



Full length article

Habitat-Dependent DNA viral communities in atmospheric aerosols: Insights from terrestrial and marine ecosystems in East Asia



Tong Jiang^{a,1}, Cui Guo^{a,b,c,1,*}, Hao Yu^a, Ziyue Wang^a, Kaiyang Zheng^a, Xinran Zhang^a, Siyuan Tang^a, Chuxiao Wang^a, Hongbing Shao^{a,b,c}, Chao Zhang^d, Yantao Liang^{a,b,c}, Liangliang Kong^{a,b,c}, Huiwang Gao^d, Andrew McMinn^{a,b,e}, Min Wang^{a,b,c,f,g,*}

^a College of Marine Life Sciences, Ocean University of China, Qingdao, China

^b Institute of Evolution and Marine Biodiversity, MoE Laboratory of Evolution and Marine Biodiversity, Frontiers Science Center for Deep Ocean Multispheres and Earth System, Center for Ocean Carbon Neutrality, Ocean University of China, Qingdao, China

^c UMT-OUC Joint Centre for Marine Studies, Qingdao, China

^d Key Laboratory of Marine Environment and Ecology, Ministry of Education of China, Ocean University of China, Qingdao, China

^e Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, TAS, Australia

^f HaideCollege, Ocean University of China, Qingdao, China

^g The Affiliated Hospital of Qingdao University, Qingdao, China

ARTICLE INFO

Keywords:

Aerosol Viral Communities
Terrestrial and marine aerosols
Pathogenic viruses
Ecological adaptation

ABSTRACT

The transmission of viruses through aerosols is of growing public health concern, yet research on aerosol-associated viral communities lags behind that of terrestrial and aquatic ecosystems. Here, DNA viral diversity in natural aerosols from both over land and ocean in the East Asia region was examined. The results showed that atmospheric environments harbor a distinct viral community that differs from those present in terrestrial and aquatic ecosystems. A comparison of aerosol samples from different locations revealed that aerosol viruses are strongly influenced by altitude and their sources. Fragments of viruses that can infect pathogenic bacteria, as well as pathogenic viruses (such as herpesviruses, Inoviruses, and Iridovirus) were detected. Anthropogenically-influenced land aerosol samples contained viral communities with greater richness and diversity as well as a higher relative abundance of pathogenic and lytic viruses compared to pristine marine airborne samples. Furthermore, habitat-specific auxiliary metabolic genes (AMGs) were observed, such as the phosphate regulon (*phoH*), which was more prevalent in ocean aerosol samples and regulates phosphate uptake under low-phosphate conditions, thereby assisting viral hosts in overcoming metabolic challenges in different environmental conditions. This study highlights the ecological distinctness of the airborne viral community and the interconnectedness between those from land, sea, and atmosphere, underscoring the importance of evaluating their potential pathogenicity in future research.

1. Introduction

Global aerosol emissions are approximately 2000 Mt per year (Shao et al., 2011). Rapid urbanization, industrial growth, and increasing energy consumption in East Asia in particular, have inevitably led to a deterioration in air quality (An et al., 2019). These human activities directly or indirectly exert pressure on the atmosphere, influencing microbial emissions from the surface, biodiversity, and metabolic activity within the air (Santl-Temkiv et al., 2022). Many studies have

highlighted the diverse nature of airborne microbial communities, which are comparable to those found in terrestrial environments (Womack et al., 2010).

Viruses have a dual significance. On the one hand, viruses that infect bacteria and archaea, known as phages, play a crucial role in ecosystem functions by influencing microbial population dynamics, facilitating nutrient cycling, and promoting genetic diversity within host organisms (Du et al., 2023; Coutinho et al., 2017). The movement of bioaerosols, including viruses, through processes like monsoons, cloud formation,

* Corresponding authors.

E-mail addresses: guocui@ouc.edu.cn (C. Guo), mingwang@ouc.edu.cn (M. Wang).

¹ These authors contributed equally to this work.

and precipitation, is thus essential for sustaining biodiversity and resilience in terrestrial and marine ecosystems (Santl-Temkiv et al., 2022; Womack et al., 2010). On the other hand, bioaerosols can also have serious health impacts by spreading pathogens in animals and plants, facilitating the transfer of antibiotic resistance genes and microbial-derived allergens (Lai et al., 2009; Brown and Hovmöller, 2002; Pal et al., 2016; Woo et al., 2013). Some of these viruses in aerosols are responsible for human diseases such as severe acute respiratory syndrome (SARS), influenza, and coronavirus disease 2019 (COVID-19) (Peiris et al., 2004; Nikitin et al., 2014; Zuo et al., 2020). Despite these critical roles, the composition and dynamics of viral communities in the air remain poorly characterized. This is primarily due to the low density of viral particles in aerosols, the absence of universally conserved marker genes (such as bacterial 16S rRNA genes) for identification, and the lack of well-annotated viral genomic databases (Prussin et al., 2014). These limitations have hindered the understanding of airborne viral communities (Prussin et al., 2014; Kuske, 2006).

To date, research on airborne viral communities has predominantly focused on viral composition in specific indoor environments (e.g., daycare center, subways, residences, dormitory, and wastewater treatment center) and outdoor areas with strong human impact (e.g., piers and public transit hubs), suggesting that the distribution of viruses is strongly influenced by human activity (Du et al., 2023; Rosario et al., 2018; Danko et al., 2021; Brisebois et al., 2018; Leung et al., 2021). For example, antimicrobial resistance genes were detected in viruses inhabiting surfaces frequently touched by occupants and in viruses found on occupants' skin (Du et al., 2023). Viral pathogens were frequently identified in the air of wastewater treatment centers (Brisebois et al., 2018), cattle processing area of animal slaughterhouse (Hall et al., 2013), and university dormitories (Rosario et al., 2018). In these studies, the diversity, composition, and metabolic functions of the viral community are found to be habitat-dependent. However, the understanding of the viral communities present in outdoor natural air remains limited. Existing studies show that the abundance of outdoor airborne viruses exhibited seasonal variations and was inversely correlated with temperature and absolute humidity (Whon et al., 2012). As regards the viral community, the most abundant viruses in PM_{2.5} and PM₁₀ (particulate matter with nominal mean aerodynamic diameters of ≤ 2.5 and $\leq 10 \mu\text{m}$, respectively) during a severe smog event were *Pseudomonas* phage F116, adenovirus C, and *Enterobacter* phage P1 (Cao et al., 2014). Viruses may travel bidirectionally between the air and sea, as suggested by the presence of shared viral populations at both the air-sea interface and in rainwater (Rahlf et al., 2023). Despite the progress made thus far, there remain important scientific questions to be explored in this field. Particularly, is the viral community present in the air distinct from those found in other ecosystems, such as soil and marine environments? What is the interconnectedness between viral communities from land, sea, and atmosphere? How do different habitats, e.g., aerosols over land and sea, affect the diversity and composition of aerosol viral communities, as well as their lifestyle and interaction with hosts?

In this study, DNA viral communities from aerosol samples collected over both land and sea in the East Asia region—specifically from Qingdao, a coastal city in China, and the East China Sea—were analyzed. The detection of a wide variety of viruses in air samples underscores the atmospheric environment as a significant yet understudied reservoir of viral diversity. The distributions of these airborne viruses reveal interconnections and variations influenced by the surrounding marine, terrestrial, and soil environments, highlighting their role in shaping the global viral ecosystem.

2. Materials and methods

2.1. Sample collection, metagenomic sequencing, and microscopic photography

Land aerosol samples were collected at Baguan Mountain in Qingdao (36.06°N, 120.34°E), a coastal city in China, using a high-volume sampler (KC-1000, Qingdao Laoshan Elec. Inc., China) in July, August, September and November 2022 (Table S1, Fig. 1). Total suspended particles in the atmosphere were collected on acid-washed cellulose filters (Whatman-41) at a constant flow rate of $1.05 \text{ m}^3 \text{ air min}^{-1}$ for 24 h. The collection method in this study may have missed capturing some free-living viruses in the air, despite the airborne viral particles tend to associate with suspended particles (Aller et al., 2005; Yang et al., 2011). However, the previous study has suggested that metagenomes, which sequence the entire microbial community (including viruses, bacteria, archaea, etc.) offer an advantage over viromes (viral metagenomics) in detecting slow-growing, low-biomass communities and lysogenic viruses (Kosmopoulos et al., 2024). The collected filters were stored at -80°C . Samples were collected once a week; the four samples from each month were pooled and sequenced to ensure the representativeness of each month. Ocean aerosol samples were collected in April; October and November of 2022 using the same sampler during two cruises in the East China Sea (Table S1, Fig. 1). Samples from two consecutive days were pooled and subjected to library preparation and sequencing. The total DNA on the cellulose filters was extracted using the CTAB Extraction Method by Novogene (Tianjin, China). Library construction and high throughput sequencing of the DNA were performed using the Illumina NovaSeq 6000 (pair-end sequencing, $2 \times 150 \text{ bp}$) platform (Gao et al., 2022).

The prepared aerosol filters were sonicated and suspended in Ultrapure water. Then, the samples were incubated with the nucleic acid stain SYBR Green I (Molecular Probes) in the dark at 80°C for 10 min. Following a 5-minute dark treatment, images were captured using an AX/AX R confocal microscope (Nikon, Tokyo, Japan).

2.2. Quality control, assembly, and identification of viral contigs

The raw reads were adapter-trimmed using fastp (v0.12.4) (Chen et al., 2018). The resulting high-quality paired-end reads were then filtered using Perl scripts, applying the following conditions: (1) no more than 20 % of bases with a quality score below 20, and (2) no more than 30 % of bases with a quality score below 30 (Gu et al., 2021). The Data volume after quality control is $55 \text{ GB} \pm 13$ (Table S1). High-quality reads from each sample were assembled using metaSPAdes (v3.13.0) (Nurk et al., 2017). Contigs shorter than 1.5 kb were discarded, and the remaining contigs ($>1.5 \text{ kb}$) were piped through DeepVirFinder (v1.0) (Ren et al., 2020) and VirSorter2 (v2.2.2) (Guo et al., 2021) to identify viral contigs. This involved using (1) DeepVirFinder with a score ≥ 0.9 and $p < 0.01$; (2) VirSorter2 with a score ≥ 0.9 ; and (3) DeepVirFinder with a score between 0.7 and 0.9 and p between 0.01 and 0.05, when VirSorter2 scores between 0.5 and 0.9. A total of 602,454 contigs with a length over 1.5 kb were assembled from the eight aerosol samples and 26,753 potential viral contigs were identified.

2.3. Dereplication and calculation of relative abundances and taxonomic profiling

Viral contigs were grouped into viral operational taxonomic units (vOTUs) using CD-HIT (v4.8.1) with a threshold of $\geq 95\%$ nucleotide identity across $\geq 80\%$ of shorter contigs (Fu et al., 2012). The longest contig in each vOTU was then selected as the representative sequence, resulting in 24,835 vOTUs. To ensure the quality and confidence of the identified vOTUs, CheckV (Nayfach et al., 2021) was used to select vOTUs based on the following criteria: 1) longer than 5 kb and 2) complete vOTUs ranging from 1.5 kb-5 kb in length. Additionally, the

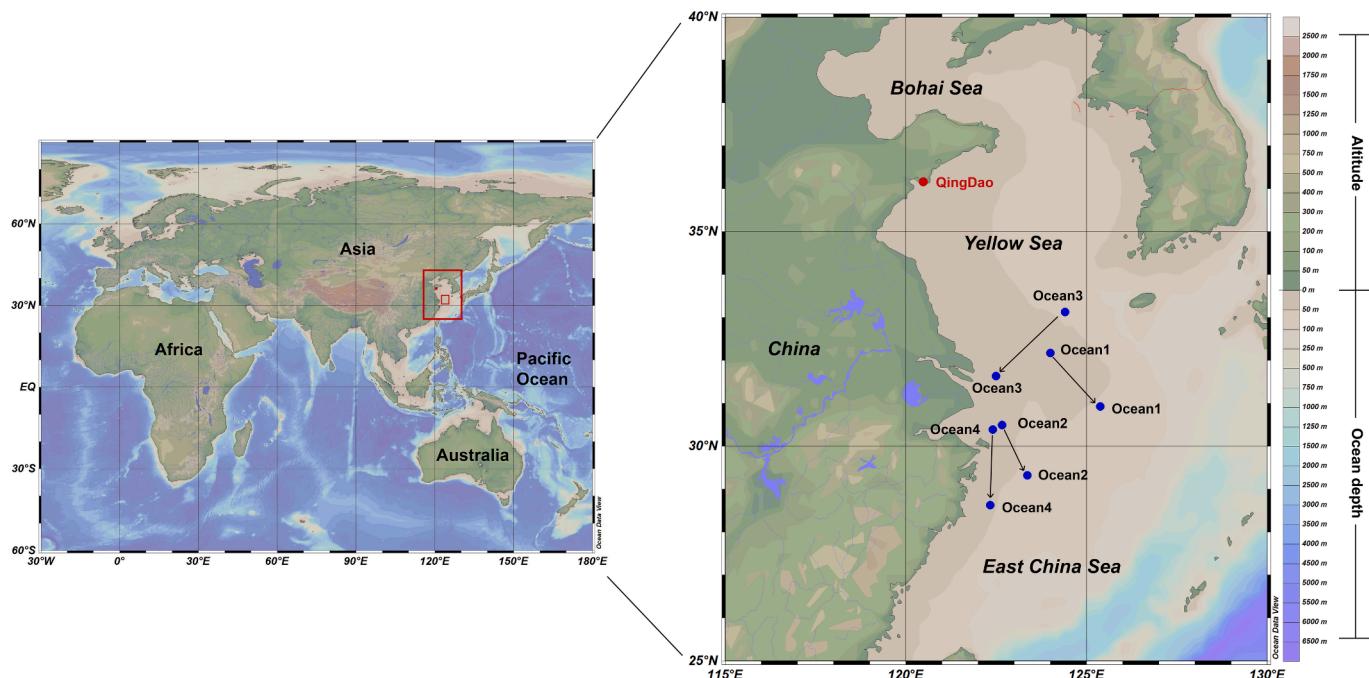


Fig. 1. Sampling stations of aerosols. As the trajectory of the vessel did not follow a perfectly straight line, the straight lines and arrows depicted here only represent where aerosol sampling was conducted during the voyage between the two stations. The colors and numbers on the right side represent the altitude of the land and the depth of the ocean.

viral and host gene counts from CheckV were used for false positive screening. Only vOTUs meeting the following conditions were retained after length-based screening: 1) viral_gene > 0 or 2) viral_gene = 0 AND host_gene = 0. After applying these criteria, 846 vOTUs were selected for subsequent analysis.

The relative abundances of these vOTUs in each sample were calculated by mapping clean reads to the vOTUs using CoverM (Aroney et al., 2025) (v0.7.0; <https://github.com/wwood/CoverM>) (with parameters –min-read-percent-identity 0.95 –min-read-aligned-percent 0.75). VITAP (v1.7) (Wang et al., 2024) and geNomad (v1.8.1) (Camargo et al., 2023) were utilized to assign the vOTUs. The lifestyle of the viruses (including the lytic and lysogenic lifestyle) was determined by VIBRANT (v1.2.1) using the default parameters (Kieft et al., 2020).

2.4. Open reading frames (ORFs) prediction and functional analyses

The ORFs of the vOTUs were predicted using Prodigal-gv (v2.11.0) with default parameters (Camargo et al., 2023; Hyatt et al., 2010). Abundance calculations of ORFs were based on the relative abundance of vOTUs in each sample (Gu et al., 2021). To further identify the protein domains, viral ORFs were compared with the PfamScan database ($e\text{-value} < 1 \times 10^{-5}$; bit score > 40) using Pfamscan (v1.6) (El-Gebali et al., 2019). The viral protein functional categories were determined by identifying the COGs (Clusters of Orthologous Groups) using eggNOG-mapper (v2.0.1) (Huerta-Cepas et al., 2017) with default parameters. KEGG Orthology pathways were predicted using KEGG GhostKOAL (<http://www.kegg.jp/ghostkoala/>) (Kanehisa et al., 2016). Genes associated with the carbon, nitrogen, sulfur, and phosphorus cycles were counted using CAZyme (Huang et al., 2018), NCycDB (Tu et al., 2019), SCycDB (Yu et al., 2020); and PCycDB (Zeng et al., 2022). Finally, DRAM-v (v1.5.0) (Shaffer et al., 2020) and manual selection (the viral region harbored at least one conserved viral protein or more than 30 % of proteins had the highest similarity to viral proteins according to the annotation) (Jian et al., 2021) were used to verify the putative auxiliary metabolic genes (AMGs).

2.5. Comparison between the aerosol viral communities and other environmental viral communities

To compare the eight aerosol viral communities with other environmental viral communities, the IMG/VR v4 database (Camargo et al., 2023), which includes complete or high-quality viral sequences (length > 10 k), was searched as well as reference genomes recognized by IMG/VR. A total of 15,238 viral genomes were retrieved from marine environments (coastal, oceanic, and intertidal zones), 9,963 from soil environments (coastal areas, wetlands, agricultural land, deserts, grasslands, temperate forests, and boreal forests/taiga), and 30 from air environments (outdoor air). For each viral contigs, ORFs were predicted using Prodigal-gv (v2.11.0) (Hyatt et al., 2010), then all-verses-all DIAMOND (v2.1.9.163) BLASTP was used to compare the protein with parameters: $e\text{-value} \leq 10^{-5}$, query coverage $\geq 50\%$, identity $\geq 25\%$ (Gu et al., 2021; Buchfink et al., 2015). All sequences were analyzed using vConTACT 2 (v 0.11.3) (Bin Jang et al., 2019) with the following parameters: –db ‘None’ –pcs-mode MCL –vcs-mode ClusterONE. The resulting network was visualized using Cytoscape (v3.9.1) (Shannon et al., 2003), and a number of viral clusters (VCs) were plotted using Evenn (<https://www.ehbio.com/test/venn/#/>). Gene-sharing networks, based on shared protein clusters (PCs) between viral genomes, reveal related genomes as a group of nodes strongly connected through multiple edges—forming a viral cluster (VC). This method has been shown to best represent genus-level groupings of viral genomes (Bin Jang et al., 2019), enabling comparisons across ecosystems at a higher taxonomic level (Ter Horst et al., 2021).

Seawater samples from China’s marginal seas (Bohai Sea, Yellow Sea, and East China Sea) were collected from multiple cruises conducted between 2019–2023. Seawater was sequentially filtered through 3.0 μm and 0.2 μm polycarbonate membrane filters (Millipore, MA, USA) to remove micozooplankton, phytoplankton, and bacteria. Planktonic viruses in 20L surface seawater from 9 stations in the Bohai and Yellow seas were enriched using the FeCl₃-mediated flocculation method (Gu et al., 2021) and then stored at 4 °C until processing. Planktonic viruses in 150L surface seawater at 8 stations in the East China Sea were concentrated by a two-step tangential flow filtration (TFF) with 50-kDa

cartridge (Millipore, MA, USA) to a final volume of 50 mL and then stored at 4 °C until processing (Gao et al., 2022). The DNA was extracted using the QIAamp DNA Mini Kit (Qiagen, REF:51304). Then, library construction and high throughput sequencing of the DNA were performed using the Illumina NovaSeq 6000 (pair-end sequencing, 2 × 150 bp) platform (Gao et al., 2022). Quality control, assembly, and identification of viral contigs were performed as described in the previous methods. The vContact2 (v0.11.3) was used to construct a shared network using aerosol samples and seawater samples from the Yellow Sea, Bohai Sea, and the East China Sea, to analyze whether aerosol samples from different sources are more similar to their geographically closer oceanic counterparts.

In addition, metagenomic data of natural aerosol samples from various locations were downloaded from public databases (NCBI and NASA GeneLab) to further compare differences between aerosol virus communities. These included aerosols over the Swedish offshore bays (Rahlf et al., 2023), dust-associated aerosols above the Red Sea (Aalismail et al., 2019), and aerosols collected at altitudes from 10,000 ft to 40,000 ft above the Sierra Nevada Mountains (Jaing et al., 2020). Similar methods for quality control, assembly, and identification of viral contigs were performed as described previously.

2.6. Generation of host metagenome-assembled genomes and taxonomic profiling of microbial communities

After the metaSPAdes (v3.13.0) assembly for the eight aerosol samples we collected, contigs were binned (-metabat2 -maxbin2 -concoct) and refined (parameters: -c 70 -x 5) using metaWRAP (v1.3.2) (Uritskiy et al., 2018; Li et al., 2021). A total of 54 bin sets were de-replicated to 39 metagenome-assembled genomes (MAGs) using dRep (v3.2.2) (parameters: -sa 0.95 -comp 70 -con 5) (Li et al., 2021; Olm et al., 2017). The taxonomy of each MAG was initially assigned using GTDB-Tk (v2.4.0) (Chaumeil et al., 2019) based on the Genome Taxonomy Database (GTDB) taxonomy 09-RS220 (Parks et al., 2020).

For microbial community analysis, the collected samples were sequenced for 16S rRNA gene amplicons. DNA extraction, PCR reactions, PCR purification, and sequencing procedures were performed as previously described (Duan et al., 2021). The samples were sequenced by Illumina MiSeq to generate the original sequence data. Subsequently, the adapter sequences were removed, and the cleaned data was imported into QIIME2 (v2023.07) (Bolyen et al., 2019) for further analyses. Taxonomic identification of the representative sequence for each Amplicon Sequence Variant (ASV) was performed using Feature-classifier (Bokulich et al., 2018) (via q2-feature-classifier) against a Silva database (version 138: <https://www.arb-silva.de/>). To enable comparisons between samples, the ASV table was randomly subsampled down to a minimum number of reads per sample (9,269 reads). In addition, 39 marine and 31 terrestrial aerosol samples collected during 2022–2023 were used for microbial diversity analyses.

2.7. Virus–host prediction

Four different host prediction strategies were used to predict the virus–host interactions, including nucleotide sequence homology, oligonucleotide frequency, clustered regularly interspaced short palindromic repeats (CRISPRs) spacer match, and tRNA match, as described in Li et al (Li et al., 2021). The microbial MAGs used for virus–host prediction were from the same metagenomes as the viral sequences in this study. These strategies were applied as follows:

(1) Nucleotide Sequence Homology: Sequences of vOTUs were queried against prokaryotic MAGs using BLASTn (query coverage ≥ 75 %, identity ≥ 70 %, bit score ≥ 50, and e-value ≤ 10⁻⁵).

(2) oligonucleotide frequency: Oligonucleotide frequency and distance between vOTUs and prokaryotic MAGs were calculated by Vir-HostMatcher (v1.0) (Ahlgren et al., 2017) with default parameters (d_2^* values ≤ 0.2).

(3) CRISPR Spacer Match: CRISPRs are a bacterial immune mechanism that recognizes and memorizes short subsequences from viral invaders (Edwards et al., 2016; Barrangou et al., 2007). CRISPR spacers are powerful tools for investigating phage–host interactions, as they link phage and host populations within complex microbial communities (Nasko et al., 2019). In this study, CRISPR arrays were assembled from prokaryotic quality-controlled reads by crass (v1.0.1) (Skennerton et al., 2013) and rated by CRISPRcasFinder (v4.3.2) (Couvin et al., 2018). Those with evidence level 4 (repeat conservation index > 70 % and spacer identity < 8 %) were retained for subsequent analysis. CRISPR spacers were then compared with viral contigs using BLASTn-short with e-value ≤ 10⁻⁵ and mismatch ≤ 1 over the whole spacer. For each matching CRISPR spacer, the corresponding repeat was then compared against the prokaryotic MAGs with the same parameters using BLASTn.

(4) tRNA Match: The tRNAs from the vOTU and prokaryotic MAG sequences were identified using ARAGORN (v1.2.38) with the ‘-t’ option (Laslett and Canback, 2004), with match requirements of ≥ 90 % length with identity ≥ 90 % of the sequences by BLASTn (Coutinho et al., 2017).

2.8. Analysis of complete and high-quality viral genomes and phylogenetic analysis

The completeness of the vOTUs was assessed using CheckV (v1.0.1) (Nayfach et al., 2021), and the selected complete and high-quality viral genomes were then matched against the NCBI database using online BLASTn. Given that 11 sequences of the *Genomoviridae* family were found in the complete or high-quality data, an in-depth analysis of the viruses of this taxon followed. The *Genomoviridae* family includes viruses with small (~2–2.4 kb), circular ssDNA genomes encoding two key proteins: the rolling-circle replication initiation proteins (Rep) and the unique capsid proteins (CP). In 2017, a sequence-based taxonomic framework was established for genomavirus classification, setting a genome-wide pairwise identity threshold of 78 % for species demarcation, whereas Rep sequence phylogeny was used to define genera (Varsani and Krupovic, 2017). From the NCBI Virus database, complete RefSeq proteins (278) belonging to the *Genomoviridae* family were downloaded. PfamScan (v1.6) (El-Gebali et al., 2019) was then used to identify rep proteins containing the Rep catalytic domain (Gemini_AL1; PF00799) and Rep protein central domain (Gemini_AL1_M; PF08283) from the aerosol viral communities sequences and the downloaded sequences (Krupovic et al., 2016). An alignment of selected *Genomoviridae* rep proteins along with reviewed Geminivirus Rep catalytic domain PF00799 sequences (50) from the InterPro database was created using MUSCLE 5 (v5.1) (Edgar, 2022) and trimmed to remove positions with gaps over 90 % using trimAL (v1.4.1) (Capella-Gutierrez et al., 2009). A maximum-likelihood phylogenetic tree was produced using IQ-TREE (v2.2.0.3) (Nguyen et al., 2015), and the resulting phylogenetic tree was visualized with iTOL v6 (<https://itol.embl.de/>) (Letunic and Bork, 2021). The average nucleotide identity between sequences was calculated using VIRIDIC (v1.1) (<https://rhea.icbm.uni-oldenburg.de/VIRIDIC/>) (Moraru et al., 2020).

For *Caudoviricetes*, four conserved domains (Terminase_1, Terminase_3, Terminase_6N, Terminase_Gpa) were searched in the ORFs of the aerosol viral communities using PfamScan (v1.6). The identified sequences were then dereplicated (Gu et al., 2021). Reference sequences containing at least one of the four conserved domains were downloaded from the NCBI Virus database and dereplicated. Sequences with less than 300 amino acids were filtered out. The combined aerosol viral community sequences and downloaded sequences were used to construct a phylogenetic tree as described above.

2.9. Statistical analysis

The α- and β-diversity indexes were calculated using vegan (2.6–6.1) in R (v 4.4.1) based on the relative abundances of vOTUs (Oksanen et al.,

2013). Significance analyses of viral diversity, lifestyle, relative abundance of family level annotations, AMGs, COG classifications, and host diversity between land and sea aerosol sample were performed using independent sample *t*-tests with the statistical software SPSS (v25).

3. Results and Discussions

3.1. Distinctness of the airborne viral communities

Viruses and bacteria are capable of attaching to aerosol particles, as evidenced by confocal microscopy (Fig. S1). The frequent association of airborne viruses with suspended particles, rather than existing individually, has also been demonstrated in previous studies (Aller et al., 2005; Yang et al., 2011). Network analyses, based on shared protein content of viruses from different habitats reveal that, although the largest VC contained viral sequences prevalent in all three habitats, each habitat also hosted a viral community distinct from the other ecosystems (Fig. 2a). Of the 94 VCs detected in aerosol samples, 70.2% (66 VCs) were exclusively found within the aerosol viral communities and were not present in the other habitats (Fig. 2b).

A comparison of aerosol samples from different locations revealed that aerosol viruses are strongly influenced by altitudes and their sources (Fig. 3a, Table S2). Aerosol viruses from low altitudes across different locations show more similarity compared to those from high altitudes (10,000 ft to 40,000 ft). Among the low-altitude natural aerosol samples, those over the East China Sea showed closer similarities to aerosol samples collected at the Swedish seaside, while aerosol viruses over East Asian lands exhibited greater resemblance to aerosols originating from the Sahara dust (Fig. 3b).

The viral sequences identified in the aerosol viral communities were predominantly from the *Caudoviricetes* class. A phylogenetic tree constructed using the terminase large subunit identified the presence of 66 phage terminase sequences (Fig. S2, Table S3). These putative phage

terminases exhibited a wide distribution across the evolutionary tree, indicating a high diversity of *Caudoviricetes* associated with the aerosols. Notably, many viral clades consisting of terminase sequences were exclusively detected in these aerosol viral communities, suggesting the possible existence of distinct aerosol *Caudoviricetes* taxa.

The distinct viral community in aerosols can be attributed to rapid fluctuations over short periods in environmental factors such as temperature, humidity, and liquid water content in the atmosphere (Santl-Temkiv et al., 2022). These fluctuations expose cells to repeated thermal and UV shocks, potentially driving microbial diversity and adaptation within aerosol environments. Distinct bacterial community structures have been reported in the atmosphere, with bacterial taxa adapted to survive under high ultraviolet (UV) irradiance, moisture limitations, and other challenges being overrepresented (Santl-Temkiv et al., 2022; Tignat-Perrier et al., 2019). This indicates a robust environmental filtering process. As obligate parasites rely entirely on hosts for reproduction and survival, viruses may undergo similar dynamics to those of other environments, akin to bacteria.

It is worth noting that three shared VCs were identified across all habitats, all belonging to *Caudoviricetes*. One of these was a P2-like phage, while the other two were unclassified below the class level (Fig. 2c). These phages are capable of switching between lytic and lysogenic modes (Nilsson and Haggard-Ljungquist, 2007) and exhibit the capacity to infect a range of Gammaproteobacteria (Nilsson and Haggard-Ljungquist, 2007; Bertani and Bertani, 1971). Their genomes are highly stable, and they can indirectly increase their own fitness by improving the fitness of the host upon lysogenization (Nilsson and Haggard-Ljungquist, 2007), thereby enabling their existence in diverse habitats.

3.2. Habitat-dependent variation in viral and host diversity

An analysis of aerosol viral communities from two distinct

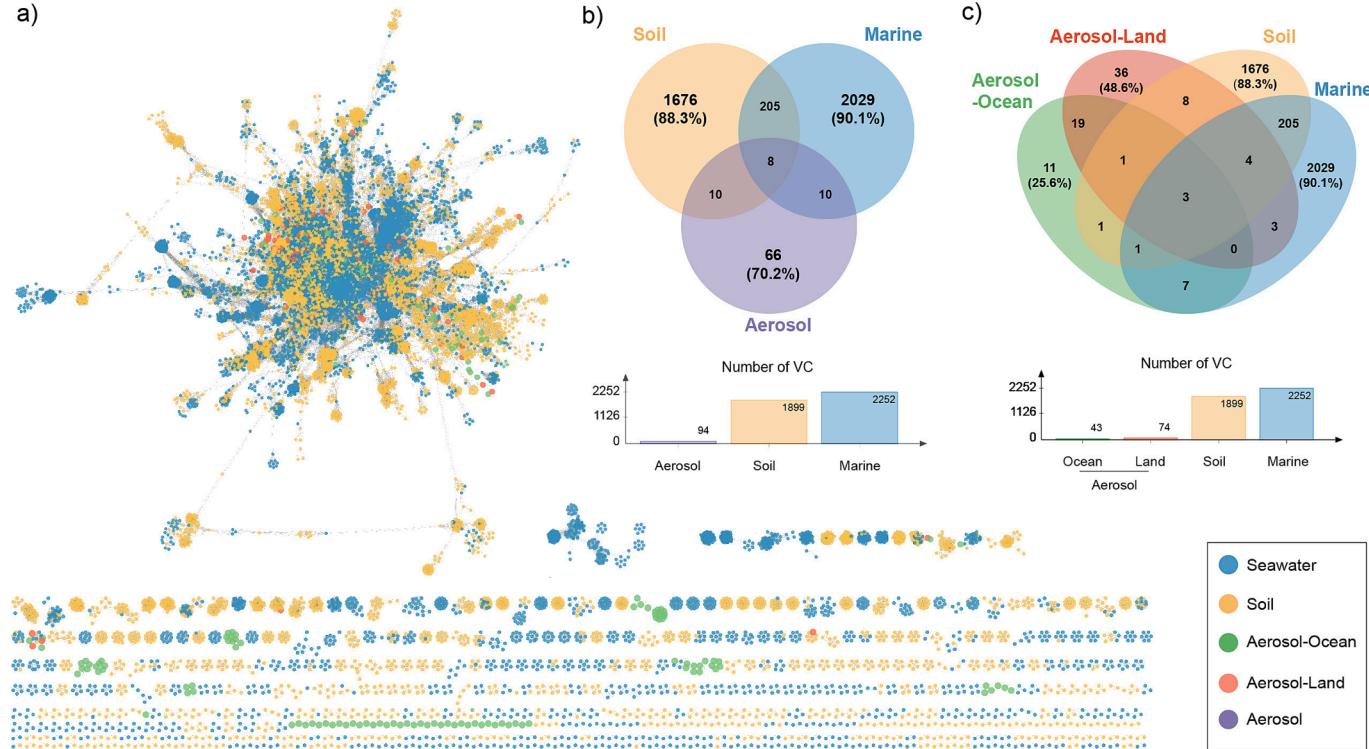


Fig. 2. Comparative analysis of the aerosol viral dataset with other environmental viral communities. (a) Gene-sharing network of viral sequences based on sequences of aerosol viral dataset and IMG/VR v4. Nodes represent viral genomes, and edges indicate similarity based on shared protein clusters. (b, c) Venn diagrams illustrate the shared and distinct viral clusters among various environmental habitats.

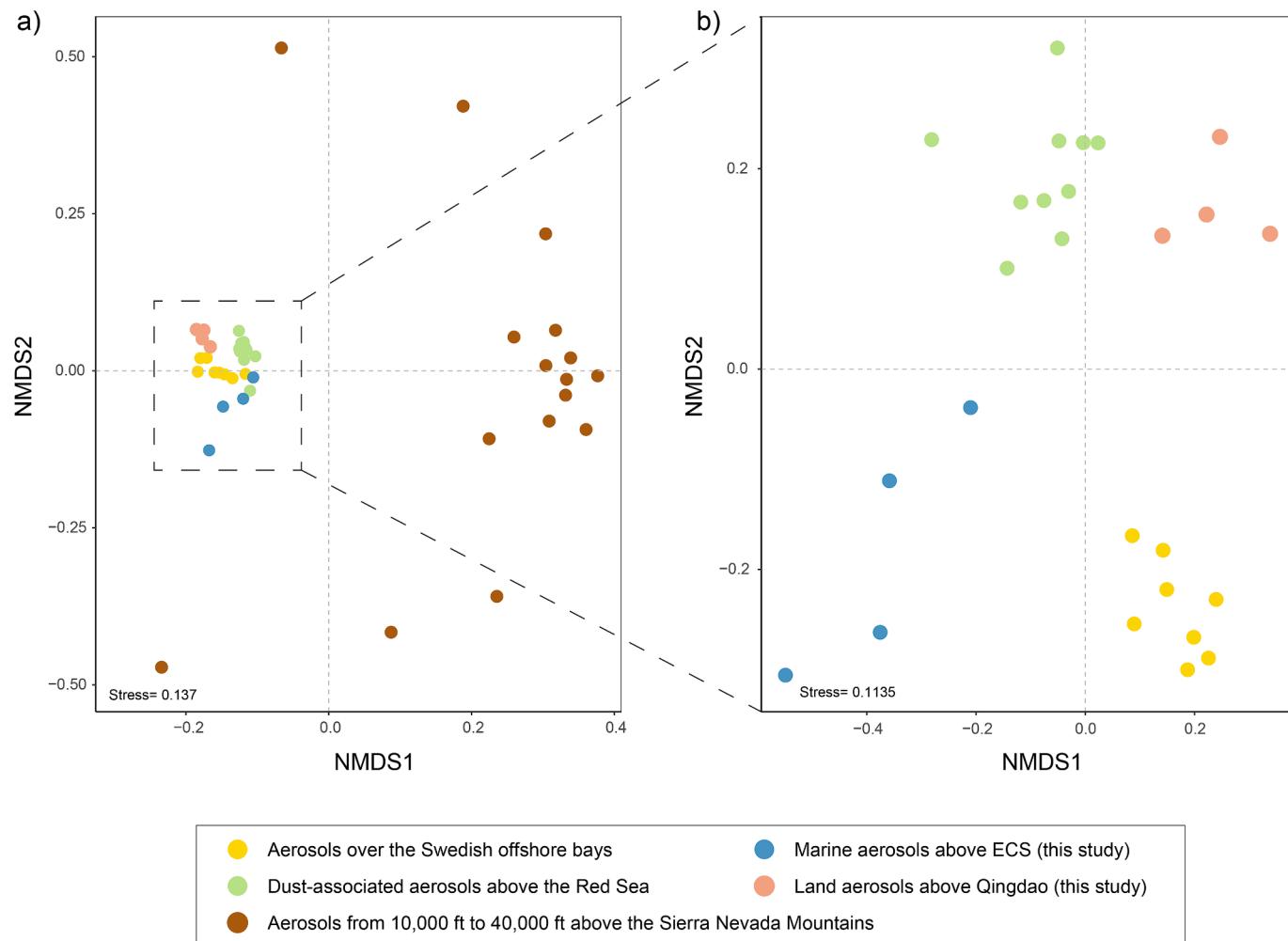


Fig. 3. Nonmetric multidimensional scaling (NMDS) analysis of aerosol virus communities from different regions. Due to the limited number of viral contigs in the dataset when using sequences > 5 kb, sequences greater than 1.5 kb were included in the comparison. (a) NMDS analysis of aerosolized viruses across different altitudes, and (b) NMDS analysis focused on low altitudes only.

ecosystems produced interesting results with regard to their habitat-dependent characteristics. In the land aerosol samples, a total of 708 VOTUs were identified, while in the ocean aerosol samples, only 163 VOTUs were found. There were significant differences in diversity and community composition at the vOTU level, with pristine marine airborne vOTUs exhibiting lower richness and Shannon diversity index compared to those from land aerosols (Fig. 4a, Table S4). The prokaryotic richness and Shannon diversity index, derived from 16S rRNA gene sequencing of 31 land aerosol samples and 39 ocean aerosol samples collected from the same locations as this study, exhibited a consistent pattern (Fig. S3, Table S4 & S5). This observation aligns with previous studies suggesting that environmental filtering, i.e., the restrictiveness of the environment, regulates bacterial diversity (Adams et al., 2015), thereby influencing the diversity of viruses. In contrast, in areas more heavily influenced by human activities, the concentration of bacteria in aerosols was observed to rise (urban areas vs. rural regions, heavy vehicular traffic area vs. quieter regions) (Harrison et al., 2005; Burrows et al., 2009; Fang et al., 2007). In such environments, the influence of environmental filtering in shaping bacterial communities is reduced, while stochastic processes play a more dominant role in shaping the community (Zhao et al., 2022). This leads to greater diversity and richness of airborne viruses. Similar patterns have also been

reported in the indoor environment, with lower viral diversity in the air of subways equipped with advanced ventilation and filtration systems than in venues relying on natural ventilation (Prussin et al., 2019).

The closer associations observed in beta diversity among samples from the same habitat (as shown in NMDS analysis, Fig. 4b), along with the variation in dominant viruses among different habitats (Fig. 4c, Table S4), both reflect the influence of habitat on shaping aerosol viral community composition. However, it should be noted that significant differences in the relative abundance of different vOTUs within each sample persisted from the same habitat, underscoring the dynamic nature of viruses in the atmosphere (Fig. S4).

At the VC level, most clusters specific to terrestrial aerosols were identified as *Caudoviricetes* and unknown taxa (Fig. S5). Another 3 VCs belonged to the *Genomoviridae* family of ssDNA. Among marine aerosol-specific VCs, 11 (92 %) were categorized as *Caudoviricetes*, including one VCs belonging to the P2-like phages. Furthermore, 28 VCs, comprising 70 % of marine aerosols and 47 % of terrestrial aerosols, were shared between the two habitats excluding the remaining reference sequences (Fig. S6). Among these, 14 (50 %) VCs were classified as *Caudoviricetes*, and others lacked annotation information. These shared VCs between marine and terrestrial aerosols could be due to the dispersion processes across different environments driven by the air circulation patterns and meteorological conditions (e.g. wind speed and direction).

Although the air ecosystem is characterized by its fluidity, allowing for long-range transport and dynamic processes, a deeper understanding

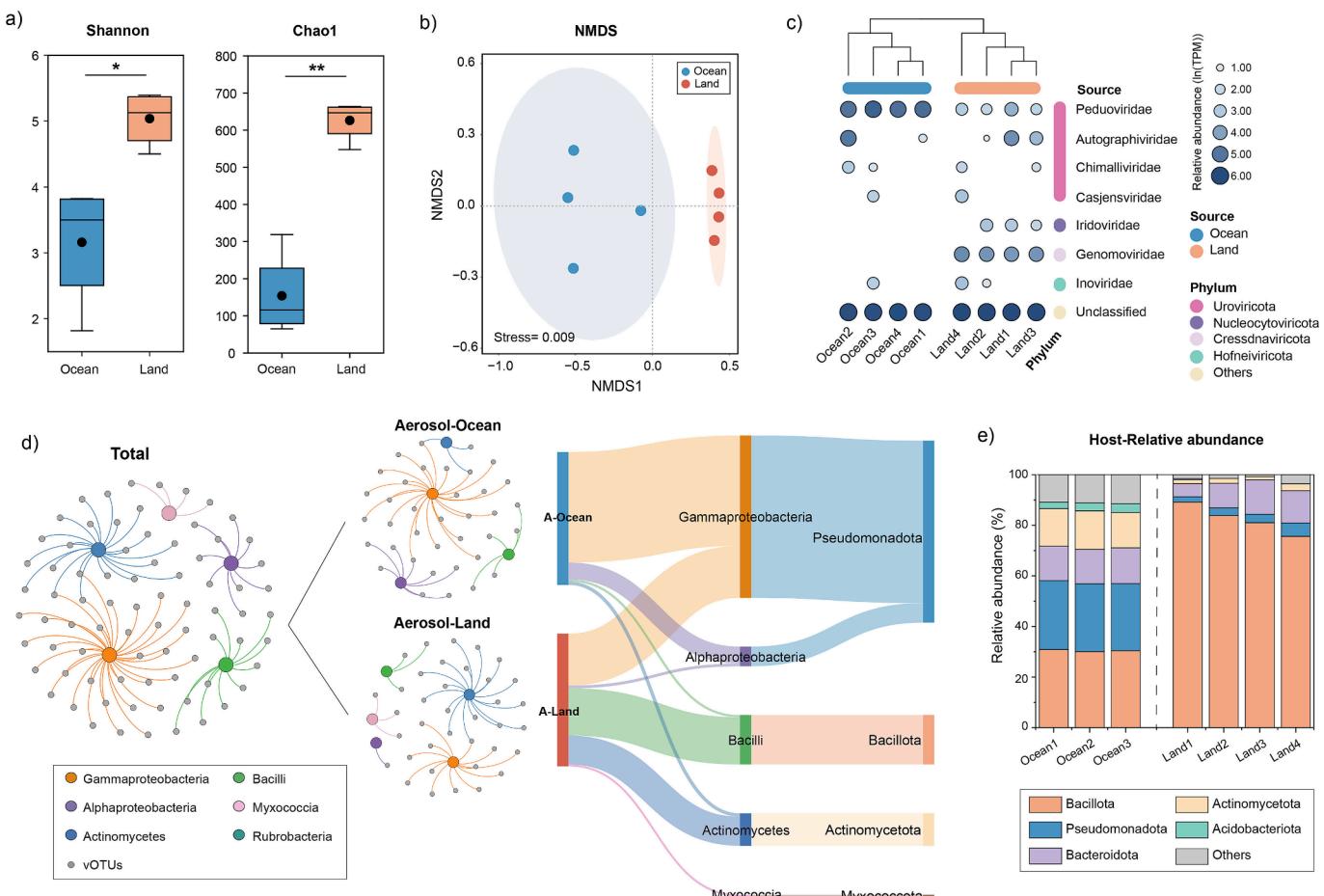


Fig. 4. Habitat-dependent diversity, community composition, life strategy, and host prediction of aerosol viruses. (a) Comparison of α -diversity indexes between aerosol viral metagenomes over the ocean and land. Black asterisks indicate significant differences between marine and terrestrial aerosol samples (t -test, $** p \leq 0.01$). (b) Non-metric multidimensional scaling analysis (NMDS) of aerosol viral metagenomes. Ellipses = 95 % confidence intervals. (c) Heat map of the distribution of identified viruses at the family level. Red asterisks indicate significant differences between the relative abundance of marine and terrestrial aerosol samples (t -test, $* p \leq 0.05$, $** p \leq 0.01$). (d) Predicted viral-prokaryotic host linkage in aerosol samples and the expression of viral relative abundance in different regions infected with different types of hosts. (e) Relative abundance of viral hosts determined from 16S rRNA gene amplicon sequencing. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

is needed to determine the degree of connectivity between the viral community and adjacent environments. Therefore, comparisons of viral communities between the aerosol environment and neighboring marine or soil habitats were conducted. Specifically, land aerosols exhibited a greater percentage of VCs shared with soil habitats (21.6 %) compared to the ocean (13.5 %), whereas marine aerosols showed a larger proportion of VCs shared with the ocean (25.6 %) than with soil (14 %) (Fig. 2c). Moreover, marine aerosols collected over the East China Sea share higher percentages of VCs with the East China Sea than with other seas (17.4 % vs. 10.9 %) (Fig. S5). These observations support that certain airborne viruses are capable of being transported from their local environmental sources. Previous studies have found that up to 2 billion tonnes of desert dust is transported into the atmosphere annually (Shepherd et al., 2016), potentially carrying viruses from the soil (Gonzalez-Martin et al., 2014). Alternatively, marine aerosols are primarily formed by the eruption of bubbles rising through the sea-surface microlayer (SML) (Aller et al., 2005), facilitating the transportation of microorganisms such as viruses from the ocean to the atmosphere. Nevertheless, it should be noted that the vast majority of the viruses were specific to aerosols or had an unclear origin of dispersal in our study.

A total of 78 vOTUs were predicted to have corresponding hosts, comprising a relative abundance of 26.2 % (Fig. 4d). Among these, 42.2 % of the vOTUs from marine-sourced aerosols were assigned to hosts,

while this percentage significantly dropped to 10.1 % for vOTUs from land sources. Coincident with the observed distinct viral community composition in the two habitats, the predicted hosts also demonstrate clear habitat differences. The predicted prokaryotic hosts for marine-sourced aerosol viruses encompassed four bacterial class-level taxa belonging to three phyla, with Gammaproteobacteria (60 % of virus-host pairs) and Alphaproteobacteria (20 %) being the most frequently predicted. In contrast, the predicted prokaryotic hosts of land-sourced aerosol viruses included six bacterial class-level taxa belonging to four phyla, with Actinomycetes (46.2 %) and Gammaproteobacteria (33.3 %), accounting for 79.5 % of the vOTUs predicted to have hosts. The predicted relative abundance of host-associated vOTUs is consistent with the bacterial relative abundance obtained through 16S rRNA gene analysis (Fig. 4e). For instance, bacteria belonging to the Pseudomonadota phylum were more prevalent in marine aerosols, along with their associated viruses, compared to land samples. This pattern may be influenced by the high occurrence of Gammaproteobacteria in the surface microlayer, which facilitates their transfer into the atmosphere (Stolle et al., 2011). The habitat-specific patterns evident in the viral-host community further emphasize the significant influence of specific features within each habitat that shape interactions between viruses and their hosts.

3.3. Airborne Viruses: Pathogens and beyond

The interest in airborne viruses stems from their potential to cause diseases (Lai et al., 2009; Leung, 2021), while some can also be beneficial to human health and the environment (Ariya et al., 2009; Barr et al., 2013). There is evidence that many common infections are caused by viruses, such as measles virus, influenza virus, norovirus, enterovirus, coronaviruses, respiratory syncytial virus, varicella-zoster virus, and adenovirus, which can be transmitted through the air (Al-Rubaey et al., 2022). In this dataset focusing on DNA viruses, fragments of herpesviruses were detected in the aerosols (Fig. 4c). Herpesviruses have a broad host range and can infect humans and other vertebrates. The relative abundance of *Orthoherpesviridae*, which contains 25 herpesviruses fragments, was significantly higher in land-sourced aerosol samples than in ocean-sourced samples (Fig. S7). It is worth noting that, although the land samples were collected from the summit of a small mountain in Qingdao, distant from human activities and near a government air quality monitoring station, human activity can still influence the composition of viral communities in aerosols.

Members of the *Inoviridae* family were detected in the dataset, with a higher relative abundance on land compared to the ocean (Fig. 4c). Filamentous bacteriophages from the *Inoviridae* family infect a number of gram-negative, and some gram-positive, bacteria, such as *Vibrio cholerae*, *Yersinia pestis*, *Neisseria meningitidis*, *Pseudomonas aeruginosa*, and some plant pathogens (Ilyina, 2015). Some Inoviruses can encode and express the major virulence factor of toxicogenic *Vibrio cholerae*, and can indirectly affect pathogenicity by altering biofilm formation and host colonization abilities (Roux et al., 2019). In our dataset, *Zonula occludens* toxin (*Zot*) (Ocean3_366_ORF1, Ocean3_460_ORF2, Land4_5924_ORF1), an enterotoxin produced by *Vibrio cholerae* and carried by Inoviruses, was detected. The *zot* gene has the ability to reversibly alter intestinal epithelial tight junctions, allowing macromolecules to pass through the mucosal barrier. Along with other genes encoding virulence factors (e.g., *ctxA*, *ctxB*, and *ace*), *zot* plays a synergistic role in the development of acute dehydrating diarrhea typical of cholera (Fasano et al., 1995).

In addition, our dataset identified viruses from the *Iridoviridae* family, which infect invertebrates and poikilothermic vertebrates, including amphibians, reptiles, and fish (Fig. 4c) (Williams, 1996). Iridovirus infections range from subclinical to severe and may lead to significant mortality (Ahne et al., 1989; Hedrick and McDowell, 1995; Hedrick et al., 1992; Langdon et al., 1986; Pozet et al., 1992). These infections have also been implicated in declines in amphibian populations and are considered emerging infectious diseases whose spread has been accelerated by human activities (Bollinger et al., 1999; Jancovich et al., 2001; Daszak et al., 2003; Jancovich et al., 2005).

A total of 66 complete and high-quality viral sequences were obtained from the eight viral metagenomes. Eleven sequences were found to be related to viruses that infect pathogenic bacteria associated with humans, animals, and plants and were detected in both land and marine aerosols (Table S6, Fig. S8). These bacterial pathogens can cause human diarrhea, septicemia, pneumonia, urinary tract infections, meningitis, and other illnesses (Knodler and Elfenbein, 2019; Wyres et al., 2020). A soil-borne bacterial plant pathogen, *Ralstonia solanacearum*, was also identified (Genin and Denny, 2012). The presence of these viruses with complete genomes suggests the potential of these airborne viruses to cause infections and thus influence the dynamics of bacterial infections in humans, plants, and animals. Furthermore, through host prediction, we identified that at the genus level, more than half of the viral hosts are pathogenic bacteria, including *Staphylococcus aureus* and *Klebsiella pneumoniae* from the ESKAPE (six highly virulent and antibiotic-resistant bacterial pathogens of urgent concern to the World Health Organization) (Fig. S9) (Taconelli, 2017). Host predictions also included *Staphylococcus gallinarum*, a relative of *Staphylococcus aureus*, as well as *Acinetobacter nosocomialis*, related to *Acinetobacter baumannii*—all of which pose significant health risks to humans. Studies

have found that bacteria tend to maintain cultivability more effectively when attached to larger particles, attributed to the protective shielding provided by these particles against environmental stresses (Burrows et al., 2009; Lighthart, 2000). Similar protective advantages may extend to viruses, potentially facilitating their infection of hosts under favorable conditions (Aller et al., 2005). However, further research is necessary to fully understand their pathogenicity and explore the extent of this influence and its implications.

Interestingly, the presence of a marker gene encoding rolling-circle replication initiation protein (Rep) from the ssDNA *Genomoviridae* was identified in the other 11 viral genomes (Table S6). This Rep protein shares two conserved domains with proteins found in members of the *Geminiviridae* family. The phylogenetic tree constructed using Rep gene sequences has distinct clusters of viral groups within *Genomoviridae* and *Geminiviridae*, which form separate sister groups (Fig. 5a, Table S7). Within *Genomoviridae*, distinct branches were observed for different genera, with 11 novel viruses affiliated with various genera (Fig. 5b), contributing to the understanding of the diversity and taxonomy of uncultured ssDNA viruses within the *Genomoviridae* family. Studies have shown that certain members of the *Genomoviridae* family can infect fungi (Li et al., 2020). The 11 sequences of *Genomoviridae* are predominantly present in terrestrial aerosols, originating from diverse sources such as the feces of egrets and giant pandas, the serum of *Sus scrofa domesticus*, as well as wastewater metagenomes and the dryland aerobiome (Fig. S8; Table S6).

3.4. Environmental conditions shaping viral Lifestyles and functional gene Profiles

The different environments present in land and ocean clearly create the distinctive ecological conditions that drive the selection and adaptation of aerosol viruses. Upon invading a host, viruses can apply different strategies to enhance their chances of survival or drive host adaptation (Colet and Roux, 2021).

One such mechanism is the insertion of large DNA fragments into the bacterial chromosome by phages with lysogenic cycles (Bobay et al., 2013). This generates genetic variation and evolutionary innovation to help the host adapt to new environments (Du et al., 2023). The relative abundance of lysogenic viruses in the ocean aerosol samples was significantly higher than in the land aerosol samples (Fig. S10; Table S4; *t*-test, $p < 0.05$). It is likely that harsh environmental conditions over the oceans, such as high UV radiation levels due to fewer air pollutants and sand activity (Elminir, 2007) and limited nutrition due to low industrial emissions (Gruber and Galloway, 2008; Falkowski et al., 2000; Mahowald et al., 2008), may contribute to the selection of a lysogenic lifestyle (Jiang and Paul, 1998). Lysogeny may serve as a strategy for viruses to evade degradation, ensuring their survival and accumulating genetic variation under non-selective conditions. The presence of lysogenic phages also contributes to the immune response of host cells against homologous phage infection (Du et al., 2023; Bobay et al., 2013). The detection of more viruses belonging to the *Peduviridae* family in the ocean aerosol samples compared with the land aerosol samples (Fig. 4c) suggests that these viruses, including P2-like viruses capable of entering a lysogenic state, may be better adapted to these environments (Nilsson and Haggard-Ljungquist, 2007; Turner et al., 2023).

In addition to lysogenic infection, another strategy to drive host adaptation involves the expression of viral auxiliary metabolic genes (AMGs) encoded by the phage but originating from the host cells. These AMGs allow the phage to fine-tune the host's metabolic processes in a way that optimally supports its own life cycle (Coutinho et al., 2017). In this study, a number of categories of AMGs associated with carbon, nitrogen, phosphorus, and lipid metabolism were detected in the aerosol viral communities. These AMGs displayed environmental variability, potentially related to resource availability, indicating their role in adapting to different environmental conditions (Fig. 6a, Table S4). Of the AMGs, carbohydrate-active genes and lipid metabolism genes had

a)

New-found Genomoviridae ★

Outer ring (I) : Family

- Genomoviridae
- Geminiviridae

Inner ring (II) : Genus

- Gemycircularvirus
- Gemykibivirus
- Gemygorvirus
- Gemykrogvirus
- Gemyvongvirus
- Gemykolovirus
- Gemyduguvirus
- Gemykroznavirus
- Gemytondvirus
- Unknown Genomoviridae

Tree scale: 1

b)

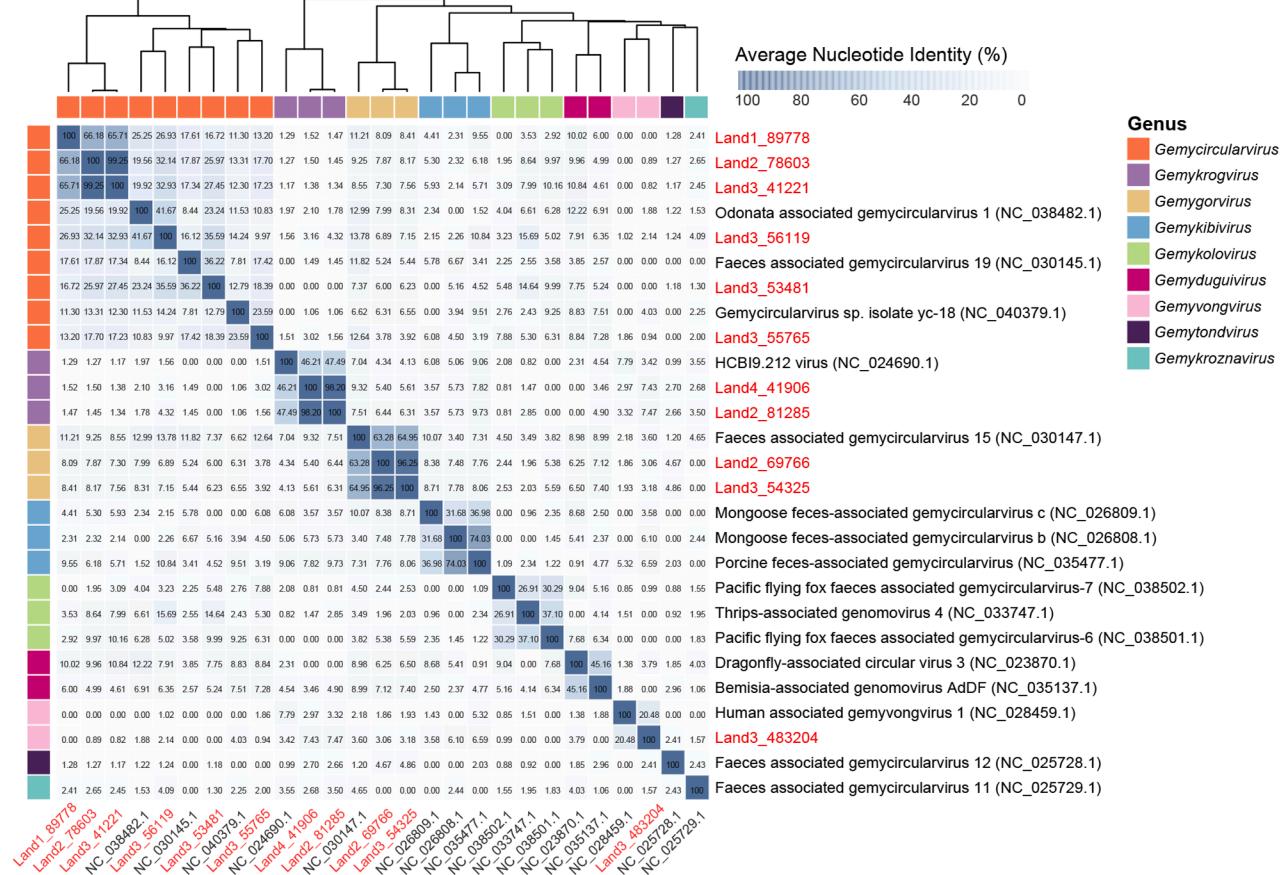


Fig. 5. Evolutionary analysis of Genomoviridae. (a) Phylogenetic tree showing the evolutionary relationships within the Genomoviridae family. The inner ring denotes genus information and the outer ring represents family information. The black branches are the viral sequences of Genomoviridae from the NCBI virus database, with details provided in Table S4. Sequences highlighted in red refer to viruses within the Genomoviridae family newly identified from our dataset. (b) Heat map displaying average nucleotide identity of selected members of the Genomoviridae family. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

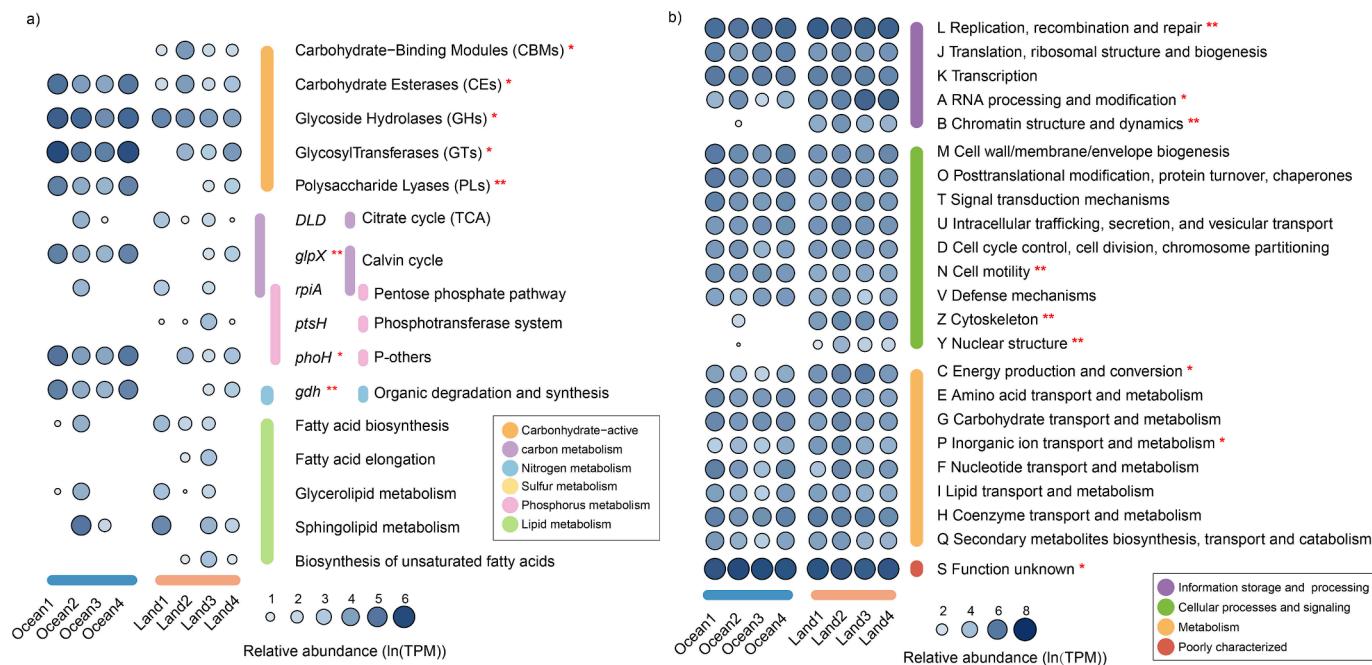


Fig. 6. Relative abundance of functional genes. a) Relative abundance of virus-encoded AMGs. b) Relative abundance of viral gene COG classification by eggNOG. Asterisks signify statistically significant differences (*t*-test, * $0.01 < p \leq 0.05$, ** $p \leq 0.01$) between marine and terrestrial aerosol samples.

the highest diversity. Genes specifically involved in the nitrogen cycle, such as *gdh*, which is associated with organic nitrogen degradation and synthesis pathways, were detected. This result is consistent with the observed high content of organic nitrogen present in the anthropogenic aerosols in East Asia (Mahowald et al., 2017) and suggests an advantage for bacterial hosts capable of degrading organic nitrogen (Chubukov et al., 2014; Guldberg et al., 2002). The phosphate regulon (*phoH*), which regulates phosphate uptake and metabolism under low-phosphate conditions, exhibited a higher relative abundance in aerosol samples above the ocean, where atmospheric phosphorus (P) load is considerably lower compared to those over continental areas. It has been reported that approximately 90 % of the total atmospheric burden of P is found over continents, primarily sourced from soil particles containing both naturally occurring and fertilizer-derived P (Graham and Duce, 1979). The expression of *phoH* genes has been shown to significantly increase as phosphorus concentration decreases (Gao et al., 2022). Therefore, the presence of *phoH* genes in ocean aerosols may assist host in overcoming limitations in phosphorus metabolism by regulating specific steps in these metabolic pathways. Other AMGs related to phosphorus metabolism (*rpiA*, *ptsH*) were also detected, indicating viral involvement in atmospheric phosphorus cycling.

While a significant number of viral proteins involved in replication, recombination, and repair were successfully identified and annotated, a considerable proportion of viral proteins still remain functionally uncharacterized. Proteins related to cell motility showed significantly higher relative abundance in the aerosol viral communities from ocean sources than those from land sources. In contrast, viruses from land sources displayed a significantly higher relative abundance of proteins associated with energy production and conversion and inorganic ion transport and metabolism (Fig. 6b, Table S4). These differences in functional gene abundance reflect the specific adaptive strategies of viruses in response to their respective habitats, highlighting the distinctive ecological conditions that drive viral-host interactions in different environments. However, we should note that this study is only based on DNA sequencing-based methods, and further validation is needed for functional genes as well as pathogens.

Our results uncovered a distinct ecological zone occupied by airborne viral communities, which was separate from marine and soil

ones. Besides aerosol-specific viruses, aerosol viruses can also be transported from nearby soil or marine environments via atmospheric circulation, comprising the whole community. Significant differences in airborne viral diversity, community composition, functional gene profile, and lifestyle were observed between environments over land and ocean. Notably, our dataset also detected the presence of pathogenic viruses associated with human diseases, particularly in aerosols collected from terrestrial environments. These findings emphasize the importance of understanding the characteristics and dynamics of viral communities in the air and their potential implications for human health.

CRediT authorship contribution statement

Tong Jiang: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation. **Cui Guo:** Writing – review & editing, Resources, Funding acquisition, Conceptualization. **Hao Yu:** Writing – review & editing, Software, Methodology. **Ziyue Wang:** Writing – review & editing, Software, Methodology. **Kaiyang Zheng:** Writing – review & editing, Software, Methodology. **Xinran Zhang:** Writing – review & editing, Investigation. **Siyuan Tang:** Writing – review & editing, Investigation. **Chuxiao Wang:** Writing – review & editing, Investigation. **Hongbing Shao:** Writing – review & editing. **Chao Zhang:** Writing – review & editing. **Yantao Liang:** Writing – review & editing. **Liangliang Kong:** Writing – review & editing. **Huiwang Gao:** Writing – review & editing. **Andrew McMinn:** Writing – review & editing. **Min Wang:** Writing – review & editing, Resources, Funding acquisition, Conceptualization.

2.10. Data availability

The raw sequence data generated in this study are deposited in the NCBI database under accession number PRJNA1028337 and PRJNA1025833.

Declaration of competing interest

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.

Acknowledgments

We sincerely acknowledge Prof. David Adelson from the University of Adelaide for the valuable discussion and comments. Marine aerosol samples and seawater samples were collected onboard R/V "XIANG YANG HONG 18" during the open research cruise (NORC2021-02 + NORC2021-301, NORC2022-02 + NORC2022-301), supported by Shiptime Sharing Project of National Natural Science Foundation of China (No. 42049906).

This study was supported by National Natural Science Foundation of China (No. 42176149, 42120104006, 42430405, 41906126, 41976117), Laoshan Laboratory (No. LSKJ202203201), and National Key Research and Development Program of China (No. 2022YFC2807500).

We thank the support of the high-performance servers of Center for High Performance Computing and System Simulation, Pilot National Laboratory for Marine Science and Technology (Qingdao), the Marine Big Data Center of Institute for Advanced Ocean Study of Ocean University of China, the IEMB-1, a high-performance computing cluster operated by the Institute of Evolution and Marine Biodiversity, and the high-performance servers of Frontiers Science Center for Deep Ocean Multispheres and Earth System.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.envint.2025.109359>.

Data availability

Data will be made available on request.

References

- Shao, Y., Wyrwoll, K.-H., Chappell, A., et al., 2011. Dust cycle: An emerging core theme in earth system science. *Aeolian Res.* 2, 181–204. <https://doi.org/10.1016/j.aeolia.2011.02.001>.
- An, Z., Huang, R.J., Zhang, R., et al., 2019. Severe haze in northern china: A synergy of anthropogenic emissions and atmospheric processes. *Proc. Natl. Acad. Sci.* 116, 8657–8666. <https://doi.org/10.1073/pnas.1900125116>.
- Santl-Temkiv, T., Amato, P., Casamayor, E.O., et al., 2022. Microbial ecology of the atmosphere. *FEMS Microbiol. Rev.* 46. <https://doi.org/10.1093/femsre/fuac009>.
- Womack, A.M., Bohannan, B.J., Green, J.L., 2010. Biodiversity and biogeography of the atmosphere. *Philos. Trans. R. Soc., B* 365, 3645–3653. <https://doi.org/10.1098/rstb.2010.0283>.
- Du, S., Tong, X., Lai, A.C.K., et al., 2023. Highly host-linked viromes in the built environment possess habitat-dependent diversity and functions for potential virus-host coevolution. *Nat. Commun.* 14, 2676. <https://doi.org/10.1038/s41467-023-38400-0>.
- Coutinho, F.H., Silveira, C.B., Gregoracci, G.B., et al., 2017. Marine viruses discovered via metagenomics shed light on viral strategies throughout the oceans. *Nat. Commun.* 8, 15955. <https://doi.org/10.1038/ncomms15955>.
- Lai, K., Emberlin, J., Colbeck, I., 2009. Outdoor environments and human pathogens in air. *Environ. Health. 8 Suppl 1*, S15. <https://doi.org/10.1186/1476-069X-8-S1-S15>.
- Brown, J.K., Hovmøller, M.S., 2002. Aerial dispersal of pathogens on the global and continental scales and its impact on plant disease. *Science* 297, 537–541. <https://doi.org/10.1126/science.1072678>.
- Pal, C., Bengtsson-Palme, J., Kristiansson, E., et al., 2016. The structure and diversity of human, animal and environmental resistomes. *Microbiome* 4, 1–15. <https://doi.org/10.1186/s40168-016-0199-5>.
- Woo, A.C., Brar, M.S., Chan, Y., et al., 2013. Temporal variation in airborne microbial populations and microbially-derived allergens in a tropical urban landscape. *Atmos. Environ.* 74, 291–300. <https://doi.org/10.1016/j.atmosenv.2013.03.047>.
- Peiris, J.S., Guan, Y., Yuen, K., 2004. Severe acute respiratory syndrome. *Nat. Med.* 10, S88–S97. <https://doi.org/10.1038/nm1143>.
- Nikitin, N., Petrova, E., Trifonova, E., et al., 2014. Influenza virus aerosols in the air and their infectiousness. *Adv. Virol.* 2014, 859090. <https://doi.org/10.1155/2014/859090>.
- Zuo, Y.Y., Uspal, W.E., Wei, T., 2020. Airborne transmission of covid-19: Aerosol dispersion, lung deposition, and virus-receptor interactions. *ACS Nano* 14, 16502–16524. <https://doi.org/10.1021/acsnano.0c08484>.
- Prussin 2nd, A.J., Marr, L.C., Bibby, K.J., 2014. Challenges of studying viral aerosol metagenomics and communities in comparison with bacterial and fungal aerosols. *FEMS Microbiol. Lett.* 357, 1–9. <https://doi.org/10.1111/1574-6968.12487>.
- Kuske, C.R., 2006. Current and emerging technologies for the study of bacteria in the outdoor air. *Curr. Opin. Biotechnol.* 17, 291–296. <https://doi.org/10.1016/j.copbio.2006.04.001>.
- Rosario, K., Fierer, N., Miller, S., et al., 2018. Diversity of DNA and RNA viruses in indoor air as assessed via metagenomic sequencing. *Environ. Sci. Technol.* 52, 1014–1027. <https://doi.org/10.1021/acs.est.7b04203>.
- Danko, D., Bezdán, D., Afshin, E.E., et al., 2021. A global metagenomic map of urban microbiomes and antimicrobial resistance. *Cell* 184, e17. <https://doi.org/10.1016/j.cell.2021.05.002>.
- Brisebois, E., Veillette, M., Dion-Dupont, V., et al., 2018. Human viral pathogens are pervasive in wastewater treatment center aerosols. *J. Environ. Sci.* 67, 45–53. <https://doi.org/10.1016/j.jes.2017.07.015>.
- Leung, M., Tong, X., Boïfot, K.O., et al., 2021. Characterization of the public transit air microbiome and resistome reveals geographical specificity. *Microbiome* 9, 112. <https://doi.org/10.1186/s40168-021-01044-7>.
- Hall, R.J., Leblanc-Maridor, M., Wang, J., et al., 2013. Metagenomic detection of viruses in aerosol samples from workers in animal slaughterhouses. *PLoS One* 8, e72226. <https://doi.org/10.1371/journal.pone.0072226>.
- Whon, T.W., Kim, M.-S., Roh, S.W., et al., 2012. Metagenomic characterization of airborne viral DNA diversity in the near-surface atmosphere. *J. Virol.* 86, 8221–8231. <https://doi.org/10.1128/jvi.00293-12>.
- Cao, C., Jiang, W., Wang, B., et al., 2014. Inhalable microorganisms in Beijing's PM_{2.5} and PM₁₀ pollutants during a severe smog event. *Environ. Sci. Technol.* 48, 1499. <https://doi.org/10.1021/es4048472>.
- Rahlf, J., Esser, S.P., Plewka, J., et al., 2023. Marine viruses disperse bidirectionally along the natural water cycle. *Nat. Commun.* 14, 6354. <https://doi.org/10.1038/s41467-023-42125-5>.
- Aller, J.Y., Kuznetsova, M.R., Jahns, C.J., et al., 2005. The sea surface microlayer as a source of viral and bacterial enrichment in marine aerosols. *J. Aerosol Sci.* 36, 801–812. <https://doi.org/10.1016/j.jaerosci.2004.10.012>.
- Yang, W., Elankumaran, S., Marr, L.C., 2011. Concentrations and size distributions of airborne influenza A viruses measured indoors at a health centre, a day-care centre and on aeroplanes. *J. R. Soc. Interface* 8, 1176–1184. <https://doi.org/10.1098/rsif.2010.0686>.
- Kosmopoulos, J.C., Klier, K.M., Langwig, M.V., et al., 2024. Viromes vs. Mixed community metagenomes: Choice of method dictates interpretation of viral community ecology. *Microbiome* 12, 195. <https://doi.org/10.1186/s40168-024-01905-x>.
- Gao, C., Liang, Y., Jiang, Y., et al., 2022. Viriplankton assemblages from Challenger Deep, the deepest place in the oceans. *iScience* 25, 104680. <https://doi.org/10.1016/j.isci.2022.104680>.
- Chen, S., Zhou, Y., Chen, Y., et al., 2018. Fastp: An ultra-fast all-in-one fastq preprocessor. *Bioinformatics* 34, i884–i890. <https://doi.org/10.1093/bioinformatics/bty560>.
- Gu, C., Liang, Y., Li, J., et al., 2021. Saline lakes on the qinghai-tibet plateau harbor unique viral assemblages mediating microbial environmental adaption. *iScience* 24, 103439. <https://doi.org/10.1016/j.isci.2021.103439>.
- Nurk, S., Meleshko, D., Korobeynikov, A., et al., 2017. Metaspades: A new versatile metagenomic assembler. *Genome Res.* 27, 824–834. <https://doi.org/10.1101/gr.213959.116>.
- Ren, J., Song, K., Deng, C., et al., 2020. Identifying viruses from metagenomic data using deep learning. *Quant. Biol.* 8, 64–77. <https://doi.org/10.1007/s40484-019-01874>.
- Guo, J., Bolduc, B., Zayed, A.A., et al., 2021. Virosorter2: A multi-classifier, expert-guided approach to detect diverse DNA and RNA viruses. *Microbiome* 9, 37. <https://doi.org/10.1186/s40168-020-00990-y>.
- Fu, L., Niu, B., Zhu, Z., et al., 2012. Cd-hit: Accelerated for clustering the next-generation sequencing data. *Bioinformatics* 28, 3150–3152. <https://doi.org/10.1093/bioinformatics/bts565>.
- Nayfach, S., Camargo, A.P., Schulz, F., et al., 2021. Checkv assesses the quality and completeness of metagenome-assembled viral genomes. *Nat. Biotechnol.* 39, 578–585. <https://doi.org/10.1038/s41587-020-00774-7>.
- Aroney ST, Newell RJ, Nissen JN et al. Coverm: Read alignment statistics for metagenomics. *arXiv preprint arXiv:25011217*. 2025 <https://doi.org/10.48550/arXiv.2501.12127>.
- Wang M, Zheng K, Sun J et al. Vitap: A high precision tool for DNA and RNA viral classification based on meta-omic data. 2024 <https://doi.org/10.21203/rs.3.rs-4406120/v1>.
- Camargo, A.P., Roux, S., Schulz, F., et al., 2023. Identification of mobile genetic elements with Genomad. *Nat. Biotechnol.* 1–10. <https://doi.org/10.1038/s41587-023-01953-y>.
- Kieft, K., Zhou, Z., Anantharaman, K., 2020. Vibrant: Automated recovery, annotation and curation of microbial viruses, and evaluation of viral community function from genomic sequences. *Microbiome* 8, 90. <https://doi.org/10.1186/s40168-020-00867-0>.
- Hyatt, D., Chen, G.-L., LoCascio, P.F., et al., 2010. Prodigal: Prokaryotic gene recognition and translation initiation site identification. *BMC Bioinf.* 11, 1–11. <https://doi.org/10.1186/1471-2105-11-119>.
- El-Gebali, S., Mistry, J., Bateman, A., et al., 2019. The pfam protein families database in 2019. *Nucleic Acids Res.* 47, D427–D432. <https://doi.org/10.1093/nar/gky995>.

- Huerta-Cepas, J., Forslund, K., Coelho, L.P., et al., 2017. Fast genome-wide functional annotation through orthology assignment by eggNOG-mapper. *Mol. Biol. Evol.* 34, 2115–2122. <https://doi.org/10.1093/molbev/msx148>.
- Kanehisa, M., Sato, Y., Morishima, K., 2016. Blastkoala and ghostkoala: Kegg tools for functional characterization of genome and metagenome sequences. *J. Mol. Biol.* 428, 726–731. <https://doi.org/10.1016/j.jmb.2015.11.006>.
- Huang, L., Zhang, H., Wu, P., et al., 2018. Dbcam-seq: A database of carbohydrate-active enzyme (cazyme) sequence and annotation. *Nucleic Acids Res.* 46, D516–D521. <https://doi.org/10.1093/nar/gkx894>.
- Tu, Q., Lin, L., Cheng, L., et al., 2019. Ncycdb: A curated integrative database for fast and accurate metagenomic profiling of nitrogen cycling genes. *Bioinformatics*. 35, 1040–1108. <https://doi.org/10.1093/bioinformatics/bty741>.
- Yu, X., Zhou, J., Song, W., et al., 2020. Scydb: A curated functional gene database for metagenomic profiling of sulphur cycling pathways. *Mol. Ecol. Resour.* 21, 924–940. <https://doi.org/10.1111/1755-0998.13306>.
- Zeng, J., Tu, Q., Yu, X., et al., 2022. Pycydb: A comprehensive and accurate database for fast analysis of phosphorus cycling genes. *Microbiome*. 10, 101. <https://doi.org/10.1186/s40168-022-01292-1>.
- Shaffer, M., Bortton, M.A., McGivern, B.B., et al., 2020. Dram for distilling microbial metabolism to automate the curation of microbiome function. *Nucleic Acids Res.* 48, 8883–8900. <https://doi.org/10.1093/nar/gkaa621>.
- Jian, H., Yi, Y., Wang, J., et al., 2021. Diversity and distribution of viruses inhabiting the deepest ocean on earth. *ISME J.* 15, 3094–3110. <https://doi.org/10.1038/s41396-021-00994-y>.
- Camargo, A.P., Nayfach, S., Chen, I.A., et al., 2023. Img/vr v4: An expanded database of uncultivated virus genomes within a framework of extensive functional, taxonomic, and ecological metadata. *Nucleic Acids Res.* 51, D733–D743. <https://doi.org/10.1093/nar/gkac1037>.
- Buchfink, B., Xie, C., Huson, D.H., 2015. Fast and sensitive protein alignment using diamond. *Nat. Methods*. 12, 59–60. <https://doi.org/10.1038/nmeth.3176>.
- Bin Jang, H., Bolduc, B., Zablocki, O., et al., 2019. Taxonomic assignment of uncultivated prokaryotic virus genomes is enabled by gene-sharing networks. *Nat. Biotechnol.* 37, 632–669. <https://doi.org/10.1038/s41587-019-0100-8>.
- Shannon, P., Markiel, A., Ozier, O., et al., 2003. Cytoscape: A software environment for integrated models of biomolecular interaction networks. *Genome Res.* 13, 2498–2504. <https://doi.org/10.1101/gr.123903>.
- Ter Horst, A.M., Santos-Medellín, C., Sorensen, J.W., et al., 2021. Minnesota peat viromes reveal terrestrial and aquatic niche partitioning for local and global viral populations. *Microbiome*. 9, 1–18. <https://doi.org/10.1186/s40168-021-01156-0>.
- Alaismail, N.A., Ngugi, D.K., Díaz-Rúa, R., et al., 2019. Functional metagenomic analysis of dust-associated microbiomes above the red sea. *Sci. Rep.* 9, 13741. <https://doi.org/10.1038/s41598-019-50194-0>.
- Jaing, C., Thissen, J., Morrison, M., et al., 2020. Sierra nevada sweep: Metagenomic measurements of bioaerosols vertically distributed across the troposphere. *Sci. Rep.* 10, 12399. <https://doi.org/10.1038/s41598-020-69188-4>.
- Uritskiy, G.V., DiRuggiero, J., Taylor, J., 2018. Metawrap-a flexible pipeline for genome-resolved metagenomic data analysis. *Microbiome*. 6, 158. <https://doi.org/10.1186/s40168-018-0541-1>.
- Li, Z., Pan, D., Wei, G., et al., 2021. Deep sea sediments associated with cold seeps are a subsurface reservoir of viral diversity. *ISME J.* 15, 2366–2378. <https://doi.org/10.1038/s41396-021-00932-y>.
- Olm, M.R., Brown, C.T., Brooks, B., et al., 2017. Drep: A tool for fast and accurate genomic comparisons that enables improved genome recovery from metagenomes through de-replication. *ISME J.* 11, 2864–2888. <https://doi.org/10.1038/ismej.2017.126>.
- Chauheim, P.A., Mussig, A.J., Hugenholtz, P., et al., 2019. Gtdb-tk: A toolkit to classify genomes with the genome taxonomy database. *Bioinformatics*. 36, 1925–1927. <https://doi.org/10.1093/bioinformatics/btz848>.
- Parks, D.H., Chuvochina, M., Chauheim, P.A., et al., 2020. A complete domain-to-species taxonomy for bacteria and archaea. *Nat. Biotechnol.* 38, 1079–1086. <https://doi.org/10.1038/s41587-020-0501-8>.
- Duan, X., Guo, C., Zhang, C., et al., 2021. Effect of east asian atmospheric particulate matter deposition on bacterial activity and community structure in the oligotrophic northwest pacific. *Environ. Pollut.* 283, 117088. <https://doi.org/10.1016/j.envpol.2021.117088>.
- Bolyen, E., Rideout, J.R., Dillon, M.R., et al., 2019. Reproducible, interactive, scalable and extensible microbiome data science using qiiime 2. *Nat. Biotechnol.* 37, 852–887. <https://doi.org/10.1038/s41587-019-0209-9>.
- Bokulich, N.A., Kaehler, B.D., Rideout, J.R., et al., 2018. Optimizing taxonomic classification of marker-gene amplicon sequences with qiiime 2's q2-feature-classifier plugin. *Microbiome*. 6, 90. <https://doi.org/10.1168/s40168-018-0470-z>.
- Ahlgren, N.A., Ren, J., Lu, Y.Y., et al., 2017. Alignment-free d₂* oligonucleotide frequency dissimilarity measure improves prediction of hosts from metagenomically-derived viral sequences. *Nucleic Acids Res.* 45, 39–53. <https://doi.org/10.1093/nar/gkw1002>.
- Edwards, R.A., McNair, K., Faust, K., et al., 2016. Computational approaches to predict bacteriophage–host relationships. *FEMS Microbiol. Rev.* 40, 258–272. <https://doi.org/10.1093/femsre/fuv048>.
- Barrangou, R., Fremaux, C., Deveau, H., et al., 2007. Crispr provides acquired resistance against viruses in prokaryotes. *Science*. 315, 1709–1712. <https://doi.org/10.1126/science.113814>.
- Nasko DJ, Ferrell BD, Moore RM et al. Crispr spacers indicate preferential matching of specific viroplankton genes. *MBio*. 2019;10:10.1128/mbio.02651-18 <https://doi.org/10.1128/mbio.02651-18>.
- Skennerton, C.T., Imelfort, M., Tyson, G.W., 2013. Crass: Identification and reconstruction of crispr from unassembled metagenomic data. *Nucleic Acids Res.* 41, e105.
- Couvin, D., Bernheim, A., Toffano-Nioche, C., et al., 2018. Crisprcasfinder, an update of crisprfinder, includes a portable version, enhanced performance and integrates search for cas proteins. *Nucleic Acids Res.* 46, W246–W251. <https://doi.org/10.1093/nar/gky425>.
- Laslett, D., Canback, B., 2004. Aragorn, a program to detect tRNA genes and tmRNA genes in nucleotide sequences. *Nucleic Acids Res.* 32, 11–16. <https://doi.org/10.1093/nar/gkh152>.
- Varsani, A., Krupovic, M., 2017. Sequence-based taxonomic framework for the classification of uncultured single-stranded DNA viruses of the family Genomoviridae. *Virus Evol.* 3, vew037. <https://doi.org/10.1093/ve/vew037>.
- Krupovic, M., Ghabrial, S.A., Jiang, D., et al., 2016. Genomoviridae: A new family of widespread single-stranded DNA viruses. *Arch. Virol.* 161, 2633–2643. <https://doi.org/10.1007/s00705-016-2943-3>.
- Edgar, R.C., 2022. Muscle5: High-accuracy alignment ensembles enable unbiased assessments of sequence homology and phylogeny. *Nat. Commun.* 13, 6968. <https://doi.org/10.1038/s41467-022-34630-w>.
- Capella-Gutiérrez, S., Silla-Martínez, J.M., Gabaldón, T., 2009. Trimal: A tool for automated alignment trimming in large-scale phylogenetic analyses. *Bioinformatics*. 25, 1972–1973. <https://doi.org/10.1093/bioinformatics/btp348>.
- Nguyen, L.T., Schmidt, H.A., von Haeseler, A., et al., 2015. IQ-tree: A fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Mol. Biol. Evol.* 32, 268–274. <https://doi.org/10.1093/molbev/msu300>.
- Letunic, I., Bork, P., 2021. Interactive tree of life (itol) v5: An online tool for phylogenetic tree display and annotation. *Nucleic Acids Res.* 49, W293. <https://doi.org/10.1093/nar/gkab301>.
- Moraru, C., Varsani, A., Kropinski, A.M., 2020. Viridic-a novel tool to calculate the intergenomic similarities of prokaryote-infecting viruses. *Viruses*. 12. <https://doi.org/10.3390/v12111268>.
- Oksanen, J., Blanchet, F.G., Kindt, R., et al., 2013. Community Ecology Package. R Package Version. 2, 321–336.
- Tignat-Perrier, R., Dommergues, A., Thollot, A., et al., 2019. Global airborne microbial communities controlled by surrounding landscapes and wind conditions. *Sci. Rep.* 9, 14441. <https://doi.org/10.1038/s41598-019-51073-4>.
- Nilsson, A.S., Haggard-Ljungquist, E., 2007. Evolution of p2-like phages and their impact on bacterial evolution. *Res. Microbiol.* 158, 311–317. <https://doi.org/10.1016/j.resmic.2007.02.004>.
- Bertani, L.E., Bertani, G., 1971. Genetics of p2 and related phages. *Adv. Genet.* 16, 199–237. [https://doi.org/10.1016/S0065-2660\(08\)60359-4](https://doi.org/10.1016/S0065-2660(08)60359-4).
- Adams, R.I., Bateman, A.C., Bik, H.M., et al., 2015. Microbiota of the indoor environment: A meta-analysis. *Microbiome*. 3, 1–18. <https://doi.org/10.1186/s40168-015-0108-3>.
- López-Leal, G., Camelo-Valera, L.C., Hurtado-Ramírez, J.M., et al., 2022. Mining of thousands of prokaryotic genomes reveals high abundance of prophages with a strictly narrow host range. *Msystems*. 7, e00326–e00422. <https://doi.org/10.1128/msystems.00326-22>.
- Harrison, R.M., Jones, A.M., Biggins, P.D., et al., 2005. Climate factors influencing bacterial count in background air samples. *Int. J. Biometeorol.* 49, 167–178. <https://doi.org/10.1007/s00484-004-0225-3>.
- Burrows, S.M., Elbert, W., Lawrence, M., et al., 2009. Bacteria in the global atmosphere—part 1: Review and synthesis of literature data for different ecosystems. *Atmos. Chem. Phys.* 9, 9263–9280. <https://doi.org/10.5194/acp-9-9263-2009>.
- Fang, Z., Ouyang, Z., Zheng, H., et al., 2007. Culturable airborne bacteria in outdoor environments in beijing, china. *Microb. Ecol.* 54, 487–496. <https://doi.org/10.1007/s00248-007-9216-3>.
- Zhao, J., Jin, L., Wu, D., et al., 2022. Global airborne bacterial community—interactions with earth's microbiomes and anthropogenic activities. *Proc. Natl. Acad. Sci.* 119, e2204465119. <https://doi.org/10.1073/pnas.2204465119>.
- Prussin, A.J., Torres, P.J., Shimashita, J., et al., 2019. Seasonal dynamics of DNA and RNA viral bioaerosol communities in a daycare center. *Microbiome*. 7, 1–14. <https://doi.org/10.1186/s40168-019-0672-z>.
- Shepherd G, Terradellas E, Baklanov A et al. Global assessment of sand and dust storms. 2016.
- Gonzalez-Martin, C., Teigell-Perez, N., Valladares, B., et al., 2014. The global dispersion of pathogenic microorganisms by dust storms and its relevance to agriculture. *Adv. Agron.* 127, 1–41. <https://doi.org/10.1016/B978-0-12-800131-8.00001-7>.
- Stolle, C., Labrenz, M., Meeske, C., et al., 2011. Bacterioneuston community structure in the southern baltic sea and its dependence on meteorological conditions. *Appl. Environ. Microbiol.* 77, 3726–3733. <https://doi.org/10.1128/AEM.00042-11>.
- Leung, N.H.L., 2021. Transmissibility and transmission of respiratory viruses. *Nat. Rev. Microbiol.* 19, 528–545. <https://doi.org/10.1038/s41579-021-00535-6>.
- Ariya, P.A., Sun, J., Eltouny, N.A., et al., 2009. Physical and chemical characterization of bioaerosols – implications for nucleation processes. *Int. Rev. Phys. Chem.* 28, 1–32. <https://doi.org/10.1080/01442350802597438>.
- Barr, J.J., Auro, R., Furlan, M., et al., 2013. Bacteriophage adhering to mucus provide a non-host-derived immunity. *Proc. Natl. Acad. Sci.* 110, 10771–10776. <https://doi.org/10.1073/pnas.1305923110>.
- Al-Rubaey, N.F., Hussain, H., Ibraheem, N., et al., 2022. A review of airborne contaminated microorganisms associated with human diseases. *Medical Journal of Babylon*. 19. https://doi.org/10.4103/mjbl.Mjbl_20_22.
- Ilyina, T., 2015. Filamentous bacteriophages and their role in the virulence and evolution of pathogenic bacteria. *Mol. Genet. Microbiol. Virol.* 30, 1–9. <https://doi.org/10.3103/S0891416815010036>.

- Roux, S., Krupovic, M., Daly, R.A., et al., 2019. Cryptic inoviruses revealed as pervasive in bacteria and archaea across earth's biomes. *Nat. Microbiol.* 4, 1895–1906. <https://doi.org/10.1038/s41564-019-0510-x>.
- Fasano, A., Fiorentini, C., Donelli, G., et al., 1995. Zonula occludens toxin modulates tight junctions through protein kinase c-dependent actin reorganization, in vitro. *J. Clin. Invest.* 96, 710–720. <https://doi.org/10.1172/JCI118114>.
- Williams, T., 1996. The iridoviruses. *Adv. Virus Res.* 46, 345–412. [https://doi.org/10.1016/S0065-3527\(08\)60076-7](https://doi.org/10.1016/S0065-3527(08)60076-7).
- Ahne, W., Schlotfeldt, H., Thomsen, I., 1989. Fish viruses: Isolation of an icosahedral cytoplasmic deoxyribovirus from sheatfish (*silurus glanis*). *J. Vet. Med. B.* 36, 333–336. <https://doi.org/10.1111/j.1439-0450.1989.tb00611.x>.
- Hedrick, R., McDowell, T., 1995. Properties of iridoviruses from ornamental fish. *Vet. Res.* 26, 423–447.
- Hedrick, R., McDowell, T., Ahne, W., et al., 1992. Properties of Three Iridovirus-like Agents Associated with Systemic Infections of Fish. <https://doi.org/10.3354/dao013203>.
- Langdon, J., Humphrey, J., Williams, L., et al., 1986. First virus isolation from australian fish: An iridovirus-like pathogen from redfin perch, *perca fluviatilis* l. *J. Fish Dis.* 9. <https://doi.org/10.1111/j.1365-2761.1986.tb01011.x>.
- Pozet, F., Morand, M., Moussa, A., et al., 1992. Isolation and preliminary characterization of a pathogenic icosahedral deoxyribovirus from the catfish *ictalurus melas*. *Dis. Aquat. Organ.* 14, 35–42. <https://doi.org/10.3354/dao014035>.
- Bollinger, T.K., Mao, J., Schock, D., et al., 1999. Pathology, isolation, and preliminary molecular characterization of a novel iridovirus from tiger salamanders in saskatchewan. *J. Wildl. Dis.* 35, 413–429. <https://doi.org/10.7589/0090-3558-35.3.413>.
- Jancovich, J.K., Davidson, E.W., Seiler, A., et al., 2001. Transmission of the ambystoma tigrinum virus to alternative hosts. *Dis. Aquat. Organ.* 46, 159–163. <https://doi.org/10.3354/dao046159>.
- Daszak, P., Cunningham, A.A., Hyatt, A.D., 2003. Infectious disease and amphibian population declines. *Divers. Distrib.* 9, 141–150. <https://doi.org/10.1046/j.1472-4642.2003.00016.x>.
- Jancovich, J., Davidson, E., Parameswaran, N., et al., 2005. Evidence for emergence of an amphibian iridoviral disease because of human-enhanced spread. *Molecular Ecology*. 14, 213–224. <https://doi.org/10.1111/j.1365-294X.2004.02387.x>.
- Knodler, L.A., Elfenbein, J.R., 2019. *Salmonella enterica*. *Trends Microbiol.* 27, 964–995. <https://doi.org/10.1016/j.tim.2019.05.002>.
- Wyres, K.L., Lam, M.M.C., Holt, K.E., 2020. Population genomics of klebsiella pneumoniae. *Nat. Rev. Microbiol.* 18, 344–359. <https://doi.org/10.1038/s41579-019-0315-1>.
- Genin, S., Denny, T.P., 2012. Pathogenomics of the ralstonia solanacearum species complex. *Annu. Rev. Phytopathol.* 50, 67–89. <https://doi.org/10.1146/annurev-phyto-081211-173000>.
- Tacconelli, E., 2017. Global priority list of antibiotic-resistant bacteria to guide research, discovery, And Development.
- Lighthart, B., 2000. Mini-review of the concentration variations found in the alfresco atmospheric bacterial populations. *Aerobiologia*. 16, 7–16. <https://doi.org/10.1023/A:1007694618888>.
- Li, P., Wang, S., Zhang, L., et al., 2020. A tripartite ssDNA mycovirus from a plant pathogenic fungus is infectious as cloned DNA and purified virions. *Sci. Adv.* 6, eay9634. <https://doi.org/10.1126/sciadv.aay9634>.
- Coclet, C., Roux, S., 2021. Global overview and major challenges of host prediction methods for uncultivated phages. *Curr. Opin. Virol.* 49, 117–126. <https://doi.org/10.1016/j.coviro.2021.05.003>.
- Bobay, L.M., Rocha, E.P., Touchon, M., 2013. The adaptation of temperate bacteriophages to their host genomes. *Mol. Biol. Evol.* 30, 737–751. <https://doi.org/10.1093/molbev/mss279>.
- Elminir, H.K., 2007. Sensitivity of ultraviolet solar radiation to anthropogenic air pollutants and weather conditions. *Atmos. Res.* 84, 250–264. <https://doi.org/10.1016/j.atmosres.2006.08.004>.
- Gruber, N., Galloway, J.N., 2008. An earth-system perspective of the global nitrogen cycle. *Nature*. 451, 293–296. <https://doi.org/10.1038/nature06592>.
- Falkowski, P., Scholes, R.J., Boyle, E., et al., 2000. The global carbon cycle: A test of our knowledge of earth as a system. *science*. 290, 290, 291. <https://doi.org/10.1126/science.290.5490.291>.
- Mahowald, N., Jickells, T.D., Baker, A.R., et al., 2008. Global distribution of atmospheric phosphorus sources, concentrations and deposition rates, and anthropogenic impacts. *Global Biogeochem. Cycles*. 22. <https://doi.org/10.1029/2008GB003240>.
- Jiang, S., Paul, J.H., 1998. Significance of lysogeny in the marine environment: Studies with isolates and a model of lysogenic phage production. *Microb. Ecol.* 35, 235–243. <https://doi.org/10.1007/s002489900079>.
- Turner, D., Shkorporov, A.N., Lood, C., et al., 2023. Abolishment of morphology-based taxa and change to binomial species names: 2022 taxonomy update of the ictv bacterial viruses subcommittee. *Arch. Virol.* 168, 74. <https://doi.org/10.1007/s00705-022-05694-2>.
- Mahowald, N.M., Scanza, R., Braheyy, J., et al., 2017. Aerosol deposition impacts on land and ocean carbon cycles. *Current Climate Change Reports*. 3, 16–31. <https://doi.org/10.1007/s40641-017-0056-z>.
- Chubukov, V., Gerosa, L., Kochanowski, K., et al., 2014. Coordination of microbial metabolism. *Nat. Rev. Microbiol.* 12, 327–340. <https://doi.org/10.1038/nrmicro3238>.
- Guldberg, L.B., Finster, K., Jørgensen, N.O., et al., 2002. Utilization of marine sedimentary dissolved organic nitrogen by native anaerobic bacteria. *Limnol. Oceanogr.* 47, 1712–1722. <https://doi.org/10.4319/lo.2002.47.6.1712>.
- Graham, W.F., Duce, R.A., 1979. Atmospheric pathways of the phosphorus cycle. *Geochim. Cosmochim. Acta*. 43, 1195–1208. [https://doi.org/10.1016/0016-7037\(79\)90112-1](https://doi.org/10.1016/0016-7037(79)90112-1).
- Gao, S., Paez-Espino, D., Li, J., et al., 2022. Patterns and ecological drivers of viral communities in acid mine drainage sediments across southern china. *Nat. Commun.* 13, 2389. <https://doi.org/10.1038/s41467-022-30049-5>.