 2003; Grasse and Spring 2017; see Table 2), one of which causes hypovirulence in its host *P. parasitica* (Grasse *et al.* 2013).

Members of the oomycete genus *Pythium* include more than a hundred species that are abundantly present in water and soil habitats. They cause diseases mainly in plant root tissues but do not generally cause a significant damage. Viruses found in *Pythium* species include an unclassified gammapartitivirus (Shiba *et al.* 2018) as well as unclassified viruses showing resemblance to members of the families *Totiviridae* and *Bunyaviridae* (Sasai *et al.* 2018), but no host effects are known.

CONCLUDING REMARKS AND FUTURE PROSPECTS

Mycoviruses have remained a largely unknown part of the microbial realm. This is highlighted by the diverse viromes detected from those fungal species investigated in more detail (e.g. Xie and Jiang 2014; Ghabrial *et al.* 2015), and the notion that mycovirus communities may be more diverse than the populations of their hosts due to a higher accumulation rate of virus taxa (Feldman, Morsy and Roossinck 2012). Moreover, even the majority of fungal species are still to be discovered, as the number of described species is around 120 000, while the estimate of the existing fungal species lies between 2.2 and 3.8 million (Hawksworth and Lücking 2017).

The recent discoveries of cross-kingdom transmission of viruses between fungi, plants and insects, as revealed by high-throughput sequencing and phylogenetic analysis (Dolja and Koonin 2018; Roossinck 2018), challenge the view that mycoviruses would have co-evolved with their hosts since ancient times. Instead, mycoviral communities may be commonly shaped by cross-species virus transmission (Yaegashi *et al.* 2011), which could lead to at least partially shared mycoviral communities between organisms dwelling at single habitats or substrates. This view resembles the phenomenon of habitat specificity observed within soil bacteriophages (Paez-Espino *et al.* 2016; Graham *et al.* 2019, unpublished). Furthermore, it is supported by the occurrence of similar viruses in fungi and oomycetes, which are phylogenetically distant but share similar lifestyles and growth substrates. However, mycoviral community and population studies have so far concentrated on single host species, and only few studies have addressed the possibility of viral transmission between fungi interacting in natural habitats (Feldman, Morsy and Roossinck 2012; Vainio *et al.* 2017). It also remains to be investigated whether cross-species or cross-kingdom viral transmissions lead to persistent infections, and whether interspecies virus transmission could regulate fungal communities due to differences in virus tolerance. Moreover, it is not known to what extent microarthropods might serve as vectors for mycoviruses or facilitate their cross-species transmission.

Another largely unknown field in mycovirus research is the effects of viruses on microbe–microbe interactions. While many mycoviruses are known to affect the pathogenicity of their host fungi towards plants, very few studies have addressed the capability of mycoviruses of altering the competitive ability of their hosts against other microbes present in the same growth substrate (Hyder *et al.* 2013). This could have an effect on the whole microbial community and also associated plants.

Finally, accumulating metatranscriptomics data are expected to enlighten the diversity of fungal and oomycete viruses present in soils. Interestingly, Žifčáková *et al.* (2016) identified that 0.2% of all annotated contigs detected in forest soils by metatranscriptomics were of viral origin, and also contained mitovirus and partitivirus sequences. However, to our knowledge, metatranscriptomics has not been systematically used to address soil mycoviromes so far.

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