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Meeting report: The first soil viral workshop 2022

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ABSTRACT

Soil viral ecology is a growing research field; however, the state of knowledge still lags behind that of aquatic systems. Therefore, to facilitate progress, the first Soil Viral Workshop was held to encourage international scientific discussion and collaboration, suggest guidelines for future research, and establish soil viral research as a concrete research area. The workshop took place at Søminestationen, Denmark, between 15 and 17th of June 2022. The meeting was primarily held in person, but the sessions were also streamed online. The workshop was attended by 23 researchers from ten different countries and from a wide range of subfields and career stages. Eleven talks were presented, followed by discussions revolving around three major topics: viral genomics, virus–host interactions, and viruses in the soil food web. The main take-home messages and suggestions from the discussions are summarized in this report.

1. Introduction

Viruses are the most abundant biological entities in aquatic systems (Suttle, 2005), and this is likely to be true in soils as well, given the high abundances of virus-like particles (VLPs; Williamson et al., 2017), thus providing an untapped reservoir of viral diversity. Studies from aquatic ecosystems show that viruses can strongly affect the mortality and metabolism of their hosts, which in turn affect biogeochemical cycles and food web dynamics (Kristensen et al., 2010). There is early evidence of similar roles of viruses in soil functioning too, however, there is still little known about the extent of their roles in soil ecosystems (Emerson, 2019; Trubl et al., 2018), which is surprising given the critical role of soils in supporting life on Earth. Furthermore, while aquatic and especially ocean viruses are well studied (Brum et al., 2015), direct extrapolations of knowledge about virus ecology from water to soil are challenging, and technological advances for aqueous systems are not always applicable in soil due to unique challenges associated with the soil matrix. As a result, soil virology is an understudied research area that is just starting to build a foundation, yet it is vital for understanding overall soil ecology.

Being an emerging research area, the soil virosphere has been studied more intensively in recent years, although scientists often have been working independently in small clusters. Therefore, the first Soil Viral Workshop (SVW) was organized to bring together leading soil viral researchers to accelerate progress in the field. The main objectives of the workshop were to: (1) encourage networking and knowledge exchange among soil viral researchers studying natural and agricultural environments; (2) shape the future directions of soil virology research; and (3) establish soil virology as a defined research area.

The 23 workshop participants came from ten different countries

(Fig. 1) and represented a variety of expertise, including molecular microbiology, plant pathology, and bioinformatics, among others. The workshop also brought together important contributions from researchers at various stages of their careers, including early career researchers. In fact, 87% of SVW participants were at the assistant professor level or below with 30% being PhD students. This was made possible in part by travel grants provided to PhD students and post-doctoral fellows. Finally, nearly half the attendees, including six out of eleven presenters, were women, a rare instance in Science, Technology, Engineering and Math (STEM) fields where women are still underrepresented. Unfortunately, there was still a strong bias towards the attendees coming from developed countries (78%) in the Northern Hemisphere, which should be improved in future workshops via, for example, advertising and collaboration possibilities. Immigration bureaucracy can be one of the issues preventing participation, which was in part remedied by using a hybrid approach, where in addition to in-person presentations and discussions, the talks were recorded and live streamed online via a link accessible to anyone who was interested. This enabled the workshop to include participants and presenters who were limited by long distances and COVID-19 restrictions. The recordings are available to the public on <https://www.soilviral.com/session-videos>.

The workshop was divided into three thematic sessions: viral genomics, virus–host interactions, and viral impacts on the food web. Each session began with a keynote speaker, followed by 2–3 presentations by other researchers. Following this, a considerable amount of time was spent on group discussions with the goal of identifying major knowledge gaps. The main take away messages from each session's talks and discussions are reported below (Table 1).

Abbreviations: MGs, Auxiliary metabolic genes; MIUViGs, Minimum Information about an Uncultivated Virus Genome; SVW, Soil Viral Workshop; VLPs, Virus-like particles.

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Fig. 1. The Soil Viral Workshop united 23 participants from 10 countries between 15 and 17 June 2022 in Denmark. Numbers inside black circles indicate the number of participants from each country.

Table 1
Summary of recommendations and important but understudied research directions raised by SVW participants.

| Session 1: Viral genomics | Session 2: Virus-host interactions | Session 3: Viruses in the soil food web |
|---|---|---|
| Sample preparation optimization for specific soil types | More non-pathological studies | Viral contribution to C, N, P cycling and availability |
| Improvement of extraction and desorption methods | Research on non-human and non-bacterial viruses | Viral contribution to organic and inorganic matter release |
| Following of MIUViG recommendations | Identification of host metabolic changes during infection | Roles of AMGs |
| Mixing of long and short read sequencing | Changes to host phenotype during infection | Viruses as regulators of community structure |
| More inclusive bioinformatics tools for viruses from a variety of hosts | Co-evolutionary dynamics | Virus roles and infection rates under different soil types, conditions, and microhabitats |
| More large-scale benchmark studies | Viral infection effects on host ecological functions | Viral roles in natural versus agricultural soils |
| Trait-based approach complementing viral taxonomy | | |
| Curated viral genome database | | |

2. Themed sessions

2.1. Viral genomics

The first session began with a plenary presentation by Richard Allen White III (PhD, UNC-Charlotte, USA), who presented a new automated method for counting VLPs using an algorithm that resolves them from epifluorescence microscopy images (unpublished data). Compared to counting manually, this method saves time and can provide unbiased, consistent results across images and thus likely more accurate estimates of viral abundance. However, there are still some limitations to the

epifluorescence microscopy approach, such as contaminating organic material, due to the complexity of the soil matrix. In the following talk, Valerie Langlois (PhD candidate, Laval University, Canada) presented seasonal changes in viral communities in thermokarst lakes, which are sinkholes formed when ice-rich permafrost thaws. She observed two distinct viral communities: a variable one at the lake surface that reestablishes every summer, and a perennial community that persists in the anoxic layer during summer but occupies the entire water column during winter (Langlois et al., 2023). She hypothesized that the seasonal viral community mostly originates from soils, such as eroding palsamounds, among other reservoirs. Furthermore, two studies on RNA viruses in soils were presented by Luke S. Hillary (PhD, UC-Davis, USA) and Cátia Carreira (postdoc, Aarhus University, Denmark). Luke found that viral communities differed across a gradient of peat, managed grassland and coastal soils in the United Kingdom, and that plant viruses were more dominant than bacteriophages in these RNA viromes (Hillary et al., 2022). Cátia found that agricultural soils had the lowest viral abundance and forest soils had the highest, and perhaps unsurprisingly, different soils (grassland, agricultural, beech and pine forest) were dominated by different virus groups (unpublished data). The two studies mentioned above did not include studies of the viral host interactions, which could be an interesting avenue of future research.

The viral genomics theme continued in the first group discussion session. With the advent of new sequencing technologies, nowadays the genomic approach often takes one of the following two forms, a total metagenomic approach (viral sequences are extracted from metagenomes of the entire microbial community) or a virome approach (the viral-sized fraction is selected prior to DNA/RNA extraction). The choice between the two methods, and which one is better suited to soil environments were discussed. It was concluded that while a total metagenome approach captures microbial hosts and, in theory, should have the potential to account for most viruses, in reality it yields a much lower diversity of viral genomes, limiting our ability to characterize viral communities (Santos-Medellin et al., 2021). The virome approach allows for substantially better recovery of viral diversity but applies a size cut-off that removes viral groups with large capsids. The virome method in particular would benefit from tailoring the sample preparation steps to their soil prior to sequencing. This includes but is not limited to optimization of the extraction and de-adsorption methods of viruses in the specific type of soil targeted in each individual study prior to sample collection and processing. Soil type, texture, and organic matter content,

among other properties, should be considered in the selection of an extraction method, since, depending on physicochemical properties, soil particles interact differently with virus particles, thus requiring different chemical suspension and/or physical separation methods (Trubl et al., 2016). Optimized methods do not yet exist for all major soil types, and more optimization studies are needed. This may result in different methods being used for different soil types, which should be clearly documented and considered when comparing studies. Furthermore, virus-host pair culturing in combination with omic approaches is likely still the most effective method for detecting certain viruses, such as mycoviruses (viruses that infect fungi). Because they often lack capsids and occur intracellularly, their detection is more challenging and therefore might require several techniques.

Difficulties in the recovery of viral genomes from uncultured viruses, particularly in complex communities such as in soils, were considered further. Participants suggested that while parameters should be set based on properties of each individual sample, the minimum threshold on quality of Uncultured Viral Genomes (MIUViGs; Roux et al., 2019) should be respected, and all associated information provided. Hybrid assembly, or the mixing of long and short read sequencing, could help reduce chimerization of multiple viral genomes, and produce longer contigs by assembly pipelines (Overholt et al., 2020). This, however, would require an important increase in financial investment into already costly research projects.

Participants reported that available bioinformatics tools and pipelines are often skewed toward bacteriophage communities and that the underlying assumptions of these tools should be reassessed to include other viral groups such as viruses of archaea or micro-eukaryotes. It was also discussed that large-scale benchmarking studies should be encouraged to assess the performance of various tools on less typical datasets such as what has been done in the Critical Assessment of Metagenome Interpretation challenge (Meyer et al., 2022). The subject of viral taxonomy was also discussed, with suggestions made to combine the typical classification approach based on sequence similarity with a trait-based approach (Santos-Medellin et al., 2022; Simmonds et al., 2023), particularly in the context of ecological datasets. Finally, the need for a single curated database of viral genomes was highlighted. This issue is not unique to soil viruses, as such a database would enhance viral ecology regardless of the ecosystem type.

2.2. Virus–host interactions

The second theme of the workshop was virus–host interactions. Suvi Sutela (PhD, Natural Resources Institute, Finland) gave a plenary talk about the search for mycoviruses in root rot pathogen (Sutela et al., 2021) and ectomycorrhizal fungi (Sutela and Vainio, 2020) from boreal forest sites in Finland, and showed that mycovirus communities were stable and persistent for several years. Further presentations by Olaoluwa Ajayi (PhD, University of Ibadan, Nigeria; presented virtually) and Živilė Buivydaitė (PhD candidate, Aarhus University, Denmark) showed how bacteria (*Rhizobia* spp.) and mycoviruses can work as biocontrol agents against plant pathogenic viruses in peas and faba beans, and against *Fusarium culmorum* in wheat, respectively (unpublished data).

During the discussion that followed, participants explored and debated important virus–host interactions, as well as which aspects require additional attention. It was generally concluded that virus–host interactions have mostly been explored from a pathological perspective with respect to higher organisms and crops. Therefore, the following areas of virus interactions should also be prioritized for future studies: virus–virus interactions, virus–mesofauna, neutral and beneficial virus–host interactions, virus transport across soil environments, and how these interactions differ in agricultural versus unmanaged soils. Relating to these interactions, the participants agreed that there is a need to determine: (1) metabolic changes associated with host fitness during infection; (2) co-evolutionary dynamics; (3) viral infection

effects on host ecology and ecophysiology; and (4) viral and host genome interactions causing the associated host phenotypic changes.

During the final point of discussion on virus–host interactions, it was agreed that there is a need to improve visualization methods and scale up nanoscale observations to ecologically relevant scales, to establish virus–host model systems, and perform experiments in ecologically relevant contexts (e.g., field, phytotron and greenhouse experiments).

2.3. Viruses in the soil food web

Joanne Emerson (PhD, UC-Davis, USA) kicked off the final session with a presentation about the dynamics and activity of soil viral communities, demonstrating strong spatial structuring (Santos-Medellin et al., 2021; 2022), as well as changes in viral communities following soil wetting (Santos-Medellin et al., 2023). Gareth Trubl (PhD, Lawrence Livermore National Laboratory, USA) followed her talk, presenting how metagenomic approaches can be combined with stable isotope probing to measure microbial and viral activities (Trubl et al. 2021; unpublished data). Kyle Mason-Jones (PhD, Netherlands Institute of Ecology, Netherlands) presented how transport by nematodes could represent one mechanism of bacteriophage motility in soils, thus affecting bacterial communities and virus–host dynamics (unpublished data). Lastly, Matthias G. Fischer (PhD, Max Planck Institute, Germany) virtually presented a high diversity of giant virus morphotypes obtained from forest soils and visualized by electron microscopy (unpublished data).

Soil viruses are most likely important for soil food webs and nutrient cycling, but research in this topic is still in its early stages (e.g., Williamson et al., 2017). Participants discussed several points that need further research to better understand the impact of viruses in soil food webs: impact of released organic and inorganic matter from cell lysis (e.g., Albright et al. 2022), impact of host metabolism modulation through expression of virus-derived auxiliary metabolic genes (AMGs; e.g., Emerson, 2019; Trubl et al., 2018; 2021), and the possibility of viruses accelerating carbon, nitrogen and phosphorus cycling, as well as changing the forms of carbon stabilized in soil. Several points were raised that need to be addressed further. For example, differences in viral contributions among soil microenvironments are expected due to extreme soil heterogeneity and complexity, both spatially and temporally, possibly resulting in different microbial and viral turnover rates. Viral infection rates are suggested to be even higher in soils compared to other environments (Kuzyakov and Mason-Jones, 2018), possibly impacting host turnover rates too. That could be measured using innovative targeted viral activity tools (e.g., stable isotope probing, nano-scale secondary ion mass spectrometry) combined with genomic tools (Pett-Ridge and Firestone, 2017). It also appears that there is a knowledge gap between soil virus research in natural and agricultural soils, wherein the research focus is concentrated either towards ecology or towards increased crop production, respectively, which the SVW participants found important to bridge.

Participants also discussed how viruses are expected to impact organisms of all trophic levels with a cascading effect throughout the soil food web, and thus the complexity of such interactions suggests that simple virus–host interactions may not be enough to understand community dynamics, but instead a more holistic view needs to be established. The topic was finalized with a discussion of how viruses can relate to the One Health approach — a concept based on understanding that the health of humans and animals, as well as environment are interconnected. Therefore, high quality and resilient soils can help prevent the spread of diseases in humans and animals, and viruses must be recognized as important members of a healthy ecosystem.

3. Conclusion

For the first time ever, researchers attended a workshop dedicated entirely to soil virology. Current research, advances in the field, as well as knowledge gaps were presented and discussed, as summarized in this

report with the hope of promoting these insights to a wider community of researchers.

3.1. Recommendations

Researchers recommended ways to improve sample preparation steps prior to sequencing and called on studies to follow MIUViG guidelines (Roux et al., 2019). Further, it was suggested to use mixed long and short read sequencing to improve virus genome assemblies, as well as to develop bioinformatics tools suitable for non-bacteriophage research. Furthermore, a trait-based classification approach for viruses was encouraged. Discussions about virus–host interactions emphasized the importance of focusing not only on single virus–host interactions but also on community-wide interactions, and how they can positively or negatively affect ecosystem functioning. Discussions about viruses in soil food webs also highlighted our lack of understanding of viral contributions to soil biogeochemistry and how they control community structure in both natural and agricultural soils. Therefore, attendees encouraged more experimental studies to complement the ongoing exploratory cataloguing of viral diversity in soil. Lastly, the increased need for non-medical studies of viruses, especially in soils, as well as the need for more international conversations in this field was brought up multiple times across different themes.

3.2. Next steps

The SVW established a strong global network of soil virologists to generate momentum for future research. The meeting adjourned with a collaboration agreement to write a workshop report, a perspective article on the roles of viruses in the soil, and to submit an application to the European Cooperation in Science and Technology (EU COST Action). The next SVW is planned to take place in California, USA in 2024, with the goal of attracting international participants with even more diverse expertise and backgrounds. Moreover, there will be discussions regarding establishment of guidelines for practical work with soil viruses to further solidify the field. Early interest can be registered using Google Forms following the link <https://forms.gle/u1zjeWj2ryPNMQoS9>.

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Authors’ Contributions

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Declaration of Competing Interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

References

- Albright, M.B.N., Gallegos-Graves, L.V., Feeser, K.L., Montoya, K., Emerson, J.B., Shakya, M., Dunbar, J., 2022. Experimental evidence for the impact of soil viruses on carbon cycling during surface plant litter decomposition. *ISME Commun.* 2, 24. <https://doi.org/10.1038/s43705-022-00109-4>.
- Brum, J.R., Ignacio-Espinoza, J.C., Roux, S., Douclier, G., Acinas, S.G., Alberti, A., Chaffron, S., Cruaud, C., de Vargas, C., Gasol, J.M., Gorsky, G., Gregory, A.C., Guidi, L., Hingamp, P., Iudicone, D., Not, F., Ogata, H., Pesant, S., Poulos, B.T., Schwenck, S.M., Speich, S., Dimier, C., Kandels-Lewis, S., Picheral, M., Searson, S., Bork, P., Bowler, C., Sunagawa, S., Wincker, P., Karsenti, E., Sullivan, M.B., 2015. Patterns and ecological drivers of ocean viral communities. *Science* 348, 1261498. <https://doi.org/10.1126/science.1261498>.
- Emerson, J., 2019. Soil viruses: a new hope. *mSystems* 4. <https://doi.org/10.1128/mSystems.00120-19>.
- Hillary, L.S., Adriaenssens, E.M., Jones, D.L., McDonald, J.E., 2022. RNA-viromics reveals diverse communities of soil RNA viruses with the potential to affect grassland ecosystems across multiple trophic levels. *ISME Commun.* 2, 34. <https://doi.org/10.1038/s43705-022-00110-x>.
- Kristensen, D.M., Mushegian, A.R., Dolja, V.V., Koonin, E.V., 2010. New dimensions of the virus world discovered through metagenomics. *Trends Microbiol.* 18, 11–19. <https://doi.org/10.1016/j.tim.2009.11.003>.
- Kuzyakov, Y., Mason-Jones, K., 2018. Viruses in soil: nano-scale undead drivers of microbial life, biogeochemical turnover and ecosystem functions. *Soil Biol. Biochem.* 127, 305–317. <https://doi.org/10.1016/j.soilbio.2018.09.032>.
- Langlois, V., Girard, C., Vincent, W.F., Culley, A.I., 2023. A tale of two seasons: distinct seasonal viral communities in a thermokarst lake. *Microorganisms* 11, 428. <https://doi.org/10.3390/microorganisms11020428>.
- Meyer, F., Fritz, A., Deng, Z.-L., Koslicki, D., Lesker, T.R., Gurevich, A., Robertson, G., Alser, M., Antipov, D., Beghini, F., Bertrand, D., Brito, J.J., Brown, C.T., Buchmann, J., Buluç, A., Chen, B., Chikhi, R., Clausen, P.T.L.C., Cristian, A., Dabrowski, P.W., Darling, A.E., Egan, R., Eskin, E., Georganas, E., Goltsman, E., Gray, M.A., Hansen, L.H., Hofmeyr, S., Huang, P., Irber, L., Jia, H., Jørgensen, T.S., Kieser, S.D., Klemetsen, T., Kola, A., Kolmogorov, M., Korobeynikov, A., Kwan, J., LaPierre, N., Lemaître, C., Li, C., Limasset, A., Malcher-Miranda, F., Mangul, S., Marcelino, V.R., Marchet, C., Marijon, P., Meleshko, D., Mende, D.R., Milanese, A., Nagarajan, N., Nissen, J., Nurk, S., Olier, L., Paoli, L., Peterlongo, P., Piro, V.C., Porter, J.S., Rasmussen, S., Rees, E.R., Reinert, K., Renard, B., Robertsen, E.M., Rosen, G.L., Ruscheweyh, H.-J., Sarwal, V., Segata, N., Seiler, E., Shi, L., Sun, F., Sunagawa, S., Sørensen, S.J., Thomas, A., Tong, C., Trajtkovski, M., Tremblay, J., Uritskiy, G., Vicedomini, R., Wang, Z., Wang, Z., Wang, Z., Warren, A., Willassen, N.

- P., Yelick, K., You, R., Zeller, G., Zhao, Z., Zhu, S., Zhu, J., Garrido-Oter, R., Gastmeier, P., Hacquard, S., Häußler, S., Khaleidi, A., Maechler, F., Mesny, F., Radutoiu, S., Schulze-Lefert, P., Smit, N., Strowig, T., Bremges, A., Szyrba, A., McHardy, A.C., 2022. Critical assessment of metagenome interpretation: the second round of challenges. *Nat. Methods* 19, 429–440. <https://doi.org/10.1038/s41592-022-01431-4>.
- Overholt, W.A., Hölzer, M., Geesink, P., Diezel, C., Marz, M., Küsel, K., 2020. Inclusion of Oxford Nanopore long reads improves all microbial and viral metagenome-assembled genomes from a complex aquifer system. *Environ. Microbiol.* 22, 4000–4013. <https://doi.org/10.1111/1462-2920.15186>.
- Pett-Ridge, J., Firestone, M.K., 2017. Using stable isotopes to explore root-microbe-mineral interactions in soil. *Rhizosphere* 3, 244–253. <https://doi.org/10.1016/j.rhisph.2017.04.016>.
- Roux, S., Adriaenssens, E.M., Dutilh, B.E., Koonin, E.V., Kropinski, A.M., Krupovic, M., Kuhn, J.H., Lavigne, R., Brister, J.R., Varsani, A., Amid, C., Aziz, R.K., Bordenstein, S.R., Bork, P., Breitbart, M., Cochrane, G.R., Daly, R.A., Desnues, C., Duhaime, M.B., Emerson, J.B., Enault, F., Fuhrman, J.A., Hingamp, P., Hugenholtz, P., Hurwitz, B.L., Ivanova, N.N., Labonté, J.M., Lee, K.-B., Malmstrom, R.R., Martínez-García, M., Mizrahi, I.K., Ogata, H., Páez-Espino, D., Petit, M.-A., Putonti, C., Rattai, T., Reyes, A., Rodríguez-Valera, F., Rosario, K., Schriml, L., Schulz, F., Steward, G.F., Sullivan, M.B., Sunagawa, S., Suttle, C.A., Temperton, B., Tringe, S.G., Thurber, R.V., Webster, N.S., Whiteson, K.L., Wilhelm, S.W., Wommack, K.E., Woyke, T., Wrighton, K.C., Yilmaz, P., Yoshida, T., Young, M.J., Yutin, N., Allen, L.Z., Kyrpides, N.C., Eloe-Fadrosh, E.A., 2019. Minimum Information about an Uncultivated Virus Genome (MIUViG). *Nat. Biotechnol.* 37, 29–37. <https://doi.org/10.1038/nbt.4306>.
- Santos-Medellín, C., Estera-Molina, K., Yuan, M., Pett-Ridge, J., Firestone, M.K., Emerson, J.B., 2022. Spatial turnover of soil viral populations and genotypes overlain by cohesive responses to moisture in grasslands. *PNAS* 119, e2209132119. <https://doi.org/10.1073/pnas.2209132119>.
- Santos-Medellín, C., Zinke, L.A., ter Horst, A.M., Gelardi, D.L., Parikh, S.J., Emerson, J.B., 2021. Viromes outperform total metagenomes in revealing the spatiotemporal patterns of agricultural soil viral communities. *ISME J.* 15, 1956–1970. <https://doi.org/10.1038/s41396-021-00897-y>.
- Santos-Medellín, C., Blazewicz, S.J., Pett-Ridge, J., Emerson, J.B., 2023. Viral but not bacterial community succession is characterized by extreme turnover shortly after rewetting dry soils. *bioRxiv*. <https://doi.org/10.1101/2023.02.12.528215>.
- Simmonds, P., Adriaenssens, E.M., Zerbin, F.M., Abrescia, N.G.A., Aiewsakun, P., Alfnas-Zerbin, P., Bao, Y., Barylski, J., Drosten, C., Duffy, S., Duprex, W.P., Dutilh, B.E., Elena, S.F., García, M.L., Junglen, S., Katzourakis, A., Koonin, E.V., Krupovic, M., Kuhn, J.H., Lambert, A.J., Lefkowitz, E.J., Lobočka, M., Lood, C., Mahony, J., Meier-Kolthoff, J.P., Mushegian, A.R., Oksanen, H.M., Poranen, M.M., Reyes-Muñoz, A., Robertson, D.L., Roux, S., Rubino, L., Sabanadzovic, S., Siddell, S., Skern, T., Smith, D.B., Sullivan, M.B., Suzuki, N., Turner, D., Van Doorslaer, K., Vandamme, A.-M., Varsani, A., Vasilakis, N., 2023. Four principles to establish a universal virus taxonomy. *PLoS Biol.* 21, e3001922 <https://doi.org/10.1371/journal.pbio.3001922>.
- Sutela, S., Piri, T., Vainio, E.J., 2021. Discovery and community dynamics of novel ssRNA mycoviruses in the conifer pathogen heterobasidion parviporum. *Front. Microbiol.* 12, 770787. <https://doi.org/10.3389/fmicb.2021.770787>.
- Sutela, S., Vainio, E.J., 2020. Virus population structure in the ectomycorrhizal fungi *Lactarius rufus* and *L. tabidus* at two forest sites in Southern Finland. *Virus Res.* 285, 197993 <https://doi.org/10.1016/j.virusres.2020.197993>.
- Suttle, C.A., 2005. Viruses in the sea. *Nature* 437, 356–361. <https://doi.org/10.1038/nature04160>.
- Trubl, G., Jang Ho, B., Roux, S., Emerson Joanne, B., Solonenko, N., Vik Dean, R., Solden, L., Ellenbogen, J., Runyon Alexander, T., Bolduc, B., Woodcroft Ben, J., Saleska Scott, R., Tyson Gene, W., Wrighton Kelly, C., Sullivan Matthew, B., Rich Virginia, L., 2018. Soil viruses are underexplored players in ecosystem carbon processing. *mSystems* 3, e00076. <https://doi.org/10.1128/mSystems.00076-18-00018>.
- Trubl, G., Kimbrel, J.A., Lique-Gonzalez, J., Nuccio, E.E., Weber, P.K., Pett-Ridge, J., Jansson, J.K., Waldrop, M.P., Blazewicz, S.J., 2021. Active virus-host interactions at sub-freezing temperatures in Arctic peat soil. *Microbiome* 9, 208. <https://doi.org/10.1186/s40168-021-01154-2>.
- Trubl, G., Solonenko, N., Chittick, L., Solonenko, S.A., Rich, V.I., Sullivan, M.B., 2016. Optimization of viral resuspension methods for carbon-rich soils along a permafrost thaw gradient. *PeerJ* 4, e1999. <https://doi.org/10.7717/peerj.1999>.
- Williamson, K.E., Fuhrmann, J.J., Wommack, K.E., Radosevich, M., 2017. Viruses in soil ecosystems: an unknown quantity within an unexplored territory. *Annu. Rev. Virol.* 4, 201–219. <https://doi.org/10.1146/annurev-virology-101416-041639>.

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