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Vegetation and microbes interact to preserve carbon in many wooded peatlands

Hongjun Wang[1,6✉], Jianqing Tian[2,1,6], Huai Chen[3], Mengchi Ho[1], Rytas Vilgalys[4], Zhao-Jun Bu[5], Xingzhong Liu[2] & Curtis J. Richardson[1✉]

Peatlands have persisted as massive carbon sinks over millennia, even during past periods of climate change. The commonly accepted theory of abiotic controls (mainly anoxia and low temperature) over carbon decomposition cannot fully explain how vast low-latitude shrub/tree dominated (wooded) peatlands consistently accrete peat under warm and seasonally unsaturated conditions. Here we show, by comparing the composition and ecological traits of microbes between *Sphagnum*- and shrub-dominated peatlands, that slow-growing microbes decisively dominate the studied shrub-dominated peatlands, concomitant with plant-induced increases in highly recalcitrant carbon and phenolics. The slow-growing microbes metabolize organic matter thirty times slower than the fast-growing microbes that dominate our *Sphagnum*-dominated site. We suggest that the high-phenolic shrub/tree induced shifts in microbial composition may compensate for positive effects of temperature and/or drought on metabolism over time in peatlands. This biotic self-sustaining process that modulates abiotic controls on carbon cycling may improve projections of long-term, climate-carbon feedbacks in peatlands.

[1] Duke University Wetland Center, Nicholas School of the Environment, Duke University, Durham, NC 27708, USA. [2] State Key Laboratory of Mycology, Institute of Microbiology, Chinese Academy of Sciences, Beijing 100101, China. [3] Key Laboratory of Mountain Ecological Restoration and Bioresource Utilization, and Sichuan Provincial Key Laboratory of Ecosystem Restoration and Biodiversity Conservation, Chengdu Institute of Biology, Chinese Academy of Sciences, Chengdu 610041, China. [4] Department of Biology, Duke University, Durham, NC 27708, USA. [5] State Environmental Protection Key Laboratory of Wetland Ecology and Vegetation Restoration, Institute for Peat and Mire Research, Northeast Normal University, Changchun 130024, China. [6] These authors contributed equally: Hongjun Wang, Jianqing Tian. ✉email: hjwang78@gmail.com; curtr@duke.edu

Peatlands cover only 3% of land surface but currently maintain 600–700 Gt of carbon (1 Gt = 10^{15} g), which exceeds global vegetation carbon stores and is close to the pool of atmospheric CO_2[1–4]. Hence, both the fate of the massive carbon stores in peat and the way peatlands, particularly their carbon-sequestration/release processes, respond to climate change are highly important to future climates. Generally, rates of carbon decomposition via soil microbial respiration increase exponentially with rising temperature in the short term[5]. Many experiments show that climate warming and drought may not only increase peat loss by accelerating decomposition[6] but also could cause substantial losses of the keystone mosses like *Sphagnum* in the vast boreal peatlands[7–9], followed by shrub/tree expansion and its uncertain effects[10–13]. Such cascading events could provoke a substantial positive feedback to global warming[6,12,14]. However, long-term warming experiments in grasslands[15,16] and studies spanning a wide range of mean annual temperature (MAT) globally[17,18] show declining microbial metabolism over time under experimental warming or in warmer regions. To date, most experimental studies in peatlands have lasted only for months to decades, and such time scales are deemed too short to detect long-term (>100 years) effects of climate change on millennial peatlands that may have complex evolutions/successions during past climatic fluctuations[19]. High-resolution stratigraphic analyses on peat profiles across boreal areas have documented that vegetation composition and net primary productivity played key roles in carbon accumulation during the last millennium[19,20]. Moreover, a recent study shows that plant taxonomic and functional turnover are decoupled across European peat bogs, which make these ecosystems much more resilient to climate change[21]. We compiled soil respiration data from >200 peatland sites across latitudes between 2°S and 75°N (Supplementary Data 1) to further test whether the dependence of decomposition on temperature applies to a wide range of MAT in peatlands. As both heterotrophic and autotrophic respirations were included here and plants with higher biomass in the tropical regions beget higher autotrophic respiration[22], we expected to see an apparent exponential rise in soil respiration along with increasing MAT. However, we found the relationship did not exist (Fig. 1). The paleontological evidence[19,20], apparent decoupling of plant taxonomic and functional turnover[21], and our large-scale soil respiration analysis (Fig. 1) together challenge the current abiotic-factor-dependent peat decay models (mainly temperature and water level) that is embedded into the Earth System Models to project climate-carbon feedback[14,23]. This discrepancy, we assume, could mainly result from the latent role of changing plant communities and their associated ecological (mainly microbial) and biogeochemical processes—a commonly occurring state shift in peatland communities induced by persistent climate change[19]. Changes in dominant plant communities among mosses, sedges, shrubs, and trees may bring forth substantial top-down and bottom-up regulations[24] on the peatland ecosystem through alteration of plant–microbe traits, specifically plant/soil chemistry[25] and microbial composition/function[10,26–28] while maintaining similar functions[29,30]. Although temperature as an abiotic factor dominantly controls microbial metabolism of soil carbon in monocultures or a constant environment, some evolutional acclimations and interactions in plant/microbial physiology and community composition, as biotic factors in response to long-term climate change in peatlands[16,26–28,31–33] are still unclear. We therefore hypothesized that the unknown biotic controls and interactions (vegetation and microbes) developed over time might be one of the major uncertainties and challenges in projecting the long-term carbon-climate feedbacks in peatlands in the Earth System Models[34], thus recognition of which could be central to the development of a meaningful framework for unraveling the future of peatlands[26,28].

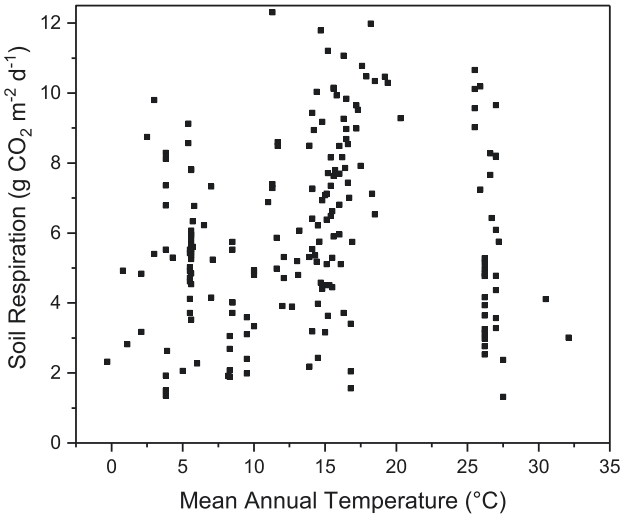

Fig. 1 Mean soil respiration from boreal to tropical peatlands. Data were compiled from 36 published studies that contain annual mean soil respirations observed in >200 sites globally (Supplementary Data 1).

Here, we set up a series of field and lab experiments in a logically progressive way and suggest that climate-change-induced shifts in dominant microbes to vegetation change, as biotic control, may sustain soil organic matter over time in peatlands facing long-term climate change. We first compared a boreal *Sphagnum*-dominated peatland with a shrub-dominated subtropical peatland in terms of the composition and functional traits of fungi—the predominant peat decomposers—and their relationships with soil physicochemical parameters. To further verify whether such functional traits exist in other wooded (shrub/tree-dominated) peatlands, we reanalyzed and compared fungal data from a subtropical peatland in China and a coastal wooded peatland in Canada. We showed that slow-growing fungi dominate many wooded peatlands globally. Finally, we verified the proposed consequence of the microbial shifts on carbon loss in peatlands through a reciprocal inoculation experiment.

Results and discussion

Slow-growing fungi dominate shrub-dominated peatlands. An ombrotrophic boreal *Sphagnum*-dominated peatland and a subtropical shrub-dominated peatland in the USA were first selected to study shifts of ecological processes in peatlands over a long term. The *Sphagnum*-dominated site is located in the Marcell Experimental Forest, MN, USA, and the shrub-dominated site is found in Pocosin Lakes National Wildlife Refuge (Pocosins), NC, USA (Supplementary Tables 1 and 2). The *Sphagnum*-dominated site is dominated by *Sphagnum* mosses (coverage >90%) with black spruce (*Picea mariana*) and scattered shrubs, while the shrub-dominated site has responded to climate change over the past 12,000 years through a transition of plant communities from boreal *Sphagnum*/spruce during late-glacial to the modern ericaceous shrubs (coverage >90%) found today[13,35]. The shrub species in Pocosins are similar in physiognomy to the expanding ericaceous shrubs found in many drained *Sphagnum*-dominated peatlands in boreal areas[10,11,36]. Peat is dominantly formed by *Sphagnum* moss in the *Sphagnum*-dominated sites, and shrubs mainly build peat in the shrub-dominated sites.

To determine the underlying microbial communities and their ecological traits, we collected triplicate soil cores from the hollows and hummocks in the boreal *Sphagnum*-dominated peatland and from three sites with different plants and water levels in the

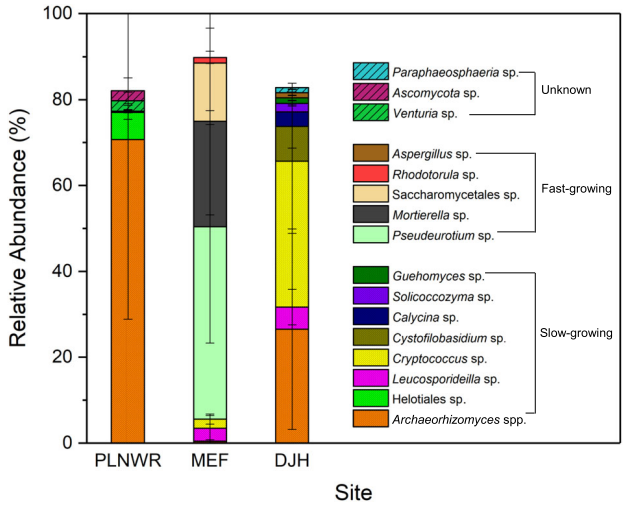

Fig. 2 Distribution of dominant fungi. Relative abundance (mean ± S.E.) of the dominant fungi (OTU relative abundance >1%) at the research sites in the shrub-dominated subtropical peatland in Pocosin Lakes National Wildlife Refuge (PLNWR), the *Sphagnum*-dominated boreal peatland in Marcell Experimental Forest (MEF), and the subtropical peatland in Dajiuhu (DJH). Ecological traits of slow-growing and fast-growing fungi were listed in Supplementary Table 3.

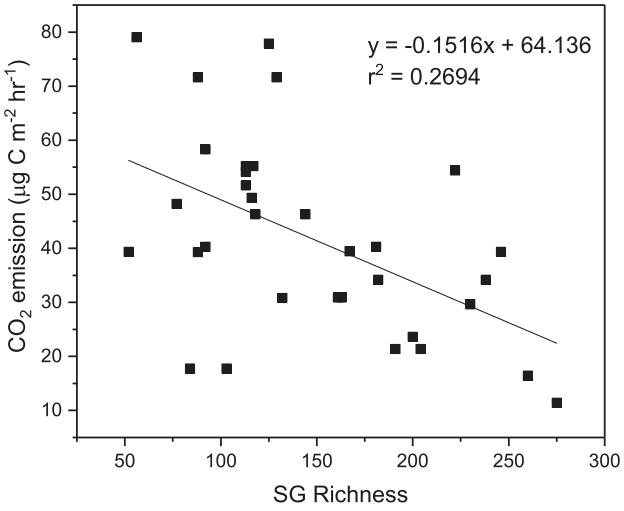

Fig. 3 The relationship between richness of slow-growing fungi and CO_2 emission in wooded peatlands in the Pacific coastal temperate rainforest in Canada. The richness of fungi was recalculated from raw amplicon reads in the European Nucleotide Arch Archive ITS(ERS1798771-ERS1799064)[41], CO_2 emission data were collected from the Hakai Institute data repository at https://doi.org/10.21966/1.715630[41]. SG = slow-growing fungi.

subtropical shrub-dominated peatland (Supplementary Table 1), and measured the composition and abundance of fungi, the relative contributions of fungi and bacteria to peat decomposition, and the associated physicochemical peat parameters. Compared to the *Sphagnum*-formed peat in the boreal site, in the shrub-formed peat in the subtropical site, the dissolved phenolics were 6–8 times higher, while soil pH, concentration of inorganic nitrogen and soil moisture were lower (Supplementary Table 1), which indicate the shrub-dominated peatland was more oligotrophic. Consistent with many previous studies[37,38], fungi were the predominant peat decomposers in the unsaturated upper layers with contributions of 93.4% and 95.2% in the *Sphagnum*- and shrub-dominated sites, respectively (Supplementary Fig. 1, also see Supplementary Note 1). The *Sphagnum*- and shrub-dominated peatlands distinctively differed in their fungal community composition (Fig. 2). Fungal communities from the *Sphagnum*-dominated sites were dominated by *Pseudeurotium*, Saccharomycetales, and *Mortierella*, whereas the shrub-dominated sites were dominated by *Archaeorhizomyces* and Helotiales characterized by slower growing rates and also forming symbiotic associations with plant roots (Fig. 2 and Supplementary Data 2). As microbial growth rates significantly affect carbon turnover in soil[29,30], we classified the dominant fungi as either fast- or slow-growing groups based on known growth traits of culturable species from each taxonomic group (Supplementary Table 3). Given current limitations on detecting growth rates of unculturable fungi, this gives us a reasonable first approximation although some inevitable biases exist in this classification. Notably, nearly 85% of dominant fungi (relative abundance of each operational taxonomic unit (OTU) > 1%) were fast-growing at the *Sphagnum*-dominated site, but at the shrub-dominated site a mere 2% were categorized as fast-growing and about 75% as slow-growing based on their ecological traits (Fig. 2 and Supplementary Table 3). Consistent with the majority of fungi found in many boreal peatlands[37], the dominant fungi at the *Sphagnum*-dominated site are members of pioneer saprobe communities that use simple carbon compounds and possibly possess *r*-selected strategy with fast growth rates[29,30,37]. Unexpectedly, 11–97% of total fungal sequences at the shrub-dominated site were assigned to *Archaeorhizomyces*, but only 0.4% on average at the *Sphagnum*-dominated site. *Archaeorhizomyces*, which represents one of the ubiquitous lineages of soil fungi, is characterized by markedly slow growth[39]. Another dominant fungal group (~5%) in the shrub-dominated site is the Helotiales, which includes certain fungi that form ericoid mycorrhizal fungi with resistant melanized cell walls (so-called dark-septate endophytes) which are also characterized by slow growth rates[40].

The fungal composition and their growth-rate traits in the *Sphagnum*-dominated site are in line with the observations found in many boreal peatlands[37], while such studies in wooded peatlands, particularly in low-latitude areas, are still rare. Hence, we further examined the fungal communities in a subtropical peatland with dense shrubs (coverage: 41%) and *Sphagnum* layer underneath in Dajiuhu peatlands in Shennongjia, China (31°29′ N, 109°59′E) and reanalyzed the fungal composition in a bog forest and a *Sphagnum*-shrub mixed peat bog (shrub coverage: 52%) in the Pacific coastal temperate rainforest in Canada[41] (Supplementary Tables 1 and 2). The majority of fungal taxa in both shrub/tree-dominated sites were also found to be slow-growing, e.g., *Archaeorhizomyces* spp. (26.5%) and *Cryptococcus* sp. (34.0%) in Dajiuhu Peatlands (Fig. 2, Supplementary Fig. 2, and Supplementary Table 3). Importantly there was a significant negative relationship between soil respiration and richness of slow-growing fungi in the Pacific coastal rainforest (Fig. 3), which indicates that the slow-growing fungi likely regulate the carbon turnover rates in these peatlands.

Further supporting the influence of shrubs on fostering slow-growing fungi, a recent study showed a boreal peatland in MN, USA, where ericaceous shrubs dominated the wooded cover, was also dominated by slow-growing fungi (Helotiales and *Archaeorhizomyces*, >80%)[42]. By comparison on an upland plateau peatland in Czech Republic, the relative abundances of Archaeorhyzomycetes were 1.4 ± 3.3%, 0.5 ± 0.6%, and 42.7 ± 28.8% in mosses-, graminoids-, and ericoid shrub-dominated sites, respectively[43]. Collectively, these studies indicate that slow-growing fungi are dominant in many wooded peatlands in North America (this study and ref. [42]), Asia (this study), and Europe[43].

Phenolics primarily control microbial communities. Mantel test and redundancy analysis (RDA) were performed to determine what soil physicochemical variables (including dissolved

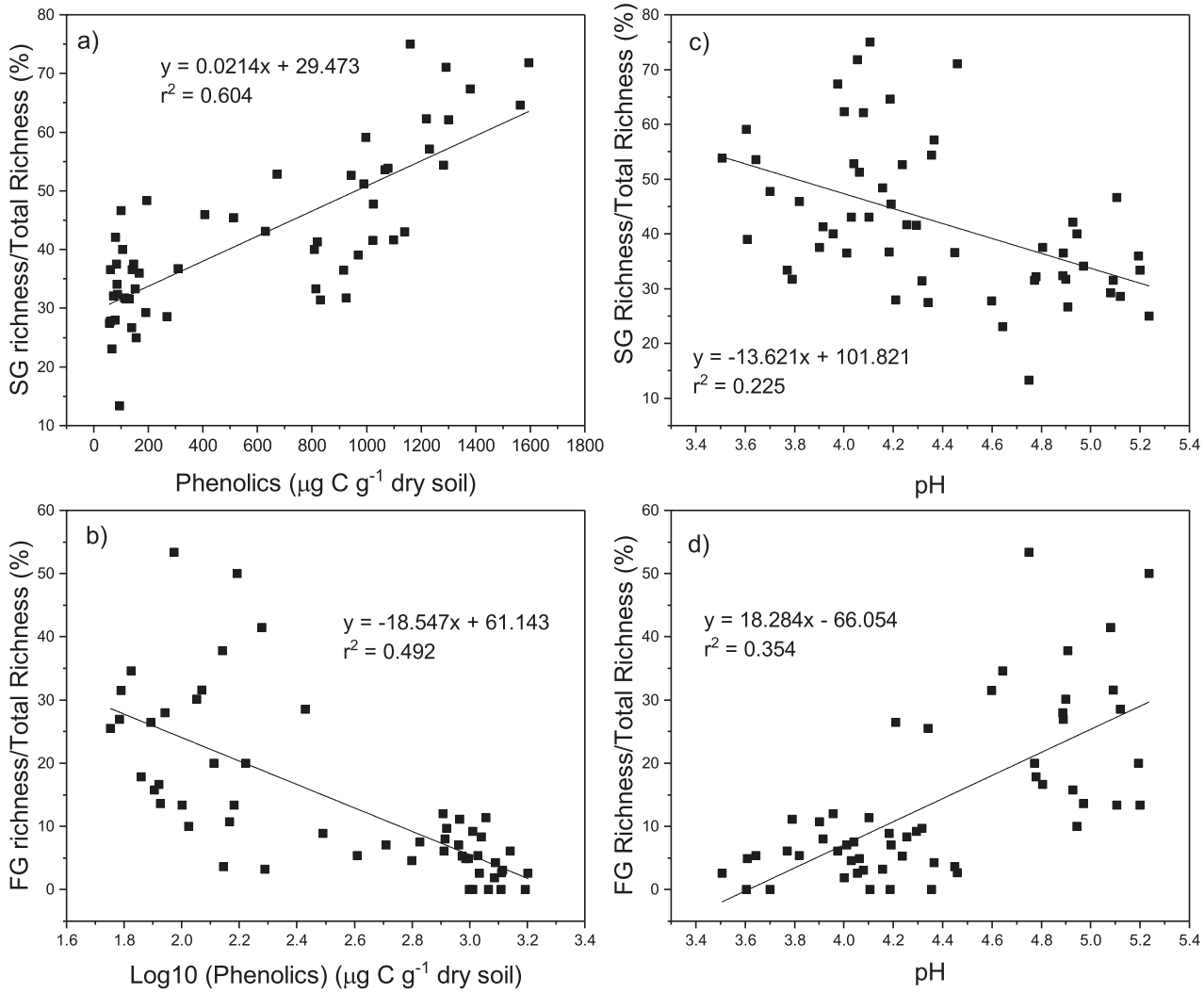

Fig. 4 Effects of phenolics and pH on ratios of slow- and fast-growing fungal richness to total fungal richness. a, **b** Phenolics effects and **c**, **d** pH effects. Species richness is the number of total OTUs observed in each sample. SG = slow-growing fungi, FG = fast-growing fungi.

organic carbon (DOC), dissolved phenolics, soil pH, soil moisture, NO_3^-–N, and NH_4^+–N) might control the fungal composition in the sites in NC and MN, USA. Both analyses showed that soluble phenolics and pH were the most important drivers (Supplementary Fig. 3 and Supplementary Table 4). Analyses of stepwise regression and correlation further show that the relative richness of slow-growing and fast-growing fungi were primarily controlled by dissolved phenolics (Fig. 4a, b) and pH (Fig. 4c, d), respectively. Because stepwise regression showed phenolics was the dominant factor controlling soil pH ($r^2 = 0.455$, $P < 0.0001$) in these sites, we speculated that phenolic content in soil primarily driven by plant communities[13] likely acted as the overarching regulator, not only directly limiting microbial activities[13,44] but also allowing slow-growing fungi to thrive while impeding fast-growing fungi. The dissolved phenolics in these peatlands might be mainly phenolic/humic acids that increase soil acidity and reduce nitrogen availability by complexing with proteins[45], thus further exacerbating the extreme oligotrophic conditions that benefit mainly the slow-growing fungi[29] while simultaneously inhibiting bacterial growth and shifting bacterial communities as well. This is further demonstrated by the relatively small contribution of bacteria to the peat decomposition at both sites (Supplementary Fig. 1). Recent measurements in bacteria composition[46,47] at the same sites in North Carolina and Minnesota showed that oligotrophic slow-growing Acidobacteria[30] dominated both peatlands. The relative abundance of Acidobacteria in the shrub-dominated sites (57%) was substantially higher than that in the *Sphagnum*-dominated sites (36%). Moreover, the fast-growing bacteria—including Betaproteobacteria and Bacteroidetes as copiotrophs[30] —were nearly absent from the shrub-dominated site[46] but contributed about 9% and 4%, respectively, in the *Sphagnum*-dominated site[47].

We postulate that these slow-growing microbes including both fungi and bacteria have adapted to high-phenolic acidic conditions and become the dominant microbes with inherent slow metabolic processes, a major underlying feature of high-phenolic wooded peatlands developed under warm and relatively dry conditions. Although higher microbial biomass carbon (MBC) was present in the shrub-formed peat (3.8 ± 0.2 mg C g^{-1} dry soil) in North Carolina relative to the *Sphagnum*-formed peat (2.6 ± 0.3 mg C g^{-1} dry soil) in Minnesota, the decomposition rate of the shrub-formed peat was much slower at the same temperature and displayed lower temperature sensitivity than the *Sphagnum*-formed peat (Supplementary Fig. 4).

Slow-growing microbes lead to slow peat decay. It is still impossible to measure the relative growth rates of the dominant

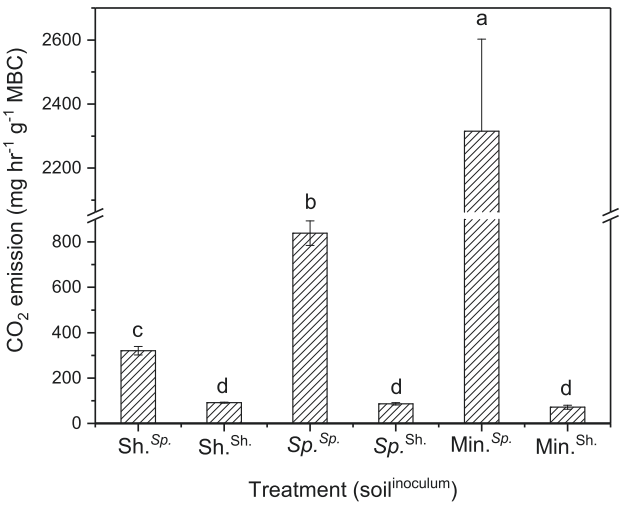

Fig. 5 Standardized CO_2 emission from sterilized soil media that include the boreal *Sphagnum*-formed peat from Minnesota, the subtropical shrub-formed peat from North Carolina and the labile carbon-enriched mineral soil. All media were inoculated by inoculum made from the *Sphagnum*-formed or shrub-formed peat. Standardized CO_2 emission (mean ± S.E.) was calculated based on the amount of MBC added to the soil media. Different letters indicate significant differences among treatments. MBC = microbial biomass carbon. Sh. = shrub-formed peat, *Sp.* = *Sphagnum*-formed peat, Min. = labile carbon-enriched mineral soil, $^{Sh.}$ = inoculum made from the shrub-formed peat, $^{Sp.}$ = inoculum made from the *Sphagnum*-formed peat.

microbes in this study, because so many of the fungi are unculturable. To further test and verify the consequences of these likely fast-growing versus slow-growing microbes including both fungi and bacteria, we compared soil respiration rates per gram MBC[17,31] in the *Sphagnum*- and the shrub-formed peats through a reciprocal inoculation experiment using inocula and peat materials from both sites. We also added each inoculum to labile carbon-enriched mineral soil to test how the microbes decompose labile carbon under a condition without phenolic inhibition. All soil media and incubators were sterilized by an autoclave before inoculation. Consistent with the microbial growth traits found in the literature (Supplementary Table 3), the microbes from the shrub-dominated peatland decomposed both labile glucose and complex peats at much slower rates than the microbes from the *Sphagnum*-dominated peatland (Fig. 5). Although the shrub-formed peat is more highly recalcitrant than the *Sphagnum*-formed peat[25], the fast-growing microbes from the *Sphagnum* inoculum decomposed the soil carbon in the shrub-formed peat 4 times faster than the microbes from the shrub-formed peat did, which indicates the reproductive strategies of decomposers (*r*- or K-selective) significantly impact the decomposition rate. Moreover, the soil respiration rates from *Sphagnum* inoculum were dependent on the source of carbon, with rates at 320, 838, and 2315 mg C h^{-1} g^{-1} MBC in the shrub-formed peat, the *Sphagnum*-formed peat, and the labile carbon-enriched mineral soil, respectively. Hence, the dominant decomposers in the *Sphagnum*-dominated peatlands are likely fast-growing copiotrophs that generally adapt to using available resource rapidly[29]. In contrast, soil media—including labile carbon—did not significantly impact the microbial activities from the shrub-formed peat inoculum (71–92 mg C h^{-1} g^{-1} MBC) in the short term. These results further support our hypothesis that microbial metabolism in high-phenolic shrub-dominated peatlands is slower and that growth traits of a specific microbial community might be inherent[29].

We postulate that the slow-growing microbes which dominate the high-phenolic shrub-dominated site behave like K-selected taxa outcompeting fast-growing *r*-selected taxa under steadily warmer and dryer conditions. The established slow-growing fungi, as well as bacteria[46,47] lead to a lower carbon turnover in soil[13,30]. The dominance of the slow-growing microbes may explain why plant necromass does not completely decompose, but continues to accumulate as peat in low-latitude wooded peatlands, despite constant warming and frequent drought over millennia[13]. This also explains the observed slow decomposition under drought in the subtropical shrub-dominated peatlands[13], which was likely caused by the anti-microbe role of increased phenolics[13,48] and also the magnified slow-growing decomposers induced by higher phenolics. Collectively, our field and lab experiments demonstrate that a phenolics-linked plant–microbe interaction may act as a natural curb on carbon loss in low-latitude wooded peatlands and would likely function in the same way in forthcoming boreal peatlands with climate-induced shrub expansion. This biotic self-sustaining process driven by consistent increases in temperature and drought over time appears to override direct abiotic controls in regulating long-term carbon-climate feedbacks in peatlands, which is critical for understanding and modeling how ongoing climate change affects peatlands across the globe.

Finally, our findings suggest that enduring peatlands that are highly resistant to increased temperature and natural drought may gradually shift to a new equilibrium state[26] with different microbes and plants that have adapted to the changed climate over time through their self-sustaining plant–microbe interactions (likely connected by plant-induced phenolics). As biotic regulators, the co-shifting microbe and plant communities that were initially triggered by climate change appear to exert very important controls on ecosystem C cycling and soil C sequestration over time, thus ensuring for continuing peat accretion in a new steady state. Though beyond the scope of this study, our findings may have more immediate applications in carbon-climate feedback models and geoengineering strategies[48,49]. Embedding dynamic biotic factors into current abiotic-factor-dependent decay models could greatly advance the accuracy of the Earth System Models in projecting the fate of boreal peatlands with shifting plant/microbe communities[10,11,42] under climate change. This mechanism added to the framework would allow models to predict how the biotic processes of a peatland could modulate abiotic controls on the carbon cycle over time. Moreover, this mechanism further indicates that peatland geoengineering[49] adding high-phenolics natural materials like woody litter[48] could be an enhanced nature-based solution, similar to a natural state shift, preserving degraded peatlands not only in the short term through increasing phenolic contents[48] but also in the long term by encouraging phenolics-magnified, slow-growing microbes.

Materials and methods

Study sites and soil sampling. Our major study sites were located in a shrub-dominated bog[13] in the Pocosin Lakes National Wildlife Refuge, NC, USA and a *Sphagnum*-dominated bog[47] in the Marcell Experimental Forest, MN, USA (Supplementary Tables 1 and 2). Three sites (>1 km apart) around Pungo Lake including Pungo West, Pungo Southwest, and Pungo East were selected at the shrub bogs in North Carolina. *Ilex glabra* and *Lyonia lucida* cover about 85% and 10%, respectively at Pungo West. *Ilex glabra* and *Lyonia lucida* also dominate Pungo Southwest but distribute evenly, also there are many *Woodwardia virginica* ferns during the growing season. The water level at Pungo Southwest is always higher than at Pungo West. Both Pungo West and Pungo Southwest have prescribed light fire every 4–5 years. There has been no fire disturbance at the Pungo East site over last 30 years, where more dominant plant species exist, including *Lyonia lucida, Ilex glabra, Zenobia pulverulenta, Gaylussacia frondosa, Vaccinium formosum*.

One hollow and one hummock were selected at the *Sphagnum*-dominated bogs in Minnesota. A lot of mature trees including *Picea mariana, Pinus resinosa, Larix laricina* with different bryophytes and shrubs grow at both the hollows and the

hummocks. *S. fallax* dominates the bryophyte layer at the hollows, and *S. angustifolium and S. magellanicum* dominate at the hummocks. The understory has a layer of ericaceous shrubs including *Rhododendron groenlandicum, Chamaedaphne calyculata, Vaccinium oxycoccos* at the hummocks, however, only scattered shrubs present in the hollows. Other site information is described in Supplementary Tables 1 and 2. We took three soil cores at each sites (with a distance >4 m from each other), and each soil core was sliced to four subsamples (0–5, 5–10, 10–15, and 15–20 cm). Big roots were removed in lab. The hair roots of all plants were included in the soil samples.

Additionally, we took three soil cores at depth 0–10 cm in the shrub-dominated area in Dajiuhu peatlands in Shennongjia, China (31°29′N, 109°59′E) in May 2017. The dominant shrub at Dajiuhu is *Betula albosinensis* and *Spiraea salicifolia* with a dense *Sphagnum* layer (detailed plant information is described in Supplementary Tables 1 and 2). The samples were transported to the laboratory in iceboxes. Half of the samples were frozen at −80 °C for DNA isolation; the other half was stored at 4 °C for chemical analysis.

Soil chemistry analysis. We used the deionized water extraction of fresh soil for DOC and soluble phenolics measurements. DOC was measured as the difference between total C and inorganic C with a total C analyzer (Shimadzu 5000 A, Kyoto, Japan). Soluble phenolics were measured by following the Folin-Ciocalteu procedure[50]. Inorganic nitrogen (NH_4^+–N and NO_3^-–N + NO_2^-–N) extract with 2 M KCl was determined colorimetrically on a flow-injection analyzer (Lachat QuikChem 8000, Milwaukee, WI, USA). Total carbon and nitrogen in soil were analyzed with combustion CN soil analyzer equipped with a TCD detector (ThermoQuest Flash EA1112, Milan, Italy). A 1:10 soil/water solution was used to measure soil pH.

DNA extraction, PCR, and sequencing. Genomic DNA was extracted from 0.25 g (fresh weight) of each homogenized soil sample using the PowerSoil DNA isolation kit (Mo Bio Laboratories, Carlsbad, CA, USA). DNA of each replicate was extracted 3 times and homogenized together as one DNA template. For Pocosin and Minnesota samples, a set of fungus-specific primers, ITS1F (3′-CTTGGTCATTTA-GAGGAAGTAA-5′) and ITS4 (3′-TCCTCCGCTTATTGATATGC-5′), were used to amplify the internal transcribed spacer (ITS) region using barcoded ITS1F primers. For Dajiuhu samples, ITS1F and ITS2 (3′-GCTGCGTTCTTCATCGAT GC-5′) were used. All PCR reactions were repeated in triplicate, together with the negative controls in which the template DNA was replaced with deionized H_2O. The amplicon concentration of each sample was determined after purification using Qubit® 2.0 Fluorometer (Invitrogen, Grand Island, NY, USA), samples pooled at equimolar concentrations, purified using AMPure Bead cleanup. The amplicons from Pocosin, Minnesota and Dajiuhu samples were submitted to the core facility at Duke University (Durham, NC, USA) and Allwegene Tech Beijing (Beijing, China) for sequencing using Illumina MiSeq (Illumina, San Diego, CA, USA), respectively.

Bioinformatics processing. Sequence data of Pocosins and Minnesota samples were obtained from both ITS1 and ITS2 gene regions. ITS sequences were quality filtered and processed using the standard QIIME pipeline, with each fungal taxon represented by an OTU at the 97% sequence similarity level. Singleton OTUs were omitted[51], and OTUs classified taxonomically using a QIIME-based wrapper of BLAST against the UNITE database[52,53] (see Supplementary Methods for further details). The quality and depth of coverage of both primers' reads were not significantly different, thus libraries from ITS4 reads were used for further analysis of fungal communities. Taxonomic-based alpha diversity was calculated as the total number of phylotypes (richness) and Shannon's diversity index (H′). A total of 150,967 ITS sequences from ITS2 region passed quality control criteria in the Pocosin and Minnesota sites. These sorted into 590 OTUs. Following the same procedure, a total of 115,936 ITS1 sequences from Dajiuhu samples were assigned into 307 OTUs. Following the processing procedure described by Wilson et al.[47], relative abundance of beta-proteobacteria at the controlled site in the boreal *Sphagnum* site was recalculated from Wilson and others' sequence data[34] available from the National Center for Biotechnology Information at SRP071256. Relative abundance of fungi from a bog forest at the Calvert Island in Canada was recalculated from the raw amplicon reads in the European Nucleotide Archive, ITS (ERS1798771-ERS1799064).

Lab incubations

The decomposing capability of microbes in the Sphagnum- *and shrub-dominated peatlands*. We tested the decomposing capability of microbes in the *Sphagnum*- and shrub-dominated peatlands by amending peat inocula from both sites in North Carolina and Minnesota to their peats and labile carbon-enriched mineral soil. Fresh *Sphagnum*- and shrub-formed peat inocula were prepared by mixing 0.5 kg of each type of fresh peat (10–20 cm) with 2 L of deionized water. After 1 h of stirring and 1-day settlement, the suspension liquid inoculum was filtered through a Buchner funnels (without filter, pore size 0.25–0.5 mm). We added 2 g of glucose to 50 g of nutrient-poor mineral soil (initially 0.05% total nitrogen, 0.64% total soil carbon) to produce a mineral soil medium with high labile carbon content. All incubation media (peat and mineral soil) and jars were sterilized by an autoclave before inoculation. About 30-g fresh *Sphagnum*-formed peat (2.5–2.8 g in dry weight) or shrub-formed peat (9.1–9.3 g in dry weight), or 50-g mineral soil with 2-g glucose was placed in Mason jars (triplicate, 8-cm diameter, 12-cm height, vacuum seal lid with a stainless-steel fitting with sampling septum), then 20 ml of its own or other's inoculum was added to the peat media, and 5 ml of inoculum from each site was added to the mineral soil. Finally, all samples were aerobically incubated at a constant temperature of 25 °C. We initially used Parafilm M® Laboratory film, which is air permeable but water resistant, to seal the top for 3-day equilibration, afterward we collected gas samples by syringe from the headspace of each jar at the beginning and end of 1-h sealed incubation and used a GC (Varian 450, CA, USA) to analyze CO_2 concentration. As microbial biomass itself is a factor regulating soil respiration rates, standardized CO_2 emissions at the microbial biomass were calculated based on the elevated CO_2 concentration, time, air volume in the jar, and the amount of added MBC from the inoculum. To prevent microbial acclimation to the assay chemistry[18,31], we only incubated the soils for a short time. A chloroform fumigation-extraction method (0.5 M K_2SO_4 to extract biomass C)[54] was used to determine soil MBC by the difference in measured carbon contents between fumigated and control replicates of each sample.

Temperature sensitivity. To test temperature sensitivity of soil respiration, nine fresh peat samples (30 g) from each site were added to jars and sealed with Parafilm M® Laboratory film. Triplicate samples were incubated at 4, 25, and 44.5 °C. The highest temperature in this incubation does not match the in situ conditions in our sites, but it may happen shortly in tropical wooded peatlands in the future. After 3-day equilibration, we used the same method as above to measure gas emission and calculated soil respiration based on soil dry weight. We conducted regression analyses for soil from each site using $R = \alpha e^{\beta T}$, where R is soil respiration, coefficient α is the intercept of soil respiration when temperature is zero, coefficient β represents the temperature sensitivity of soil respiration, and T is soil temperature.

The relative contributions of fungi and bacteria to peat decomposition. We subsampled 20 g each of our archived material from the *Sphagnum*-dominated bog in Minnesota and the shrub-dominated peatland in North Carolina, then subsamples were well mixed to make two composite bulk samples (one for *Sphagnum*-formed peat, one for shrub-formed peat) for the following incubations.

A total of nine broad-spectrum antibiotics were tested either alone or in combination for their inhibition on bacteria or/and fungal respiration using a selective inhibition (SI) technique[55] without glucose. The antibiotics include 5 fungicides (cycloheximide, benomyl, nystatin, natamycin, amphotericin B) and 4 bactericides (streptomycin, penicillin, oxytetracycline hydrochloride, neomycin). Both fungicide and bactericide were used alone or combined at concentrations of 0, 10, 20, 100, 500, and 1000 μg g^{-1} soil for the shrub-formed peat or 0, 35, 71, 357, 1785, and 3571 μg g^{-1} soil for the *Sphagnum*-formed peat. Each concentration of antibiotics (triplicate) was added to a 3-g fresh peat placed in a 50-ml tube. Mason jars (8-cm diameter, 12-cm height, vacuum seal lid with a stainless-steel fitting with sampling septum) are used to incubate the treated samples. CO_2 accumulation rates over 24 h was measured and calculated as same as testing temperature sensitivity of soil respiration above. We found that all bactericides used in this study increased CO_2 emission along with their concentrations. The results suggest that: (1) the contribution of bacteria to peat decomposition in general was simply very little, (2) the bacteria that were inhibited by bactericide contribute negligibly to peat decomposition, (3) the non-targeted bacteria were stimulated after the targeted-bacteria were inhibited, although the bactericides are broad-spectrum antibiotics, they did not inhibit the dominant bacteria at all in our sites, and /or (4) both bacteria and fungi in our sites may utilize these bactericides as a carbon source. As to the fungicide, only cycloheximide at a concentration of 357 μg g^{-1} soil slightly decrease CO_2 emission in the *Sphagnum*-formed peat, but not the shrub-formed peat. Other fungicides did not suppress the CO_2 emission regardless of their concentrations, or increased the CO_2 emission along with increase in concentrations of fungicide, which suggest that these fungicides did not inhibit the dominant fungi in our sites. Therefore, we found no evidence that SI technique could detect the relative contribution of bacteria and fungi to peat decomposition in our sites. To further examine our fungal dominance hypothesis, we next used filtration by size to assess dominant decomposers.

According to the literature (e.g., refs. [56–58]), the average size of most bacteria is between 0.2 and 2.0 μm in diameter, with most of them less than 1.5 μm; while most fungi grow as hyphae in soil, which are cylindrical, thread-like structures 1.5–10 μm in diameter and up to several centimeters in length[57,59,60]. The sizes of most fungal spore are more than 2.0 μm in diameter[61–63]. Theoretically, porous filters could physically separate bacteria from fungi[58]. Domeignoz-Horta et al.[64] used 0.8-μm filter to exclude fungi successfully[64]. In our test, filters with pore sizes of 0.22, 0.45, 1.2, and 1.5 μm were selected. The filtrates through 1.2- and 1.5-μm filters contain most of the bacteria, in which a small portion of larger bacteria and small fungi may pass through pores due to a lack of rigidity of their cells[58].

Sphagnum- and shrub-formed peat inocula were made by mixing 50 g of each type of fresh peat with 250 ml of sterilized deionized water. After 1 h of stirring and 1-day settlement, the suspension liquid inoculum was first filtered through a Buchner funnels (without filter, pore size 0.25–0.5 mm). The filtrate, we assumed,

contain all bacteria and fungi while removing large decomposers like insects and worms. The 0.25–0.5 mm filtrate was used to make other inocula containing no-bacteria/fungi, nanobacteria and non-fungi, and most bacteria and non-fungi by filtering through 0.22- (nylon), 0.45- (nylon), 1.2- (glass fiber), and 1.5-μm (glass fiber) filters, separately. In total, 6 treatments including 5 inocula (filtrates through 0.22, 0.45, 1.2, 1.5, and 250–500-μm filters) and control (sterilized deionized water) were established. Either inoculum or sterilized deionized water was added to a 3-g sterilized *Sphagnum*- or shrub-formed peat (triplicate) and incubated at 25 °C. CO_2 emission was measured within 24 h.

Statistical analysis. One-way ANOVA with Duncan's multiple-range test was used to compare the means of soil physicochemical parameters. Standard error of the mean was calculated for each mean. The significant level of the test was set at a probability of 0.05. The ANOSIM function in the *vegan* package in R was used to test statistical significance in fungal composition within and among sites in the shrub- and the *Sphagnum*-dominated peatlands (999 permutations), which shows that fungal communities were significantly different within sites at the shrub-dominated peatlands (Pungo East, Pungo West, and Pungo Southwest) and at the *Sphagnum*-dominated peatlands (hollows and hummocks) (Supplementary Fig. 5). Mantel test and redundancy analysis (RDA) were employed to explain the relative roles of soil physicochemical factors in fungal community composition using *vegan* package in R. The correlation of the redundancy axes with the explanatory matrix was determined with the general permutation test (anova.cca function; 999 permutations). Stepwise regression was further run to test what primarily control the slow-growing versus fast-growing fungi and soil acidity.

Data availability

The generated sequence data are available from the National Center for Biotechnology Information at SRP122579 and SRP158553. Data files containing compiled mean soil respirations from boreal to tropical peatlands, soil physicochemical parameters and results of incubation experiments are available from https://doi.org/10.17632/8zx2mczz6d.1.

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Author contributions

H.W., J.T., and C.J.R. conceived the ideas and designed this research; C.J.R., H.W., R.V., and H.C. obtained funding; H.W., M.H., C.J.R., H.C., and Z.B. collected field samples; J.T., H.C., and X.L. did microbial measurement and analyzed microbial community data; H.W. measured soil chemistry and conducted incubation experiments; M.H. and Z.B. analyzed plant information. H.W. and J.T. compiled data of soil respiration from literatures; H.W. wrote the manuscript with J.T. and C.J.R.; and all other authors discussed results and commented on the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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Correspondence and requests for materials should be addressed to H.W. or C.J.R.

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