Web links to the author's journal account have been redacted from the decision letters as indicated to maintain confidentiality.

9th Jun 20

Dear Dr Wang,

Your manuscript titled "Vegetation and Microbes Interact to Preserve Organic Matter in Wooded Peatlands" has now been seen by 3 reviewers, whose comments are appended below. You will see that they find your work of some potential interest. However, they have raised quite substantial concerns that must be addressed. In light of these comments, we cannot accept the manuscript for publication, but would be interested in considering a revised version that fully addresses these serious concerns.

We hope you will find the reviewers' comments useful as you decide how to proceed. Should additional work allow you to
• address these criticisms(that is, either to incorporate the suggestions or provide a compelling argument why the point made by the reviewer is not valid, or relevant to the editorial threshold as outlined below)
AND
• meet our editorial thresholds as outlined below,

then we would be happy to look at a substantially revised manuscript. However, please bear in mind that we will be reluctant to approach the reviewers again in the absence of substantial revisions.

In the following, we list our main editorial concerns:

****Provide compelling evidence that the soil fungal community composition has a greater influence on organic matter decay rate and carbon dynamics in two US peatlands than previously recognised****

****Rigorously justify all your interpretations and claims with evidence presented in the manuscript, or soften these statements appropriately****

****Ensure your work is placed firmly and accurately in the context of all relevant existing literature****

In addition, please supply point-by-point responses to all the reviewers' comments.

If the revision process takes significantly longer than three months, we will be happy to reconsider your paper at a later date, as long as nothing similar has been accepted for publication at Communications Earth & Environment or published elsewhere in the meantime.

We understand that due to the current global situation, the time required for revision may be longer than usual. We would appreciate it if you could keep us informed about an estimated timescale for resubmission, to facilitate our planning. Of course, if you are unable to estimate, we are happy to

accommodate necessary extensions nevertheless.

We are committed to providing a fair and constructive peer-review process. Please do not hesitate to contact us if you wish to discuss the revision in more detail.

Please use the following link to submit your revised manuscript, point-by-point response to the referees' comments (which should be in a separate document to any cover letter) and any completed checklist:

[link redacted]

** This url links to your confidential home page and associated information about manuscripts you may have submitted or be reviewing for us. If you wish to forward this email to co-authors, please delete the link to your homepage first **

Please do not hesitate to contact me if you have any questions or would like to discuss the required revisions further. Thank you for the opportunity to review your work.

Best regards,

Joe Aslin

Associate Editor,
Communications Earth & Environment
https://www.nature.com/commsenv/
Twitter: @CommsEarth

EDITORIAL POLICIES AND FORMAT

If you decide to resubmit your paper, please ensure that your manuscript complies with our editorial policies and complete and upload the checklist below as a Related Manuscript file type with the revised article:

Editorial Policy Policy requirements

For your information, you can find some guidance regarding format requirements summarized on the following checklist:
Communications Earth & Environment formatting checklist

REVIEWER COMMENTS:

Reviewer #1 (Remarks to the Author):

Dear authors,
With much interest I have read and assessed you manuscript that describes a series of observations that show that peatland differ in the composition of of fungal communities and that these different communities have different life-history traits that relate to carbon dynamics. These results are claimed to solve the paradox that with warming peatlands still sequester C.

The introduction is quite clear, although I feel that the connection between paleo-evidence on the role of vegetation on C dynamics and the current approach ¬– i.e. environmental gradient study – needs to be made more explicit. Perhaps interesting in the context of the present study is this paper: https://www.nature.com/articles/s41467-017-01350-5

With disqualifying the 'current abiotic-factor-dependent peat decay models¬' based in Fig.1, I feel he authors are taken a short-cut. The figure only shown soil respiration against MAT, while water table is ignored but stated are a major driver for the models they disqualify.

In the introduction i.m.o. a few references are not used correctly:
Ref 1& 2 (l42)are not at all making a statement on the peatland C pool. I'd suggest to have a look at https://agupubs.onlinelibrary.wiley.com/doi/10.1029/2010GL043584 & https://www.nature.com/articles/s41561-019-0454-z.
Ref 7 (l49) does not deal with feedbacks, but shows that only slight increase in temperature lead to respiration of old carbon. See https://onlinelibrary.wiley.com/doi/pdf/10.1111/gcb.14140 for an alternative.
Refs 17 (l70), 19-21 (l72) are not dealing with the effects of plant community composition on microbial communities in peatlands. Yet, a wealth of research has been published recently which I think is actually much ignored in the introduction. Some examples: https://besjournals.onlinelibrary.wiley.com/doi/pdf/10.1111/1365-2745.12413, https://www.sciencedirect.com/science/article/pii/S0038071714004027.

When describing the site locations for the first part of the story (l81-93), I find it hard to link this to a space-for-time approach. Only the data in Fig 1 can be linked to a space-for-time approach, the others part of this work are site comparisons. Clarity needs to be given. As written now, the sampling efforts seem all ad-hoc; samples were taken at two sites, then some extra sites were measured. I would urge the authors to ty to build a narrative. This actually becomes even more apparent when in the discussion part, suddenly data on a Chinese peatland surfaces, and later a re-analysis of data on pacific-coast peatlands. In my opinion, the way the manuscript is presented is more like a gathering of data-sets that if alone would not warrant publication, and which are now forcedly brought together.

(l90-91) what are these pilot results?
(l97-98) can you underpin, by literature, that fungi are the main decomposers in peat? I think you need to explain this choice a bit better. Prokaryotes are actually quite important in peatlands, especially when condition get wetter. Similarly, how can you be sure that soil respiration rates as presented in Fig. 4 are fungal-driven and not by bacteria?

(l100) 'The Sphagnum and shrub peatlands distinctively differed in the fungal community'. Sure they do but the sites are hardly comparable in environmental conditions! Are we now not comparing two different types of peatland and they start guessing if observed differences are plant driven or

environment driven?

I wonder if it would not be better to perform a numerical test (e.g. PCA, RDA) to determine which physicochemical parameters control fungal community composition?

I thin that the conclusion that these findings provide new insights that enduring peatlands …. gradually shift to a new equilibrium state… (l206-209) is inappropriate. A comparison between peatlands has been made, but the nature of the research makes it hard to tell what the underlying drivers for differences are.

Reviewer #2 (Remarks to the Author):

Wang et al. 2020 – Nature – Earth & Environment
Very well written abstract and informative. This is a nice study presenting a synthesis of soil respiration data (although not quite comprehensive for North America), soil analyses at two contrasting bog in term of vegetation and climate settings and an incubation experiment. I find the result very interesting BUT way too highly out of bound and speculative to apply the results to the vast expanses of the boreal peatlands of North America and Russia. The authors have conducted very good work but should be more rigorous with their inferences. Besides this main comment, I have no problem with the article. It is a very popular topics currently and the scientific findings will open the doors to a lot more investigations (to prove or disprove the conclusions of this paper). The data are well analysed. So in all I would recommend the publication of the manuscript.
Introduction
Line 46-48: be careful with such big claim: Climate warming and drought not only increase peat loss by accelerating decomposition but also cause substantial losses of the keystone mosses like Sphagnum in the vast boreal peatlands, followed by shrub expansion and its uncertain effects4-6 – First, I am a boreal peatland ecologist and this is largely untrue. Also we cannot check Talbot ref (incomplete), Bragazza and Swiss colleagues only worked and did their study in Switzerland and then made large inferences from analytical work. The alpine peatlands of Switzerland are very different then the vast boreal peatlands. And your own citation, Wang et al are studies done in the Pocosin peatlands (NC) so far from the vast boreal peatlands which as far as I know have not lost their Sphagnum cover.

Line 57-58: I am surprised to see so little data from Canada and the one cited dates. What about: Solondz et al. 2008 (Ecohydrology); Munir et al 2017 (Forests); Bubier et al 2003 (Ecosystems); Dalva et al. 2001 (JGR). I would be surprised that most Canadian studies do not meet the author selection criteria.

Results and Discussion:
Line 89-90: I would strongly challenge this claim: These shrub species in pocosins are similar to the expanding shrubs found in Sphagnum peatlands across boreal areas4, 5. I would say absolutely not true. Also easy to see from your Table 1 comparing Marcell bog with the studied pocosin.
I find it disturbing to see a conclusive sentence such as: line 90-92: Our pilot results in the Sphagnum site are in line with the observations in many boreal peatlands, while such studies in low latitude system are still rare. While we have not yet seen any data. In general I do not like to see a section of Results and Discussion together, harder to first assess only the results based on the reviewer

expertise. I would strongly suggest to present results first and then discussed it.

Line 86: the authors keep talking about shrubs but no species are mentioned – it appears that all is mixed up (kalmia, birch, willows etc).

Line 89-90: Again the authors write: These shrub species in pocosins are similar to the expanding shrubs found in Sphagnum peatlands across boreal areas4, 5. But this is totally not substantiated as discussed above.

Line 98-99: this result appears to be an important one to the whole discussion of the paper – I do not understand the choice to put the evidence data in a supplementary table.

Line 124-125: This is core to the argument the relationship between pH and fungi dynamic, so Supplementary Fig. 1 should be part of the main text of the article.

Line 166: Was really a field experiment done? I understand that soil was sampled and analysed at two different locations (Marcell bog and Pocosin) but was an experimental design implemented?

Line 168: this statement is highly speculative. We are not at the point of making this jump in conclusion.

Line 180-181: this is the original results from this study – I do not understand 1) why not presented in main text and 2) why coming much later in the logic of the discussion. This confirms that it would be much better to present results first and then have sub-heading in the discussion for the 1, 2 or 3 messages the authors want to convey.
Line 186: as said before the Swiss study is an altitudinal study not a climate change one – yes a proxy – but to apply their results of the very tiny peat wholes they have in Switzerland to the vast mires of northern Europe and North America is way too large of a step. The authors have enough interesting results without doing these speculations.
Line 188-190: All my life I walked in peatlands where some parts are open, some are very shrubby with close to no Sphagnum and some are treed. Studying a patch of a shrubby Sphagnum bogs does not mean shrubs are expanding in their abundance. I still have to see a solid study on that claim.
Line 190: The authors of citation 37 absolutely do not report as done here: which shows that the on-going shrub expansion in some boreal peatlands have shifted in 191 sync from fast-growing to slow-growing microbes - wrongly cited.

Line 191-197: while I agree with was is reported here, it is clear that fungi composition depends on the surface plant community but there is no implication about shrub expansion into bogs.

Detailed comments:
Line 40: better cite a more recent estimate of 2.84% see: Xu, J., Morris, P. J., Liu, J., & Holden, J. (2018). PEATMAP: Refining estimates of global peatland distribution based on a meta-analysis. Catena, 160, 134-140.
Line 202 : write : the no exponential rise (to make it an enumeration of reasons before the statement.
Line 209 : plant? And not plan
Line 228: when switching back to Lake Pungo, tell the reader that you are back in NC.

Line 226 to 237: the sites description would be more easily grasps if presented in a table format.
Line 240 and 560 : the species name of Ledum groenlandicum is now Rhodendron groenlandicum
Line 248: with dense and layer not in italics

Reviewer #3 (Remarks to the Author):

H. Wang, J. Tian, H. Chen, M. Ho, R. Vilgalys, X. Liu, and CJ Richardson. Vegetation and microbes interact to preserve organic matter in wooded peatlands.

Summary

In this paper, Wang et al., cite the prevalence of low latitude peat accumulation under warm and seasonally oxic conditions to challenge the widespread view that cold anoxic conditions are the primary inhibition of organic matter decomposition facilitating accumulation of peat. Instead Wang et al. proffer a microbial explanation wherein slow-growing microorganisms types dominate wooded peatlands accounting for slow organic matter decomposition rates despite warmer temperatures.

General Impression

Although the manuscript is based on an intriguing hypothesis, a few key points seem to be lacking rigorous support. For example, much is made of the trade-off between slow-growing and fast-growing microorganisms in Sphagnum-dominated versus woody peatlands. However, it is unclear how microorganisms (and after reading further it's really just fungi since bacteria were not measured) were assigned to these groups since line 136 states "It is impossible to measure the relative growth rates of the dominant microbes in this study, because so many of the fungi are unculturable." How can effects be attributed to a factor that is unmeasurable?

Another example is that the authors claim differences in carbon lability among the sites, but it is not clear how carbon lability was either defined or quantified. For example, in line 144, how were "labile and complex organic material" differentiated? Or in line 145, how was it determined that the shrub peat is more highly recalcitrant than the Sphagnum peat? And what do the authors mean by "recalcitrant" since they state on line 182, that "the fast-growing microbes decomposed highly recalcitrant peat more quickly than the slow-growing microbes"? If the material is truly recalcitrant it should not be degraded quickly. From the statement on line 182, it seems more likely that the OM under consideration is not recalcitrant per se, but rather is simply not a preferred substrate of the slow-growing microorganisms.

Further, in line 148, the authors suggest that "the decomposers ultimately determine the decomposition rate", however, that conclusion is in direct contradiction to the results presented in Figure 4 which demonstrate that the rates of the Sphagnum inoculum are, in fact, modified by the available substrate. If decomposers ultimately determine the decomposition rate, there would be no significant differences among the various Sphagnum inoculated incubations.

With further regard to the incubations, why were incubations conducted at 25°C (line 306) which is much higher than the MAT at any of the sites in Table S1. Given the extreme differential

temperature sensitivity of the Sphagnum community relative to the shrub community (Fig S2) could the results in Fig 4 be influenced by this temperature difference in addition to substrate? It seems that the Sphagnum community would be favorably selected at this warmer temperature, which I think is a consistent alternate (or at least contributing) explanation for the results in Fig 4.

It's not clear to me why carbon-enriched mineral soil was chosen for the incubations (line 141) instead of adding labile carbon to peat. Changing to mineral soil seems to me to introduce many more variables besides just the labile C, e.g. pH and potentially essential cations that may alter microbial activity. I think this part of the experiment should be more fully explained and the implications carefully considered.

The study sites in China and Canada seem like a last-minute add-on that were not well-incorporated into the rest of the study. They are treated very briefly; if the results were presented, I missed them and they were scarcely explained. I would encourage the authors to more fully explain how the results from these sites support their hypothesis.

Specific Comments

The abstract includes phrases such as "…we present a…natural course that curbs carbon loss against climate change" and "…high-phenolic shrub/tree induced shifts in microbial composition may compensate for positive effects of temperature and/or drought" these phrases hint to me of a trade-off between fast-growing microorganisms in Sphagnum-dominated peatlands where OM quality is low versus slow-growing microorganisms in woody peatlands where OM quality is high. However, this interpretation seems contradictory to the statement on line 32 which suggests that Sphagnum-associated OM is labile while woody OM is high(ly?) recalcitrant (line 29). I am left puzzled whether the authors intend to convey a trade-off between microbial growth rates and OM quality which offset to more or less maintain slow overall decomposition rates across all peatlands or whether instead the trade-off is between microbial growth rates and environmental conditions? (and indeed, after finishing the manuscript this question appears to me to remain unresolved).

The abstract frequently refers to "microbes" and "microbial composition" as factors controlling decomposition, so I was surprised to learn on line 130 that bacterial composition was not measured at all in this study. I would recommend making it clear in the abstract that this study focuses solely on fungi to avoid the implication that the whole microbial community was measured.

Introduction

Lines 47-48, this reference seems relevant to the discussion: Norby, R.J., Childs, J., Hanson, P.J. and Warren, J.M., 2019. Rapid loss of an ecosystem engineer: Sphagnum decline in an experimentally warmed bog. Ecology and Evolution, 9(22), pp.12571-12585.

Line 48, I'm not sure "invoke" is the right word here, perhaps "provoke"?

Line 50: Was MAP or MAT meant?

Results and Discussion

Line 81, I don't think you need "as an alternative" in this sentence.

Line 90-91, "Our pilot results in the Sphagnum site are in line with the observations in many boreal

peatlands," this statement is rather vague. What results?

Line 92-93, Where in China and Canada? Is the Canada site not boreal? Can you give lat/long as was done for Marcell and the Pocosins?

Line 111: It would seem relevant to consider these results in the context of Woodcroft et al, (2018) who discuss the abundance of single C utilizers in Sphagnum peatlands: Woodcroft, B. J., Singleton, C. M., Boyd, J. A., Evans, P. N., Emerson, J. B., Zayed, A. A., et al., (2018) Genome-centric view of carbon processing in thawing permafrost. Nature, 560(7716), 49

Line 120-121, This line seems to suggest that the relationships between species richness and DOC, moisture, nitrate/nitrite and ammonium were tested, but I don't see those results presented. Further, there appears to be a significant relationship between species richness and pH (Fig. S1), so how was it concluded that phenolics were the primary driver and not pH or the interaction between the two? Perhaps some multivariate statistics (MANOVA) could be useful for further exploring these relationships.

Line 130, the microbial data for Marcell was somewhat limited in Wilson et al., (2016) I would recommend reviewing Lin et al., for a more thorough characterization of the microbial community at Marcell.
Lin X, Tfaily MM, Steinweg JM, Chanton P, Esson K, Yang ZK, Chanton JP, Cooper W, Schadt CW, Kostka JE. Microbial community stratification linked to utilization of carbohydrates and phosphorus limitation in a boreal peatland at Marcell Experimental Forest, Minnesota, USA. Appl. Environ. Microbiol.. 2014 Jun 1;80(11):3518-30.

Lin X, Tfaily MM, Green SJ, Steinweg JM, Chanton P, Imvittaya A, Chanton JP, Cooper W, Schadt C, Kostka JE. Microbial metabolic potential for carbon degradation and nutrient (nitrogen and phosphorus) acquisition in an ombrotrophic peatland. Appl. Environ. Microbiol.. 2014 Jun 1;80(11):3531-40.

Line 181 and Fig S2, it seems curious that the Sphagnum community appears to be so strongly sensitive to such high temperatures (>40°C) despite their apparent acclimation to a much lower MAT (~3°C). What is the significance of that particularly with regard to the observation that these organisms do not seem to compete well at warmer, low-latitude sites?

Lines 187-191, This is a long run-on sentence which is also difficult to parse. I would suggest breaking this sentence into smaller thoughts and rewording for clarity.

Line 209, "(likely bridged by plan-induced phenolics)", I don't know what this means, what are plan-induced phenolics and what do they bridge?

Methods

Line 236, should be "One hollow and one hummock"

Line 243, should be "three soil cores at each site"

Lines 252-259, Where were the DOC, nitrate/nitrite, ammonium and TON results presented?

Line 305 why was only 5 mL of inoculum added to the mineral soil while 20 mL were added to the others?

Vegetation and Microbes Interact to Preserve Organic Matter in Wooded Peatlands

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This PDF file includes:

Abstract

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 explain how vast low-latitude wooded peatlands consistently accrete peat under warm and seasonally unsaturated conditions. Similarly, that theory cannot accurately project the decomposition rate in boreal peatlands where warming and drought have decreased *Sphagnum* and increased shrub expansion. Here, by comparing composition and ecological traits of microbes between *Sphagnum*- and shrub-dominated peatlands, we present a previously unrecognized natural course that curbs carbon loss against climate change. Slow-growing microbes decisively dominate the studied wooded peatlands, concomitant with plant-induced, high recalcitrant carbon and phenolics. The slow-growing microbes inherently metabolize organic matter slowly. However, the fast-growing microbes that dominate our *Sphagnum* site (most boreal peatlands as well) decomposed labile carbon >50 times faster than the slow-growing microbes. We show 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 help better project long-term, climate-carbon feedbacks in peatlands.

Main Text

Introduction

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, 2]. 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[3]. Climate warming and drought not only increase peat loss by accelerating decomposition but also cause substantial losses of the keystone mosses like *Sphagnum* in the vast boreal peatlands, followed by shrub expansion and its uncertain effects[4-6]. Such cascading events could invoke a catastrophic positive feedback to global warming[7-9]. However, long-term warming experiments in grasslands[10, 11] and studies spanning a wide range of mean annual temperature (MAP) globally[12, 13] show declining microbial metabolism over time under experimental warming or in warmer regions. By now 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[14]. High-resolution stratigraphic analyses on peat profiles across boreal areas documented that vegetation composition and net primary productivity played key roles in carbon accumulation during the last millennium[14, 15]. We compiled soil respiration data from >150 peatland sites across latitudes between 2°S and 75°N (Supplementary Data 1) to test whether the dependence of decomposition on temperature applies to a wide range of mean annual

temperature (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[16], we expected to see an apparent exponential rise in soil respiration along with increasing MAT. However, we found the idea unsustainable (Fig. 1). The paleontological evidence[14, 15] and our large-scale soil respiration analysis 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[7, 9]. This disagreement, we assume, could result from the latent role of changing plant communities and their associated ecological and biogeochemical processes—a commonly occurring state shift in peatlands induced by persistent climate change[14]. Changes in plant communities among mosses, sedges, shrubs and trees may bring forth substantial top–down and bottom–up regulations[17] on the peatland ecosystem through alteration of plant–microbe traits, specifically plant/soil chemistry[18] and microbial composition/function[5, 19-21]. Although temperature dominantly controls microbial metabolism of soil carbon in monoculture or a constant environment, the long-term feedback between climate change and soil carbon processes (especially some evolutional acclimations in plant/microbial physiology and community composition in peatlands[11, 19-24] is still unclear and possibly one of the major uncertainties and challenges in projecting future climate in the Earth System Models[25]. Thus, recognition of the biotic control can be central to the development of a meaningful framework for unravelling the long-term responses of the perpetual peatlands to climate change[19, 21].

Results and Discussion

We used space-for-time substitution as an alternative to study shifts of ecological processes in peatlands over time. An ombrotrophic boreal *Sphagnum* peatland and a subtropical shrub

peatland in the U.S.A were first selected. The *Sphagnum* site is located in the Marcell Experimental Forest, Minnesota (47°30′N, 93°27′W), USA, and the shrub site is in Pocosin Lakes National Wildlife Refuge, North Carolina (35°40′N, 76°32′W), USA. The *Sphagnum* site is dominated by *Sphagnum* mosses with scattered shrubs and black spruce (*Picea mariana*), while the shrub 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 today[6, 26]. These shrub species in pocosins are similar to the expanding shrubs found in *Sphagnum* peatlands across boreal areas[4, 5]. Our pilot results in the *Sphagnum* site are in line with the observations in many boreal peatlands, while such studies in low latitude system are still rare. Hence, two wooded peatlands were further tested in subtropical southern China and temperate western Canada.

To determine the underlying microbial communities and their ecological traits, we collected triplicate soil cores from the hollows and hummocks in the boreal *Sphagnum* peatlands and from 3 sites with different plants and water levels in the subtropical shrub peatlands (Supplementary Table 1) and measured the composition and abundance of fungi—the predominant peat decomposers—and associated physiochemical peat parameters. Compared to the *Sphagnum* peat, dissolved phenolics in the shrub peat were about 6–10 times higher (Supplementary Table 1). The *Sphagnum* and shrub peatlands distinctively differed in the fungal community composition (Fig. 2). At the *Sphagnum* site, the fungal groups were dominated by *Pseudeurotium*, Saccharomycetales and *Mortierella*, whereas at the shrub site, by *Archaeorhizomyces* and Helotiales (Fig. 2, Supplementary Data 2). As microbial growth rates significantly affect carbon turnover in soil[27, 28], we roughly 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 2). This is the best way we can approach by now although some inevitable biases exist in this classification. Notably, nearly 85% of fungi were likely fast-growing at the *Sphagnum* site, but at the shrub site a mere 2% were categorized as fast-growing and about 75% as slow-growing based on their ecological traits (Fig. 2, Supplementary Table 2). Consistent with the majority of fungi found in many boreal peatlands[29], the dominant fungi at the *Sphagnum* site are members of pioneer saprobe communities that use simple carbon compounds and possibly possess *r*-selected strategy with fast growth rates[27-29]. Unexpectedly, 11–97% of fungal sequences at the shrub site were assigned to *Archaeorhizomyces*, but only 0.4% on average at the *Sphagnum* site. *Archaeorhizomyces*, which represents one of the ubiquitous lineages of soil fungi, is characterized by markedly slow growth [30]. Another dominant fungal group (~5%) in the subtropical shrub 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 slower growth rates[31]. To determine what might control the fungal composition, we examined the relationship between fast- versus slow-growing fungal richness and physicochemical variables including dissolved organic carbon, dissolved phenolics, soil pH, soil moisture, NO_3^-–N and NH_4^+–N. Dissolved phenolics likely acted as the overarching regulator, not only directly limiting microbial activities[6, 32] but also allowing slow-growing fungi to thrive while hampering fast-growing fungi (Fig. 3). We also found soil acidity positively related to the relative richness of slow-growing fungi while negatively related to that of fast-growing fungi (Supplementary Fig. 1). As there was a significant negative relationship between soil pH and dissolved phenolics ($r^2 = 0.428$, $P<0.0001$), the dissolved phenolics in these peatlands might be mainly phenolic acids that increase soil acidity, thus further worsening

128 extreme conditions that benefit the slow-growing fungi[28] or under which only slow-growing
129 fungi can survive.

130 Although we did not measure bacterial composition in this experiment, recent measurements[33, 34]
131 at several of the same shrub and *Sphagnum* sites show that oligotrophic slow-growing
132 Acidobacteria[27] dominated both peatlands. The relative abundance of Acidobacteria in the shrub
133 sites (57%) was substantially higher than that in the *Sphagnum* sites (36%). Moreover, the fast-
134 growing bacteria—including Betaproteobacteria and Bacteroidetes as copiotrophs[27] —were nearly
135 absent from the shrub site[33] but contributed about 9% and 4%, respectively, in the *Sphagnum* site[34].

136 It is impossible to measure the relative growth rates of the dominant microbes in this study, because
137 so many of the fungi are unculturable. To further test and verify the consequences of these likely
138 fast-growing versus slow-growing microbes, we compared soil respiration rates per gram
139 microbial biomass carbon (MBC)[12, 24] in the *Sphagnum* and the shrub peats through a reciprocal
140 inoculation experiment using inocula and peat materials from both sites. We also added each
141 inoculum to labile carbon-enriched mineral soil to test how the microbes decompose labile carbon.
142 All soil media and incubators were sterilized by an autoclave before inoculation. Consistent with
143 the microbial growth traits found in the literatures (Supplementary Table 2), the microbes from
144 the shrub peat decomposed both labile and complex organic material at much slower rates than the
145 microbes from the *Sphagnum* peat (Fig. 4). Although the shrub peat is more highly recalcitrant
146 than the *Sphagnum* peat, the fast-growing microbes from the *Sphagnum* inoculum decomposed the
147 shrub peat 4 times faster than the microbes from the shrub peat did, which means the decomposers
148 ultimately determine the decomposition rate. Moreover, the soil respiration rates from *Sphagnum*
149 inoculum were dependent on the source of carbon, with rates at 320, 838 and 2315 mg C hr^{-1} g^{-1}
150 MBC in the shrub peat, the *Sphagnum* peat and the labile carbon-enriched mineral soil,

151 respectively. Hence, the dominant decomposers in the *Sphagnum* peatlands are likely fast-growing
152 copiotrophs that generally adapt to using available resource rapidly[28]. In contrast, soil media—
153 including labile carbon—did not impact the microbial activities from the shrub inoculum (71–92
154 mg C hr^{-1} g^{-1} MBC). These results support our hypothesis that microbial metabolism in high-
155 phenolic shrub peatlands is slower and that such a growth trait of a specific microbial community
156 might be inherent[28].

157 The slow-growing microbes that dominate the high-phenolic shrub site behave like *K*-selected taxa
158 that may have outcompeted fast-growing *r*-selected taxa under steadily warmer and dryer
159 conditions. The established slow-growing fungi, as well as bacteria[33, 34] lead to a lower carbon
160 turnover in soil[6, 27]. The dominance of the slow-growing microbes may explain why plant
161 necromass does not completely decompose, but continues to accumulate as peat in low-latitude
162 wooded peatlands, despite constant warming and frequent drought over millennia[6]. This also
163 further uncovers the observed slow decomposition under drought in the subtropical shrub
164 peatlands[6], which was likely caused not only by the anti-microbe role of increased phenolics[6, 35]
165 but also the magnified slow-growing decomposers induced by higher phenolics. Collectively, our
166 field and lab experiments demonstrate for the first time that a phenolics-linked plant-microbe
167 interaction acts as a natural curb on carbon loss in low-latitude wooded peatlands and will likely
168 also in future boreal peatlands with climate-induced shrub expansion. This biotic self-sustaining
169 process driven by consistent increases in temperature and drought over time appears to be more
170 important than direct abiotic controls in regulating long-term carbon–climate feedbacks in
171 peatlands, which is critical for understanding and modeling how ongoing climate change affects
172 peatlands across the globe.

We postulate that these slow-growing microbes 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. This hypothesis is further supported by a temperature sensitivity experiment, a fungal composition measurement in a subtropical peatland in Asia and a reanalysis of fungal composition in a wooded peatland in Canada[36]. Although higher microbial biomass carbon was present in the shrub peat (3.8 ± 0.2 mg C g^{-1} dry soil) in North Carolina relative to the *Sphagnum* peat (2.6 ± 0.3 mg C g^{-1} dry soil) in Minnesota, the decomposition rate of the shrub peat was much slower at the same temperature and displayed lower temperature sensitivity than the *Sphagnum* peat (Supplementary Fig. 2). As we have shown the fast-growing microbes decomposed highly recalcitrant peat more quickly than the slow-growing microbes did (Fig. 4), thus current fast-growing microbes in most boreal peatlands[29] could decompose stored carbon more quickly when temperature is higher, but the microbes in peat soil may gradually shift to slow-growing species with increasing phenolic contents through shrub expansion under climate change[5] or even by adding wood litter—a new appearing geoengineering in degraded peatlands[35]. A recent study showed that the relative abundance of slow-growing fungi (Helotiales and *Archaeorhizomyces*) was over 80% in a *Sphagnum* peatlands where ericaceous shrubs dominated the wooded cover in Meadowlands, MN, USA[37], which shows that the on-going shrub expansion in some boreal peatlands have shifted in sync from fast-growing to slow-growing microbes. In addition, we examined a shrub-dominant subtropical peatland with *Sphagnum* layer underneath in Shennongjia, China (31°29′N, 109°59′E), where the majority of fungal taxa (80.4%) are also found slow-growing (Fig. 5), e.g. *Archaeorhizomyces* spp. (26.5%) and *Cryptococcus* sp. (34.0%). We also reanalyzed the fungal composition in a bog forest and a *Sphagnum*-shrub mixed peat bog in the Pacific coastal temperate

196 rainforest in Canada[36]. Slow-growing fungi also dominated these wooded peatlands
197 (Supplementary Fig. 3, Supplementary Table 2). Importantly there was a significant negative
198 relationship between soil respiration and richness of slow-growing fungi (Fig. 6), which indicates
199 that the slow-growing fungi regulate the carbon turn-over rates in the wooded peatlands. Our
200 research suggests that slow-growing microbes, which are less effective in decomposition under
201 warmer climates, may dominate most wooded peatlands, particularly in low-latitude areas. The
202 dominance of slower-growing microbes in these wooded peatlands, its exponential rise in soil
203 respiration with increasing MAT from boreal to tropical regions (Fig. 1), and the vast amount of
204 carbon stored in tropical wooded peatlands[2, 38] together support this deduction, even though our
205 study sites included only three wooded peatlands in North America and Asia.

206 Finally, our findings provide new evidence that enduring peatlands that are highly resistant to
207 increased temperature and drought may gradually shift to a new equilibrium state[19] with different
208 microbes and plants that have adapted to the changed climate over time through their self-
209 sustaining plant-microbe interactions (likely bridged by plan-induced phenolics). As biotic
210 regulators, the co-shifting microbe and plant communities that were initially triggered by climate
211 change appear to exert dominant controls on ecosystem C cycling and soil C sequestration, thus
212 ensuring for continuing peat accretion in the new state. Though beyond the scope of this study,
213 our findings may have more immediate applications in carbon-climate feedback models and
214 geoengineering strategies[35, 39]. Embedding dynamic biotic factors into current abiotic-factor-
215 dependent decay models could greatly advance the accuracy of the Earth System Models in
216 projecting the fate of boreal peatlands with shifting plant/microbe communities[4, 5, 37] under
217 climate change. This mechanism like a new framework would allow models to predict how the
218 biotic processes of a peatland could modulate abiotic controls on the carbon cycle over time.

Moreover, this mechanism further indicates that peatland geoengineering[39] adding high-phenolics natural materials like woody litter[35] could be an accelerated nature-based solution, similar to a natural state shift, preserving degraded peatlands not only in the short term through increasing phenolic contents[35] 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 bog[6] in the Pocosin Lakes National Wildlife Refuge, North Carolina, USA and a *Sphagnum* bog[34] in the Marcell Experimental Forest in Minnesota, USA. Three sites (>1 km apart) around Lake Pungo including Pungo West, Pungo Southwest and Pungo East were selected at the shrub bogs. *Ilex glabra* and *Lyonia lucida* cover about 85% and 10%, respectively at Pungo West. *Ilex glabra* and *Lyonia lucida* are also dominate Pungo Southwest but distribute evenly, also there are many *Woodwardia virginica* 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 is no disturbance at Pungo East site over 30 years, where more dominant plant species exist, including *Lyonia lucida, Ilex glabra, Zenobia pulverulenta, Gaylussacia frondosa, Vaccinium formosum.* One hollows and one hummocks were selected at the *Sphagnum* bogs. 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 thick layer of ericaceous shrubs including *Ledum groenlandicum, Chamaedaphne calyculata, Vaccinium oxycoccos* at the hummocks, however,

only scattered shrubs happen at the hollows. Other site information is described in Supplementary Table 1. We took three soil cores at each sites (with a distance >4 m from each other), and each soil core was sliced to four sub-samples (0–5 cm, 5–10 cm, 10–15 cm, 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-dominant area in Dajiuhu peatlands in Shennongjia, China (31°29′N, 109°59′E) in May 2017. The dominant shrub at Dajiuhu is *Crataegus wilsonii with dense Sphagnum layer*. 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 dissolved organic carbon (DOC) and soluble phenolics measurements. DOC was measured as the difference between total C and inorganic C with a total C analyzer (Shimadzu 5000A, Kyoto, Japan). Soluble phenolics were measured by following the Folin-Ciocalteu procedure[40]. 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, Wisconsin, 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 three times and homogenized together as one DNA template. For Pocosin

and Minnesota samples, a set of fungus-specific primers, ITS1F (3'-CTTGGTCATTTAGAGGAAGTAA-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'- GCTGCGTTCTTCATCGATGC-5') were used. All PCR reactions were repeated in triplicate, together with the negative controls in which the template DNA was replaced with sterile H_2O. The amplicon concentration of each sample was determined after purification using Qubit® 2.0 Fluorometer (Invitrogen, Grand Island, USA), samples pooled at equimolar concentrations, purified using AMPure Bead cleanup, and submitted to the core facility at Duke University (Durham, NC, USA) for sequencing using Illumina MiSeq (Illumina, San Diego, CA, USA).

Bioinformatics processing

Sequence data of Pocosin and Minnesota samples are 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 operational taxonomic unit (OTU) at the 97% sequence similarity level. Singleton OTUs were omitted[41], and OTUs classified taxonomically using a QIIME-based wrapper of BLAST against the UNITE database[42, 43] (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. Follow 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[34], 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

We tested the decomposing capability of microbes in the *Sphagnum* and shrub 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 peat inocula were prepared by mixing 0.5 kg of each type of fresh peat (10–20 cm) with 2 liters of deionized water. After 1 hour 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* peat (2.5–2.8 g in dry weight) or shrub 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-hour sealed incubation and used a GC (Varian 450, California,

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 and air volume in the jar and the amount of added microbial biomass carbon from the inoculum. To prevent microbial acclimation to the assay chemistry[13, 24], we only incubated the soils shortly. A chloroform fumigation-extraction method (0.5 M K_2SO_4 to extract biomass C)[44] was used to determine soil microbial biomass carbon by the difference in measured carbon contents between fumigated and control replicates of each sample.

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. Triplicate samples were incubated at 4°C, 25°C 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 future. After 3-day equilibration, we used the same method as above to measure gas emission and calculated soil respiration based on soil 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.

Statistical analysis

One-way ANOVA with Duncan's multiple-range test was used to compare the means. 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 peatlands and the *Sphagnum* peatlands (999 permutations), which shows that fungal communities were

significantly different within sites at the shrub peatlands (Pungo East Pungo West and Pungo Southwest) and at the *Sphagnum* sites (hollows and hummocks) (Supplementary Fig. 4).

Data availability

The generated sequence data are available from the National Center for Biotechnology Information at SRP122579 and SRP158553. All other data in this study are available within the paper and its Datasets.

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Acknowledgements We would like to thank Drs. David J. Levy-Booth and William W. Mohn at University of British Columbia and Dr. Joel E. Kostka at Georgia Institute of Technology for sharing their published data, Dr. William H. Schlesinger at the Cary Institute of Ecosystem Studies for his detailed comments on experimental design and data interpretation, Dr. Jeff Chanton at Florida State University, Dr. Dorothy Peteet at Columbia University, Dr. Christopher W. Schadt at Oak Ridge National Laboratory, Dr. Scott Neubauer at Virginia Commonwealth University, and Dr. Louis James Lamit at Syracuse University for their comments, Belen de la Barrera for laboratory measurement, Dr. Randy Neighbarger for technical editing. US DOE Office of Science, Terrestrial Ecosystem Sciences (DE-SC0012272), Key Research Program of Frontier Sciences,

CAS (QYZDB-SSW-DQC007), the Duke University Wetland Center Endowment, and China Scholarship provided financial support.

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., and H.C. 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; 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 financial interests.

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Figures

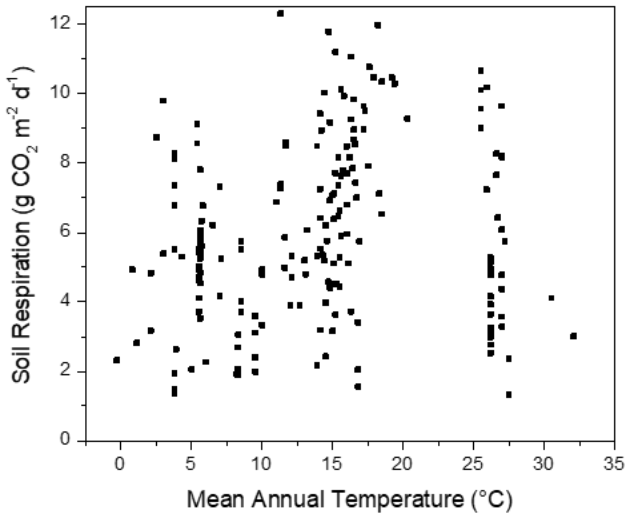


Fig. 1 Mean soil respiration from boreal to tropical peatlands. Data were compiled from 31 published studies that contain annual mean soil respirations observed in >150 sites globally (Supplementary Data 1).

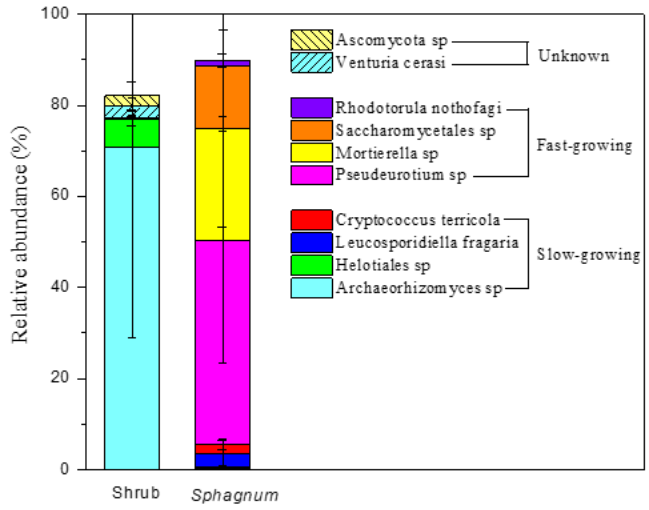
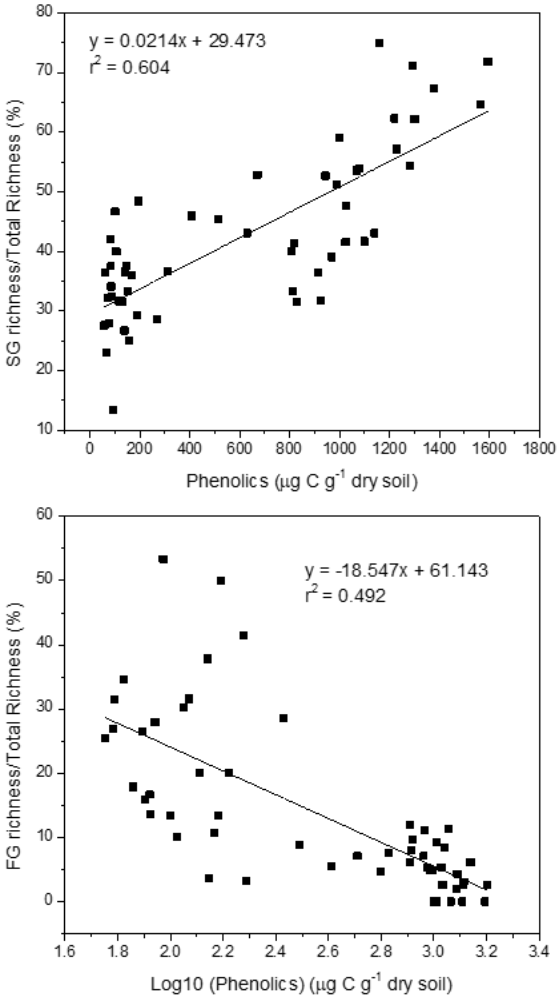


Fig. 2 Dominant fungal composition (relative abundance >1%, see Supplementary Data 2 for detailed OTUs distribution) **and relative abundance** (mean ± S.E.) **of slow-growing and fast-growing fungi** (see Supplementary Table 2 for ecological traits of the dominant fungi) **in the subtropical shrub and the boreal *Sphagnum* peatlands**.



466

467 **Fig. 3 Effects of phenolics on ratios of slow- and fast-growing fungal richness to total**

468 **richness.** Species richness is the number of total OTUs observed in each sample. SG = slow-

469 growing fungi, FG = fast-growing fungi.

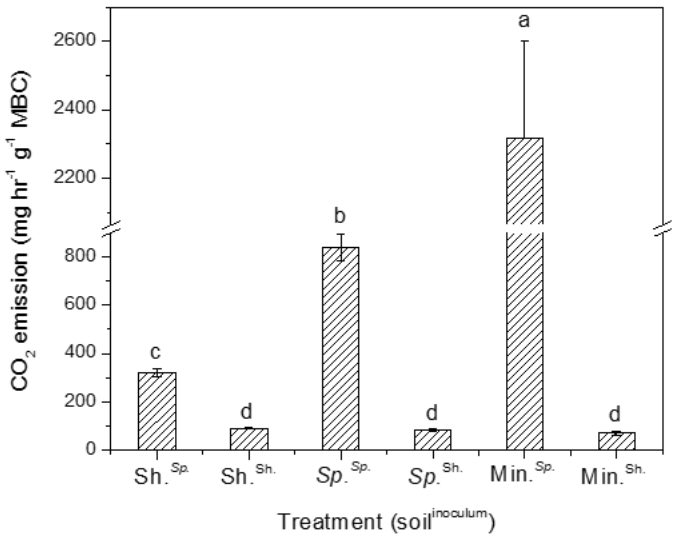


Fig. 4 Standardized CO_2 emission (mean ± S.E.) **from sterilized soil media that include the boreal *Sphagnum* peat from Minnesota (*Sp.*), the subtropical shrub peat from North Carolina (Sh.) and the labile carbon–enriched mineral soil (Min.).** All media were inoculated by inoculum made from the *Sphagnum*($^{Sp.}$) or shrub ($^{Sh.}$) peat. MBC represents microbial biomass carbon. Standardized CO_2 emission was calculated based on the amount of MBC added to the soil media. Different letters indicate significant differences among treatments.

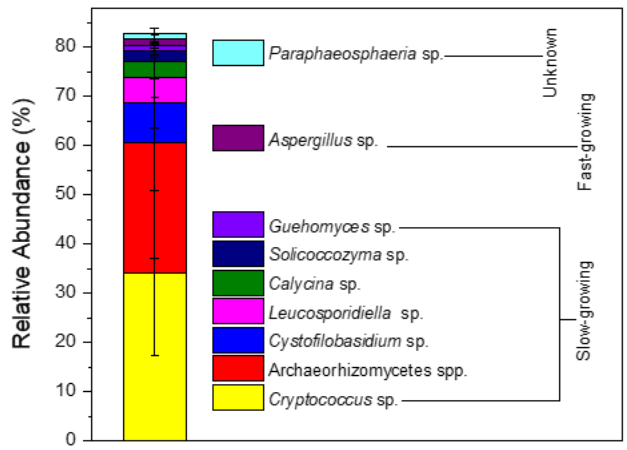


Fig. 5 Relative abundance (mean ± S.E.) **of the dominant fungi** (OTU relative abundance >1%) **in Dajiuhu subtropical peatland in China** (see Supplementary Table 2 for ecological traits of the dominant fungi).

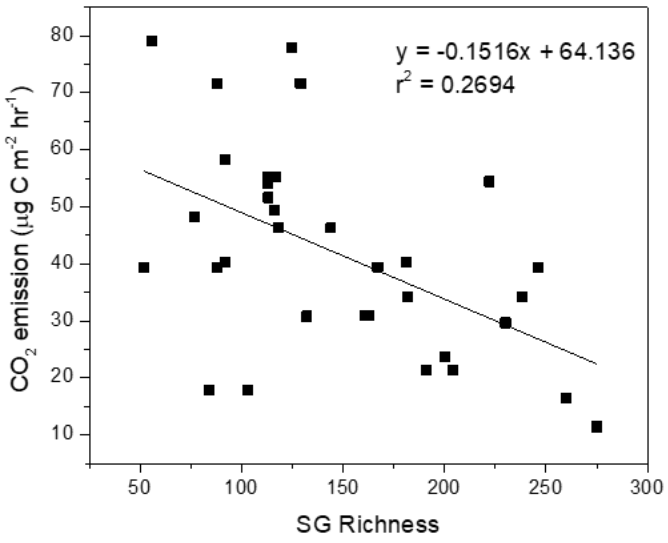


Fig. 6 The relationship between richness of slow-growing fungi and CO_2 emission in wooded peatlands in the Pacific coastal temperate rainforest in Canada. The richness of fungi was recalculated from raw amplicon reads in the European Nucleotide Arch Archive ITS(ERS1798771-ERS1799064), CO_2 emission data were collected from the Hakai Institute data repository at https://doi.org/10.21966/1.715630. SG = slow-growing fungi.

Supplementary Information (SI)

Vegetation and Microbes Interact to Preserve Organic Matter in Wooded Peatlands.

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This SI includes:

Methods

Supplementary Figures 1, 2, 3 and 4

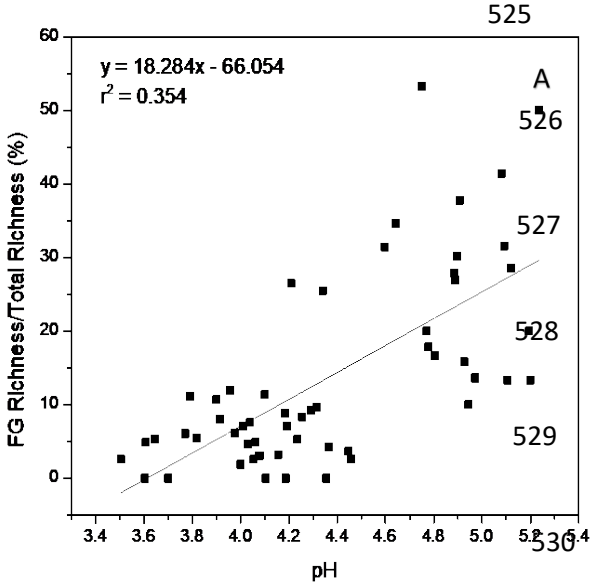
Supplementary Tables 1 and 2

References for SI only

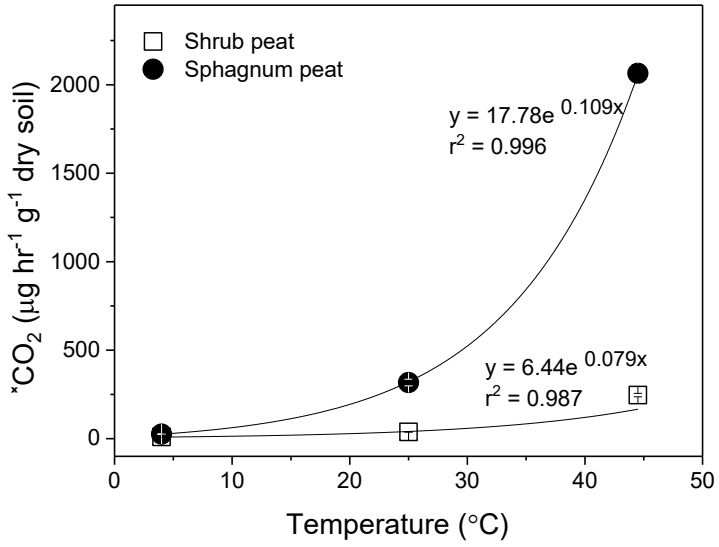
Methods

Bioinformatic analysis

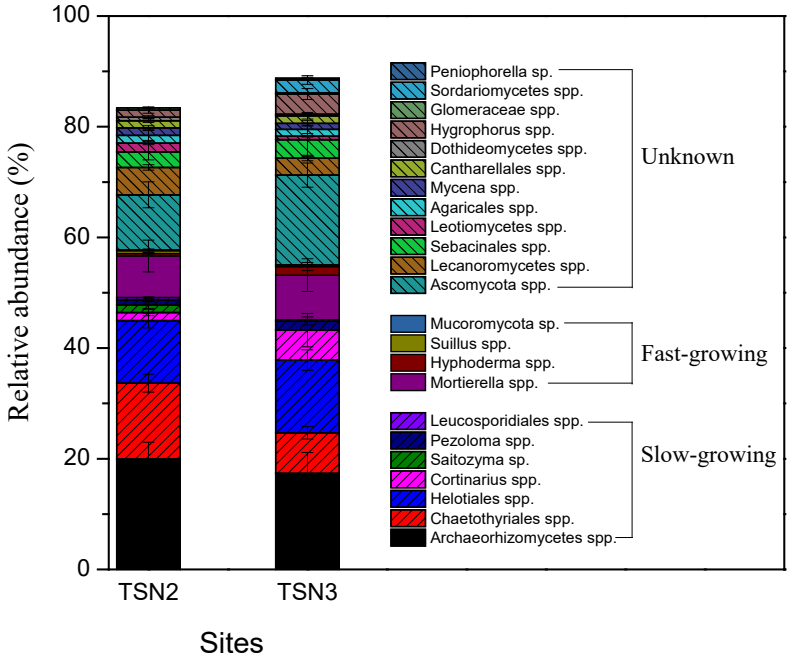
The trimming, sorting and quality filtering of reads were processed using the QIIME Pipeline[45]. All sequences were demultiplexed into samples based on unique identification barcodes using the split_libraries_fastq.py script. As ITS1f and ITS4 are too long to pair-end, the sequences from both primers were processed separately. Sequences were sorted by gene region and primers were removed using cutadapt, and then reads were trimmed to 220 bp using -fastq_filter with a q10 minimum value as a quality filter. Sequences were dereplicated and singletons were removed. The ITS2 region from the remaining sequences was identified and extracted using the fungal ITSx software[46]. Chimeras were detected and eliminated using the UCHIME program [47] referenced with the UNITE database (https://unite.ut.ee/) [48]. Non-chimera sequences that passed the filtering processes were binned into operational taxonomic units (OTUs) at a 97% similarity cutoff using the UPARSE pipeline[47]. All singletons OTU were excluded from the dataset. Subsequently, the taxonomic identity of each OTU was determined based on BLAST search against the UNITE reference database. The quality and depth of coverage of both primers reads were not significant difference, thus libraries from ITS1f reads were used for further analysis of fungal communities.



Supplementary Figure 1. Effects of pH on ratios of (A) fast- and (B)slow-growing fungal richness to total richness. Species richness is the number of total OTUs observed in each sample. SG = slow-growing fungi, FG = fast-growing fungi

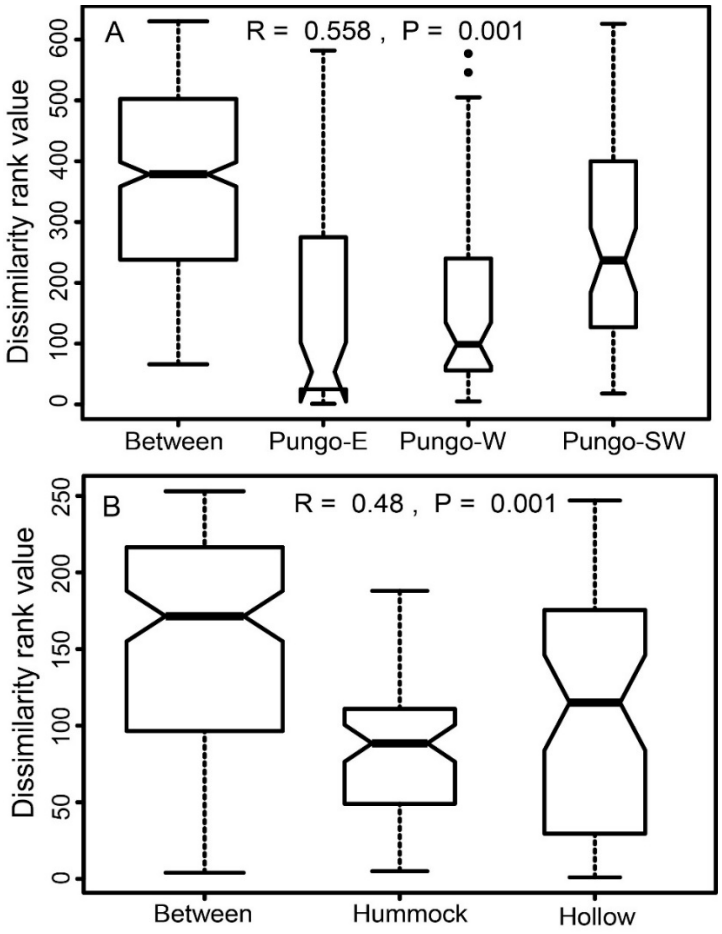


Supplementary Fig. 2 Temperature sensitivity of soil respiration (mean ± S.E.) in the subtropical shrub and the boreal *Sphagnum* peats through a lab incubation experiment. Regression analyses were run using $R = \alpha e^{\beta T}$, where R is soil respiration, coefficient α is the intercept of soil respiration when temperature is zero, coefficient β represents the temperature sensitivity of soil respiration and T is soil temperature.



546

547 **Supplementary Fig. 3 Relative abundance (mean ± S.E.) of the dominant fungi (OTU**
548 **relative abundance >0.1%) in a bog forest (TSN2) and a *Sphagnum*-shrub mixed peat bog**
549 **(TSN3) in the Pacific coastal temperate rainforest in Canada** (ref.36). The ecological traits of
550 the dominant fungi present in Supplementary Table 1. The relative abundances were recalculated
551 from raw amplicon reads in the European Nucleotide Archive [ITS(ERS1798771-ERS1799064)].



552

553 **Supplementary Fig. 4 Analysis of similarities (ANOSIM) plot showing dissimilarity**
554 **between and within sites at (A) the shrub peatlands in NC and (B) the *Sphagnum* peatlands**
555 **in MN.** Bold horizontal bar in the box indicates median; bottom of the box indicates 25th
556 percentile; top of the box indicates 75th percentile; whiskers extend to the most extreme data
557 point, which is no more than the range (i.e. 1.5) times the interquartile range from the box; width
558 of the bar is directly proportional to sample size.

Supplementary Table 1 Characterization of research sites at Pocosin Lakes National Wildlife Refuge, Marcell Experimental Forest and Dajiuhu, add Canada sites

	Pocosin Lakes National Wildlife Refuge, USA			Marcell Experimental Forest, USA		Dajiuhu Peatlands,China	Calvert Island Field Station (ref. 36),Canada	
Sites	Pungo West	Pungo Southwest	Pungo-East	S1H4S1 (Hollow)	S1H4L1 (Hummock)	N/A	TSN2 (Bog forest)	TSN3 (*Sphagnum*/shrub bog)
Coordinate	35.68882°, -76.56437°	35.673478°, -76.5581°	35.69078°, -76.52856°	47.50871°, -93.45240°	47.5084°, -93.45163°	31.48333°, 109. 98333°	51.65222°, -128.19272°	51.65139°, -128.12861°
Dominant Species	*Ilex glabra, Lyonia lucida*	*Ilex glabra, Lyonia lucida, Woodwardia virginica*	*Lyonia lucida, Ilex glabra, Zenobia pulverulenta, Gaylussacia frondosa, Vaccinium formosum, Pinus serotina*	*S. fallax S. angustifolium, Picea mariana, Pinus resinosa, Larix laricina,*	*S. angustifolium, S. magellanicum, Ledum groenlandicum, Chamaedaphne calyculata, Vaccinium oxycoccos, Picea mariana, Pinus resinosa, Larix laricina,*	*Sphagnum palustre Crataegus wilsonii*	*Pinuscontorta, Chamaecyparis nootkatensis, andThuja plicata.*	Abundant ericaceous shrubs and *Sphagnum* spp
Mean Water Level	*-39.6**	*-22.0**	*-30.5**	N/A	N/A	N/A	*-31.7*	*-40.7*
MAT(°C)	16.8			3.3		7.2	N/A	N/A
Soluble Phenolics in soil (μg C/g dry soil)	858±64	1171±98	658±137	114±11	107±21	89±26	N/A	N/A
TIN (μg N/g dry soil)	76±8	37±10	49±4	202±28	130±23	90±16	30.1±4.5	55.7±8.2
TN	1.89±0.08	1.88±0.07	1.11±0.04	1.42±0.14	1.35±0.24	N/A	1.13±0.04	1.40±0.05
TC (%)	55.91±0.78	51.33±0.71	50.09±0.93	43.69±1.02	44.52±2.58	38.0±7.4	55.5±0.9	57.6±1.1
pH	4.06±0.05	4.19±0.04	3.86±0.08	5.00±0.06	4.76±0.09	4.7±0.12	3.76±0.04	3.72±0.06
SM (%)	241±33	322±15	253±29	1214±91	1328±117	398±104	`966±43	820±54

MAT = Mean Annual Temperature
TIN =Total Soil Inorganic Nitrogen (NO_x-N + NH_4-N)
TN =Total Soil Nitrogen
SM =Soil Moisture
TC = Total Soil Carbon
N/A = not available
* mean water level from 3/17/2015 to 10/05/2017 at Pocosin Lakes National Wildlife Refuge

Supplementary Table 2 Growth rates of dominant fungi in the subtropical shrub and the boreal *Sphagnum* peatlands

Division	Lower taxa	Growth rates	Dominant Fungi		Ref.
			Shrub sites	*Sphagnum* site	
Ascomycota	*Archaeorhizomyces* spp.	Slow	+	−	30, 49
Ascomycota	*Pseudogymnoascus roseus*	Slow	−	+	50
Ascomycota	Helotiales sp.	Slow	+	−	31, 51
Basidiomycota	*Cryptococcus* sp.= *Saitozyma* sp.	Slow	+	−	52-54
Basidiomycota	*Solicoccozyma* sp.	Slow	+	−	52
Basidiomycota	*Guehomyces* sp.	Slow	+	−	54
Basidiomycota	*Cystofilobasidium* sp.	Slow	+	−	52-54
Basidiomycota	*Leucosporidiella* sp.	Slow	+	−	53
Ascomycota	*Calycina* sp.	Slow	+	−	55
Ascomycota	*Chaetothyriales* spp.	Slow	+	−	56, 57
Basidiomycota	*Cortinarius* spp	Slow	+	−	58
Ascomycota	*Pezoloma* spp.	Slow	+	−	59
Ascomycota	*Pseudeurotium* sp.	Fast	−	+	60
Ascomycota	*Penicillium* sp.	Fast	−	+	61, 62
Ascomycota	Saccharomycetales sp.	Fast	−	+	63
Basidiomycota	*Rhodotorula* sp.	Fast	−	+	64
Zygomycota	*Mortierella* spp.	Fast	−	+	65, 66
Basidiomycota	*Bullera* sp.	Fast	+	−	67, 68
Ascomycota	*Aspergillus* sp.	Fast	+	−	29
Basidiomycota	*Hyphoderma* spp.	Fast	+	−	69
Basidiomycota	*Suillus* spp.	Fast	+	−	70
Zygomycota	Mucoromycota sp.	Fast	+	−	71

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Rebuttal Letter

Thank you for the helpful comments on our manuscript. We have carefully reviewed each comment and have made changes where appropriate. Here are our point-to-point responses:

Reviewer #1 (Remarks to the Author):

Dear authors,

With much interest I have read and assessed you manuscript that describes a series of observations that show that peatland differ in the composition of fungal communities and that these different communities have different life-history traits that relate to carbon dynamics. These results are claimed to solve the paradox that with warming peatlands still sequester C.

Reviewer's Comment 1: The introduction is quite clear, although I feel that the connection between paleo-evidence on the role of vegetation on C dynamics and the current approach, i.e. environmental gradient study – needs to be made more explicit. Perhaps interesting in the context of the present study is this paper: https://www.nature.com/articles/s41467-017-01350-5

Response: Thanks for bringing up this interesting paper, which, consistent with our research, shows that shifts in plant communities in bogs are a biotic factor and could adapt to climate change and maintain similar ecological functioning. In our revision this paper is added to strengthen our deduction on the importance of biotic factors in the section of Introduction.

Reviewer's Comment 2: With disqualifying the 'current abiotic-factor-dependent peat decay models' based in Fig.1, I feel the authors are taken a short-cut. The figure only shown soil respiration against MAT, while water table is ignored but stated are a major driver for the models they disqualify.

Response: Water levels were added to Supplementary Data 1 in the revision. However, we did not find any significant relationship between water level and SR in the whole data set or under similar MATs.

Reviewer's Comment 3: In the introduction i.m.o. a few references are not used correctly: Ref 1& 2 (l42) are not at all making a statement on the peatland C pool. I'd suggest to have a

look

at https://agupubs.onlinelibrary.wiley.com/doi/10.1029/2010GL043584 & https://www.nature.com/articles/s41561-019-0454-z.

Response: After pursuing the suggestions, we found that Yu et al. provided a reliable source[1], while Nichols and Peteet's results[2] were questionable (see 10.31223/osf.io/kafcu, and 10.31223/osf.io/hynm7). Carbon stores in both boreal and tropical peatlands were added together, and the references were updated accordingly in the revision.

Reviewer's Comment 4: Ref 7 (l49) does not deal with feedbacks, but shows that only slight increase in temperature lead to respiration of old carbon.

See https://onlinelibrary.wiley.com/doi/pdf/10.1111/gcb.14140 for an alternative.

Refs 17 (l70), 19-21 (l72) are not dealing with the effects of plant community composition on microbial communities in peatlands. Yet, a wealth of research has been published recently which I think is actually much ignored in the introduction. Some

examples: https://besjournals.onlinelibrary.wiley.com/doi/pdf/10.1111/1365-2745.12413, https://www.sciencedirect.com/science/article/pii/S0038071714004027.

Response: Ref 7 was replaced with the recommended Ref [3]. Ref 17 shows the top-down and bottom-up regulations, Refs 20 and 21 clarify roles of microbe and plant shifts, respectively, in ecosystem functioning. Ref 19 is a synthesis of Refs 20 and 21, which shows the complex adaption of peatlands. Therefore, we kept the original Refs 17, 19-21 in the revision.

There are many good papers about the feedbacks, however, due to limited numbers of references allowed in this journal, we did not add the recommended two papers that mainly focus on methanogens and methanotrophs in peatlands.

Reviewer's Comment 5: When describing the site locations for the first part of the story (l81-93), I find it hard to link this to a space-for-time approach. Only the data in Fig 1 can be linked to a space-for-time approach, the others part of this work are site comparisons. Clarity needs to be given. As written now, the sampling efforts seem all ad-hoc; samples were taken at two sites, then some extra sites were measured. I would urge the authors to ty to build a narrative. This actually becomes even more apparent when in the discussion part, suddenly data on a Chinese peatland surfaces, and later a re-analysis of data on pacific-coast peatlands. In my opinion, the

way the manuscript is presented is more like a gathering of data-sets that if alone would not warrant publication, and which are now forcedly brought together.

Response: Yes, we added several experiments based on several experts' comments (see the Acknowledgement) and the questions raised from our initial results at the sites in North Carolina and Minnesota. Rather than a single experiment, our study also included a literature synthesis, three field experiments and three lab incubations, all of which made a logical progression to solve our major scientific questions.

Combined the second and third Reviewer's comments on the structure of this manuscript (comments 15, 20, 21 and 43), we reorganized it in a more coherent way. Briefly, we first focused on our results with some short discussion in the context, then had a discussion with some implications.

Sphagnum mosses might be gradually replaced by shrubs in boreal peatlands under climatic warming and drought in future evidenced by aerial photo comparisons, plot-scale observations, and many climate-change manipulation experiments [e.g.3-16], which would likely be similar to our shrub site that 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. Therefore, this could be a model for space-for-time substitution study in peatlands. The sentence is rephrased to "We used space-for-time substitution to study shifts of ecological processes in peatlands over a long term" Finally, we have added a new paragraph organizing our combined studies at the end of the Introduction and new subheadings in the R& D to aid the reader in following our experimental and supporting evidence.

Reviewer's Comment 6: (l90-91) what are these pilot results?

Response: Initially the sentences of "Our pilot results… Hence, two wooded peatlands were further tested in subtropical southern China and temperate western Canada." was a short context that showed readers the reason why we add two more sites in this study. After restructuring this manuscript, we deleted these sentences in the revision.

Reviewer's Comment 7: (l97-98) can you underpin, by literature, that fungi are the main decomposers in peat? I think you need to explain this choice a bit better. Prokaryotes are actually

quite important in peatlands, especially when condition get wetter. Similarly, how can you be sure that soil respiration rates as presented in Fig. 4 are fungal-driven and not by bacteria?
Response: Based on most published studies, we initially speculated that fungi were the dominant decomposers in peatlands, which dominantly happened in the surface aerobic layers. After digging deeper into literature, we did find several studies indicating that bacteria play a role as important as fungi in decaying acidic and recalcitrant peat. To fully address this question, we added new experiments to test the relative contributions of bacteria and fungi to aerobic peat decomposition. Key to carbon accumulation is the amount of recent organic matter at the surface aerobic layer (acrotelm) that can be partially kept until it can later be buried under anaerobic zone, where the decomposition is much slower than in the surface layer. Therefore, our test focused on aerobic peat decomposition. Our results show that fungi dominantly control peat decomposition in the unsaturated layers (Supplementary Fig.1). Please see all details in the section of Methods and the Supplemental introduction and results for separating the relative contributions of fungi and bacteria to peat decomposition.
The inoculum for Fig. 4 was the filtrate passing through a Buchner funnel (without filter, pore size 0.25–0.5 mm). Other than macro-decomposers like insects and worms, all microbes including both prokaryotes and eucaryotes were presented in the incubation experiment.

Reviewer's Comment 8: (l100) 'The *Sphagnum* and shrub peatlands distinctively differed in the fungal community'. Sure they do but the sites are hardly comparable in environmental conditions! Are we now not comparing two different types of peatland and they start guessing if observed differences are plant driven or environment driven?
Response: Yes, the environmental conditions between two sites are different after thousands of years, which have shaped different plant communities as well as microbial communities. They all are peatlands while at different states.

Reviewer's Comment 9: I wonder if it would not be better to perform a numerical test (e.g. PCA, RDA) to determine which physicochemical parameters control fungal community composition?
Response: In the revision, we performed both Mantel and RDA tests to determine which soil physiochemical parameters control fungal community composition. Both tests indicated that

soluble phenolics and pH were most important drivers for fungal communities (Supplementary Fig. 3, Supplementary Table 3). 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. 5 A,B) and pH (Fig. 5 C,D), respectively. As showed by stepwise regression phenolics were the dominant factor controlling soil pH ($r^2 = 0.455$, $P < 0.0001$) in these sites, and thus we speculated that phenolics may act as the overarching regulator. New Supplementary Fig. 3 and Supplementary Table 3 were added, and the detailed statistical methods as well. The whole paragraph was also rephrased.

Reviewer's Comment 10: I think that the conclusion that these findings provide new insights that enduring peatlands …. gradually shift to a new equilibrium state… (l206-209) is inappropriate. A comparison between peatlands has been made, but the nature of the research makes it hard to tell what the underlying drivers for differences are.
Response: We made this claim a little softer although we believe our data and analysis when combined with other literature, support our view of differences in the underlying drivers. The sentence was rephrased as "our findings suggest that enduring peatlands that are highly resistant to increased temperature and natural drought may gradually shift to a new equilibrium state 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)."

Reviewer #2 (Remarks to the Author):
Wang et al. 2020 – Nature – Earth & Environment
Very well written abstract and informative.

Reviewer's Comment 11: This is a nice study presenting a synthesis of soil respiration data (although not quite comprehensive for North America), soil analyses at two contrasting bog in term of vegetation and climate settings and an incubation experiment. I find the result very interesting BUT way too highly out of bound and speculative to apply the results to the vast expanses of the boreal peatlands of North America and Russia. The authors have conducted very good work but should be more rigorous with their inferences. Besides this main comment, I have

no problem with the article. It is a very popular topics currently and the scientific findings will open the doors to a lot more investigations (to prove or disprove the conclusions of this paper). The data are well analysed. So in all I would recommend the publication of the manuscript.
Response: We have added new information and clarified our position as noted in comment 10. We have also toned down our inferences about all peatlands.

Reviewer's Comment 12: Line 46-48: be careful with such big claim: Climate warming and drought not only increase peat loss by accelerating decomposition but also cause substantial losses of the keystone mosses like Sphagnum in the vast boreal peatlands, followed by shrub expansion and its uncertain effects4-6 – First, I am a boreal peatland ecologist and this is largely untrue. Also we cannot check Talbot ref (incomplete), Bragazza and Swiss colleagues only worked and did their study in Switzerland and then made large inferences from analytical work. The alpine peatlands of Switzerland are very different then the vast boreal peatlands. And your own citation, Wang et al are studies done in the Pocosin peatlands (NC) so far from the vast boreal peatlands which as far as I know have not lost their Sphagnum cover.
Response: We are so glad to know that the reviewer has not seen massive *Sphagnum* lost in the vast boreal peatlands, although many studies including aerial photo comparisons, plot-scale observations, and climate-change manipulation experiments [e.g.3-16] have shown that shrubs have been expanding in some boreal peatlands, particularly in some drained area. After reviewing more literature, we kept this claim with more specifications. It was rephrased as "Many experiments have shown that climate warming and drought may not only increase peat loss by accelerating decomposition but also cause substantial losses of the keystone mosses like *Sphagnum* in the vast boreal peatlands, followed by shrub expansion and its uncertain effects." in the revision.

Reviewer's Comment 13: Line 57-58: I am surprised to see so little data from Canada and the one cited dates. What about: Solondz et al. 2008 (Ecohydrology); Munir et al 2017 (Forests); Bubier et al 2003 (Ecosystems); Dalva et al. 2001 (JGR). I would be surprised that most Canadian studies do not meet the author selection criteria.
Response: More data from Canada were added in the revision and strengthen the paper.

Reviewer's Comment 14: Line 89-90: I would strongly challenge this claim: These shrub species in pocosins are similar to the expanding shrubs found in *Sphagnum* peatlands across boreal areas4, 5. I would say absolutely not true. Also easy to see from your Table 1 comparing Marcell bog with the studied pocosin.

Response: Many studies[e.g.3-7] found shrubs encroachment, Ericaceae in particular, happened in long-term climate-change manipulation experiments and drained peatlands in boreal area. Therefore, we specifically rephrased this sentence as: "These shrub species in pocosins are similar to the expanding ericaceous shrubs found in some drained *Sphagnum* peatlands in boreal areas"

Reviewer's Comment 15: I find it disturbing to see a conclusive sentence such as: line 90-92: Our pilot results in the Sphagnum site are in line with the observations in many boreal peatlands, while such studies in low latitude system are still rare. While we have not yet seen any data. In general I do not like to see a section of Results and Discussion together, harder to first assess only the results based on the reviewer expertise. I would strongly suggest to present results first and then discussed it.

Response: Thanks for this constructive comment. We restructured our manuscript in a more coherent way. Briefly, we first mainly focused on our results with some short discussions in the context, then had discussions with implications. Some short discussions in the results were still kept helping readers understand the content smoothly, hence we did not fully separate the section of Results from Discussions in the revision. The sentence **"**Our pilot results in the *Sphagnum* site are in… Hence, two wooded peatlands were further tested in subtropical southern China and temperate western Canada" was deleted in the revision.

Reviewer's Comment 16: Line 86: the authors keep talking about shrubs but no species are mentioned – it appears that all is mixed up (kalmia, birch, willows etc).

Response: Plant species and other site information for all sites were listed in Supplementary Table 1. In the revision, Supplementary Table 1 was cited when first introducing the sites. Also, species were described in detail only in the section of Methods due to the word limit in the main text in this journal.

Reviewer's Comment 17: Line 89-90: Again the authors write: These shrub species in pocosins are similar to the expanding shrubs found in Sphagnum peatlands across boreal areas4, 5. But this is totally not substantiated as discussed above.
Response: Please see our response to Reviewer's Comment 14

Reviewer's Comment 18: Line 98-99: this result appears to be an important one to the whole discussion of the paper – I do not understand the choice to put the evidence data in a supplementary table.
Response: Thanks for this suggestion. Due to only limited figures and table allowed in the main text, we still think this table is not as important as other figures. To add other essential information in this table to the main text, we rephrased the results in this table as "Compared to the *Sphagnum* peat, in the shrub peat soil pH, concentration of inorganic nitrogen and soil moisture were lower, while dissolved phenolics were 6-8 times higher (Supplementary Table 1)".

Reviewer's Comment 19: Line 124-125: This is core to the argument the relationship between pH and fungi dynamic, so Supplementary Fig. 1 should be part of the main text of the article.
Response: This figure was combined into Figure 3 in the revision.

Reviewer's Comment 20: Line 166: Was really a field experiment done? I understand that soil was sampled and analysed at two different locations (Marcell bog and Pocosin) but was an experimental design implemented? Line 168: this statement is highly speculative. We are not at the point of making this jump in conclusion.
Response: In the revision, we restructured the whole manuscript and put these conclusive sentences to the end of discussion.

Reviewer's Comment 21: Line 180-181: this is the original results from this study – I do not understand 1) why not presented in main text and 2) why coming much later in the logic of the discussion. This confirms that it would be much better to present results first and then have sub-heading in the discussion for the 1, 2 or 3 messages the authors want to convey.
Response: These results were moved into a better location with other results in the revision.

Reviewer's Comment 22: Line 186: as said before the Swiss study is an altitudinal study not a climate change one – yes a proxy – but to apply their results of the very tiny peat wholes they have in Switzerland to the vast mires of northern Europe and North America is way too large of a step. The authors have enough interesting results without doing these speculations.
Response: This speculation was deleted in the revision

Reviewer's Comment 23: Line 188-190: All my life I walked in peatlands where some parts are open, some are very shrubby with close to no Sphagnum and some are treed. Studying a patch of a shrubby Sphagnum bogs does not mean shrubs are expanding in their abundance. I still have to see a solid study on that claim.
Response: After carefully reviewing the literature, we find there are many observations that do show shrubs have been expanding in boreal *Sphagnum* peatland [e.g. 5,8-16]. In the revision, we reduced these speculations. Also see our response to Reviewer's Comment 12.

Reviewer's Comment 24: Line 190: The authors of citation 37 absolutely do not report as done here: which shows that the on-going shrub expansion in some boreal peatlands have shifted in 191 sync from fast-growing to slow-growing microbes - wrongly cited.
Response: This speculation was deleted.

Reviewer's Comment 25: Line 191-197: while I agree with was what is reported here, it is clear that fungi composition depends on the surface plant community but there is no implication about shrub expansion into bogs.
Response: We primarily presented the evidence that slow-growing fungi were found dominant in these shrub peatlands. One more recent paper[17] was also added, in which the relative abundances of slow-growing Archaeorhyzomycetes were 1.4±3.3%, 0.5±0.6%, and 42.7±28.8% in mosses-, graminoids- and ericoid shrub- dominated sites, respectively on an upland plateau peatland in Czech Republic. Therefore, plant community shift may significantly affect microbial composition underneath.

Reviewer's Comment 26: Line 40: better cite a more recent estimate of 2.84% see: Xu, J., Morris, P. J., Liu, J., & Holden, J. (2018). PEATMAP: Refining estimates of global peatland distribution based on a meta-analysis. Catena, 160, 134-140.
Response: This reference was added in the revision.

Reviewer's Comment 27: Line 202: write: the no exponential rise (to make it an enumeration of reasons before the statement.
Response: This statement was deleted in the revision.

Reviewer's Comment 28: Line 209: plant? And not plan
Response to Reviewer's Comment 28: It was corrected.

Reviewer's Comment 29: Line 228: when switching back to Lake Pungo, tell the reader that you are back in NC.
Response to Reviewer's Comment 29: It was added.

Reviewer's Comment 30: Line 226 to 237: the sites description would be more easily grasps if presented in a table format.
Response: The sites information was presented in Supplementary Table 1, which was cited in the revision.

Reviewer's Comment 31: Line 240 and 560: the species name of Ledum groenlandicum is now Rhodendron groenlandicum
Response: It was updated.

Reviewer's Comment 32: Line 248: with dense and layer not in italics
Response: It was corrected.

Reviewer's Comment 33: L32 replace > with "more than"
Response: It was replaced.

Reviewer's Comment 34: L46-47 this is untrue
Response: See the detailed response in our response to Comment 12.

Reviewer's Comment 35: "… a catastrophic positive.." is alarmist the tone here.
Response: Word "catastrophic" was replaced with "substantial"

Reviewer's Comment 36: L56 the authors might be interested to see this study: Bérubé, (2018). Production and decomposition rates of different fen species, Ecological indicators, 91, 105-115. Where detailed stratigraphic analyses demonstrated the importance of the presence of bryophytes in peatland vegetation of boreal fen to lead to greater peat accumulation.
Response: Thank you for the recommendation. However, we feel this is a short-term study, thus we did not add it to our manuscript.

Reviewer's Comment 37: L90, The logic of discussion here is not clear
Response: These sentences were deleted after restructuring the whole manuscript.

Reviewer #3 (Remarks to the Author):

H. Wang, J. Tian, H. Chen, M. Ho, R. Vilgalys, X. Liu, and CJ Richardson. Vegetation and microbes interact to preserve organic matter in wooded peatlands.

Summary

In this paper, Wang et al., cite the prevalence of low latitude peat accumulation under warm and seasonally oxic conditions to challenge the widespread view that cold anoxic conditions are the primary inhibition of organic matter decomposition facilitating accumulation of peat. Instead Wang et al. proffer a microbial explanation wherein slow-growing microorganisms types dominate wooded peatlands accounting for slow organic matter decomposition rates despite warmer temperatures.

General Impression

Reviewer's Comment 38: Although the manuscript is based on an intriguing hypothesis, a few key points seem to be lacking rigorous support. For example, much is made of the trade-off between slow-growing and fast-growing microorganisms in Sphagnum-dominated versus woody peatlands. However, it is unclear how microorganisms (and after reading further it's really just fungi since bacteria were not measured) were assigned to these groups since line 136 states "It is impossible to measure the relative growth rates of the dominant microbes in this study, because so many of the fungi are unculturable." How can effects be attributed to a factor that is unmeasurable?

Response: Please first see our response to the Reviewer's Comment 7, we found fungi were the predominant decomposers in our sites. Although we did not measure the bacterial composition, other measurements at the same sites in North Carolina and Minnesota show the dominant bacteria in both sites also grew slowly. It is common that microbes are unculturable in vitro. We were eager to culture them, but we had to give it up after many tries. Hence, we can't directly detect the growth of dominant fungi. This is also the reason why we moved to indirect measurements in this study. Through the incubation experiment, we verified that the microbial metabolism in high-phenolic shrub peatlands is slower than in the *Sphagnum* peatlands.

Reviewer's Comment 39: Another example is that the authors claim differences in carbon lability among the sites, but it is not clear how carbon lability was either defined or quantified. For example, in line 144, how were "labile and complex organic material" differentiated? Or in line 145, how was it determined that the shrub peat is more highly recalcitrant than the Sphagnum peat? And what do the authors mean by "recalcitrant" since they state on line 182, that "the fast-growing microbes decomposed highly recalcitrant peat more quickly than the slow-growing microbes"? If the material is truly recalcitrant it should not be degraded quickly. From the statement on line 182, it seems more likely that the OM under consideration is not recalcitrant per se, but rather is simply not a preferred substrate of the slow-growing microorganisms.

Response: To make it clear, we replaced "labile and complex organic material" with "labile glucose and complex peats". Recalcitrant carbon is organic material resistant to decomposition, which general contains high aromatic content. We cited a paper[18], which provide evidence that

the recalcitrance increases from boreal *Sphagnum*-dominated to tropical/subtropical wooded peatlands on the original line 145.

Thanks for raising this question on line 182. As we had a short-term incubation to avoid microbial acclimation to the assay chemistry[19,20] in this experiment, the higher rates of microbial respiration happened in the *Sphagnum*-inoculum inoculated than shrub-inoculum inoculated shrub peat. This means that fast-growing microbe from the *Sphagnum* inoculum can decay carbon in labile or recalcitrant form in the shrub peat in higher rates than the original microbes did in the shrub peat. Although we can't identify whether labile or recalcitrant compounds in the shrub peat contributed most to the observed respiration from the microbes in the *Sphagnum* inoculum, the shrub peat relative to the *Sphagnum* peat is for sure more recalcitrant with higher aromatic contents[18]. In the revision, this sentence was rephased as "Although the shrub peat is more highly recalcitrant than the *Sphagnum* peat[18], the fast-growing microbes from the *Sphagnum* inoculum decomposed the soil carbon in the shrub peat 4 times faster than the microbes from the shrub peat did." Instead of "…decomposed the shrub peat…" we used "…decomposed the soil carbon in the shrub peat..." to include both labile and recalcitrant organic compounds.

Reviewer's Comment 40: Further, in line 148, the authors suggest that "the decomposers ultimately determine the decomposition rate", however, that conclusion is in direct contradiction to the results presented in Figure 4 which demonstrate that the rates of the Sphagnum inoculum are, in fact, modified by the available substrate. If decomposers ultimately determine the decomposition rate, there would be no significant differences among the various Sphagnum inoculated incubations.

Response: Here we emphasized that the reproductive strategies of microbes significantly impact the decomposition rate, more specifically the responses of fast-growing *r*-selective vs. slow-growing K-selective microbes to the provided food are different. To make it specific, the sentence was rephrased as "which indicates the reproductive strategies of decomposers (*r*- or K-selective) significantly impact the decomposition rate."

Reviewer's Comment 41: With further regard to the incubations, why were incubations conducted at 25°C (line 306) which is much higher than the MAT at any of the sites in Table S1.

Given the extreme differential temperature sensitivity of the Sphagnum community relative to the shrub community (Fig S2) could the results in Fig 4 be influenced by this temperature difference in addition to substrate? It seems that the Sphagnum community would be favorably selected at this warmer temperature, which I think is a consistent alternate (or at least contributing) explanation for the results in Fig 4.

Response: MAT represent mean annual temperature. Temperatures of 25°C occur in both sites in summer. To our knowledge, experiments comparing decomposing capabilities of different microbial communities are operated under a similar temperature. In Fig. S2, we showed several temperature responses and even at 4 °C the rate of soil respiration in the *Sphagnum* peat was about 3 times higher than the shrub peat. The higher temperature sensitivity of the *Sphagnum* microbes relative to the microbes in the shrub peat post a higher risk of carbon loss in boreal peatlands under a warming climate.

Reviewer's Comment 42: It's not clear to me why carbon-enriched mineral soil was chosen for the incubations (line 141) instead of adding labile carbon to peat. Changing to mineral soil seems to me to introduce many more variables besides just the labile C, e.g. pH and potentially essential cations that may alter microbial activity. I think this part of the experiment should be more fully explained and the implications carefully considered.

Response: To avoid the effect of peat chemistry, we added glucose to a low-nutrient poor mineral soil to make the labile-carbon medium. We aimed to see how these microbes respire labile carbon alone, not the priming effects of labile carbon on peat decomposition.

Reviewer's Comment 43: The study sites in China and Canada seem like a last-minute add-on that were not well-incorporated into the rest of the study. They are treated very briefly; if the results were presented, I missed them and they were scarcely explained. I would encourage the authors to more fully explain how the results from these sites support their hypothesis.

Response: We reformatted our manuscript and incorporated these results to provide additional support to our objectives and main hypotheses.

Reviewer's Comment 44: The abstract includes phrases such as "…we present a…natural

course that curbs carbon loss against climate change" and "…high-phenolic shrub/tree induced shifts in microbial composition may compensate for positive effects of temperature and/or drought" these phrases hint to me of a trade-off between fast-growing microorganisms in Sphagnum-dominated peatlands where OM quality is low versus slow-growing microorganisms in woody peatlands where OM quality is high. However, this interpretation seems contradictory to the statement on line 32 which suggests that Sphagnum-associated OM is labile while woody OM is high(ly?) recalcitrant (line 29). I am left puzzled whether the authors intend to convey a trade-off between microbial growth rates and OM quality which offset to more or less maintain slow overall decomposition rates across all peatlands or whether instead the trade-off is between microbial growth rates and environmental conditions? (and indeed, after finishing the manuscript this question appears to me to remain unresolved).

Response: The terms of OM quality and carbon recalcitrance are different. Compared with shrub peat, the OM in the *Sphagnum* peat contains more labile carbon and is easier decompose, which translates to a high quality (more labile) carbon. This is the reason why low-temperature and anoxic conditions are so important in preserving these *Sphagnum* peat. In this paper, we show that the co-shifting microbe and plant communities that were initially triggered by climate change appear to exert important biotic controls on ecosystem C cycling and soil C sequestration over time, thus ensuring continuation of peat accretion in different climate states.

Reviewer's Comment 45: The abstract frequently refers to "microbes" and "microbial composition" as factors controlling decomposition, so I was surprised to learn on line 130 that bacterial composition was not measured at all in this study. I would recommend making it clear in the abstract that this study focuses solely on fungi to avoid the implication that the whole microbial community was measured.

Response: Although we did not measure bacterial composition, we reanalyzed the data recently available from other research in the same sites in North Carolina and Minnesota, where slow-growing bacteria dominate. We also added another experiment to test the relative contributions of fungi and bacteria to peat decomposition and found fungi to be the dominant peat decomposer. Moreover, we took both bacteria and fungi into account in the incubation experiment about the decomposing capabilities of microbes from both sites.

Reviewer's Comment 46: Lines 47-48, this reference seems relevant to the discussion: Norby, R.J., Childs, J., Hanson, P.J. and Warren, J.M., 2019. Rapid loss of an ecosystem engineer: Sphagnum decline in an experimentally warmed bog. Ecology and Evolution, 9(22), pp.12571-12585.
Response: We agree and include this reference in the revision.

Reviewer's Comment 47: Line 48, I'm not sure "invoke" is the right word here, perhaps "provoke"?
Response: "provoke" was used in the revision

Reviewer's Comment 48: Line 50: Was MAP or MAT meant?
Response: MAP should read MAT, and it has been corrected in the revision

Reviewer's Comment 49: Line 81, I don't think you need "as an alternative" in this sentence.
Response: It has been omitted.

Reviewer's Comment 50: Line 90-91, "Our pilot results in the Sphagnum site are in line with the observations in many boreal peatlands," this statement is rather vague. What results?
Response: This part has been removed.

Reviewer's Comment 51: Line 92-93, Where in China and Canada? Is the Canada site not boreal? Can you give lat/long as was done for Marcell and the Pocosins?
Response: All coordinates of the locations are now listed in the Supplementary Table 1.

Reviewer's Comment 52: Line 111: It would seem relevant to consider these results in the context of Woodcroft et al, (2018) who discuss the abundance of single C utilizers in Sphagnum peatlands: Woodcroft, B. J., Singleton, C. M., Boyd, J. A., Evans, P. N., Emerson, J. B., Zayed, A. A., et al., (2018) Genome-centric view of carbon processing in thawing permafrost. Nature, 560(7716), 49

Response: Woodcroft et al. provided an accurate prediction of carbon processing in peatlands based on meta-omics analysis. However, they focused on bacterial and archaeal communities in their whole paper. The single C utilizers are mostly from bacteria such as Methanotrophs and acetogens. In our sites, bacteria and archaeal communities only had a small contribution to peat decomposition. Therefore, we did not include this paper in our context.

Reviewer's Comment 53: Line 120-121, This line seems to suggest that the relationships between species richness and DOC, moisture, nitrate/nitrite and ammonium were tested, but I don't see those results presented. Further, there appears to be a significant relationship between species richness and pH (Fig. S1), so how was it concluded that phenolics were the primary driver and not pH or the interaction between the two? Perhaps some multivariate statistics (MANOVA) could be useful for further exploring these relationships.
Response: Please refer to the Response to Reviewer's Comment 9 where we explain our use of multivariate techniques in the revision.

Reviewer's Comment 54: Line 130, the microbial data for Marcell was somewhat limited in Wilson et al., (2016) I would recommend reviewing Lin et al., for a more thorough characterization of the microbial community at Marcell.
Lin X, Tfaily MM, Steinweg JM, Chanton P, Esson K, Yang ZK, Chanton JP, Cooper W, Schadt CW, Kostka JE. Microbial community stratification linked to utilization of carbohydrates and phosphorus limitation in a boreal peatland at Marcell Experimental Forest, Minnesota, USA. Appl. Environ. Microbiol.. 2014 Jun 1;80(11):3518-30.
Lin X, Tfaily MM, Green SJ, Steinweg JM, Chanton P, Imvittaya A, Chanton JP, Cooper W, Schadt C, Kostka JE. Microbial metabolic potential for carbon degradation and nutrient (nitrogen and phosphorus) acquisition in an ombrotrophic peatland. Appl. Environ. Microbiol.. 2014 Jun 1;80(11):3531-40.
Response: We have read through these papers before working on our manuscript. The relative abundance of Acidobacteria in Lin et al. were consistent with raw sequence data in Wilson et al. We hoped to reanalyze the sequence data from both Lin et al. and Wilson et al., in which the soil samples were collected in 2012 and 2014, respectively. However, the sequence data of Lin et al.

were not publicly available, and the required relative abundance of Betaproteobacteria was unavailable. As a result, we only reanalyzed the raw sequence data from Wilson et al. We did not include Lin et al. due to reference limits for the journal.

Reviewer's Comment 55: Line 181 and Fig S2, it seems curious that the *Sphagnum* community appears to be so strongly sensitive to such high temperatures (>40°C) despite their apparent acclimation to a much lower MAT (~3°C). What is the significance of that particularly with regard to the observation that these organisms do not seem to compete well at warmer, low-latitude sites?
Response: The reasons why these fast-growing microbes can't compete well in the shrubby low-latitude sides may be stemmed from highly recalcitrant carbon (low quality), lower nutrient, and higher C/N ratio in the shrub peat.

Reviewer's Comment 56: Lines 187-191, This is a long run-on sentence which is also difficult to parse. I would suggest breaking this sentence into smaller thoughts and rewording for clarity.
Response: We have reworded the sentence in the revision as "a *Sphagnum* peatland in Minnesota, USA, similar to our site in Dajiuhu peatlands, where ericaceous shrubs dominated the wooded cover, was also dominated by slow-growing fungi (Helotiales and Archaeorhizomyces, >80%)."

Reviewer's Comment 57: Line 209, "(likely bridged by plan-induced phenolics)", I don't know what this means, what are plan-induced phenolics and what do they bridge?
Response: Our study and analyses showed that phenolics from plants are the overarching factor impacting the fungal composition, this suggests that plant-induced phenolics link aboveground plant biomass quality with belowground microbes via decomposition byproducts like phenolics and aromatics.

Reviewer's Comment 58: Line 236, should be "One hollow and one hummock"
Response: The error has been corrected.

Reviewer's Comment 59: Line 243, should be "three soil cores at each site"

Response: The error has been corrected.

Reviewer's Comment 60: Lines 252-259, Where were the DOC, nitrate/nitrite, ammonium and TON results presented?

Response: These soil parameters were used as independent variable in the Mantel test and redundancy analysis (RDA), regression and correlation analyses (Supplementary Fig. 3 and Supplementary Table 3)

Reviewer's Comment 61: Line 305 why was only 5 mL of inoculum added to the mineral soil while 20 mL were added to the others?

Response: To maintain the soil medium aerobic conditions, 5 ml of inoculum was sufficient to moisten but not alter the aerobic soil environment.

References:

1 Yu, Z., Loisel, J., Brosseau, D. P., Beilman, D. W. & Hunt, S. J. Global peatland dynamics since the Last Glacial Maximum. *Geophys. Res. Lett.* **37**, n/a-n/a, doi:10.1029/2010gl043584 (2010).

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3 Gavazov, K. *et al.* Vascular plant-mediated controls on atmospheric carbon assimilation and peat carbon decomposition under climate change. *Global Change Biol.* **24**, 3911-3921, doi:10.1111/gcb.14140 (2018).

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6 Norby, R. J., Childs, J., Hanson, P. J. & Warren, J. M. Rapid loss of an ecosystem engineer: Sphagnum decline in an experimentally warmed bog. *Ecol. Evol.* **9**, 12571-12585, doi:10.1002/ece3.5722 (2019).

7 Breeuwer, A. *et al.* Decreased summer water table depth affects peatland vegetation. *Basic Appl. Ecol.* **10**, 330-339, doi:https://doi.org/10.1016/j.baae.2008.05.005 (2009).

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10 Gałka, M. *et al.* Vegetation Succession, Carbon Accumulation and Hydrological Change in Subarctic Peatlands, Abisko, Northern Sweden. *Permafrost and Periglacial Processes*, doi:10.1002/ppp.1945 (2017).

11 Harris, L. I., Roulet, N. T. & Moore, T. R. Drainage reduces the resilience of a boreal peatland. *Environmental Research Communications* **2**, 065001, doi:10.1088/2515-7620/ab9895 (2020).

12 McPartland, M. *et al.* Characterizing Boreal Peatland Plant Composition and Species Diversity with Hyperspectral Remote Sensing. *Remote Sensing* **11**, 1685, doi:10.3390/rs11141685 (2019).

13 McPartland, M. Y. *et al.* The response of boreal peatland community composition and NDVI to hydrologic change, warming, and elevated carbon dioxide. *Global Change Biol.* **25**, 93-107, doi:10.1111/gcb.14465 (2019).

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12th Jan 21

Dear Dr Wang,

Your manuscript titled "Vegetation and Microbes Interact to Preserve Carbon in Wooded Peatlands" has now been seen by our reviewers, whose comments appear below. In light of their advice we are happy, in principle, to publish a suitably revised version in Communications Earth & Environment under the open access CC BY license (Creative Commons Attribution v4.0 International License) provided you are transparent and clear in the naming and terminology for the different sites and strongly consider Reviewer #2's suggestion of a table outlining the structure, composition and estimated biomass distribution in the different types of peatland discussed.

We therefore invite you to revise your paper one last time to address the remaining concerns of Reviewer #2. In particular please consider further caveating your comments on large scale changes to boreal peatlands and remove this from the abstract. At the same time we ask that you edit your manuscript to comply with our format requirements and to maximise the accessibility and therefore the impact of your work.

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Best regards,

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REVIEWERS' COMMENTS:

Reviewer #1 (Remarks to the Author):

The authors did good work in improving the manuscript. I am totally satisfied with most of the answers and the revisions made based on my earlier comments. The manuscript is clearly written and most of the conclusions that earlier I found to punch above their weight are now toned down. I like the work and certainly think it will instigate novel ideas and research.

Reviewer #2 (Remarks to the Author):

Abstract:
Line 23: Delete such a wide speculation: Similarly, that theory alone cannot accurately project the decomposition rate in 23 boreal peatlands where warming and drought have decreased Sphagnum and increased 24 shrub/forest expansion.
It is a little arrogant from the authors that after 3 reviewers tell that their results are out of bound with vast inferences to boreal ecosystems (very speculative) that they argue and maintain that point in the abstract. The researchers have good results about the 2 different substrates they studied and

they should more closely stick to that. What they have told us the reviewers in their rebuttal letter is that they more thoroughly review the literature and they found further evidence from experiments and drained peatlands. That is exactly it: when a peatland is drained it becomes shrubbier. It is very specific and localised results that should not be infer to 2/3 of the peatland on the planets whereas more than 80% are still intacts. Such speculation cannot remains in the abstract. And this is not a modelling study where GCM scenarios are applied to the northern hemisphere. Only the soil analysis results of the two sites (and the lately add-on data from China) should be discussed at the process level without the inference. If maintain I would reject the publication of the manuscript.
Line 26: also the authors – which slowly I am tempting to say that they have seen little of the dominant muskeg, bogs and fens in the northern boreal biomes – are making too much of a striking difference between Sphagnum – shrub/tree-dominated peatlands. Over the 40 years of my careers I have seen several sites of both climatic locations (spruce bog and pocosins). There is not such a thing really in the boreal biome as a dominating Sphagnum peatlands – they are always full of ericaceous shrubs and associated with black spruce or larch trees. So the distinction is not so contrasted. We should read more something like: Sphagnum-ericaceous peatland (north) vs shrub-treed (pocosin) peatlands. Only on Tierra del Fuego I have seen truly dominated Sphagnum peatlands. When one knows that 80% of the ericaceous biomass in a bog is below-ground it tunes down this difference in peat composition between the two sites. One can also found dominating pure Sphagnum carpets around pools in the boreal zone.
Line 26-27: we present a natural course that curbs carbon loss against climate change. Should not come at this point in the abstract before presentation of the study results. This should be deleted as line34-36 is ending very well the implication of the study.
Line 85: what is really meant by… climate-change-induced shifts in dominant microbes… meaning that a warming experiment was performed? Modelling scenario were applied. I think that such a conclusion in the proposal of the objectives has not its place here.
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Line 103-106: Please do start by giving your results – all this is so far stretch - while the shrub 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 found today13,35. The shrub species in pocosins are similar to the expanding ericaceous shrubs found in

many drained Sphagnum peatlands in boreal areas10,11,36. First present your results and stick to it – you have good results and making advancement in our thinking but your story is too diluted and speculative when couple to climate change.

Line 114: which indicate the shrub peatland was more oligotrophic. Oligotrophy is defined by nutrients not by phenolic compounds. Rewrite your sentence.

Line 117: Bacteria only contributed about 6.6% and 4.8% to peat decomposition in the Sphagnum and the shrub peats, respectively I think for the whole argumentation a very good description of the structure and biomass associated with each strata component should be given in M&M. and hereafter the text could be written like this: Bacteria only contributed about 6.6% and 4.8% to peat decomposition in the boreal and the pocosin peats, respectively Consequently no biais would be introduced.

Line 142: The authors should in their writing make sure to be consistent with the naming of the sites and the terminology used to convey the right idea. Here they compare boreal to a wooded peatlands. It should be a boreal vs a sub-tropical peatlands or Sphagnum-shrub versus a Shrub-treed peatlands (I think the later showing in all transparency that there is shrubs in both ecosystems is better.

Line 144 to 149: the data from China and Canada are equivalent and needed to support the point of view of the authors, why present part of the data in figure 3 and the other in a supplementary figure even if reanalysed. In the figure caption it could be said: A composite figure of author's own data and published data. And here again, we cannot just believed the other with the naming of the site to get a good accurate view of the structure, and biomass distribution among the strata need to be added to Supplementary Table 1. This article needs a table describing well the 4 sites in term of structure (average height of the different strata), composition (dominant species) and estimated biomass of each strata. The data do exist for the boreal and pocosin peatlands, it remains to be seen for China but most likely. What is needed here is not the exact site data but what they represent in general as the authors are making so many large inferences.

Secondly (and after reading the whole paper) a synthesis of Supplementary Table 1 should be presented in the paper. First only pocosin vs marcell bog vs Dajiuhu and Canada peatland are the 4 sites discussed and not the individual sampling sites. I would keep Supplementary Table 1 but would produce a synthetic one with only a combined description of the 4 sites and of what is important to know to follow your argumentation. So a 5 columns table with the following lines and it is allright if estimated from other studies of the same regions – the discussion is at a large scale:
Average height:
- trees
- shrubs – ericaceous
- shrubs - others
- herb strata (sedge or else)

Average abundance (% cover)
- trees
- shrubs – ericaceous
- shrubs - others
- herbs
- mosses

Average biomass (if aerial can be separated from the below-ground even better
- trees
- shrubs – ericaceous
- shrubs - others
- herbs
- mosses

This is what is really needed in support of your whole argumentation.

Line 153-154: this is not clear. Further supporting the influence of shrubs on fostering slow-growing fungi, a Sphagnum peatland 153 in Minnesota, USA, similar to our site in Dajiuhu peatlands, where ericaceous shrubs dominated 154 the wooded cover, a reader gets loss in all the interchange of site naming. A clear descriptive table as described above should solve that problem.

Line 174: the authors do not have a good comprehension of the definition of an oligotrophic-eutrophic gradient. Higher acidity is not related to higher oligotrophy. See textbook by Rydin and Jeglum 2012 or Wieder and Vitt 2006. Looking at Supplementary Table 1 – TN is pretty homogeneous across sites

Line 178: …that oligotrophic slow-178 growing Acidobacteria30 dominated both peatlands. Clarify if really oligotrophic is meant – such as these bacteria can grow in very low P or N environment and is it acidic that is meant?

Line 214: it is the more tree component or total lignin components and not the shrubs that should be the conclusion and shrubs are just present at both sites. The pocosin site can have more than just ericaceous shrubs than a boreal bog – this can make a difference. Again why a descriptive table of the sites is needed.

Line 232- 249: implications of the research is well written.

Reviewer #3 (Remarks to the Author):

The authors have done a thorough job of responding to the reviewer comments and have revised the manuscript accordingly. I find that the current version is suitable for publication.

Reviewer #1 (Remarks to the Author):

The authors did good work in improving the manuscript. I am totally satisfied with most of the answers and the revisions made based on my earlier comments. The manuscript is clearly written and most of the conclusions that earlier I found to punch above their weight are now toned down. I like the work and certainly think it will instigate novel ideas and research.

Reviewer #2 (Remarks to the Author):

Abstract:

Comment 1: Line 23: Delete such a wide speculation: Similarly, that theory alone cannot accurately project the decomposition rate in boreal peatlands where warming and drought have decreased *Sphagnum* and increased shrub/forest expansion.

It is a little arrogant from the authors that after 3 reviewers tell that their results are out of bound with vast inferences to boreal ecosystems (very speculative) that they argue and maintain that point in the abstract. The researchers have good results about the 2 different substrates they studied and they should more closely stick to that. What they have told us the reviewers in their rebuttal letter is that they more thoroughly review the literature and they found further evidence from experiments and drained peatlands. That is exactly it: when a peatland is drained it becomes shrubbier. It is very specific and localised results that should not be infer to 2/3 of the peatland on the planets whereas more than 80% are still intacts. Such speculation cannot remains in the abstract. And this is not a modelling study where GCM scenarios are applied to the northern hemisphere. Only the soil analysis results of the two sites (and the lately add-on data from China) should be discussed at the process level without the inference. If maintain I would reject the publication of the manuscript.

Response: Thanks for this suggestion. It was deleted.

Comment 2: Line 26: also the authors – which slowly I am tempting to say that they have seen little of the dominant muskeg, bogs and fens in the northern boreal biomes – are making too much of a striking difference between Sphagnum – shrub/tree-dominated peatlands. Over the 40 years of my careers I have seen several sites of both climatic locations (spruce bog and pocosins). There is not such a thing really in the boreal biome as a dominating Sphagnum

peatlands – they are always full of ericaceous shrubs and associated with black spruce or larch trees. So the distinction is not so contrasted. We should read more something like: Sphagnum-ericaceous peatland (north) vs shrub-treed (pocosin) peatlands. Only on Tierra del Fuego I have seen truly dominated Sphagnum peatlands. When one knows that 80% of the ericaceous biomass in a bog is below-ground it tunes down this difference in peat composition between the two sites. One can also found dominating pure Sphagnum carpets around pools in the boreal zone.

Response: We agree that there are shrubs in *Sphagnum*-dominated peatlands, and herbs as well. Here the term of *Sphagnum*-dominated peatlands does not mean that *Sphagnum* is the only plant community in the ecosystem. *Sphagnum*-dominated peatlands refer to the peatlands where *Sphagnum* is the most abundant and has the most live and dead biomass, thus play a major role in shaping the community structure. Peat is dominantly formed by *Sphagnum* moss in the *Sphagnum*-dominated peatlands, and Shrubs mainly build peat in the shrub-dominated peatlands. We have done a literature review about *Sphagnum*- or sedge-, or shrub-, or tree-dominated peatlands, including textbook by Rydin & Jeglum 2012 and Wieder & Vitt 2006. *Sphagnum* mosses dominate most boreal peatlands, and this term is commonly used in many published papers (e.g. Kuhry, 1994; Kuhry et al., 1993; McPartland et al., 2019a; Rydin et al., 2006; Vitt et al., 1990; Vitt and Slack, 1975; Wieder et al., 1994), including our study site in S1 bogs in Minnesota (e.g. McPartland et al., 2019b; Norby et al., 2019; Zalman et al., 2018). We actually can not find the term "*Sphagnum* – shrub dominated peatlands" by google. We also discussed this issue with several peatland experts in Europe and North America who have seen many *Sphagnum*-dominated peatlands in boreal areas. They feel that the terms of "*Sphagnum*-dominated peatland" vs "shrub-dominated peatland" make more sense. Therefore, in our paper we believe the evidence from our review of the literature and our discussions with northern peatland experts allows us to keep these terms, and we also make them consistent throughout the paper.

Comment 3: Line 26-27: we present a natural course that curbs carbon loss against climate change. Should not come at this point in the abstract before presentation of the study results. This should be deleted as line34-36 is ending very well the implication of the study.

Response: It was deleted.

Comment 4: Line 85: what is really meant by… climate-change-induced shifts in dominant microbes… meaning that a warming experiment was performed? Modelling scenario were applied. I think that such a conclusion in the proposal of the objectives has not its place here.

Response: The word ”demonstrate” was changed to “suggest”. As to the mechanism found here, we don’t think the general warming experiment within decades could detect such changes, which may take over centuries. More studies are still needed for its application in models. This conclusion here is a brief summary of the major results and conclusions that are required by the Journal.

Comment 5: Line 87: it should be we compared a boreal Sphagnum-ericaceous shrub dominated peatland with a shrub-tree dominated sub-tropical peatland. This would convey better the idea that shrubs are largely present in boreal Sphagnum peatlands to the readers less familiar with these ecosystems. In fact throughout the paper, the authors should make it clear that there is a lot of shrubs in both ecosystems: the main difference is one has a good carpet of peat mosses with the shrubs and the other one (the pocosin) has more trees with the shrubs. That is the real structural and composition difference and the discussion of the results should reflect that.

Response: Thanks for this suggestion, although there are shrubs in our boreal site, shrubs’ contribution to peat formation over there is much smaller compared to *Sphagnum* moss. Also, we saw most samples we collected were *Sphagnum* in the boreal site. But in our shrub-dominated subtropical site, shrubs covers over 90% of land (only about 1% of land is covered by tree) and build peat there. To us, our boreal site is distinctively different from the subtropical site, the peat composition and texture in particular. Therefore, the terms were kept in our revision. Also, please see our responses to **Comment 2**.

Comment 6: Results and discussion: I am still of the opinion that the two should be two distinct section but I will let the editor-in-chief to decide.

Response: In this manuscript we presented our study that included several experiments in a coherent way that represented a logical progression into the study of the patterns being explored. We first mainly focused on our results with some short discussions in the context, then had discussions with implications. Some short discussions in the results can help readers understand the content smoothly.

Comment 7: Line 97-98 : We used space-for-time substitution to study shifts of ecological processes in peatlands over a long term. It is really not a good model of space-for-time substitution. The authors should present their experimental and analytical results – they have plenty – without making these large steps of inference.

Response: It was deleted.

Comment 8: Line 98-99: this is even more misleading: An ombrotrophic boreal Sphagnum peatland and a subtropical shrub peatland in the U.S.A were first selected. As said the shrub component is the common strata to both peatlands what differs is one has a well-developed Sphagnum carpet and the other has a lot more trees. Not conveying this difference is throwing doubts to if the authors know well these ecosystems they are discussing. And later the authors state: The Sphagnum site … the shrub site … creating a biais in the argumentation.

Response: Please see our responses to Comments 2 &5 first. To make it clear and consistent through the paper, we use terms of *Sphagnum*-dominated or shrub-dominated peatlands. Also actually there are more trees in our boreal sites than in the subtropical sites (please see our new Supplementary Table 2).

Comment 9: Line 103-106: Please do start by giving your results – all this is so far stretch - while the shrub 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 found today[13,35]. The shrub species in pocosins are similar to the expanding ericaceous shrubs found in many drained Sphagnum peatlands in boreal areas[10,11,36]. First present your results and stick to it – you have good results and making advancement in our thinking but your story is too diluted and speculative when couple to climate change.

Response: Climate change is an important element in this paper. The reason why we brought up the history of pocosin was to indicate that the phenomenon we observed in the shrub peatlands may represent the climate-change induced changes in boreal peatland in the face of long-term climate changes. This also suggests that the general climate-change manipulation experiment may not detect the long-term (at least >100 years) responses of peatland to climate changes.

Comment 10: Line 114: which indicate the shrub peatland was more oligotrophic. Oligotrophy is defined by nutrients not by phenolic compounds. Rewrite your sentence.

Response: It was rephrased as “Compared to the Sphagnum peat, the shrub peat 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 peatland was more oligotrophic.”

Comment 11: Line 117: Bacteria only contributed about 6.6% and 4.8% to peat decomposition in the Sphagnum and the shrub peats, respectively I think for the whole argumentation a very good description of the structure and biomass associated with each strata component should be given in M&M. and hereafter the text could be written like this: Bacteria only contributed about 6.6% and 4.8% to peat decomposition in the boreal and the pocosin peats, respectively Consequently no biais would be introduced.

Response: Thanks for this sharp view on the context. It was rephrased as “Consistent with many previous studies[e.g.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 the shrub peats, respectively (Supplementary Fig.1, also see Supplemental introduction and results for separating the relative contributions of fungi and bacteria to peat decomposition).”

Comment 12: Line 142: The authors should in their writing make sure to be consistent with the naming of the sites and the terminology used to convey the right idea. Here they compare boreal to a wooded peatlands. It should be a boreal vs a sub-tropical peatlands or Sphagnum-shrub versus a Shrub-treed peatlands (I think the later showing in all transparency that there is shrubs in both ecosystems is better.

Response: We consider shrub/tree dominated peatlands are wooded peatlands. All terms are consistent now.

Comment 13: Line 144 to 149: the data from China and Canada are equivalent and needed to support the point of view of the authors, why present part of the data in figure 3 and the other in a supplementary figure even if reanalysed. In the figure caption it could be said: A composite figure of author’s own data and published data. And here again, we cannot just believed the other with the naming of the site to get a good accurate view of the structure, and biomass distribution among the strata need to be added to Supplementary Table 1. This article needs a table describing well the 4 sites in term of structure (average height of the different strata),

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Average abundance (% cover)

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- shrubs - others

- herbs

- mosses

Average biomass (if aerial can be separated from the below-ground even better

- trees

- shrubs – ericaceous

- shrubs - others

- herbs

- mosses

This is what is really needed in support of your whole argumentation.

Response: Thanks for this suggestion. A table was added to show the heights, coverage and aboveground biomass in our four sites. Please see the detailed method and plant information in the Supplementary file. We could not separate shrubs-ericaceous from other shrubs, then all shrubs were included in the table. We don't have belowground biomass. A reference was added to Figure 3.

Comment 14: Line 153-154: this is not clear. Further supporting the influence of shrubs on fostering slow-growing fungi, a Sphagnum peatland 153 in Minnesota, USA, similar to our site in Dajiuhu peatlands, where ericaceous shrubs dominated 154 the wooded cover, a reader gets loss in all the interchange of site naming. A clear descriptive table as described above should solve that problem.

Response: A table about plant information was added. Also, it was rephrased as "…a recent study showed a boreal peatland in Minnesota, USA, where ericaceous shrubs dominated the wooded cover, was also dominated by slow-growing fungi (Helotiales and *Archaeorhizomyces*, >80%)".

Comment 15: Line 174: the authors do not have a good comprehension of the definition of an oligotrophic-eutrophic gradient. Higher acidity is not related to higher oligotrophy. See textbook by Rydin and Jeglum 2012 or Wieder and Vitt 2006. Looking at Supplementary Table 1 – TN is pretty homogeneous across sites

Response: Thank you for recommending the textbook. The concentrations of total N among sites were similar, but the available N were different. High phenolics generally reduce N availability by complexing with proteins (Hättenschwiler and Vitousek, 2000). To clarify this, we rephrased the sentence as "The dissolved phenolics in these peatlands might be mainly phenolic/humic acids that increase soil acidity and reduce N availability by complexing with proteins, thus

further exacerbating the oligotrophic conditions that benefit the slow-growing fungi while simultaneously inhibiting bacterial growth and shifting bacterial communities as well."

The related reference was added.

Comment 16: Line 178: …that oligotrophic slow-growing Acidobacteria dominated both peatlands. Clarify if really oligotrophic is meant – such as these bacteria can grow in very low P or N environment and is it acidic that is meant?

Response: Based a research by (Fierer et al., 2007), Acidobacteria belong to slow-growing oligotrophic bacteria that are more tolerant to substrate depletion and grow well in a nutritionally deprived environment. Low pH may contribute to the slow growing rate.

Comment 17: Line 214: it is the more tree component or total lignin components and not the shrubs that should be the conclusion and shrubs are just present at both sites. The pocosin site can have more than just ericaceous shrubs than a boreal bog – this can make a difference. Again why a descriptive table of the sites is needed.

Response: Yes, both sites have shrubs, but *Sphagnum* mainly forms peat in the boreal site, and shrubs in the subtropical site. Our previous study showed that shrub contain the highest phenolics (Wang et al., 2015), then shrub does matter here.

Line 232- 249: implications of the research is well written.

Reviewer #3 (Remarks to the Author):

The authors have done a thorough job of responding to the reviewer comments and have revised the manuscript accordingly. I find that the current version is suitable for publication.

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