








Draft Metagenome Sequences of the *Sphagnum* (Peat Moss) Microbiome from Ambient and Warmed Environments across Europe

 Bryan T. Piatkowski,^a Dana L. Carper,^a Alyssa A. Carrell,^a I-Min A. Chen,^b  Alicia Clum,^b Chris Daum,^b  Emiley A. Eloë-Fadrosh,^b Daniel Gilbert,^c Gustaf Granath,^d Marcel Huntemann,^b Sara S. Jawdy,^a Ingeborg Jenneken Klarenberg,^{e,*} Joel E. Kostka,^f Nikos C. Kyrpides,^b Travis J. Lawrence,^a Supratim Mukherjee,^b Mats B. Nilsson,^g Krishnaveni Palaniappan,^b  Dale A. Pelletier,^a Christa Pennacchio,^b  T. B. K. Reddy,^b Simon Roux,^b A. Jonathan Shaw,^h Denis Warshan,ⁱ Tatjana Živković,^j David J. Weston^a

^aBiosciences Division, Oak Ridge National Laboratory, Oak Ridge, Tennessee, USA

^bDepartment of Energy Joint Genome Institute, Berkeley, California, USA

^cLaboratoire Chrono-Environnement/UMR 6249, CNRS, University of Bourgogne Franche-Comté, Montbéliard, France

^dDepartment of Ecology and Genetics, Uppsala University, Uppsala, Sweden

^eUniversity of Akureyri, Akureyri, Iceland

^fGeorgia Institute of Technology, Atlanta, Georgia, USA

^gDepartment of Forest Ecology and Management, Swedish University of Agricultural Sciences, Umeå, Sweden

^hDepartment of Biology, Duke University, Durham, North Carolina, USA

ⁱFaculty of Life and Environmental Sciences, University of Iceland, Reykjavik, Iceland

^jDepartment of Biology, Dalhousie University, Halifax, Nova Scotia, Canada

ABSTRACT We present 49 metagenome assemblies of the microbiome associated with *Sphagnum* (peat moss) collected from ambient, artificially warmed, and geothermally warmed conditions across Europe. These data will enable further research regarding the impact of climate change on plant-microbe symbiosis, ecology, and ecosystem functioning of northern peatland ecosystems.

Peat mosses (*Sphagnum* spp.) are keystone species of northern peatlands and have an extraordinary impact on global biogeochemical cycles. These northern latitude ecosystems harbor over one-quarter of terrestrial carbon in the form of peat, or incompletely decomposed biomass, but cover roughly 3% of Earth's land mass (1). Furthermore, peatlands store approximately 9 to 16% of global soil nitrogen (2, 3), which is largely derived from the biological fixation of atmospheric nitrogen by microbes that live in symbiosis with peat mosses (4, 5). Recently, much effort has been dedicated to understanding how *Sphagnum* will respond to projected scenarios of climate change (e.g., see references 6 and 7), but gaps exist in our knowledge about how such changes might affect the community composition and functioning of the *Sphagnum* microbiome. Here, we present microbiome metagenome assemblies for 49 samples of *Sphagnum*, representing 11 species collected from ambient, artificially warmed, and geothermally warmed environmental conditions.

Samples were collected from seven sites across three countries in Europe (Fig. 1), and the dominant species of *Sphagnum* were sampled at each site. Artificial warming experiments have been conducted since 1994 at the Degerö Stormyr peatland in Sweden (8) and since 2008 at the Forbonnet peatland in France (9). The average temperatures of moss samples were 12.2°C under ambient conditions, 14.7°C under artificially warmed conditions, and 27.2°C under geothermally warmed conditions (Table 1). Samples in the *Sphagnum magellanicum* species complex, i.e., *Sphagnum divinum* and *Sphagnum medium*, were identified on the basis of morphological and genetic analyses.

Editor Jason E. Stajich, University of California, Riverside

Copyright © 2022 Piatkowski et al. This is an open-access article distributed under the terms of the [Creative Commons Attribution 4.0 International license](https://creativecommons.org/licenses/by/4.0/).

Address correspondence to Bryan T. Piatkowski, piatkowskibt@ornl.gov.

*Present address: Ingeborg Jenneken Klarenberg, Systems Ecology, Department of Ecological Science, Faculty of Science, Vrije Universiteit Amsterdam, Amsterdam, Netherlands.

The authors declare no conflict of interest.

Received 21 April 2022

Accepted 16 August 2022

Published 7 September 2022

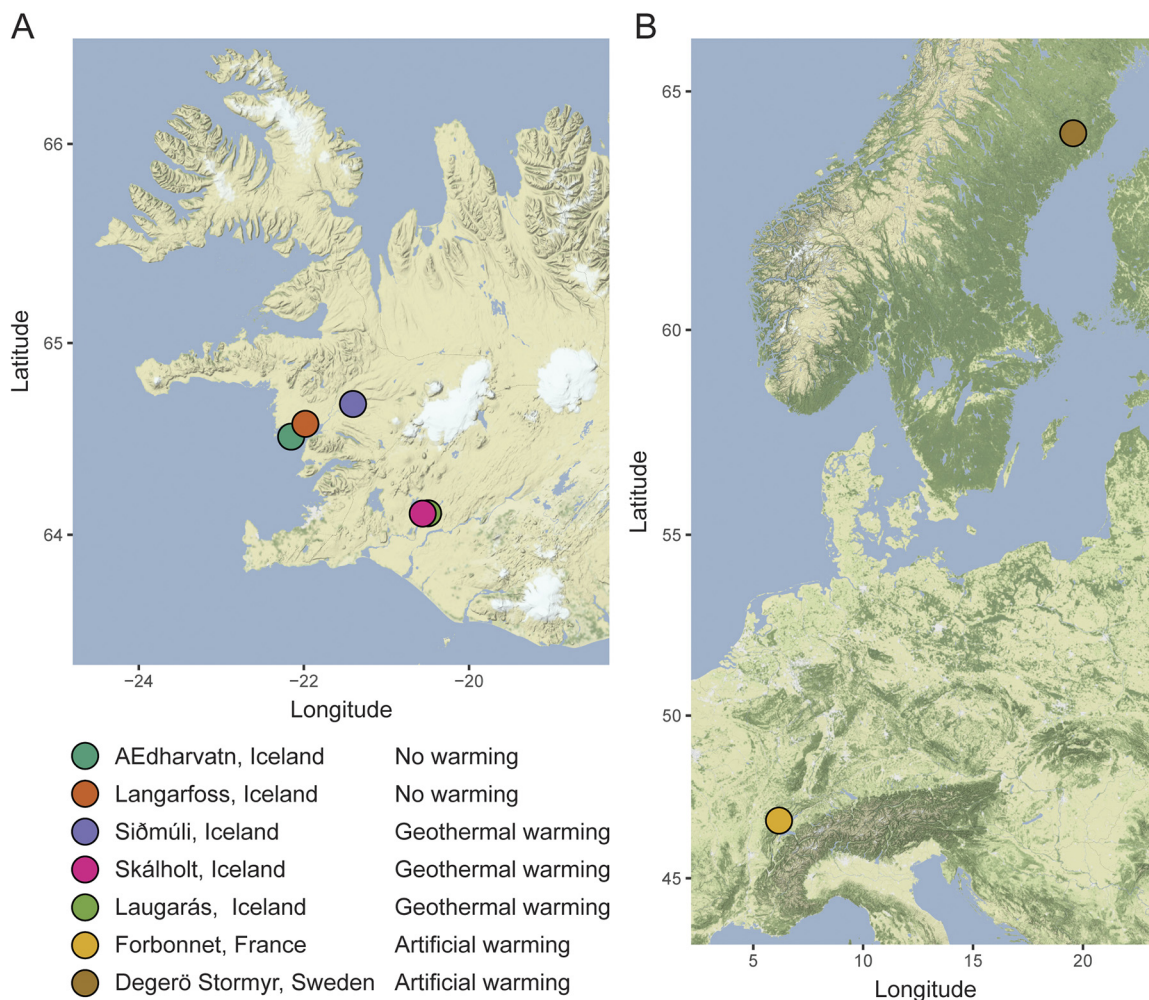


FIG 1 Collection sites for *Sphagnum* metagenome samples. (A) Plants at Icelandic sites were collected from only ambient or both ambient and geothermally warmed conditions. (B) Plants in France and Sweden were collected from both ambient and artificially warmed conditions.

Samples were flash frozen in the field using liquid nitrogen. Genomic DNA extractions were performed using DNeasy Plant Pro DNA extraction kits (Qiagen) according to the manufacturer's instructions. Illumina library construction using KAPA DNA library kits and 2×151 -bp sequencing using the Illumina NovaSeq S4 platform were performed by the U.S. Department of Energy's (DOE) Joint Genome Institute (JGI). All metagenomes were processed by the DOE JGI Metagenome Workflow (10). In brief, reads were quality controlled using the BBTtools package v38.92 (<https://bbtools.jgi.doe.gov>), metagenomes were assembled using metaSPAdes v3.15.2 (11), and the assemblies were annotated using the IMG Annotation Pipeline v5.0.24 (10). MetaBAT v0.32.4 (12) was used to identify genome bins, with a 3-kb minimum contig cutoff value, contig coverage information included, and the $-superspecific$ parameter enforced. Genome bins of at least medium quality were kept according to the minimum information on a metagenome-assembled genome (MIMAG) standards (13). Relevant statistics for these metagenome assemblies and annotations can be found in Table 1. Metadata and annotations can be obtained through the Genome OnLine Database (GOLD study identification number [Gs0154043](https://gold.jgi.doe.gov)) (14) and Integrated Microbial Genomes and Microbiomes (IMG/M) online system (15), respectively.

Data availability. The data have been deposited in the European Nucleotide Archive (ENA) at EMBL-EBI (project number [PRJEB54621](https://www.ebi.ac.uk/ena/record/PRJEB54621)).

TABLE 1 Properties of the *Sphagnum* metagenomes

| <i>Sphagnum</i> species | Sample name | Country of isolation | Region of isolation | Temp treatment | Moss temp (°C) | IMG genome identification no. | ENA sample accession no. | ENA run accession no. |
|-------------------------|-------------|----------------------|---------------------|----------------|----------------|-------------------------------|--------------------------|-----------------------|
| <i>S. angustifolium</i> | NH_ANG_ICE | Iceland | Langarfoss | None | 10.0 | 3300047495 | ERS12393009 | ERR9963747 |
| <i>S. auriculatum</i> | 1_AUR_ICE | Iceland | Laugarás | Geothermal | 34.0 | 3300047328 | ERS12393010 | ERR9963748 |
| <i>S. auriculatum</i> | 3_AUR_ICE | Iceland | Laugarás | Geothermal | 22.0 | 3300047494 | ERS12393011 | ERR9963749 |
| <i>S. auriculatum</i> | 5_AUR_ICE | Iceland | Laugarás | Geothermal | 27.0 | 3300047169 | ERS12393012 | ERR9963750 |
| <i>S. balticum</i> | 16OTC_BA_DE | Sweden | Degerö Stormyr | Artificial | 18.1 | 3300047167 | ERS12393013 | ERR9963751 |
| <i>S. balticum</i> | 11C_BA_DE | Sweden | Degerö Stormyr | None | 14.8 | 3300047166 | ERS12393014 | ERR9963752 |
| <i>S. balticum</i> | 19C_BA_DE | Sweden | Degerö Stormyr | None | 14.8 | 3300047165 | ERS12393015 | ERR9963753 |
| <i>S. divinum</i> | 20TC_MAG_FR | France | Forbonnet | Artificial | 13.4 | 3300047335 | ERS12393016 | ERR9963754 |
| <i>S. divinum</i> | 30TC_MAG_FR | France | Forbonnet | Artificial | 13.4 | 3300047332 | ERS12393017 | ERR9963755 |
| <i>S. divinum</i> | 60TC_MAG_FR | France | Forbonnet | Artificial | 13.4 | 3300047324 | ERS12393018 | ERR9963756 |
| <i>S. divinum</i> | 1C_MAG_FR | France | Forbonnet | None | 11.4 | 3300047326 | ERS12393019 | ERR9963757 |
| <i>S. divinum</i> | 4C_MAG_FR | France | Forbonnet | None | 11.4 | 3300047325 | ERS12393020 | ERR9963758 |
| <i>S. divinum</i> | 5C_MAG_FR | France | Forbonnet | None | 11.4 | 3300047175 | ERS12393021 | ERR9963759 |
| <i>S. fallax</i> | 10OTC_SF_FR | France | Forbonnet | Artificial | 13.4 | 3300047177 | ERS12393022 | ERR9963760 |
| <i>S. fallax</i> | 12OTC_SF_FR | France | Forbonnet | Artificial | 13.4 | 3300047174 | ERS12393023 | ERR9963761 |
| <i>S. fallax</i> | 30TC_SF_FR | France | Forbonnet | Artificial | 13.4 | 3300047176 | ERS12393024 | ERR9963762 |
| <i>S. fallax</i> | 60TC_SF_FR | France | Forbonnet | Artificial | 13.4 | 3300047333 | ERS12393025 | ERR9963763 |
| <i>S. fallax</i> | 80TC_SF_FR | France | Forbonnet | Artificial | 13.4 | 3300047179 | ERS12393026 | ERR9963764 |
| <i>S. fallax</i> | 11C_SF_FR | France | Forbonnet | None | 11.4 | 3300047178 | ERS12393027 | ERR9963765 |
| <i>S. fallax</i> | 1C_SF_FR | France | Forbonnet | None | 11.4 | 3300049214 | ERS12393028 | ERR9963766 |
| <i>S. fallax</i> | 4C_SF_FR | France | Forbonnet | None | 11.4 | 3300047330 | ERS12393029 | ERR9963767 |
| <i>S. fallax</i> | 5C_SF_FR | France | Forbonnet | None | 11.4 | 3300047329 | ERS12393030 | ERR9963768 |
| <i>S. fallax</i> | 7C_SF_FR | France | Forbonnet | None | 11.4 | 3300047334 | ERS12393031 | ERR9963769 |
| <i>S. fallax</i> | 9C_SF_FR | France | Forbonnet | None | 11.4 | 3300047331 | ERS12393032 | ERR9963770 |
| <i>S. gigensohnii</i> | 12_GIR_ICE | Iceland | Skálholt | Geothermal | 20.0 | 3300047171 | ERS12393033 | ERR9963771 |
| <i>S. lindbergii</i> | 16OTC_LL_DE | Sweden | Degerö Stormyr | Artificial | 18.1 | 3300047164 | ERS12393034 | ERR9963772 |
| <i>S. lindbergii</i> | 40TC_LL_DE | Sweden | Degerö Stormyr | Artificial | 18.1 | 3300047173 | ERS12393035 | ERR9963773 |
| <i>S. lindbergii</i> | 11C_LL_DE | Sweden | Degerö Stormyr | None | 14.8 | 3300047473 | ERS12393036 | ERR9963774 |
| <i>S. lindbergii</i> | 19C_LL_DE | Sweden | Degerö Stormyr | None | 14.8 | 3300047327 | ERS12393037 | ERR9963775 |
| <i>S. medium</i> | H_MAG_ICE | Iceland | Siðmúli | Geothermal | 28.0 | 3300047499 | ERS12393038 | ERR9963776 |
| <i>S. medium</i> | H1_MAG_ICE | Iceland | Siðmúli | Geothermal | 28.0 | 3300049255 | ERS12393039 | ERR9963777 |
| <i>S. medium</i> | H2_MAG_ICE | Iceland | Siðmúli | Geothermal | 28.0 | 3300048014 | ERS12393040 | ERR9963778 |
| <i>S. medium</i> | H3_MAG_ICE | Iceland | Siðmúli | Geothermal | 28.0 | 3300048015 | ERS12393041 | ERR9963779 |
| <i>S. medium</i> | C_MAG_ICE | Iceland | Siðmúli | None | 12.0 | 3300047493 | ERS12393042 | ERR9963780 |
| <i>S. medium</i> | C1_MAG_ICE | Iceland | Siðmúli | None | 12.0 | 3300049217 | ERS12393043 | ERR9963781 |
| <i>S. medium</i> | C2_MAG_ICE | Iceland | Siðmúli | None | 12.0 | 3300049218 | ERS12393044 | ERR9963782 |
| <i>S. medium</i> | C3_MAG_ICE | Iceland | Siðmúli | None | 12.0 | 3300049617 | ERS12393045 | ERR9963783 |
| <i>S. subnitens</i> | SUB_ICE | Iceland | Langarfoss | None | 10.0 | 3300047170 | ERS12393046 | ERR9963784 |
| <i>S. teres</i> | NH_TE_ICE | Iceland | AEdharvatn | None | 10.0 | 3300047498 | ERS12393047 | ERR9963785 |
| <i>S. teres</i> | H_TE_ICE | Iceland | Siðmúli | Geothermal | 10.0 | 3300047172 | ERS12393048 | ERR9963786 |
| <i>S. teres</i> | H1_TE_ICE | Iceland | Siðmúli | Geothermal | 28.0 | 3300047462 | ERS12393049 | ERR9963787 |
| <i>S. teres</i> | H2_TE_ICE | Iceland | Siðmúli | Geothermal | 28.0 | 3300049215 | ERS12393050 | ERR9963788 |
| <i>S. teres</i> | C_TE_ICE | Iceland | Siðmúli | None | 12.0 | 3300047168 | ERS12393051 | ERR9963789 |
| <i>S. teres</i> | C1_TE_ICE | Iceland | Siðmúli | None | 12.0 | 3300047994 | ERS12393052 | ERR9963790 |
| <i>S. teres</i> | C2_TE_ICE | Iceland | Siðmúli | None | 12.0 | 3300047678 | ERS12393053 | ERR9963791 |
| <i>S. teres</i> | C3_TE_ICE | Iceland | Siðmúli | None | 12.0 | 3300049216 | ERS12393054 | ERR9963792 |
| <i>S. teres</i> | 7_TE_ICE | Iceland | Skálholt | Geothermal | 34.0 | 3300047497 | ERS12393055 | ERR9963793 |
| <i>S. teres</i> | 9_TE_ICE | Iceland | Skálholt | None | 16.0 | 3300047496 | ERS12393056 | ERR9963794 |
| <i>S. warnstorffii</i> | 11_WAR_ICE | Iceland | Skálholt | Geothermal | 20.0 | 3300047163 | ERS12393057 | ERR9963795 |

TABLE 1 (Continued)

| ENA analysis accession no. | No. of filtered reads | Genome size (bp) | No. of contigs | Contig N_{50} (bp) | Contig L_{50} (bp) | Avg coverage of assembled sequences (x) | No. of genes | No. of genome bins | Estimated no. of genomes |
|----------------------------|-----------------------|------------------|----------------|----------------------|----------------------|---|--------------|--------------------|--------------------------|
| ERZ12298656 | 1.3E+08 | 1.2E+09 | 1.4E+06 | 1.7E+05 | 1,287 | 9.2 | 2.2E+06 | 12 | 172 |
| ERZ12293583 | 1.1E+08 | 1.4E+09 | 1.2E+06 | 1.4E+05 | 2,092 | 9.1 | 2.1E+06 | 31 | 140 |
| ERZ12293588 | 1.3E+08 | 1.5E+09 | 1.6E+06 | 1.7E+05 | 1,266 | 9.8 | 2.3E+06 | 56 | 235 |
| ERZ12293627 | 1.1E+08 | 1.3E+09 | 1.4E+06 | 2.5E+05 | 1,291 | 9.6 | 2.0E+06 | 22 | 105 |
| ERZ12293049 | 1.1E+08 | 1.2E+09 | 1.6E+06 | 2.0E+05 | 1,112 | 8.5 | 2.3E+06 | 6 | 150 |
| ERZ12293046 | 1.0E+08 | 1.3E+09 | 1.7E+06 | 2.7E+05 | 1,053 | 8.0 | 2.4E+06 | 19 | 195 |
| ERZ12298654 | 1.2E+08 | 1.4E+09 | 1.8E+06 | 3.1E+05 | 968 | 8.2 | 2.6E+06 | 16 | 207 |
| ERZ12293584 | 1.4E+08 | 1.5E+09 | 2.1E+06 | 3.9E+05 | 853 | 7.3 | 2.9E+06 | 14 | 238 |
| ERZ12293337 | 1.3E+08 | 1.2E+09 | 1.9E+06 | 4.2E+05 | 633 | 7.0 | 2.4E+06 | 12 | 279 |
| ERZ12293629 | 1.4E+08 | 1.5E+09 | 2.3E+06 | 4.6E+05 | 728 | 7.8 | 2.9E+06 | 17 | 257 |
| ERZ12293615 | 1.3E+08 | 1.5E+09 | 2.0E+06 | 3.3E+05 | 919 | 8.2 | 2.7E+06 | 17 | 237 |
| ERZ12293589 | 1.6E+08 | 1.6E+09 | 2.3E+06 | 4.5E+05 | 767 | 7.9 | 3.1E+06 | 15 | 324 |
| ERZ12293624 | 1.3E+08 | 1.4E+09 | 1.9E+06 | 2.9E+05 | 959 | 9.0 | 2.5E+06 | 21 | 234 |
| ERZ12293045 | 9.4E+07 | 1.0E+09 | 1.5E+06 | 3.2E+05 | 776 | 7.6 | 1.9E+06 | 7 | 170 |
| ERZ12293614 | 1.3E+08 | 1.3E+09 | 1.6E+06 | 2.7E+05 | 1,054 | 9.5 | 2.3E+06 | 16 | 208 |
| ERZ12293587 | 9.6E+07 | 9.0E+08 | 1.0E+06 | 1.5E+05 | 1,310 | 8.3 | 1.5E+06 | 9 | 104 |
| ERZ12297591 | 1.3E+08 | 1.4E+09 | 2.1E+06 | 4.1E+05 | 809 | 7.7 | 2.8E+06 | 9 | 233 |
| ERZ12298564 | 1.3E+08 | 1.3E+09 | 1.7E+06 | 2.3E+05 | 1,075 | 10.8 | 2.4E+06 | 5 | 169 |
| ERZ12293047 | 1.3E+08 | 1.3E+09 | 1.9E+06 | 3.4E+05 | 844 | 9.1 | 2.5E+06 | 21 | 255 |
| ERZ12293582 | 1.2E+08 | 1.4E+09 | 1.8E+06 | 2.8E+05 | 1,004 | 8.7 | 2.6E+06 | 13 | 204 |
| ERZ12293621 | 1.4E+08 | 1.4E+09 | 1.5E+06 | 1.4E+05 | 1,350 | 10.7 | 2.3E+06 | 7 | 171 |
| ERZ12295550 | 1.3E+08 | 1.3E+09 | 2.0E+06 | 4.0E+05 | 819 | 8.1 | 2.4E+06 | 7 | 174 |
| ERZ12298487 | 1.9E+08 | 2.0E+09 | 2.5E+06 | 3.9E+05 | 1,032 | 9.4 | 3.6E+06 | 18 | 341 |
| ERZ12293631 | 1.1E+08 | 1.1E+09 | 1.3E+06 | 1.8E+05 | 1,146 | 9.0 | 1.9E+06 | 4 | 124 |
| ERZ12295332 | 1.1E+08 | 9.9E+08 | 6.4E+05 | 3.1E+04 | 5,777 | 14.1 | 1.4E+06 | 28 | 111 |
| ERZ12298653 | 1.2E+08 | 1.3E+09 | 1.3E+06 | 1.2E+05 | 1,894 | 9.2 | 2.2E+06 | 15 | 183 |
| ERZ12298655 | 1.4E+08 | 1.4E+09 | 1.6E+06 | 2.2E+05 | 1,153 | 9.0 | 2.5E+06 | 26 | 265 |
| ERZ12295331 | 9.4E+07 | 1.2E+09 | 2.0E+06 | 4.5E+05 | 615 | 7.5 | 2.5E+06 | 12 | 212 |
| ERZ12295333 | 1.1E+08 | 1.1E+09 | 8.1E+05 | 3.7E+04 | 4,496 | 10.3 | 1.7E+06 | 19 | 146 |
| ERZ12295052 | 1.5E+08 | 1.6E+09 | 1.3E+06 | 8.6E+04 | 2,974 | 11.4 | 2.4E+06 | 67 | 206 |
| ERZ12298643 | 5.4E+08 | 2.6E+09 | 1.7E+06 | 4.4E+04 | 7,822 | 29.3 | 3.1E+06 | 158 | 335 |
| ERZ12294360 | 3.6E+08 | 2.4E+09 | 2.3E+06 | 1.4E+05 | 2,584 | 19.8 | 3.0E+06 | 96 | 290 |
| ERZ12298651 | 3.4E+08 | 2.3E+09 | 2.7E+06 | 1.8E+05 | 1,940 | 19.6 | 3.0E+06 | 77 | 301 |
| ERZ12293733 | 1.2E+08 | 1.5E+09 | 1.5E+06 | 1.9E+05 | 1,636 | 8.3 | 2.5E+06 | 21 | 222 |
| ERZ12293632 | 4.6E+08 | 2.3E+09 | 3.4E+06 | 2.9E+05 | 1,361 | 24.7 | 3.2E+06 | 61 | 319 |
| ERZ12298641 | 3.7E+08 | 2.3E+09 | 2.4E+06 | 1.4E+05 | 2,432 | 20.9 | 2.9E+06 | 86 | 283 |
| ERZ12293637 | 3.7E+08 | 2.3E+09 | 2.6E+06 | 1.8E+05 | 1,957 | 19.9 | 3.0E+06 | 69 | 304 |
| ERZ12295330 | 1.2E+08 | 1.3E+09 | 1.8E+06 | 3.7E+05 | 796 | 7.8 | 2.4E+06 | 16 | 227 |
| ERZ12295321 | 1.4E+08 | 1.4E+09 | 1.7E+06 | 2.5E+05 | 1,195 | 7.6 | 2.5E+06 | 6 | 166 |
| ERZ12298652 | 1.1E+08 | 1.2E+09 | 1.2E+06 | 1.2E+05 | 1,512 | 9.9 | 1.9E+06 | 54 | 206 |
| ERZ12298644 | 5.1E+08 | 2.9E+09 | 2.8E+06 | 1.5E+05 | 2,554 | 23.6 | 3.7E+06 | 152 | 406 |
| ERZ12294693 | 4.2E+08 | 2.1E+09 | 2.2E+06 | 1.0E+05 | 2,547 | 27.0 | 2.7E+06 | 154 | 387 |
| ERZ12293768 | 3.6E+08 | 1.3E+09 | 1.1E+06 | 3.6E+04 | 3,842 | 10.8 | 2.0E+06 | 38 | 190 |
| ERZ12293633 | 3.6E+08 | 2.4E+09 | 2.8E+06 | 1.7E+05 | 2,009 | 18.8 | 3.1E+06 | 119 | 392 |
| ERZ12298642 | 3.5E+08 | 2.5E+09 | 3.3E+06 | 3.6E+05 | 1,424 | 16.4 | 3.4E+06 | 127 | 475 |
| ERZ12293692 | 4.5E+08 | 2.6E+09 | 2.5E+06 | 1.2E+05 | 2,899 | 23.2 | 3.2E+06 | 129 | 394 |
| ERZ12293630 | 1.3E+08 | 1.3E+09 | 8.2E+05 | 4.4E+04 | 5,424 | 10.9 | 1.9E+06 | 76 | 217 |
| ERZ12298640 | 1.3E+08 | 1.4E+09 | 1.6E+06 | 2.2E+05 | 1,301 | 7.6 | 2.5E+06 | 28 | 274 |
| ERZ12293048 | 1.2E+08 | 1.3E+09 | 1.8E+06 | 3.2E+05 | 868 | 7.7 | 2.5E+06 | 30 | 235 |

ACKNOWLEDGMENTS

Oak Ridge National Laboratory is managed by UT-Battelle, LLC, for the U.S. DOE under contract DE-AC05-00OR22725. Sample collection, processing, and manuscript writing were supported by the U.S. DOE BER Early Career Research Program. The work (<https://www.osti.gov/award-doi-service/biblio/10.46936/10.25585/60001200>) conducted by the U.S. DOE JGI (<https://ror.org/04xm1d337>), a DOE Office of Science User Facility, is supported by the Office of Science of the U.S. DOE operated under contract DE-AC02-05CH11231. This work was supported in part by the National Science Foundation (Division of Environmental Biology grant 1754756 to J.E.K. and D.J.W.) and by a U.S. DOE, Office of Science, Office of Biological and Environmental Research, Genomic Science Program Grant to D.J.W. under award DESC0020362. The manuscript has been authored by UT-Battelle, LLC, under contract DE-AC05-00OR22725 with the U.S. DOE.

REFERENCES

1. Yu Z, Loisel J, Brosseau DP, Beilman DW, Hunt SJ. 2010. Global peatland dynamics since the Last Glacial Maximum. *Geophys Res Lett* 37:L13402. <https://doi.org/10.1029/2010GL043584>.
2. Limpens J, Heijmans MMPD, Berendse F. 2006. The nitrogen cycle in boreal peatlands, p 195–230. *In* Wieder RK, Vitt DH (ed), *Boreal peatland ecosystems*. Springer-Verlag, Berlin, Germany.
3. Loisel J, Yu Z, Beilman DW, Camill P, Alm J, Amesbury MJ, Anderson D, Andersson S, Bochicchio C, Barber K, Belyea LR, Bunbury J, Chambers FM, Charman DJ, Vleeschouwer FD, Fialkiewicz-Kozielec B, Finkelstein SA, Galka M, Garneau M, Hammarlund D, Hinchcliffe W, Holmquist J, Hughes P, Jones MC, Klein ES, Kokfelt U, Korhola A, Kuhry P, Lamarre A, Lamentowicz M, Large D, Lavoie M, MacDonald G, Magnan G, Mäkilä M, Mallon G, Mathijssen P, Mauquoy D, McCarroll J, Moore TR, Nichols J, O'Reilly B, Oksanen P, Packalen M, Peteet D, Richard PJH, Robinson S, Ronkainen T, Rundgren M, Sannel ABK, et al. 2014. A database and synthesis of northern peatland soil properties and Holocene carbon and nitrogen accumulation. *Holocene* 24:1028–1042. <https://doi.org/10.1177/0959683614538073>.
4. Vile MA, Wieder RK, Živković T, Scott KD, Vitt DH, Hartssock JA, Iosue CL, Quinn JC, Petix M, Fillingim HM, Popma JMA, Dynarski KA, Jackman TR, Albright CM, Wykoff DD. 2014. N₂-fixation by methanotrophs sustains carbon and nitrogen accumulation in pristine peatlands. *Biogeochemistry* 121:317–328. <https://doi.org/10.1007/s10533-014-0019-6>.
5. Kolton M, Weston DJ, Mayali X, Weber PK, McFarlane KJ, Pett-Ridge J, Somoza MM, Lietard J, Glass JB, Lilleskov EA, Shaw AJ, Tringe S, Hanson PJ, Kostka JE. 2022. Defining the *Sphagnum* core microbiome across the North American continent reveals a central role for diazotrophic methanotrophs in the nitrogen and carbon cycles of boreal peatlands ecosystems. *mBio* 13:e03714-21. <https://doi.org/10.1128/mbio.03714-21>.
6. Norby RJ, Childs J, Hanson PJ, Warren JM. 2019. Rapid loss of an ecosystem engineer: *Sphagnum* decline in an experimentally warmed bog. *Ecol Evol* 9:12571–12585. <https://doi.org/10.1002/ece3.5722>.
7. Jassey VEJ, Signarbieux C. 2019. Effects of climate warming on *Sphagnum* photosynthesis in peatlands depend on peat moisture and species-specific anatomical traits. *Glob Chang Biol* 25:3859–3870. <https://doi.org/10.1111/gcb.14788>.
8. Wiedermann MM, Nordin A, Gunnarsson U, Nilsson MB, Ericson L. 2007. Global change shifts vegetation and plant-parasite interactions in a boreal mire. *Ecology* 88:454–464. <https://doi.org/10.1890/05-1823>.
9. Jassey VE, Chiapusio G, Gilbert D, Buttler A, Toussaint M-L, Binet P. 2011. Experimental climate effect on seasonal variability of polyphenol/phenoxidase interplay along a narrow fen-bog ecological gradient in *Sphagnum fallax*. *Glob Chang Biol* 17:2945–2957. <https://doi.org/10.1111/j.1365-2486.2011.02437.x>.
10. Clum A, Huntemann M, Bushnell B, Foster B, Foster B, Roux S, Hajek PP, Varghese N, Mukherjee S, Reddy TBK, Daum C, Yoshinaga Y, O'Malley R, Seshadri R, Kyrpides NC, Eloe-Fadrosh EA, Chen IA, Copeland A, Ivanova NN. 2021. DOE JGI Metagenome Workflow. *mSystems* 6:e00804-20. <https://doi.org/10.1128/mSystems.00804-20>.
11. Nurk S, Meleshko D, Korobeynikov A, Pevzner PA. 2017. metaSPAdes: a new versatile metagenomic assembler. *Genome Res* 27:824–834. <https://doi.org/10.1101/gr.213959.116>.
12. Kang DD, Froula J, Egan R, Wang Z. 2015. MetaBAT, an efficient tool for accurately reconstructing single genomes from complex microbial communities. *PeerJ* 3:e1165. <https://doi.org/10.7717/peerj.1165>.
13. Bowers RM, Kyrpides NC, Stepanauskas R, Harmon-Smith M, Doud D, Reddy TBK, Schulz F, Jarett J, Rivers AR, Eloe-Fadrosh EA, Tringe SG, Ivanova NN, Copeland A, Clum A, Becraft ED, Malmstrom RR, Birren B, Podar M, Bork P, Weinstock GM, Garrity GM, Dodsworth JA, Yooseph S, Sutton G, Glöckner FO, Gilbert JA, Nelson WC, Hallam SJ, Jungbluth SP, Etema TJG, Tighe S, Konstantinidis KT, Liu W-T, Baker BJ, Rattei T, Eisen JA, Hedlund B, McMahon KD, Fierer N, Knight R, Finn R, Cochrane G, Karsch-Mizrachi I, Tyson GW, Rinke C, Genome Standards Consortium, Lapidus A, Meyer F, Yilmaz P, Parks DH, Eren AM, Schriml L, Banfield JF, Hugenholtz P, Woyke T. 2017. Minimum information about a single amplified genome (MISAG) and a metagenome-assembled genome (MIMAG) of bacteria and archaea. *Nat Biotechnol* 35:725–731. <https://doi.org/10.1038/nbt.3893>.
14. Mukherjee S, Stamatis D, Bertsch J, Ovchinnikova G, Sundaramurthi JC, Lee J, Kandimalla M, Chen IA, Kyrpides NC, Reddy TBK. 2021. Genomes OnLine Database (GOLD) v.8: overview and updates. *Nucleic Acids Res* 49:D723–D733. <https://doi.org/10.1093/nar/gkaa983>.
15. Chen IA, Chu K, Palaniappan K, Ratner A, Huang J, Huntemann M, Hajek P, Ritter S, Varghese N, Seshadri R, Roux S, Woyke T, Eloe-Fadrosh EA, Ivanova NN, Kyrpides NC. 2021. The IMG/M data management and analysis system v.6.0: new tools and advanced capabilities. *Nucleic Acids Res* 49:D751–D763. <https://doi.org/10.1093/nar/gkaa939>.