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Review

Towards the forest virome: next-generation-sequencing drastically expands our understanding on virosphere in temperate forest ecosystems

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Abstract: Forest health is dependent on the variability of microorganisms interacting with the host tree/holobiont. Symbiotic microbiota and pathogens engage in a permanent interplay, which influences the host. Thanks to the development of NGS technologies, a vast amount of genetic information on the virosphere of temperate forests has been gained the last seven years. To estimate the qualitative/quantitative impact of NGS in forest virology, we have summarized viruses affecting major tree/shrub species and their fungal associates, including fungal plant pathogens, mutualists and saprotrophs. The contribution of NGS methods is extremely significant for forest virology. Reviewed data about viral presence in holobionts, allowed us to address the role of the virome in the holobionts. Genetic variation is a crucial aspect in hologenome, significantly reinforced by horizontal gene transfer among all interacting actors. Through virus-virus interplays synergistic or antagonistic relations may evolve, which may drastically affect the health of the holobiont. Novel insights of these interplays may allow practical applications for forest plant protection based on endophytes and mycovirus biocontrol agents. The current analysis is conceived in light of the prospect that novel viruses may initiate an emergent infectious disease and that measures for avoidance of future outbreaks in forests should be considered.

Keywords: virome, microbiome, next generation sequencing, mycoviruses, plant pathogenic viruses

1. Introduction

Forests represent a major natural resource and provider of ecosystem services, products and jobs in Europe. They cover 35% of Europe's total land area [1] their ecological importance being equally significant as the economic one. The majority of the countries have 30 - 45% of their land area covered with forests, while countries in the North Europe have larger forest areas, with three-quarters of the total land area in Finland and 69% in Sweden being covered by forests. The forest sector consisting of wood industry and paper industry contributes 1.97% to total gross domestic product (GDP) in North Europe and on average 0.72% to the total GDP of Europe [1, 2]. Pests and diseases were reported as important causes of damage among wildlife and grazing by domestic animals, fires and weather extremes such as storms. Insect attacks, weather extremes and fungal diseases were reported as the most common and widespread factors associated with tree defoliation [1]. Forest health is a "public good" and multiple categories of end-users are benefited from it. The forest industry, the seed producers, nurseries, producers of non-timber birch and spruces products, the broader society are end-users of forests and urban green areas as providers of multiple ecosystem services. The need of indicators to provide information on forest ecosystem health and vitality - which may make possible an evaluation of its resilience - is clearly undelined [2]. Healthy trees and healthy forests is translated into forests providing better regulating services (associated with natural catastrophes), better maintenance/habitat services (increased biodiversity) and better multiple ecosystem services (affecting humans and animals).

Virus diseases of forests tree species represent a so far underestimated threat for the forest health [3, 4]. Losses from virus diseased trees have to be assumed referring to experience from virus infected fruit trees. But data are still missing and have to be gained urgendly in the close future. But current data regarding monitoring for symptom appearance, disease dispersal and epidemic severity assessment form a essential basisn. Collecting data for virus diseases occurrence is a demanding work that should be done by specialized staff. Often viral symptoms are difficult

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to determine and distinguish from other causes as they appear mainly in leaves and rarely in fruits. Their irregular distribution within the tree and the low concentration also contributes to this challenge. Additionally, an infected tree may be mistaken to be healthy when the upper part of the tree is affected, which is quite common in forest trees; European mountain ash may reach 15 m, the silver birch up to 30 m, while some oak and elm species may reach huge volume and height up to 40 m.

Still, forest tree viruses are ranking high in regard to their risk for introduction and establishment in forests and crops and this lies mainly upon the wide distribution of susceptible plant germplasm, the often extended host range and the rapid emergence of new genotypes (virus strains or variants). Most common reports by the international sociaty for infectious diseases ProMED (http://www.promedmail.org/) are reports of newly arrived viruses and viroids (36.6%) among approximately 140 emerging infectious diseases (EIDs) in plants [5]. Concerning forest trees, from own investigations and existing references we suggest that viruses contribute as a remarkable factor to emerging infectious diseases and confirm Nienhaus [3] who made already in the 80s aware about. A serious recent epidemic of viral species is related with the birch leafroll disease (BLRD) in birches (*Betula* spp.) [6, 7]. Another current viral epidemic in Europe correlated with emaraviruses from the the genus *Emaravirus* within the family *Fimoviridae,* which comprises several species with European mountain ash ringspot-associated virus (EMARaV) as the type species and the causal agent of the 'European mountain ash ringspot disease' in *Sorbus aucuparia* [8, 9].

Due to the utilization of next generation sequencing methodologies (NGS), forest virology has gained a significant momentum in identifying viruses infecting forest trees [10 - 13]. These platforms offer the possibility of metagenomic analysis, the study of microbial populations in samples by analyzing their nucleotide sequence content. RNA viruses, viroids and the RNA stages of actively replicating DNA viruses can be directly sequenced. Applying RNA-Seq, birch viromes in relation with BLRD were unraveled revealing a complex of novel and known viruses (Badna-, Nepo- and Capillovirus [14], while a novel badna virus was associated with the BLD symptoms and was genetically characterized [15]. Regarding EMARaV, it was initially reported only in European mountain ash, lately, however and with the use of NGS several emaraviruses were detected in new hosts as there are e.g. *Karpatiosorbus x hybrid* in Finland [16], and *Sorbus intermedia* [17] and *Amelanchier spp.* in Germany [18].

Significant amount of data derive from the last decade through metagenomic analyses [11, 19], as these viruses were not targeted earlier, because - based on the traditional principles of phytopathology - they were out of consideration as non-plant pathogens. However, as fungal plant pathogens and mutualists may have a major effect on the plant growth, it is important to characterize viruses that could regulate the balance between the pathogen and host plant. The host in the review is considered as a holobiont, defined as the tree/shrub organism and all its microbiome, explicitly symbiotic microbiota and pathogenic fraction (bacteria, oomycetes, other protists and viruses) [definition by Margulis, 1993; 20]. Viruses that reduce the pathogenicity or growth of fungal plant pathogens can be considered beneficial for the holobiont, as they protect the tree from disease. In turn, viruses that would cause debilitation of mutualistic mycorrhizal fungi are harmful in the viewpoint of the host plant. Therefore, mycoviruses will be addressed here based on the ecological guild of the host fungus: viruses of plant pathogens and viruses of mutualistic fungi. Many different approaches have been used to study the biodiversity of mycoviruses, including enrichment of virus-like particles, extraction of dsRNA, and the NGS of small RNA and total RNA. In this review, we will we will summarize how the NGS era has changed our view of mycoviral diversity.

This review aims to describe and comprehend the current status of the virosphere of a forest by summarizing the viral species coexisting in a forest. We name this “forest virome” and consider all existing genetic information of viral origin related to common forest trees and shrubs. Although the interactions between host and viral agent are not always adequately defined, we have consired the following big categories of interactions: a. pathogenic virus versus tree/shrub host, b. non-pathogenic virus versus tree/shrub host, c. pathogenic virus versus fungal host or d. non-pathogenic virus versus fungal host. In the term “forest” we consider the natural forest ecosystems in the north Hemisphere as well as urban parks and urban green mainly covered by forest trees and shrubs and constitute separate ecosystems within urban environments. What, however, is beyond the aim of the the present review remains, is to list down all studies performed until now; this work has been thoroughly done before [3]. The aim in the present work is to update the list of pathogens considered as present in the forest ecosystem in light of the sequencing efforts and discoveries achieved the last 5-7 years. Glancing at our aim to describe the forest virome, we will not consider here observations that lack genetic characterization and sequence data availability.

The need for a current review about forest viruses is further strengthened by the fact the advances in plant virology are traditionally restricted in crop or fruit tree pathogenic viruses. This becomes apparent when considering the latest reviews [21, 22] resuming viral discoveries by the use of deep sequencing techniques in fruit trees, where virus discoveries in the forest ecosystem are not included. It is true, that few groups worldwide lay their focus of plant pathology research on forest ecosystems and this may be partially attributed to the difficulties in quantitatively estimating the importance of forest ecosystems and the economic impact due to viral epidemics. Despite this fact, it is shown through the present work, that substancial progress has been achieved in this field and in many cases this has radically changed our understanding about forest viral diseases.

Finally, this review presents various lines of evidence regarding why further research on forest virome is urgently required in order to a. characterize biologically the newly described pathogens, including their modes of dispersal and possible vectors, b. build the knowledge base of virus-host interactions as well as of virus-fungal endophyte/fungal pathogen interactions, c. gather knowledge on the behavior of the forest parasites, in preparation for future outbreaks as consequence of significant changes in the climate and the environment, d. explore alternative means of controlling fungal and viral forest diseases. As our understanding of the viruses of fungal endophytes and forest pathogens is only at the very beginning, it is an ideal time to apply the most modern sequenced-based tools in favour forest virology.

2. Methods

The current analysis was based on two main principles. First, the hologenome theory of evolution was taken into consideration [23, 24]. According to this theory, a holobiont is a single dynamic entity in which a vast amount of its genetic information and variability is contributed by the microorganisms [25]. We considered a forest tree/shrub as a holobiont and in this study and focused on a part of its microbiome, the virome, considering all virus communities (as dependent biological agents) affecting the tree (plant pathogenic or latent viruses) and affecting the exosymbionts and endosymbionts of the tree (mycoviruses). Secondly, the “forest” was considered as an ecosystem with multiple holobionts (diverse tree species); our focus was put on the virus variation that characterizes the whole system, and this we called “forest virome”.

To explore the studies involved in the described subject, we have first listed viruses alphabetically, ordering them in three categories; 1. plant viruses infecting tree/shrub hosts and cryptoviruses (Section 3.1.1; Table 1), 2. mycoviruses occurring in plant pathogenic fungi (Section 3.1.2; Table 2) and 3. mycoviruses occurring in mutualistic fungi and saprotrophs (Section 3.1.3; Table 3). To systematically handle the data, we have listed in a following step the 11 most important forest tree or shrub genera known to be affected by viruses; a separate section is devoted to the virome of each plant genus (Section 3.2.1 - 3.2.11). A sub-section is devoted to “other trees” where less information is yet available (3.2.12). For all searches to detect all related articles, the search-machine of Elsevier's Scopus, a big citation database of peer-reviewed literature, was applied (www.scopus.com/search/).

Table 1. Plant viruses infecting tree/shrub hosts and cryptoviruses. For each virus the name, the genus and family it is classified or putatively ordered, its host(s), the country it was reported and the related references are given. Viruses that were discovered by means of NGS methods are indicated by the note "NGS" next to their number of order.

	Virus	Genus, Family	Host	Location, Country*	Reference
1	Apple chlorotic leaf spot virus (ACLSV)	*Trichovirus, Betaflexiviridae (+)ssRNA*	*Aesculus hippocastanum, S. aucuparia*	Germany	121, 181
2	Apple mosaic virus ApMV	*Ilarvirus, Bromoviridae (+)ssRNA*	*Carpinus, Sorbus, Aesculus, Betula*	Canada, Europe	69 (*Sorbus, Aesculus, Betula, Carpinus*); 182 (*Betula*); 183 (*Rubus*); 184
3	Arabis mosaic virus (ArMV)	*Nepovirus, Secoviridae (+)ssRNA*	*Acer spp., Fraxinus spp., Populus spp., Sambucus nigra,* *Betula spp.*	Europe, USA	70, 95 (*Populus spp.*); 82, 83 (*Fraxinus spp.*); 109 (*Sambucus nigra*); 65, 66 (*Acer*)
4 **NGS**	Aspen mosaic-associated virus (AsMaV)	*Emaravirus, Fimoviridae (-)ssRNA*	*Populus tremula*	Germany	26
5 **NGS**	Birch leafroll-associated virus (BLRaV)	*Badnavirus, Caulimoviridae dsDNA*	*Betula spp.*	Germany, Finland	14, 15
6 **NGS**	Birch idaeovirus (BIV)	*Idaeovirus, Mayoviridae (+)ssRNA*	*Betula spp.*	Germany	14
7 **NGS**	Birch capillovirus (BCV)	*Capillovirus, Betaflexiviridae (+)ssRNA*	*Betula spp.*	Germany	14
8 **NGS**	Birch carlavirus (BiCV)	*Carlavirus, Betaflexiviridae (+)ssRNA*	*Betula spp.*	Germany	14
9	Blueberry scorch virus (BlScV)	*Carlavirus, Betaflexiviridae (+)ssRNA*	*Sambucus nigra*	Poland	31, 110
10	Brome mosaic virus (BMV)	*Bromovirus, Bromoviridae (+)ssRNA*	*Salix*		185
11	Cherry leaf roll virus (CLRV)	*Nepovirus, Secoviridae (+)ssRNA*	*Betula spp., Aesculus, Fagus, Fraxinus spp., Sambucus nigra; Sorbus; Ulmus armeniaca*	Europe, USA	3 (*Fagus*); 71 (*Betula*); 121 (*Aesculus spp.*); 84 (*Fraxinus spp.*); 7, 186 (*Betula spp.*); 111, 114 (*Sambucus*);

					122 (*Sambucus nigra, Sorbus*); 187 (*Ulmus armeniaca, Fagus*); 232
12	Cherry rasp leaf virus (ChRLV)	*Cheravirus, Secoviridae (+)ssRNA*	*Sambucus nigra subsp. caerulea,*	USA	112
13 **NGS**	Chestnut mosaic virus (ChMV)	*Badnavirus, Caulimoviridae dsDNA*	*Castanea sativa*	Italy, France	30
14 **NGS**	Common oak ringspot-associated virus (CORaV)	*Emaravirus, Fimoviridae (-)ssRNA*	*Quercus robur*	Germany	27, 28
15 **NGS**	Elderberry aureusvirus 1 (ElAV1)	*Aureusvirus, Tombusviridae (+)ssRNA*	*Sambucus nigra*	Czech Republic	118
16-20 **NGS**	Elderberry carlaviruses A,B,C,D,E (ElVA-ElVE).	*Carlavirus, Betaflexiviridae (+)ssRNA*	*Sambucus nigra*	USA	32, 33
21 **NGS**	Elm carlavirus (ECV)	*Carlavirus, Betaflexiviridae (+)ssRNA*	*Ulmus laevis*	Germany	34, 129, 130
22	Elderberry latent virus (ELV)	*Pelarspovirus or Carmovirus (acc. CABI), Tombusviridae (+)ssRNA*	*Sambucus nigra*	Austria, Poland, USA	32, 111
23	Elm mottle virus (EMoV)	*Ilarvirus, Bromoviridae (+)ssRNA*	*Ulmus* sp.	central Europe, Russia, UK	123; 124 188
24 **NGS**	European mountain ash ringspot-associated virus (EMARaV) NGS: + 2 RNA segments in *S. intermedia* (17)	*Emaravirus, Fimoviridae (-)ssRNA*	*Sorbus aucuparia, Aronia melanocarpa, Amelanchier spp., Karpatiosorbus × hybrid, S. intermedia**	Germany, Sweden, Norway, UK, Check Republic, Poland, UK, Russia *Sweden	189, 190, 191 8, (Germany) 192 (Check Republic); 193 (Poland); 194 (Russia); 195 (*S. aucuparia*); 16 (*Karpatiosorbus × hybrida*); 18 (*Amelanchier spp.*); 17 (*S. intermedia*)
25 **NGS**	Maple mottle-associated virus	*Emaravirus, Fimoviridae (-)ssRNA*	*Acer pseudoplatanus*	Germany	29
26	Peanut stunt virus (PSV)	*Cucumovirus, Bromoviridae*	*Robinia pseudoacacia*	Italy, Coatia,	196; 197 (Croatia);

		(+)ssRNA		Iran	198 (Italy); 199 (Iran)
27 NGS	Pinus nigra virus 1	unclassified *Caulimoviridae dsDNA*	air samples, *Pinus nigra*	Spain	141
28 NGS	Pinus patula amalgavirus 1	unclassified *Amalgaviridae* dsRNA	*Pinus patula*	NGS Transcriptome Shotgun Assembly database	134
29	Pinus sylvestris partitivirus NL-2005	putative *Cryptovirus*, unclassified *Partitiviridae* dsRNA	*Pinus sylvestris*	Germany	140
30	Poplar mosaic virus (PopMV)	*Carlavirus, Betaflexiviridae (+)ssRNA*	*Populus* spp.	UK, Germany, China	96; 98; 99
31 NGS	Sambucus virus S (SVS)	*Bromovirus, Bromoviridae (+)ssRNA*	*Sambucus nigra*	Czech Republic	119
32	Strawberry latent ringspot virus (SLRV)	*Stralarivirus (according to Dullemans et al., 2020), Secoviridae (+)ssRNA*	*Aesculus hippocastanum*, *Robinia pseudoacacia*	Germany, Poland	181 (*Aesculus*); 200 (*Robinia*, Poland); 201 , 202 (*Robinia, Aesculus*); 203 (*Robinia*, Poland)
33	Tomato black ring virus (ToBRV)	*Nepovirus Secoviridae (+)ssRNA*	*Sambucus nigra, Populus spp.*	Poland	95, 115
34	Tomato bushy stunt virus (TBSV)	*Tombusvirus, Tombusviridae (+)ssRNA*	*Sambucus nigra, S. canadensis, Ulmus*	USA, Czech Republic	113 (USA); Jones, 1972 (*S. canadensis*); 116 (Czech Rep.)
35	Tomato mosaic virus (ToMV)	*Tobamovirus, Virgaviridae (+)ssRNA*	*Picea rubens Sarg., Picea mariana, Abies balsamea, ,Salix*	Canada, USA	17; 18; 143; 144; 185
36	Tomato ringspot virus (ToRSV)	*Nepovirus, Secoviridae (+)ssRNA*	*Betula spp., Fraxinus spp., Populus spp. Ulmus americana*	UK, USA	70 (Betula); 125 (Ulmus)
37	Tobacco mocaic virus (TMV)	*Tobamovirus, Virgaviridae (+)ssRNA*	*Fraxinus spp. Quercus*	USA, Hungary (*Quercus*) ; Germany (Quercus)	86 87; 88; 204 (Fraxinus); 102 (*Quercus*); 103; 104; 105
38	Tobacco necrosis virus	*Alphanecrovirus, Tombusviridae,*	*Betula, Fagus, Fraxinus spp.*	Europe	3, 70 (birch, beech, pine,

	(TNV)	*(+)ssRNA*	*Pinus, Quercus, Sambucus nigra*		oak, *Salix*); 101, 85; 97 (*Populus*) 113, 116 (*Sambucus nigra*)
39	Tobacco rattle virus (TRV)	*Tobravirus, Virgaviridae (+)ssRNA*	*Fraxinus* spp., *Populus* spp.	Germany	205
40	Tobacco ringspot virus (TRSV)	*Nepovirus Secoviridae (+)ssRNA*	*Fraxinus* spp., *Sambucus nigra*	USA	83, 87 - 90; 206; 207 (*Fraxinus*); 117 (*S. nigra*)
41	White ash mosaic virus (WAMV)	unclassified *Flexiviridae (+)ssRNA*	*Fraxinus americana*	USA	91
42 NGS	putative Cryptovirus	Partitiviridae dsRNA	*Fraxinus americana*		92
43 NGS	putative Caulimovirus	Caulimoviridae Reverse-Transcribing DNA	*Fraxinus americana*		92

* The virus distribution data were retrieved from the Invensive Species Compedium CABI in combination with information from the publications referred in the present review.

Table 2. Mycoviruses occurring in plant pathogenic fungi. For each virus the name, the genus and family it is classified or putatively ordered, its host(s), the country it was reported and the related references are given. Viruses that were discovered by means of NGS methods are indicated by the note "NGS" next to their number of order.

	Virus	**Genus, Family**	**Fungal species**	**Tree species**	**Location, Country**	**Reference**
1 NGS	Armillaria borealis mycovirgavirus 1	unclassified *Virgaviridae* (+)ssRNA	*Armillaria borealis*	*Populus spp.*	Russia	39
2-4 NGS	Armillaria borealis ambi-like virus 1, 2, 3	unclassified *Riboviria*	*Armillaria borealis*	*Populus spp.*	Russia, Finland	39
5 NGS	Armillaria mellea negative strand RNA virus 1	*Mymonaviridae* (-)ssRNA	*Armillaria mellea*	*Quercus robur*	South Africa	39
5 NGS	Armillaria mellea botourmia-like virus 2	*Botourmiaviridae* (+)ssRNA	*Armillaria mellea*	*Quercus robur*	South Africa	39
7-11 NGS	Cronartium ribicola mitovirus 1-5	*unclassified Mitovirus, Mitoviridae* (+)ssRNA	*Cronartium ribicola*	*Pinus strobus*	North America	43
12-14	Cryphonectria hypovirus 1, 2, 3	*Hypovirus, Hypoviridae* (+)ssRNA	*Cryphonectria parasitica*	*Castanea sp., Aesculus hippocastanum*	Europe (England, Croatia, Slovenia, Slovakia, Italy, Spain, Greece), Turkey,	208; 209; 210; 211; 212; 228

					USA	
15 **NGS**	Cryphonectria parasitica ambivirus 1- NB631 (CpaV1)	*Riboviria; unclassified Ambivirus* (-)ssRNA	*Cryphonectria parasitica*	*Castanea sativa*	Azerbaijan	40
16	Cryphonectria parasitica mitovirus 1	*Mitovirus, Mitoviridae* (+)ssRNA	*Cryphonectria parasitica*	*Castanea sativa*	USA	35
17 **NGS**	Cryphonectria parasitica sclerotimonavirus 1	*unclassified Sclerotimonavirus, Mymonaviridae* (-)ssRNA	*Cryphonectria parasitica*	*Castanea sativa*	Azerbaijan	40
18-20 **NGS**	Heterobasidion mitovirus 1, 2, 3 (HetMV1)	*Mitovirus, Mitoviridae* (+)ssRNA	*H. annosum and H. parviporum*	*Pinus sylvestris, Picea abies*	Poland, Finland, Russia	213; 214; 215
21	Heterobasidion orthocurvulavirus (HetRV6*)	*Orthocurvulavirus, Curvulaviridae* dsRNA	*Heterobasidion abietinum, H. annosum, H. parviporum, H. occidentale*	*Abies alba, A. sibirica, A. cephalonica, A. cilicica, A. equi-trojani, A. concolor; Pinus sylvestris, P. nigra, P. obovata; Picea abies; Fagus sp.*	Europe, USA	215
22-35	Heterobasidion partitivirus 1, 3, 4*, 5, 8, 9, 10, 11, 12 13*, 14, 15, 16, 20	*Alphapartitivirus, Partitiviridae* dsRNA	*Heterobasidion abietinum, H. ecrustosum, H. parviporum, H. occidentale, H. australe, H. annosum, H. irregulare*	*Abies cephalonica A. concolor Pinus massoniana P. wallichiana, P. sylvestris P. elliottii P. abies, P. pinea, Picea likiangensis*	Greece, China, Finland, Italy, Poland, Russia, USA, Bhutan	48; 162; 216-219; 146; 213; 231
36-38	Heterobasidion partitivirus 2*, 7*, 8	*Betapartitivirus, Partitiviridae* dsRNA	*Heterobasidion parviporum, H. annosum, H. irregulare*	*Picea abies, P. sylvestris, P. pinea*	Finland, Italy	233
39	Hymenoscyphus fraxineus mitovirus 1 (HfMV1)	unclassified *Mitovirus, Mitoviridae* (+)ssRNA	*Hymenoscyphus fraxineus*	*Fraxinus spp.*	Switzerland, Japan, Poland, Germany,	37

					Lithuania, Norway	
40-42 **NGS**	Fusarium circinatum mitovirus 1, 2-1 and 2-2	unclassified *Mitovirus, Mitoviridae* (+)ssRNA	*Fusarium circinatum*	*Pinus. radiate, P. pinaster, P. nigra, P. sylvestris*	Spain	135; 136; 230
43-44	Gremmeniella mitovirus 1, 2	*Mitovirus,Mitoviridae* (+)ssRNA	*Gremmeniella abietina*	mainly *Pinus sylvestris, Picea, Abies* and *Larix*	Northern and Central Europe, North America and Japan, Spain, Turkey	36
45	Gremmeniella abietina RNA virus L1	*Victorivirus, Totiviridae* dsRNA	*Gremmeniella abietina*	mainly *Pinus sylvestris, Abies* and *Larix*	Finland	36
46	Gremmeniella abietina RNA virus MS1	*Gammapartitivirus, Partitiviridae* dsRNA	*Gremmeniella abietina*	*Pinus sylvestris, (Abies and Larix)*	Finland	36
47	Gremmeniella abietina RNA virus 6	*Curvulaviridae* dsRNA	*Gremmeniella abietina*	*Pinus halepensis*	Spain	42
48	Gremmeniella betaendornavirus (XL)	*Endornaviridae* (+)ssRNA	*Gremmeniella abietina*	*Pinus sylvesris, P. contorta*	Finland	220
49	Gremmeniella fusarivirus 1	unclassified Riboviria, proposed family “*Fusariviridae*” (+)ssRNA	*Gremmeniella abietina*	*Pinus hapepensis*	Spain	42
50-52	Mycoreovirus 1, 2, 3 (MyRV-1, -2, -3)	*Mycoreovirus, Reoviridae* dsRNA	*Cryphonectria parasitica*	*Castanea sativa, Prunus spp.*		49; 221; 41 229;
53-60	Ophiostoma mitoviruses 1a, 1b, 1c, 3a, 3b, 4, 5, 6	*Mitovirus, Mitoviridae* (+)ssRNA	*Ophiostoma novo-ulmi*	*Ulmus*	UK, Canada	38; 132
61 **NGS**	Phytophthora alphaendornavirus 1	*Alphaendornavirus, Endornaviridae* (+)ssRNA	*Phytophthora ramorum, Phytophthora* taxon douglasfir	*Pseudotsuga menziesii, Quercus agrifolia, Viburnum sp., Laurus nobilis, Rhododendron sp.*	USA, UK, Netherlands	107
62 **NGS**	Phytophthora cactorum RNA virus	unclassified *Totiviridae*	*Phytophthora cactorum*	*Betula pendula*	Denmark	76

	1 (PcRV1)	dsRNA				
63 **NGS**	Rosellinia necatrix megabirnavirus 1 (RnMBV1)	*Megabirnavirus, Megabirnaviridae* dsRNA	*Rosellinia necatrix*	*Prunus spp.* and a wide range of fruit trees (*Malus, Pyrus, Citrus* etc.)	Spain, Italy, Israel	41
64 **NGS**	Rosellinia necatrix virus 1	*Betapartitivirus, Partitiviridae* dsRNA	*Rosellinia necatrix*	*Prunus spp.* and a wide range of fruit trees (*Malus, Pyrus, Citrus* etc.)	Spain, Italy, Israel	222
65	Sphaeropsis sapinea RNA virus 1	*Victorivirus, Totiviridae* dsRNA	*Diplodia pinea, D. scrobiculata*	*Pinus roxburghii*	South Africa	223

Table 3. Mycoviruses occurring in mutualistic fungi and saprotrophs. For each virus the name, the genus and family it is classified or putatively ordered, its host(s), the country it was reported and the related references are given. Viruses that were discovered by means of NGS methods are indicated by the note "NGS" next to their number of order.

	Virus	**Genus, Family**	**Fungal species**	**Tree species**	**Location, Country**	**Reference**
1 **NGS**	Hygrophorus penarioides partitivirus 1	unclassified *Alphapartitivirus, Partitiviridae* dsRNA	*Hygrophorus penarioides*	*Quercus petraea*	Turkey	52
2 **NGS**	Geopora sumneriana mitovirus 1	unclassified *Mitovirus, Mitoviridae Narnaviridae* (+)ssRNA	*Geopora sumneriana*	*Cedrus libani*	Turkey	54
3 **NGS**	Gyromitra esculenta endornavirus 1	unclassified *Endornaviridae* (+)ssRNA	*Gyromitra esculenta*	*Pinus brutia* (fungal RNA-Seq dataset)	Turkey	139
4 **NGS**	Gyromitra esculenta partitivirus 1	unclassified Partitiviridae dsRNA	*Gyromitra esculenta*	*Pinus brutia*	Turkey	53
5	Lactarius rufus RNA virus 1	*Orthocurvulavirus, Curvulaviridae* dsRNA	*Lactarius rufus, L. tabidus*	*Pinus sylvesrtris, Picea abies*	Finland	234
6	Lactarius tabidus RNA virus 1	*Orthocurvulavirus, Curvulaviridae* dsRNA	*Lactarius rufus, L. tabidus*	*Pinus sylvesrtris, Picea abies*	Finland	58
7 **NGS**	Picoa juniperi mycovirus 1	unclassified *Riboviria*, newly proposed Megatotivirida	*Picoa juniperi*	various forest tree species	Turkey	50

		e dsRNA				
8	Tuber aestivum virus 1	*Totivirus, Totiviridae* dsRNA	*Tuber aestivum* Vittad.	Mixed beech forest	Hungary	224
9	Tuber aestivum endornavirus	*Betaendornavirus, Endornaviridae* ssRNA(+)	*Tuber aestivum* Vittad.	Mixed oak forest	Hungary	225
10	Tuber aestivum mitovirus	*unclassified Mitovirus, Mitoviridae* ssRNA(+)	*Tuber aestivum* Vittad.	Mixed oak forest	Hungary	226
11	Tuber excavatum mitovirus	*unclassified Mitovirus, Mitoviridae* ssRNA(+)	*Tuber excavatum*	mixed beech forest	Germany	227
12-13 NGS	putative Alphapartitivirus and Betapartitivirus	*Partitiviridae* dsRNA	*Sarcosphaera coronaria*	*Pinus brutia*	Turkey	51

3. Results

3.1. *Interaction of viral agents with other organisms*

3.1. 1. Plant viruses infecting tree/shrub hosts and cryptoviruses

In the present review we have listed 38 plant viruses that affect 19 forest tree and shrub species present in the temperate forest and urban zone (Table 1 and references). The majority of these viruses are single-stranded positive-sense RNA viruses ((+)ssRNA) of the families *Betaflexiviridae* (11 viruses), *Secoviridae* (seven viruses), *Bromoviridae* (five viruses), *Tombusviridae* (four viruses), *Virgaviridae* (three viruses) and *Mayoviridae* (one virus). Apart from the (+)ssRNA viruses, there is also a genus of negative-sense RNA ((-)ssRNA), the *Emaravirus*, which is represented in the forest virome with four different species. There are also two reverse-transcribing double-stranded DNA viruses, the birch leafroll-associated virus (BLRaV) in *Betula* spp. and the chestnut mosaic virus in *Castanea sativa*, both belonging to the *Badnavirus* genus (Family *Caulimoviridae*). Additionally, first genetic evidence for the presence of one more reverse-transcribing DNA virus has been reported in white ash (*Fraxinus americana*).

21 viruses were newly discovered within the last five years applying NGS methodologies, which represent the 49% of the total number of viral species in forest trees. Among these, three virus genera are overwhelmingly represented. These are the genus *Emaravirus* with up to now four species (aspen mosaic-associated virus [26]; common oak ringspot-associated virus [27, 28]; maple mottle-associated virus [29]; European mountain ash ringspot-associated virus [9]), the genus *Badnavirus* with two species (birch leafroll-associated virus [15]; chestnut mosaic virus [30]) and the genus *Carlavirus* with eight species (birch carlavirus [14]; blueberry scorch virus [31]; elderberry carlaviruses A, B, C, D, E [32-33]; elm carlavirus [34]). All the novel emara- and badnaviruses are found to be associated with the corresponding symptoms and are, consequently, plant pathogenic, while the role of the carlaviruses is not yet clarified. Apart from these, single species are discovered from four other genera with ssRNA(+); an *Idaeovirus* (unassigned species and family), a *Capillovirus* (*Betaflexiviridae*), a *Bromovirus* (*Bromoviridae*) and a *Aureusvirus* (*Tombusviridae*).

From the current knowledge the majority of viruses detected in forest/shrub tree species exhibit a broad host range and they were isolated in many other crops or trees (apple, cherry, tomato, tobacco, strawberry, blueberry a.o.) before their report in forest trees, but we are on the way to reform this knowledge base, as there is a remarkable increasing number of novel viruses. The so far 21 novel viruses discovered through NGS are, however, host-specific and, following the nomenclature principles, the host name is included in the new species name. As a result, all novel virus species are named after their forest tree host. Only four viruses were named after a forest tree name before the discovery of the NGS - the poplar mosaic virus, the European mountain ash rinspot-associated virus, the elm mottle virus and the white ash mosaic virus.

3.1. 2. Mycoviruses occurring in plant pathogenic fungi

In this study we have summarized 65 viral species infecting eleven highly important fungal or oomycete pathogens occurring in more than 15 genera of forest trees (Table 2 and references). In contrary to the plant pathogenic viruses, this group of viruses includes many double-stranded RNA (dsRNA) viruses mainly affiliated with the *Partitiviridae* family (26 viruses), but also families *Totiviridae* (three viruses) and *Curvulaviridae* (two viruses), while the families *Reoviridae* and *Megabirnaviridae* were represented by one virus species. As dsRNA viruses can be readily detected based on classical cellulose chromatography analysis, most of these viruses were already known before the employment of NGS methods. Similarly, some (+)ssRNA viruses, including members of *Hypoviridae*, *Endornaviridae* and *Mitoviridae* had been already discovered prior to the NGS era based on their dsRNA replicative intermediates. NGS analysis has, however, revealed mitoviruses to be highly common in fungi, also in fungal species where members of this family were not detected by classical virus screening methods. From the total of 33 (+)ssRNA viruses detected, 23 belong to the family *Mitoviridae;* 11 novel mitoviruses have been detected during the last five years applying NGS, while Cryphonectria parasitica mitovirus 1 [35], Gremmeniella mitoviruses 1 and 2 [36], Hymenoscyphus fraxineus mitovirus 1 [37] and Ophiostoma mitoviruses [38] were known earlier. Other (+)ssRNA viruses revealed by NGS methodology include a virga-like virus (unclassified *Virgaviridae*) and a botourmia-like virus (family *Botourmiaviridae*) in *Armillaria spp* [39]. NGS methodology has also allowed for first time the detection of (-)ssRNA RNA viruses in our target pathogens: Armillaria mellea negative strand RNA virus 1 [39] and Cryphonectria parasitica sclerotimonavirus 1 [40] (both putative members of *Mymonaviridae*). Finally, new unclassified ambisense viruses were very recently identified and characterized: Cryphonectria parasitica ambivirus 1- NB631 [40] and Armillaria ambi-like viruses [39]. Considering the soilborne pathogen fungus *Rosellinia necatrix* that infects many fruit trees and related natural trees, NGS has been shown to be a very efficient tool for the detection of viral diversity and led to the discovery of members of *Hypoviridae*, as well as unclassified „fusagraviruses“ and „megatotiviruses“ [41]. Similarly, unclassified (+)ssRNA viruses of the proposed family „Fusariviridae“ (proposal submitted to ICTV in June 2021) were discovered for the first time in Gremmeniella abietina by NGS 9 [42].

Thus far, only fungal gemycircularviruses, which are related to plant geminiviruses have been shown to be transmitted by insect vectors in white pine [43]. These represent one of the few DNA viruses found in fungi. The vast majority of fungal viruses are transmitted intracellularly, which enables them to spread without movement proteins and even without being protected by protein capsids. Due to this close host association and long co-evolution, most mycoviruses do not cause a major host debilitation. However, as described in more detail in the discussion below, there are several important exceptions where mycoviruses reduce the virulence or growth rate of their host and hence improve the health of the holobiont. The most important example is the chestnut blight pathogen, *Cryphonecria parasitica*, that can be controlled via the introduction of hypoviruses [44, 45], while also two alphapartitiviruses of *Heterobasidion spp*. [46] and a mycoreovirus of *R. necatrix* have shown promising results [47] (see discussion). However, the outcome of a mycovirus-host association is complex and may be dependent on environmental conditions, interacting fungi or coinfecting viruses [46, 48, 49].

3.1. 3. Mycoviruses occurring in mutualistic fungi and saprotrophs

In Table 3 we have summarized 12 viral species infecting eleven species of ectomycorrhizal (ECM) fungi associated with both broadleaved and conifer trees. Again, dsRNA viruses predominate; most of them belong to the family *Partitiviridae* (four viruses), and the rest in the families *Curvulaviridae* (two viruses) and *Totiviridae* (two viruses). Thanks to NGS, novel dsRNA viruses were detected for first time in several species of ECM fungi in Turkey: *Picoa juniperi* (dsRNA virus of the proposed family Megatotiviridae, [50]), *Sarcosphaera coronaria* (putative Partitiviridae member, [51]), *Hygrophorus penarioides* (partitivirus, [52]), as well as in the false morel mushroom *Gyromitra esculenta* [53]. Regarding ssRNA(+) viruses, they had already been identified with traditional methods, including putative members of *Mitoviridae* (three viruses) and *Endornaviridae* (two viruses). For first time, a mitovirus was by means of NGS fully genetically characterized in the ectomycorrhizal fungus *Geopora sumneriana* [54].

The first viruses infecting ECM fungi were discovered in commercially valuable truffles (genus *Tuber*), and only recently viral diversity in mycorrhizal fungi has been addressed more from an ecological viewpoint. While NGS studies have already revealed hitherto unknown evolutionary trajectories and new viral genome organizations in ECM fungi and other mycorrhizae [55], the phenotypic effects of most of these viruses have not been systematically studied.

Saprotrophs that consume coarse or fine woody debris are somewhat less intimately connected with the plant host than mycorrhizal fungi and pathogens, and most of them cannot be connected to a single genus of host trees. Some of them produce edible fruiting bodies and for this reason have been subjected to virus screening studies by NGS. The shiitake mushroom (*Lentinula edodes*) is found on many broadleaved tree species, and although virus-like particles were found in this species already in the 1970s, NGS has recently revealed many new virus taxa, most notably ssRNA(-) viruses not detected by traditional methods [56, 57]. Very recently, a novel ssRNA(-) virus of the family *Mymonaviridae* and a partitivirus was also identified with the use of RNA-Seq in the *Bondarzewia berkeleyi* from oak wood [58]. Other important wood decay fungi known to be infected by symptomatic viruses (e.g. [59, 60]) but not yet subjected to NGS include for example the oyster mushroom (*P. ostreatus*), and the enokitake (*F. velutipes*) favouring broadleaved trees.

3.2. Virome of specific plant hosts

3.2. **1. *Acer spp.*** arabis mosaic virus, cucumber mosaic virus, maple mottle-associated virus

Maples are abundantly found in temperate forests and urban parks, with the most common species *A. pseudoplatanus* (sycamore) and *A. platanoides* (Norway maple) representing a natural component of birch (*Betula spp*.) and fir (*Abies spp*.) forests [61]. Several *Acer* species provide valuable timber and are the main sources of maple sugar and maple syrup [62].

Viral diseases in different maple species have been since long reported [63, 64]. Arabis mosaic virus [65, 66] has been reported to infect *Acer* sp. Still, until recently, *Acer* sp. has never been unambiguously described as a host for any well-characterized viral agent. Employing RNA-Seq methodology a novel emaravirus was recently reported in sycamore maple (*A. pseudoplatanus*) exhibiting mottle symptoms in Germany and was genetically characterized [29]. Maple mottle-associated virus comprises 6 RNA segments and evidence is provided that it may be the symptom-inducing virus in the diseased trees.

3.2 2. *Betula spp.* apple mosaic virus, arabis mosaic virus, birch leafroll-associated virus, birch idaeovirus, birch capillovirus, birch carlavirus, cherry leaf roll virus, tobacco necrosis virus, tomato ringspot virus, Phytophthora cactorum RNA virus 1

Birch as a colonizer and pioneer tree species of open areas tree has an extraordinary geographical distribution in the Northern Hemisphere (Europe, Asia, North America, also introduced to Australia) and highly significant role in sylviculture [67]. The genus contains 60 taxa of which 11 are on the IUCN 2011 Green List of Threatened Species. Birch is distributed throughout Eurasia and has the widest range of all European broadleaved tree species. Its ecological impact is unique, as it constitutes part of the few remaining old-growth forests growing in Europe, the proportion of which is rapidly decreasing across the entire boreal zone. Additionally, it contributes to forest resilience and rapid restoration of wood production after disturbance [68].

Several common tree viruses have been since long reported in birch; apple mosaic virus [69], arabis mosaic virus [70], cherry leaf roll virus [71], tobacco necrosis virus [70], tomato ringspot virus [70]. A severe birch decline was first observed in Finnland in 2002 involving leaf symptoms like vein banding, leaf roll, chlorosis and subsequent necrosis and leading the trees to loss of vigour and degeneration. The disease has been widely distrubuted the last two dacedes so far being reported in five European countries with diverse climate conditions (Finland, Sweden, Norway, Germany, France) [7, 72, 73]. The emerging phenomenon was descibed as “birch leaf-roll disease” (BLRD) (6, 72) and was in the beginning related to the presence of CLRV in the affected trees - based on standard molecular diagnostic tools - (6, 7, 73). However, the employment of NGS radically changed our concept regarding the causal agent of the BLRD. RNA-Seq revealed the presence of a novel badnavirus in affected birches [15], while a complex virome involving novel and known viruses was reaveled; birch idaeovirus, birch capillovirus, birch carla virus and cherry leaf roll virus arepresent in symptomatic trees [14]. Based on the metagenomic analysis of three birches that exhibited symptoms and two that did not exhibit symptoms and on further analysing from a considerable number of samples [74], it is suggested that the novel birch leafroll-associated badnavirusis (BLRaV) is the main causal agent of BLRD, however, the other viruses could possibly still contribute in symptom development in cases of mixed infection with BLRaV and/or CLRV.

The oomycete *Phytophthora cactorum* (Leb. and Cohn) Schröeter is a birch pathogen that causes stem lesions and infects mostly nursery seedlings [75]. Besides birch, it infects over 200 species of trees, ornamentals, and fruit crops. A recent NGS study revealed alphaendornaviruses, bunya-like viruses, a toti-like virus and viruses affiliated to the unclassified dsRNA virus group tentatively called "ustiviruses" in *P. cactorum* isolated from strawberry plants [76]. Furthermore, birch may be infected with Armillaria root rot fungi, which typically attack trees weakened by drought or other pathogens. A recent NGS study detected a novel virus group called "ambiviruses" in *Armillaria borealis* growing on birch wood [39].

3.2 **3. *Castenea sativa*** chestnut mosaic virus, Cryphonectria hypovirus 1, mycoreovirus 1

European chestnut (*Castanea sativa* Mill.) has a long-standing tradition of cultivation in many European countries. It is an important species, economically and ecologically as a source of timber and fruit and through the multiple ecosystemic services it provides [77].

The case of the chestnut mosaic disease (ChMD) represents one more case in the forest pathology, where knowledge concerning the causal agent was gained thanks to NGS and bioinformatics analysis. The disease was described several decades ago in Italy [78] associated with viral symptoms like mosaic, shoots with asymmetric leaf blade deformation. Later, it was reported in France in 1987 [79] involving necrotic lesions in the bark and wood that turns into cankers, chlorotic lesions and yellow stripes on leaf veins and partial limb atrophy and, consequently, heavily affecting the production [80]. By using RNA-Seq analysis, two independent isolates of the same novel virus were identified [30]. The novel chestnut mosaic virus belongs to the genus *Badnavirus*, family *Caulimoviridae*, it is unambiguously proven to be episomal and is strongly suggested to play causal role in the disease development.

Another serious disease of chestnut is caused by the ascomycete *Cryphonectria parasitica*. As stated above, hypoviruses infecting the pathogen have been successfully used to control the fungus and subsequent natural spread of these viruses has protected European chestnut trees from complete devastation [44, 45]. Also other viruses (including Mycoreovirus 1 and Cryphonectria mitovirus 1) infect this pathogen, and these have been recently examined for their biocontrol and transmission potential in planta. Some promise was shown, but the use of the viruses is highly dependent on their transmission efficacy [81].

3.2 **4. *Fraxinus* spp**. arabis mosaic virus, cherry leaf roll virus, tobacco necrosis virus, tobacco mocaic virus, tobacco ringspot virus, white ash mosaic virus, putative Cryptovirus, putative Caulimovirus, Hymenoscyphus fraxineus mitovirus 1

Although several viruses are reported in ash trees, all of them are generalists and none of them is host specific. The most common are arabis mosaic virus (82, 83), cherry leaf roll virus [84], tobacco necrosis virus [85], tobacco mocaic virus [86; 87; 88], tobacco ringspot virus [87 - 89], tomato ringspot virus [90], white ash mosaic virus [91].

With the use of NGS a novel putative partitivirus and a novel putative caulimovirus have been identified in *Fraxinus americana* [92] exhibiting symptoms distinct from those caused by the already reported ones, namely chlorotic patches and necrotic lesions on leaves. Generally, members of *Partitiviridae* family do not produce symptoms in their host, recently, however, new members of the family seem no be associated with symptom appearance. Still, further studies are needed in order to fully characterize the new viruses in ash. Because of enough evidence lacking about the causal role of these viruses, they are not included in the Table 1.

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A recently discovered mycovirus related to the ash microbiome/virome is Hymenoscyphus fraxineus mitovirus 1 (HfMV1) [37]. *H. fraxineus* is a pathogen recently introduced to Europe from Asia causing ash dieback and threatening ash stands all across the continent [93]. *H. fraxineus* isolates from Europe were previously shown to harbour HfMV1, while later a viral population with higher genetic diversity was detected in *H. albidus*, a harmless litter saprotroph native in Europe, which suggests multiple interspecific virus transfers from *H. albidus* to *H. fraxineus* [93].

3.2 5. ***Populus spp.***

arabis mosaic virus, , poplar mosaic virus, tomato black ring virus, tobacco ne crosis virus, aspen mosaic-associated virus Armillaria borealis mycovirgavirus 1, Armillaria borealis ambi-like viruses 1 and 2

Populus is a tree native to most of the Northern Hemisphaere including 25-30 species. Six of these aspen species play a disproportionately important role in promoting biodiversity, sequestering carbon, limiting forest disturbances, and providing other ecosystem services [94]. Importantly, aspen are commonly designated "keystone species," meaning their sustained existence supports an inordinate number of dependent plants and animals.

Regarding viruses affecting poplars, only four viruses have been since long time identified; arabis mosaic virus [95, 96], tomato black ring virus [95], tobacco necrosis virus [97] and poplar mosaic virus [98, 99]. The latest is one of the few viruses discovered in the before-NGS-era that is a specialist. Very recently, based on RNA-Seq analysis, a novel emaravirus was discovered in aspen, named aspen mosaic-associated virus [26].

Poplars, as many other hardwood trees are also readily infected by species of *Armillaria*. One of the most common species is *A. borealis* occurring in both conifers and hardwoods. Recently, NGS analysis revealed a Siberian isolate of *A. borealis* from *Populus spp*. to be infected by multiple viruses, including a novel ssRNA(+) virus named Armillaria borealis mycovirgavirus 1 and three ambi-like viruses [39].

3.2 6. ***Quercus spp*.**

common oak ringspot-associated virus, tobacco necrosis virus, tobacco mocaic virus, Armillaria mellea negative strand RNA virus 1, Armillaria mellea ourmia-like virus 2

The genus *Quercus* (oak) contains over 500 species. Oaks are amongst the most economically and ecologically important deciduous trees in Europe providing wood for fuel, bark for tanning, timber for construction, and acorns for livestock [100]. Here we present existing virome data described about *Q. robur* (common oak), *Q. petraea, Q. variabilis* (chinese oak), and *Q. rubra* that are native in Europe, N. America and Asia.

Apart from two viruses with wide host spectrum reported to occur in oaks - tobacco necrosis virus [101] and tobacco mocaic virus [102 - 105], still the main virus disease affecting the species remained until recently unidentified. The `chlorotic ringspot´ disease of oaks originating from the USA was reported already from the 70´s in Europe [105] and its occurrence was estimated to be relatively high in Germany and Scandinavia [3]. The disease was also found to affect 11-19% of oak seedling in propagation stations, threatening with wider spread of the disease through the infected oak propagation material [3]. Due to the employment of NGS strategies the causal agent of the disease could very lately be identified; the common oak ringspot-associated virus (CORaV) [27, 28] represents a new member of the genus *Emaravirus* comprising five RNA segments. For one more time, metagenomic analysis provided the diagnostic answer to a problem remaining unsolved for long time.

Apart from the virus diseases, oaks suffer also by the "Sudden Oak Death" caused by *Phytophthora ramorum* - an oomycete that can kill oaks within few weeks - and from "Oak Wilt", caused by the fungus *Ceratocystis fagacearum*. The oak forest decline is a serious problem in North and South America. In the USA, entire oak ecosystems have declined due to a combination of factors still imperfectly known [106] (Lorimer, 2003), it is, however, hypothesized that viral diseases are part of this complex syndrome. Notably, endornavirus strains have been found in *Phytophthora ramorum* isolates from various host plants including *Rhododendron* and *Viburnum* species both in the United States and Europe, but unfortunately they do not seem to cause host debilitation that could be used for disease mitigation [107]. Already declining oak trees also readily suffer from infections by *Armillaria* root rot fungi. Recent discoveries of viruses in *Armillaria spp*. [39] prompt for the search of debilitation-associated viruses also in these species. However, the viruses found thus far (Armillaria mellea negative strand RNA virus 1 and Armillaria mellea ourmia-like virus 2) in *A. mellea* from oak trees in South Africa, seemed not to reduce the growth of their host in laboratory conditions.

Oaks are known to form mycorrhizal associations with both ascomycetes, such as true truffles (*Tuber spp*.) and *Cenococcum geophilus*, as well as basidiomycetes, such as species of *Lactarius, Russula and Cortinarius*. Viruses have been found in the ectomycorrhizal fungus *Hygrophorus penarioides*, but their possible effects on the tree-fungus association are yet unknown [52]. Moreover, *Tuber spp*. (*T. excavatum* and *T. aestivum*) have been shown to harbor diverse viruses of families *Totiviridae, Endornaviridae* and *Mitoviridae* (Table 2).

3.2 7. *Sambucus spp.*

arabis mosaic virus, blueberry scorch virus, cherry leaf roll virus, cherry rasp leaf virus, elderberry carlaviruses A, B, C, D, E, elderberry latent virus, elderberry aureusvirus 1, Sambucus virus S, tomato bushy stunt virus, tomato black ring virus, tobacco necrosis virus, tobacco ringspot virus

Elderberry (*Sambucus nigra* L.) is a deciduous tree native to Europe and North America. Its flowers and berries are used to prepare infusions, syrups and jellies and in traditional medicine. The popularity of this plant has increased in recent years in the pharmaceutical and food industries, due to its antiseptic and antiviral properties as well as to the interest in the colour compounds present in the berries [108].

From the abundant viruses affecting elderberry, eight are generalists and seven are specialists. Arabis mosaic virus [109], blueberry scorch virus [110], cherry leaf roll virus [111], cherry rasp leaf virus [112], tomato bushy stunt virus [113, 114], tomato black ring virus [115], tobacco necrosis virus [113, 116], tobacco ringspot virus [117] have been since long reported in elderberries and in other forest species worldwide. One of the specialists is elderberry latent virus [32, 112] reported in the USA. NGS technology contributed to our knowledge on viral diseases in elderberry with the discovery of seven host specific viruses. The elderberry aureusvirus 1 is either asymptomatic or associated with mild chlorotic mosaics and was detected by applying Illumina sequencing in double-stranded RNAs (ds-RNAs) [118]. Through dsRNAs Illumina sequencing was also the bromovirus sambucus virus S identified [119]. Five elderberry carlaviruses A, B, C, D, E were detected with the use of a degenerate oligonucleotide primed (DOP) RT-PCR method with multiple barcodes for NGS, involving VirFind, a novel and automated bioinformatics tool specifically for virus detection and discovery [32, 33].

3.2 8. *Sorbus aucuparia*

apple mosaic virus, apple chlorotic leaf spot virus, cherry leaf roll virus, European mountain ash ringspot-associated virus

S. aucuparia is an important deciduous tree or shrub, native to most of Europe and parts of Asia, as well as northern Africa. It serves as an ornamental urban species, it is also cultivated for its fruits and its timber [120].

The major disease affecting *S. aucuparia* is the 'European mountain ash ringspot disease' caused by European mountain ash ringspot-associated virus (EMARaV) inducing chlorotic ringspots, mottle and line pattern on leaves, and is widespread in central/northern Europe and England [8, 9]. Apart from symptoms development, EMARaV also causes symptomless infections, it is therefore assumed to be more common in the wild mountain ash trees than previously thought. Monitoring EMARaV in European forests revealed a very important aspect in viral epidemiology, the ability of viral pathogens to have an extended host range. Concretely, EMARaV was recently detected in new hosts, namely in *Amelanchier spp*. in Germany [18], in *Karpatiosorbus x hybrid* in Finland [16] and in *Sorbus intermedia* in Sweden [17]. Concretely, in *S. aucuparia* (Swedish whitebeam) it was revealed through high-throughput Illumina RNASeq that EMARaV in this host posseses two additional RNA segments, in contrast to the four RNAs possessed by EMARaV in mountain ash [17]. The biological function of these previously unrecorded genome segments remains to be elucidated.

Apart from EMARaV, only a few viruses have been detected in mountain ash; the apple mosaic virus [116], the apple chlorotic leaf spot virus [121] and the cherry leaf roll virus [122].

3.2 9. *Ulmus spp.*

cherry leaf roll virus, elm carlavirus, elm mottle virus, tomato bushy stunt virus, tomato ringspot virus, Ophiostoma mitoviruses

Several viruses have been reported to affect elms; elm mottle virus [123, 124], tomato ringspot virus [125], tomato bushy stunt virus [126] and cherry leaf roll virus [122, 127]. Recently, a disease affecting elms attributed to a non-characterized virus was investigated with the use of RNA-Seq methodology. This method revealed the presence of a novel carlavirus, the elm carlavirus [129, 130] strongly suggested to be the causal agent of dieback and leaf symptoms like chlorotic ringspots, mottling and necroses in elms.

Mitoviruses are common in *Ophiostoma ulmi* and *O. novo-ulmi*, the causal agents of the dutch elm disease (DED) devastating american elms but causing also epidemics in Europa and N. America after new introductions. Some of these mitoviruses are associated with reduced growth and sporulation of the host fungus [131]. Eight independently replicating mitoviruses were detected by Doherty et al. [38] in one diseased isolate of *O. novo-ulmi*, while two more mitoviruses were detected in a Candian isolate of *O. novo-ulmi* [132]. The use of virus-induced hypovirulence as a biological control relies on the ability to transfer the virus between isolates within a population of the target pathogen. RNA viruses that have been found in *O. novo-ulmi* to date are located in mitochondria and can only be transmitted during anastomosis between compatible hyphae, or induced forms of cytoplasmic mixing [132]. These findings raise the potential for engineering these viruses to include other genetic elements, such as anti-sense or interfering RNAs, to create novel and highly specific biological controls.

3.2 10. ***Pinus spp***.

Heterobasidion partitiviruses, Gremmeniella abietina mitochondrial RNA virus S1, Gremmeniella abietina RNA virus L1, Gremmeniella abietina RNA virus MS1, Fusarium circinatum mitovirus 1, 2-1 and 2-2, Pinus sylvestris partitivirus NL-2005, Pinus patula amalgavirus 1, Pinus nigra virus 1, Tobacco necrosis virus

Pinus spp. are attacked by various fungal pathogens including the root rot fungi *Heterobasidion annosum* (Europe) and *H. irregulare* (North America and Europe as an introduced invasive species). These pine pathogens host viruses of the families *Partitiviridae,* and *Mitoviridae* and both virus families have also apparently cryptic members infecting plants [133, 134]. The alphapartitivirus HetPV13-an1 of *H. annosum* is associated with host debilitation (133; see Discussion). *H. parviporum* also hosts HetRV6, a member of a newly classified family *Curvulaviridae* (Table 2). The spore-mediated dispersal of *H. parviporum* and *H. annosum* can be controlled by a preparation of the saprotroph *Phlebiopsis gigantea* that acts as an antagonist to *Heterobasidion spp*. and occurs very commonly in newly cut conifer wood, especially Scots pine. *P. gigantea* is infected by mycoviruses tentatively named "phlegiviruses" according to their host fungus (Table 2).

Pines also suffer from needle diseases such as *Scleroderris* cancer caused by *Gremmeniella abietina* and wilting disease caused by the globally spreading pathogen *Fusarium circinatum*. The ascomycete *G. abietina* (Lagerberg) Morelet causes shoot blight and stem canker of several conifers in Europe and North America. The fungus hosts a diverse virus community (Table 2; 42). One of the viruses, representing virus family *Curvulaviridae*, has been associated with phenotypical changes in the host (enhanced mycelial growth) [42]. *F. circinatum* is also commonly infected with mitoviruses (Table 2, [135-136]). Viruses of the families *Totiviridae* and *Mitoviridae* also occur in the pine needle pathogens *Diplodia pinea* and *Cronartium ribicola*, respectively (Table 2).

On the other hand, pines have several fungi as their symbiotic partners forming ectomycorrhizal associations. One of the most common is *Thelephora terrestris* that hosts a "phlegivirus" that was also detected in soil oribatid mites, suggesting that even some RNA mycoviruses could have arthropod vectors [137]. Also the basidiomycete *Lactarius rufus* is a highly common ectomycorrhizal symbiont of pine trees, and has been shown to be commonly infected by members of family *Curvulaviridae* (Table 3; [138]). Remarkably, a single ascocarp of the ectomycorrhizal crown cup fungus *Sarcosphaera coronaria* associated with *Pinus brutia*, was shown to be infected with ~34 different partitiviruses [51]. The same research group found a partitivirus in another ectomycorrhizal partner of *P. brutia, Gyromitra esculenta* [53], which may be also infected by endornaviruses as revealed by in silico analysis of transcriptomic datasets [139].

Not many viruses are known from the *Pinus* trees themselves. One of the rare ones is the cryptovirus Pinus sylvestris partitivirus NL-2005 (Table 1, [140]). Also Pinus patula amalgavirus 1 has been reported in a transcriptome shotgun assembly (TSA) database [134], illustrating the value of mining the TSA and other databases for novel viral sequences.

Pinus nigra virus 1, an unclassified *Caulimoviridae* member, was discovered through air metagenomics (using Illumina technology) in a Spain and was later PCR-detected in *Pinus nigra* samples from the vicinity of where the air samples were collected. This suggests that this new virus is likely pathogen of *Pinus* (Rastojo 2018). Another pathogenic virus reported in *Pinus* is tobacco necrosis virus [101], but since long it has not been further investigated.

3.2 11. *Picea spp.* tomato mosaic virus, picea mariana tenuivirus, Heterobasidion partitiviruses, Heterobasidion orthocurvulavirus, Heterobasidion mitovirus 3, tomato mosaic virus

Concerning Norway spruce, it is a long-living species (>200 years-old) with a long tradition of cultivation for its straight trunk, particularly used for timber constructions, pulpwood for paper and furniture [142]. Its high economic and ecological significance calls for taking proactive measures against potential viral emergence. Starting from the 1980s, spruce forests have shown symptoms of decline in mountainous areas of central Europe including yellowing, loss of needles, die-back of branches and reduced growth. Due to widespread spruce pathogens and pests such as *Heterobasidion parviporum* and *Ips typographus*, as well as health problems of unidentified etiology, its popularity for reforestation, particularly outside its natural range in central European forests has been reduced although it remains to be the commercially most valuable tree species in the Nordic countries.

From the plant pathogenic viruses only tomato mosaic virus has been reported in spruce [143, 144]. *Picea mariana* has been reported to host ssRNA(-) viruses of the genus *Tenuivirus* (Castello 2000).

The most important fungal pathogen infecting Norway spruce is *Heterobasidion parviporum*, which causes economic losses of hundreds of millions of euros annually in Europe [145]. Like the related species *H. annosum* preferring pines as its host, also *H. parviporum* hosts partiti-, curvula- and mitoviruses (Table 2). The alphapartitivirus HetPV15-pa1 of *H. annosum* is associated with debilitation of its fungal host [146]. The ectomycorrhizal symbionts of spruce include e.g. species of *Lactarius, L. tabidus* being one of the most common ones. This species also harbors members of family *Curvulaviridae* (Table 3). The ectomycorrhizal symbionts of spruce include e.g. species of *Lactarius, L. tabidus* being one of the most common ones [58]. This species also harbors members of family *Curvulaviridae* (Table 3).

3.2 12. Other tree species

1. ***Prunus spp.***: Prunus trees may suffer from infections by *Chondrostereum purpureum* that causes silver leaf disease and has been developed as a biocontrol tool for prevention of sprouting. The fungus hosts an alphapartitivirus called Chondrostereum cryptic virus 1 [147]. This tree genus may also be attacked by the notorious white root rot fungus *R. necatrix* that has a very broad host range including both tropical and temperate fruit and forest trees. *R. necatrix* viruses are exemplified above and in Table 2.
2. ***Aesculus spp.*:** Some plant pathogenic viruses have been reported in *Aesculus* (apple chlorotic leaf spot virus, apple mosaic virus, cherry leaf roll virus, strawberry latent ringspot virus) (Table 1). Cryphonectria hypovirus 1 affecting *Cryphonectria parasitica* most commonly in chestnut, is also present in *Aesculus hippocastanum* (Table 2).
3. ***Fagus spp.*:** Earlier reports exists about occurrence of cherry leaf roll virus and tobacco necrosis virus in beech. Recent RNA-Seq investigation has revealed a novel carlavirus related with leaf symtoms in trees in Germany [129].
4. ***Robinia spp.***: Strawberry latent ringspot virus and peanut stunt virus (Iran) (Table 1) have been reported.
5. ***Salix spp.*:** A few generalist viruses may occur in Salix, like brome mosaic virus, tomato mosaic virus and tobacco necrosis virus.
6. ***Cedrus libani***: The ectomycorrhizal ascomycete *Geopora sumneriana* associates with Lebanon cedar. Recently a Geopora sumneriana mitovirus 1 was identified in this fungal species (Sahin an Akata 2019).
7. ***Abies spp.***: No plant pathogen reported. Several partitivirus are reported in *Heterobasidion* basidiomycetes infecting diverse *Abies* species; Heterobasidion partitivirus 1 in *A. cephalonica*, Heterobasidion partitivirus 10 in *A. concolor* and Heterobasidion RNA virus 6 (an orthocurvulavirus) in *A. alba, A. sibirica, A. cephalonica, A. cilicica, A. equi-trojani* and *A. concolor* (Table 2). Finally, a mitovirus is detected in *Fusarium circinatum* infesting in *A. alba* (*Mitovirus, Mitoviridae).*

8. ***Pseudotsuga menziesii***: Aphaendornaviruses infect members of *Phytophthora ramorum* and *Phytophthora* taxon douglasfir [107].

4. Discussion

NGS technology has quantitatively considerably impacted on pathogen detection in forest pathology and virology. Based on the data presented in the current review, it has become obvious that NGS has significantly contributed to the discovery of novel viruses in organisms (trees, fungi) that comprise what a forest is. Analogically, our knowledge regarding virus communities in urban parks has considerably increased. Almost the half of the plant pathogenic viruses and cryproviruses in plants (21 out of 43), 36% of the mycoviruses infecting pathogenic fungi (23 out of 65) and 58% of the mycoviruses occurring in non-pathogenic fungi (7 out of 12) were discovered due to the employment of NGS strategies. Specifically considering the phytopathogenic viruses, the novel viruses were not identified in random environmental or host samplings, but after targeting diseased trees, where the disease was since long described, the disease distribution was for long monitored, but still, the causal agent had not been identified due to limitations in the existing conventional molecular diagnostic methods. As far as mycoviruses are concerned, even in species that have been extensively investigated, NGS of a small amount of isolates has revealed virus families not detectable by traditional methods, most notably (+)ssRNA and (-)ssRNAviruses. The ability of NGS methods to extend the genetic investigation to a depth that had not been earlier achieved, resulted in extraordinary discoveries that radically changed the view of forest pathology.

The massive discoveries of viruses in the forest ecosystem based on NGS technologies refer usually only to the full or partial genome sequence of the novel viruses, while little is probably known about its biology and symptom-expression. To provide a basis for assessing the risk the novel viruses pose and take scientifically-based decisions, a series of unavoidable steps need to be taken [148]. The early steps include the confirmation of infection using complementary methods, the provisional taxonomy assignment, the sample documentation adding information like symptomatology and geographical origin, the full genome sequencing and annotation (in cases of incomplete viral sequences), development of a diagnostic protocol accessible to all affected parties, as well as small-scale epidemiological surveys at the discovery location. The in-depth characterization is a mid- or longterm goal that involves transmission experiments to explore modes of dispersal as well as possible vectors and future large-scale surveys, organized on a national or international scale. This framework has been already actively followed by the numerous research groups that focus on plant virology [149]. Regarding the forest virology, however, as mentioned in the introduction the progress is anticipated to be too slow, due to the few groups that focus on these issues and if research in this field will not be drastically financed, we may face unpleasant consequences in the future.

Based on the data of the last five years, it has been revealed that the genetic variation of the forest virome is much larger than estimated. After gathering information about the viral presence in the holobionts, we could - as a next step - estimate the role of this virome in the holobionts, the need for which was highlighted by Rosenbeng and Zilber-Rosenberg [150]. One of the four basic principles of the hologenome theory is that genetic variation in the hologenome can also be brought by changes in the microbiome genome [150]. Following, we attempt to make suggestions on how the novel genetic information may qualitatively influence our view regarding forest health.

An important source of genetic variation is the horizontal gene transfer (HZT). As an example, 128 genes were identified in the genome of moss *Physcomitrella patens,* which were acquired by HGT from prokaryotes, fungi or viruses [151]. Acquisition of genomic segments by HGT has been found in plants in relation also with infections by pararetroviruses. With the use of NGS two novel badnaviruses, which are dsDNA pararetroviruses of the family *Caulimoviridae* are discovered in birch and in chestnut and one unclassified *Caulimoviridae* member in pines. Pararetroviruses are often present as integrated, complete or fragmented and/or re-arranged genomic sequences in some host plant genomes and are then referred to as endogenous viral elements (EVEs). Some banana streak viruses are found in episomal form having an endogenous counterpart (eBSV) [152]. In a few cases, badnavirus EVEs are known to be activated to generate viral infection (like Banana streak OL, GF or IM viruses) [153]. Moreover, it is shown that genes of totiviruses and partitiviruses have widespread homologs in the nuclear genomes of eukaryotic organisms. Evidence has been provided that some of the transferred genes are conserved and expressed in eukaryotic organisms, suggesting that these viral genes are also functional in the recipient genomes [154]. Whether the integration of the viral DNA of the novel caulimoviruses into the birch, chestnut and pine genome may play a role in its evolution remains to be untangled.

Viruses often coinfect single holobionts - in our study trees/shrubs - in nature. This was already known before the development of NGS technology, but the deep sequencing methods profoundly revealed the complexity of plants and tree viromes. Novel data about the birch virome clearly demonstrate in holobionts mixed infections by multiple plant viruses as well as multiple variants of the same virus species [14, 15, 74]. This is the case also in other non-forest plant species like peach [155], or grapevine [156, 157]. As a consequence, it is not easy to establish a correlation between such viral complexes and the appearance of symptoms or to differentiate symptomatology in cases of infection by a single virus or by two virus species. It is, however, suggested [74] that alterations in the viral communities in a holobiont may result in alteration in the symptom development.

Viruses often coinfect single fungal hosts in nature and there are interesting virus/virus interplays in coinfected hosts have been reported that may be synergistic, apparently neutral or antagonistic [49]. Strong virus interference between unrelated RNA viruses were detected in *Cryphonectria parasitica*; for example, the (+)ssRNA virus Cryphonectria hypovirus 1 (CHV1) exerts a one-way synergistic effect on a co-infecting mycoreovirus 1 (MyRV1), resulting in enhanced virus accumulation and increased vertical transmission of MyRV1 [158]. In another interplay, the replication of Rosellinia necatrix victorivirus 1 (RnVV1) was strongly impaired by coinfection with MyRV1 or a mutant of CHV1 lacking the RNA silencing suppressor [47]. Recently, a unique mutualistic virus/virus interplay was reported, where the capsidless (+) ssRNA yado-kari (YkV1) virus is hosted by an unrelated dsRNA virus, yado-nushi virus (YnV1); while YnV1 can complete its replication cycle, YkV1 relies on YnV1 for its viability [159]. In another interaction system, the hypovirulence-associated mycoreovirus, named Sclerotinia sclerotiorum mycoreovirus 4 (SsMYRV4), could suppress host non-self recognition and facilitate horizontal transmission of heterologous viruses among vegetatively incompatible *S. sclerotiorum* individuals to create a bridge donor strain for mycovirus spread under natural conditions [160]. Such examples provide insight into the potential for broad-spectrum virus control mediated by RNA silencing.

Interspecific virus transmission is often being suggested in mycoviruses [93, 161]. In vitro experiments have shown that Cryphonectria hypovirus 1 was transmitted horizontally between the chestnut blight fungus *Cryphonectria parasitica*, and a sympatric unidentified *Cryphonectria* species via hyphal anastomosis [161]. Similarly, highly similar *Heterobasidion* RNA virus 1 (HetRV1) strains with 98 % nucleotide level similarity were found from *H. parviporum* and *H. australe* growing in the same region in Bhutan, an observation that suggests recent virus transmission between these taxonomically distant *Heterobasidion* species in nature [162]. In another host, *Fraxinus spp*., hyphal anastomosis and transfer of the mitovirus Hymenoscyphus fraxineus mitovirus 1 (HfMV1) between both *Hymenoscyphus albidus* and *H. fraxineus* in ash is also hypothesized [93]. Having in mind that interspecies virus transmission is possible between viruses occurring in distantly related organisms like infecting fungi, plants, oomycetes and invertebrates [163, 164], this evolutionary potential should be taken into consideration also in view of the forest virome.

The efforts to untangle the complex world of micobiota-virome interaction has been initiated for the human holobiont. Evidence is provided that bacteria aid in the antiviral response to certain viruses, however, occasionally they may act as promoters of viral infection [165]. The present review constitutes a conceptual change by putting under the same umbrella communities of microbiota and virome in a forest. This way it becomes obvious how many possibilities for interactions are open, with all consequences these may have for all “partners” within a holobiont. An important consequence could be, that since the microbiome genome can adjust to environmental dynamics more rapidly and by more processes than the host genome, it can play a fundamental role in the adaptation and evolution of the holobiont [150].

The accumulation of knowledge regarding abundant mycoviruses in plant pathogenic fungi in forests offers new possibilities for pathogen control and management. There were already promises raised that endophytes might be utilized as biocontrol agents in integrated pest and disease management [166]. Practical applications for forest protection based on endophytes are still rare. As stated above, the major mycoviral biocontrol agent used in field conditions is the hypovirus CHV1 that significantly reduces the pathogenicity of the ascomycetous chestnut blight fungus (*Cryphonectria parasitica*) in Europe [44, 45]. Moreover, in *C. parasitica*, introduction of a partitivirus and a megabirnavirus originating from another host fungus, *Rosellinia necatrix*, was also shown to reduce host virulence [167, 168]. Several *R. necatrix* viruses, including a fungal reovirus, show as well potential for controlling their native host [169 - 172]. Additionally, Heterobasidion partitiviruses 13 and 15 have been shown to restrict host growth and alter mycelial morphology of the conifer root rot fungi *H. annosum* and *H. parviporum* [46, 133]. The recently generated data that are summarized in the present review could trigger further novel, modern, sustainable and environmentally friendly pest control applications. More knowledge can lead to mechanisms being unravelled in a direction that humans can use the latest level of knowledge to positively influence the health of the tree and environment.

In the present review, we have not addressed viruses of arthropods; however, it should be noted that baculoviruses of insect pests of temperate forest trees have been investigated for their biocontrol potential. The most prominent, that we mention here, are the nuclear polyhedrosis virus affecting *Lymantria dispar* on birches [173], oaks and poplars [174], the Condylorrhiza vestigialis multiple nucleopolyhedrovirus affecting *Condylorrhiza vestigialis* on poplars [175], the Orgyia leucostigma nucleopolyhedrovirus infesting *Orgyia leucostigma* on birches, firs and spruces [176, 177] and the Neodiprion abietis nucleopolyhedrovirus (NeseSNPV) affecting *Neodiprion abietis* on conifers [178]. As part of the effort to control the sawfly, NeseSNPV was introduced from Sweden into Canada and spread rapidly through the cohort and ultimately the population resulting in long-term suppression of *N. sertifer* [179]. To our knowledge, NGS application has not contributed some further progress on this field.

Regarding vectors that transmit viruses little is known. The only corresponding reference in the past is given in 1971 when Nienhaus detected tobamoviruses in Califonian oak leaves and assumed due to the experiments a virus transmissible fungus (*Sphaerotheca lanestris*). Vector studies of forest viruses were not continued later up to 2012 when Mielke and Mühlbach [9] highlighted the confirmed vector transmission by eriophyid mites (*Phytoptus pyri*) conclusively shown with several emaraviruses: European mountain ash ringspot-associated virus (EMARaV), Fig mosaic virus (FMV), rose rosette virus (RRV), raspberry leaf blotch virus (RLBV), pigeonpea sterility mosaic virus.

The characterization of many novel - pathogenic or non-pathogenic - viruses in a short time raises the question of how to profit from these new data in order to avoid forest disease outbreaks in the future. How possible is for a pathogen to initiate an emerging infectious disease (EID)? According to the pathogen-host-environment interplay theory [180] emergence starts with an existing disease complex or pathogen–host–environment complex - based on paradigms from human and animal disease. The drivers of pathogen's emergence cause a shift to the overall pattern of the pathogen–host–environment interactions leading to an emergence infectious disease (EID) event. Examples of drivers in regard to forest comprise deforestation and logging, other forms of human encroachment of forests and game reserves, and increased interspecies contacts at the wildlife/agriculture interface. Impending climate change may support the spread of forest pathogens and diseases and play a role in dispersal of forest epidemics. Based on significant changes in the environment, alterations in the interactions within the holobiont may underlie future outbreaks of diseases. In light of the current detrimental and on-going COVID-19 epidemic in humans, we propose that driver analysis in forest pathogens should be conducted coordinated and similarly across the fields of human, animal and plant health.

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