



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

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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.

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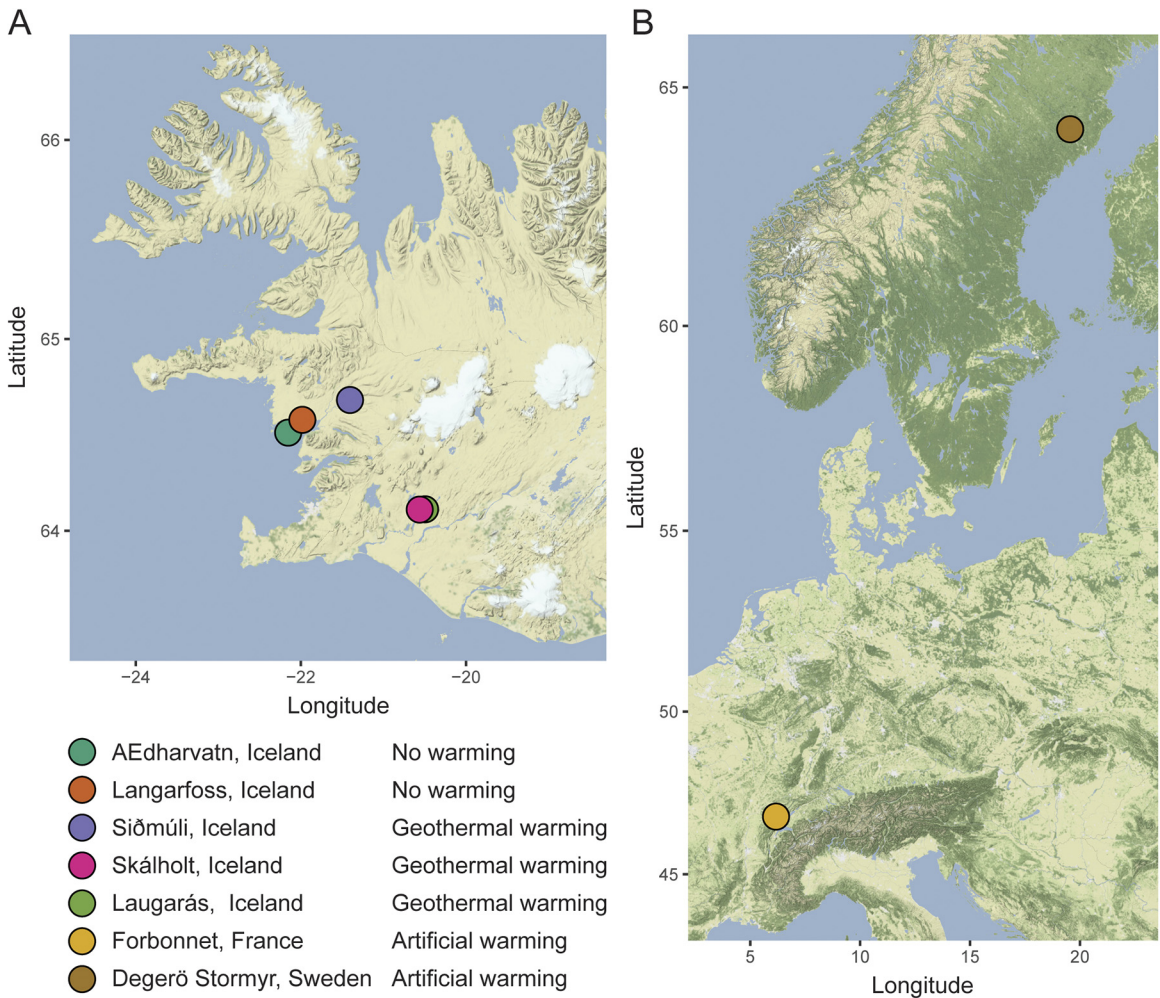


FIG 1 Collection sites for *Sphagnum* metagenome samples. (A) Plants at Icelandic sites were collected from only ambient or both ambient and geothermally warmed conditions. (B) Plants in France and Sweden were collected from both ambient and artificially warmed conditions.

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 BBTools 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 $-\text{superspecific}$ 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://doi.org/10.26434/chemrxiv-2022-gs015)) (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://doi.org/10.6019/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. girgensohnii</i>	12_GIR_ICE	Iceland	Skálholt	Geothermal	20.0	3300047171	ERS12393033	ERR9963771
<i>S. lindbergii</i>	16OTC_LI_DE	Sweden	Degerö Stormyr	Artificial	18.1	3300047164	ERS12393034	ERR9963772
<i>S. lindbergii</i>	40TC_LI_DE	Sweden	Degerö Stormyr	Artificial	18.1	3300047173	ERS12393035	ERR9963773
<i>S. lindbergii</i>	11C_LI_DE	Sweden	Degerö Stormyr	None	14.8	3300047473	ERS12393036	ERR9963774
<i>S. lindbergii</i>	19C_LI_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	28.0	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
ERZ12298657	1.1E+08	1.4E+09	1.2E+06	1.4E+05	2,092	9.1	2.1E+06	31	140
ERZ12298658	1.3E+08	1.5E+09	1.6E+06	1.7E+05	1,266	9.8	2.3E+06	56	235
ERZ12298659	1.1E+08	1.3E+09	1.4E+06	2.5E+05	1,291	9.6	2.0E+06	22	105
ERZ12298660	1.1E+08	1.2E+09	1.6E+06	2.0E+05	1,112	8.5	2.3E+06	6	150
ERZ12298661	1.0E+08	1.3E+09	1.7E+06	2.7E+05	1,053	8.0	2.4E+06	19	195
ERZ12298662	1.2E+08	1.4E+09	1.8E+06	3.1E+05	968	8.2	2.6E+06	16	207
ERZ12298663	1.4E+08	1.5E+09	2.1E+06	3.9E+05	853	7.3	2.9E+06	14	238
ERZ12298664	1.3E+08	1.2E+09	1.9E+06	4.2E+05	633	7.0	2.4E+06	12	279
ERZ12298665	1.4E+08	1.5E+09	2.3E+06	4.6E+05	728	7.8	2.9E+06	17	257
ERZ12298666	1.3E+08	1.5E+09	2.0E+06	3.3E+05	919	8.2	2.7E+06	15	237
ERZ12298667	1.6E+08	1.6E+09	2.3E+06	4.5E+05	767	7.9	3.1E+06	15	324
ERZ12298668	1.3E+08	1.4E+09	1.9E+06	2.9E+05	959	9.0	2.5E+06	21	324
ERZ12298669	9.4E+07	1.0E+09	1.5E+06	3.2E+05	776	7.6	1.9E+06	7	170
ERZ12298670	1.3E+08	1.3E+09	1.6E+06	2.7E+05	1,054	9.5	2.3E+06	16	208
ERZ12298671	9.6E+07	9.0E+08	1.0E+06	1.5E+05	1,310	8.3	1.5E+06	9	104
ERZ12298672	1.3E+08	1.4E+09	2.1E+06	4.1E+05	809	7.7	2.8E+06	9	233
ERZ12298673	1.3E+08	1.3E+09	1.7E+06	2.3E+05	1,075	10.8	2.4E+06	5	169
ERZ12298674	1.3E+08	1.3E+09	1.9E+06	3.4E+05	844	9.1	2.5E+06	21	255
ERZ12298675	1.2E+08	1.4E+09	1.8E+06	2.8E+05	1,004	8.7	2.6E+06	13	204
ERZ12298676	1.4E+08	1.4E+09	1.5E+06	1.4E+05	1,350	10.7	2.3E+06	7	171
ERZ12298677	1.3E+08	1.3E+09	2.0E+06	4.0E+05	819	8.1	2.4E+06	7	174
ERZ12298678	1.1E+08	2.0E+09	2.5E+06	3.9E+05	1,032	9.4	3.6E+06	18	341
ERZ12298679	1.1E+08	1.1E+09	1.3E+06	1.8E+05	1,146	9.0	1.9E+06	4	124
ERZ12298680	1.1E+08	9.9E+08	6.4E+05	3.1E+04	5,777	14.1	1.4E+06	28	111
ERZ12298681	1.2E+08	1.3E+09	1.3E+06	1.2E+05	1,894	9.2	2.2E+06	15	183
ERZ12298682	1.4E+08	1.4E+09	1.6E+06	2.2E+05	1,153	9.0	2.5E+06	26	265
ERZ12298683	9.4E+07	1.2E+09	2.0E+06	4.5E+05	615	7.5	2.5E+06	12	212
ERZ12298684	1.1E+08	1.1E+09	8.1E+05	3.7E+04	4,496	10.3	1.7E+06	19	146
ERZ12298685	1.5E+08	1.6E+09	1.3E+06	8.6E+04	2,974	11.4	2.4E+06	67	206
ERZ12298686	5.4E+08	2.6E+09	1.7E+06	4.4E+04	7,822	29.3	3.1E+06	158	335
ERZ12298687	3.6E+08	2.4E+09	2.3E+06	1.4E+05	2,584	19.8	3.0E+06	96	290
ERZ12298688	3.4E+08	2.3E+09	2.7E+06	1.8E+05	1,940	19.6	3.0E+06	77	301
ERZ12298689	1.2E+08	1.5E+09	1.5E+06	1.9E+05	1,636	8.3	2.5E+06	21	222
ERZ12298690	4.6E+08	2.3E+09	3.4E+06	2.9E+05	1,361	24.7	3.2E+06	61	319
ERZ12298691	3.7E+08	2.3E+09	2.4E+06	1.4E+05	2,432	20.9	2.9E+06	86	283
ERZ12298692	3.7E+08	2.3E+09	2.6E+06	1.8E+05	1,957	19.9	3.0E+06	69	304
ERZ12298693	1.2E+08	1.3E+09	1.8E+06	3.7E+05	796	7.8	2.4E+06	16	227
ERZ12298694	1.4E+08	1.4E+09	1.7E+06	2.5E+05	1,195	7.6	2.5E+06	6	166
ERZ12298695	1.1E+08	1.2E+09	1.2E+06	1.2E+05	1,512	9.9	1.9E+06	54	206
ERZ12298696	5.1E+08	2.9E+09	2.8E+06	1.5E+05	2,554	23.6	3.7E+06	152	406
ERZ12298697	4.2E+08	2.1E+09	2.2E+06	1.0E+05	2,547	27.0	2.7E+06	154	387
ERZ12298698	3.6E+08	1.3E+09	1.1E+06	3.6E+04	3,842	10.8	2.0E+06	38	190
ERZ12298699	3.6E+08	2.4E+09	2.8E+06	1.7E+05	2,009	18.8	3.1E+06	119	392
ERZ12298700	3.5E+08	2.5E+09	3.3E+06	3.6E+05	1,424	16.4	3.4E+06	127	475
ERZ12298701	4.5E+08	2.6E+09	2.5E+06	2.3E+05	2,899	23.2	3.2E+06	129	394
ERZ12298702	1.3E+08	1.3E+09	8.2E+05	4.4E+04	5,424	10.9	1.9E+06	76	217
ERZ12298703	1.3E+08	1.4E+09	1.6E+06	2.2E+05	1,301	7.6	2.5E+06	28	274
ERZ12298704	1.2E+08	1.3E+09	1.8E+06	3.2E+05	868	7.7	2.5E+06	30	235

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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, Hartsock JA, Iosue CL, Quinn JC, Petix M, Fillingim HM, Popma JMA, Dynarski KA, Jackman TR, Albright CM, Wyckoff 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/pheno-oxidase 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, Elo-Fadrosch 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, Elo-Fadrosch 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, Ettema 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, Elo-Fadrosch 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>.